Frameworks used in Invasion Science

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EDITORIAL

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Frameworks used in invasion science: progress and prospects

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Abstract

Our understanding and management of biological invasions relies on our ability to classify and conceptualise the phenomenon. This need has stimulated the development of a plethora of frameworks, ranging in nature from conceptual to applied. However, most of these frameworks have not been widely tested and their general applicability is unknown. In order to critically evaluate frameworks in invasion science, we held a workshop on 'Frameworks used in Invasion Science' hosted by the DSI-NRF Centre of Excellence for Invasion Biology in Stellenbosch, South Africa, in November 2019, which led to this special issue. For the purpose of the workshop we defined a framework as "a way of organising things that can be easily communicated to allow for shared understanding or that can be implemented to allow for generalisations useful for research, policy or management". Further, we developed the Stellenbosch Challenge for Invasion Science: "Can invasion science develop and improve frameworks that are useful for research, policy or management, and that are clear as to the contexts in which the frameworks do and do not apply?". Particular considerations identified among meeting participants included the need to identify the limitations of a framework, specify how frameworks link to each other and broader issues, and to improve how frameworks can facilitate communication. We believe that the 24 papers in this special issue do much to meet this challenge. The papers apply existing frameworks to new data and contexts, review how the frameworks have been adopted and used, develop useable protocols and guidelines for applying frameworks to different contexts, refine the frameworks in light of experience, integrate frameworks for new purposes, identify gaps, and develop new frameworks to address issues that are currently not adequately dealt with. Frameworks in invasion science must continue to be developed, tested as broadly as possible, revised, and retired as contexts and needs change. However, frameworks dealing with pathways of introduction, progress along the introduction-naturalisation-invasion continuum, and the assessment of impacts are being increasingly formalised and set as standards. This, we argue, is an important step as invasion science starts to mature as a discipline.

Keywords
CBD introduction pathway classification framework, Environmental Impact Classification for Alien Taxa (EICAT), invasive alien species, invasive species, Socio-Economic Impact Classification of Alien Taxa (SEICAT), Unified Framework for Biological Invasions

The origins, purposes, and challenges facing frameworks in invasion science

The study of biological invasions has a rich history of developing and refining hypotheses, frameworks, theories, and other conceptual constructs with the aim of assisting with resolving particular problems and in some cases moving beyond case studies (observations of a small number of invasive taxa, invaded habitats or invasion events) to arrive at generalisations or principles that apply more widely. These conceptual constructs often link insights from fundamental research to policy and management responses. Frameworks, in particular, are an important way to communicate concepts and ideas between people. As humans, we like to structure the world around us; to some extent frameworks are scientific models of how we think the world works that allow us to test our ideas, debate edge cases, and build new hypotheses. Just like any scaffolding, frameworks are intended to be built upon. Reviewing developments in "implementation science", Nilsen (2015) posits that a framework usually denotes "a structure, overview, outline, system or plan consisting of various descriptive categories, e.g., concepts, constructs or variables, and the relations between them that are presumed to account for a phenomenon". In this typology, frameworks are not explanatory but "only describe empirical phenomena by fitting them into a set of categories". Frameworks are especially useful when they are used to collate, organise, combine, simplify, and synthesise a large volume of new information; to classify and integrate insights from various perspectives and disciplines; to bridge gaps between science and policy and between disciplines; and to provide roadmaps to guide further research inquiries. These endeavours all rely on frameworks to circumscribe and classify the problem.

However, as invasion science originates from various discipline-specific questions and problems, attempts at circumscription and classification have arisen from multiple different origins. These differences in origin largely align with traditional disciplinary boundaries (zoology, botany, marine biology) and debates (e.g., utilisation vs. protection or humans as a part of nature vs. humans as a threat to nature). In consequence, there are a plethora of terminologies, differences in emphasis, and similar ideas are expressed in slightly different formats. Taking the development of hypotheses as an analogy, many hypotheses used to explain aspects of biological invasions overlap, some are vague, and some can be collapsed to general ecological theories that need not be related to biological invasions at all (Catford et al. 2009; Enders et al. 2020). Furthermore, as only a few hypotheses in invasion science have attracted sustained attention, few hypotheses have consistent and strong evidentiary support (Jeschke et al. 2012; Ricciardi et al. 2013; Traveset and Richardson 2020). As such, it is difficult to differentiate between hypotheses that provide insights into the processes at play and those that should not be the basis for developing scientific models and management recommendations as they are misleading (Crystal-Ornelas and Lockwood 2020).

The challenge for those working on invasion frameworks is similar–that of demonstrating the utility of frameworks, being clear as to the contexts under which particular frameworks apply, and adapting (or abandoning) frameworks in response to new evidence or needs. Frameworks are needed both to address particular specific problems, to improve general understanding, and ideally to facilitate the transfer of lessons learnt from the general to specific and vice versa (Lawton 1996). This tension between generalisation and utility is crucial [cf. invasion syndromes for one practical approach of addressing it (Novoa et al. 2020)]. The context-dependency of the biological invasions phenomenon means there is substantial value in taking an idiographic approach, i.e., studying case by case to uncover mechanisms and consequences (Simberloff 2004); tailored frameworks can be very valuable in such cases. However, a major goal of some frameworks has been to facilitate generalisations and comparisons across scales, taxa, and biological realms, and more broadly to formalise frameworks as standards that are intended to be used by all stakeholders involved (Box 1). For example, the so called Unified Framework for Biological Invasions aimed to link frameworks developed by botanists and zoologists (Blackburn et al. 2011); the EICAT impact classification framework (Blackburn et al. 2014), which has been recently adopted as a standard of the IUCN, aims to facilitate the measurement and reporting of invasive species impacts in a consistent manner (IUCN 2020) (Box 2); and the CBD has proposed an introduction pathway classification framework that bridges decades of debate on how invasive species are transported out of their native range (CBD 2014) (Box 3). These frameworks have been proposed to be incorporated into biodiversity standards (Groom et al. 2019) with a view to developing a standardised system for monitoring and reporting on biological invasions that can be applied across scales from local to global, across habitats from coral reefs to mountain tops, across taxa from fungi to ferns to frogs, and across pathways from hitchhikers on plastic debris to seeds sent through e-commerce (McGeoch and Jetz 2020). There is thus some evidence that invasion science is coalescing around a few frameworks and formalising them as standards (Boxes 1–3). However, the frameworks are still rarely explicitly used in practice (Wilson et al. 2020, this issue), and our experience when applying the most commonly cited frameworks to real data and situations has been that they are very useful but that there are a number of practical challenges to be resolved, some of which are fundamental to the field (see the section on 'Putting frameworks to the test' below).

So, are current frameworks fit for purpose? How do they perform in practice? Can they be adapted to deal with new contexts? Do they need to be revised and adapted to deal with new information? Can frameworks be linked together to facilitate the transfer of lessons learnt from the general to the particular? What gaps are there that need addressing?

Box 1. Moving from frameworks to standards.

A framework, in the sense used here, provides a structure on which other ideas or applications are built. Frameworks can often be used flexibly, with details modified so they fit particular contexts (Wilson et al. 2020, this issue). However, for a framework to be a tool that is routinely used and shared, then definitions and terms need to be fixed, and, ideally, guidelines for use formalised. In such cases a framework becomes a standard. Adopting a standard has several advantages, notably that it facilitates the exchange of data within science, represents an agreed basis for the communication of the issue to a wider community, and provides an incontrovertible basis for policy. Data standards allow us to aggregate, compare, communicate, validate, and share data. They may include entity relationships, term definitions, controlled vocabularies, and formats. They have to be used precisely if data are to be readable by a machine.

Frameworks and standards are both abstractions of the real world. The confrontation of a framework or standard with real world data can lead to the realisation that the framework or standard needs to be revised, that it only applies to specific contexts or that it is fundamentally not fit for purpose. However, while a framework might be informally updated or adapted to particular contexts, any change to a standard needs to be formally documented and ideally reviewed and discussed by other users, i.e., there should be a clear process for consulting on, and implementing, changes. There is thus an interplay of frameworks, standards, and the stakeholders using them that leads to an evolution of ideas and data (see Boxes 2, 3).

A leading organisation in the development of biodiversity standards is the Biodiversity Information Standards (https://www.tdwg.org/). This organisation is a heterogeneous group of biodiversity data managers created in response to the need to manage biodiversity data. It liaises with a wide variety of international individuals and organisations, such as the Research Data Alliance (https://www.rd-alliance.org/), the International Union for Conservation of Nature (https://www.iucn.org/) and its Invasive Species Specialist Group (http://www.issg.org/), and the Global Biodiversity Information Facility (https://www.gbif.org/).

Box 2. The IUCN's Environment Impact Classification for Alien Taxa (EICAT)–a standard for categorising alien species impact.

The EICAT can be used to classify alien taxa according to the magnitude of their impacts on native taxa, with impact magnitude based on the organisational level in the affected community. Impact categories range from Minimal Concern to Massive (IUCN 2020). If only individual performance is affected, it is considered a Minor impact; if a native taxon is removed from the community (locally extinct or extirpated), it is considered Major or Massive, based on the reversibility of the change (IUCN 2020). For more details see IUCN (2020), Kumschick et al. (2020a, this issue), and Volery et al. (2020, this issue).

The IUCN EICAT Standard is the product of a long process of developing and adapting frameworks to quantify impacts. EICAT has its origins in the Generic Impact Scoring System (GISS) which was first published by Nentwig et al. (2010). The idea of GISS was to develop a system capturing all kinds of impacts from all alien taxa and classifying them according to their magnitude. As the impacts of an increasing variety of taxa were scored using GISS, several issues emerged, including that the description of impact magnitudes was not always clear (Strubbe et al. 2011) and that the way scores were summed across different types of impact did not always make logical sense (Game et al. 2013). Blackburn et al. (2014) designed a new framework to address these issues, specifically by providing consistent descriptions of impact magnitudes for different types of environmental impact and by classifying taxa based on the maximum impact seen for any one type of impact.

In parallel to the development of these impact classification frameworks, the Parties to the CBD invited the IUCN SSC Invasive Species Specialist Group (ISSG) in 2014 "to develop a system for classifying invasive alien species based on the nature and magnitude of their impacts" (COP XII Decision 17), Guidelines were then developed for the application of the framework by Hawkins et al. (2015), and the name EICAT was suggested. The IUCN then conducted a global consultation process, developed a standard, and revised the guidelines in response to the comments and suggestions received. EICAT was also revised in the light of the experiences of those using it (e.g., Kumschick et al. 2017; Evans et al. 2018; Volery et al. 2020, this issue). A final version of the standard was accepted by the IUCN Council in February 2020, and the standard was launched and published in September 2020 (IUCN 2020).

Circumscribing the problem–the workshop

In light of rapid developments in the field, we decided it was important to take stock and assess the current state of frameworks used in invasion science. We invited a wide range of researchers focussing on biological invasions to a workshop to discuss, develop, and revise ideas. In particular, we asked prospective attendees to develop draft manuscripts before the meeting with the aim of formalising their thoughts and sharing

Box 3. The CBD's pathway classification framework–a standard for classifying the pathways along which alien species are introduced.

Similar to classifying impact (Box 2), the need to classify introduction pathways into a small number of practical categories to better communicate pathway information and improve the monitoring and regulation of those pathways has long been recognised (Puth and Post 2005; Lodge et al. 2006). In 2008, Hulme and others published a framework of six broad introduction pathways that endeavoured to be globally applicable, suitable for terrestrial and aquatic organisms, and relevant for policy and management. Parallel to this, the need to focus research and management to identify, prioritise, and manage pathways of invasive alien species was set as part of the Aichi Biodiversity Target 9 adopted by the CBD in 2010. To help facilitate the achievement of this target, in 2014, the CBD proposed an introduction pathway classification framework that was developed based on extending the framework proposed by Hulme et al. (2008) to include sub-categories that could facilitate inclusion of data in other databases [in particular the Global Invasive Species Database, the Invasive Species Compendium (ISC) of CABI, Delivering Alien Invasive Species Inventories for Europe (DAISIE), and peer-reviewed literature (CBD 2014)]. A manual was produced in 2017 to assist users with interpreting the categories (Harrower et al. 2017).

The framework proposed by the CBD has been applied in numerous settings, not least to integrate pathway information across major alien species databases (Saul et al. 2017). However, to achieve this without manual intervention the vocabulary needs to be further formalised and incorporated into digital data standards, i.e., set as a formal standard rather than just a framework. As part of this, the Invasive Organism Information Task Group of the Biodiversity Information Standards organisation has proposed changes to the Darwin Core to incorporate pathway information (Groom et al. 2019) [the Darwin Core aims to provide a stable standard reference for sharing information on biological diversity (Wieczorek et al. 2012)].

This is not, however, the end of the story. New recommendations for changes will have to navigate the, often circuitous, route to ratification (Pergl et al. 2020, this issue), and several major issues have emerged—the pathway framework is arguably Euro-centric in origin and use (Faulkner et al. 2020, this issue; Wilson et al. 2020, this issue), and the sub-categories do not have many of the desirable properties that an introduction pathway classification framework should have (Faulkner et al. 2020, this issue). So even after more than a decade, a high degree of consultation, and the framework verging on being adopted in a formal data standard used by the whole biodiversity community, the CBD's introduction pathway classification framework is likely not appropriate to all contexts where it is intended to apply, and it might need a substantive overhaul if this were to be achieved.

them in advance of the discussions. The workshop itself, 'Frameworks used in Invasion Science', was held 11–13 November 2019 in Stellenbosch, South Africa, and was hosted by the DSI-NRF Centre of Excellence for Invasion Biology (for details of the workshop and how the special issue developed see Suppl. material 1).

One of the main areas of discussion at the workshop was to define what is meant by a framework and to clarify the overall aim of such a framework. It was felt that frameworks should be useful, and the broader, the better. However, generalisations are only worthwhile if they do not come at the cost of the utility of the framework for its original purpose. Frameworks are often used for purposes for which they were not initially intended and in some cases for which they are not suited (see examples in Wilson et al. 2020, this issue). Frameworks created in one context and naively used in other contexts might mean important details are missed by those applying the frameworks or that the problem is made much more complicated than it actually is. In other words, the sensitivity and specificity of frameworks are not always clear.

Over the course of the workshop, the question 'What is a framework?' was repeatedly debated, with such debate providing a valuable anchor for our discussions. We eventually settled on the following working definition:

A framework is a way of organising things that can be easily communicated to allow for shared understanding or that can be implemented to allow for generalisations useful for research, policy, or management.

Building on this, we developed an overall goal of the workshop, dubbed 'the Stellenbosch Challenge for Invasion Science':

Can invasion science develop and improve frameworks that are useful for research, policy or management, and that are clear as to the contexts in which the frameworks do and do not apply?

Putting frameworks to the test

A major goal of the workshop was for participants to formalise their thoughts in manuscripts, and to 'stress-test' the frameworks–indeed a survey conducted as part of this special issue found that while invasion scientists feel some of the major frameworks are very influential, the frameworks still lack serious critical examination (Wilson et al. 2020, this issue). The 24 papers in this special issue revisit many of the philosophical underpinnings and practical challenges associated with attempts to integrate, reconcile, and synthesise thoughts and concepts in invasion science (Appendix 1).

In achieving these aims, this special issue, we argue, addresses the Stellenbosch Challenge. The papers address the utility of frameworks for research, policy, and management; they clarify the contexts in which the frameworks do and do not apply; and they discuss how the frameworks need to be developed and improved to facilitate shared understanding. In particular, the special issue addresses all these above issues with respect to the rapidly developing field of impact assessment.

Can invasion science develop and improve frameworks that are useful for research…

Several of the papers show how frameworks can structure and guide research. Pyšek et al. (2020, this issue) build on a rich literature on the macroecology of introductions, naturalisations, and invasions, to explicitly outline the factors that must be considered when studying invasions, viz. species, location, event, and their interactions. This highlights that the required level of complexity has not often been adequately elucidated in previous macroecological analyses, leading to a high probability of spurious results. By contrast, Liebhold et al. (2020, this issue) propose a potential way to reduce complexity. They argue that the two basic processes of population growth and dispersal underlie several phases of the introduction-naturalisation-invasion continuum, which means that similar models can be used across scales and stages, thereby simplifying the problem. The value of rethinking biological invasions is also addressed by Hulme et al. (2020, this issue), who show how reconnecting invasion science to the rich theory in epidemiology can improve both understanding and management. They show how viewing habitats as hosts could potentially change the way we manage invasive species, and argue that concepts such as super-spreaders, herd immunity, ring vaccination, and cordon sanitaire are all promising areas for future applied research on biological invasions.

...policy...

Frameworks also provide valuable systematic means to phrase policy goals. At a broad level Essl et al. (2020b, this issue) show how frameworks can underpin global goals and targets, specifically the proposed revised CBD biodiversity targets, and to ensure that the indicators to track such targets are based on agreed standards and methods. At a more local scale, Kumschick et al. (2020b, this issue) present a novel risk analysis framework that combines existing frameworks on impact assessment, pathway classification, and scoring of introduction status to produce a method that integrates international best practice with local contexts to provide recommendations for South African regulations. Datta et al. (2020, this issue) explore another policy area in more detail– how regulations should deal with taxa at levels other than the species, and in particular what is needed to regulate 'safe' cultivars of invasive horticultural plants. They develop the foundation on which a new framework to address this issue can be built.

…[and] management…

Many of the papers go beyond the policy arena and explicitly use frameworks to address pressing on-the-ground management issues. Bertolino et al. (2020, this issue) and Ziller et al. (2020, this issue) develop approaches to prioritising management efforts (for mammals in Italy and for control efforts in protected areas in Brazil respectively). Such prioritisation efforts build on information from risk and impact assessments and ecological studies. In the same vein, Latombe et al. (2020, this issue) provide insights for the allocation of biosecurity resources across a network (e.g., of countries, islands or lakes) which is in the process of being invaded. They combine a framework considering categories of abundance and extent with a metapopulation model to show how the efficacy of management and synchronisation in management efforts together can reduce spread rates. Brock and Daehler (2020, this issue) tried to classify the whole alien flora of Hawai'i according to the Unified Framework for Biological Invasions (Blackburn et al. 2011). They found that while much of the framework is conceptually sound, in practice, and for management, some categories needed to be merged and new ones created. By combining the revised framework with information from risk assessments they propose a monitoring tool that is tailored to address the needs of managers in Hawai'i and likely other countries as well.

…and that are clear as to the contexts in which the frameworks do and do not apply?

The context dependency in invasions is not always well addressed by existing frameworks, but is an explicit focus of several papers in the special issue. Potgieter and Cadotte (2020, this issue) examine the 'urban effect' on invasions within the context of existing frameworks, both by demonstrating how different barriers to invasions tend to be weaker in cities and how the impacts differ. Paap et al. (2020, this issue) explore available frameworks in invasion science in the context of forest pathology. They found that most studies of forest pathogens have been undertaken without any connection with, or consideration of, the frameworks of invasion science. They argue that this is a consequence of the mechanistic approach required in forest pathology to investigate specific interactions between hosts and pathogens, the aim being to control resulting disease problems. In terms of pathways, Pergl et al. (2020, this issue) test the utility of the CBD pathway classification in Europe and demonstrate how recently published guidelines provide clarity and can improve the usefulness of the framework. However, Faulkner et al. (2020, this issue) found that while the main categories of the CBD pathway framework have many desirable features, the sub-categories are not useful; they note that the current framework performs poorly in some non-European settings. They propose a hybrid approach, using broad categories for global generalisations and reporting, and context-specific categories to serve local needs and purposes.

A framework is a way of organising things that can…allow for shared understanding

A notable emerging feature of this special issue is that while the papers cover a wide range of topics, taxa, habitats, and environments, there is some evidence of a growing consensus. Together, the 24 papers of the special issue cite well over a thousand different publications, but many of the papers cite the same handful of frameworks (Fig. 1, Appendix 1). The authors of this special issue are certainly not divided into distinct camps that use different frameworks. The leading frameworks are widely cited and highly influential (Wilson et al. 2020, this issue). Moving forward, we posit that it is critical to ensure frameworks in invasions' science are designed to also respond to the multitude of growing, changing, and interacting global change drivers under which biological invasions are playing out. For example, Robinson et al. (2020, this issue) highlight how climate change will have dramatic and varied impacts on biological invasions that will require new ways of thinking, emphasising the imperative of collecting foundational data and monitoring change. And, as outlined by Sinclair et al. (2020, this issue), frameworks should be explicit in how humans affect biological invasions, and how biological invasions affect humans.

A developing standard for impact assessments

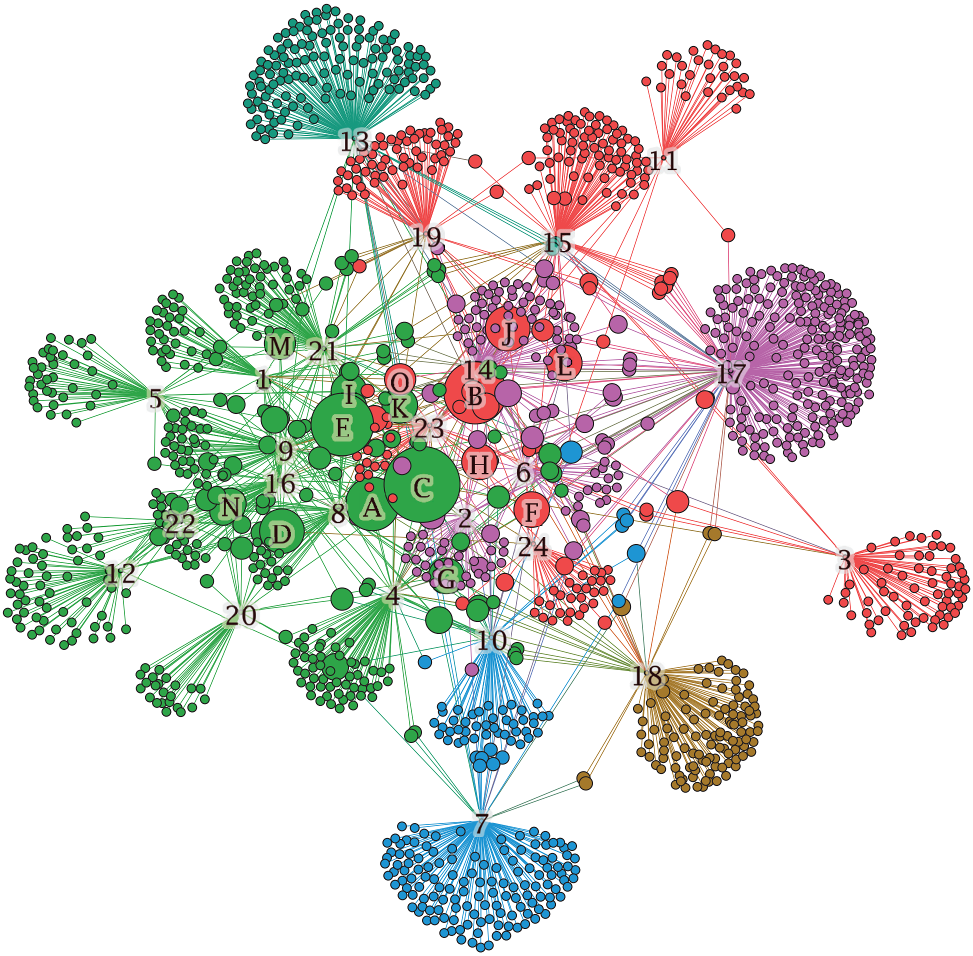
One of the major criticisms of invasion science has been that, at least historically, assessments of 'impact' magnitude have been subjective. However, recent developments in the field are explicitly addressing this (Simberloff et al. 2013; Blackburn et al. 2014; Bacher et al. 2018; Ireland et al. 2020). One of the main focus areas of the special issue, and one that cuts across the themes above, is the need to standardise impact assessments. Kumschick et al. (2020a, this issue) provide important insights on the dos and don'ts when using EICAT. Volery et al. (2020, this issue) build on the developing global experiences of applying EICAT and on feedback that emerged from an extensive IUCN consultation exercise to update guidelines for using EICAT. Probert et al. (2020, this issue) provide recommendations on how to categorise uncertainty in ICAT assessments (i.e., both EICAT and SEICAT). Invasion scientists appreciate the benefits alien species provide to society (Ewel et al. 1999). However, for practical purposes, most impact assessments focus on negative impacts. Vimercati et al. (2020, this issue) examine which frameworks in invasion science have considered positive impacts of alien taxa and argue that a systematic understanding of all types of impact is important for management and regulatory decisions. The test of such frameworks is, of course, when they are applied in practice. Van der Colff et al. (2020, this issue), using data on gastropods, demonstrate how EICAT assessments and Red List assessments provide complementary information valuable to evaluations of the impact of biological invasions on native biodiversity; they recommend that both should be used to inform policy and management decisions.

The more one looks, the more impacts are found

Evans et al. (2020, this issue) apply SEICAT to alien bird impacts and Measey et al. (2020, this issue) update EICAT and SEICAT assessments for amphibians providing the first detailed assessment of the cost of the research on which impact assessments are based. They both show that data on impact are limited and that varying levels of data availability have the potential to create biases–if an invasion is poorly studied (e.g., due to a lack of resources to conduct a detailed investigation of impact) the current recorded impact will likely be considered to be lower than it actually is. However, both studies agree that a major benefit of the ICAT frameworks is that they make data needs explicit; they also show that these frameworks serve an important function in directing and guiding research. On this point, Kumschick et al. (2020a, this issue) recommend that decision makers should use EICAT in conjunction with information on how likely it is that current recorded impact is underreported or the likelihood of significant increases in negative impacts in future.

A hierarchy of frameworks

While each paper in the special issue tackles specific parts of the Stellenbosch Challenge and draws from particular frameworks (Appendix 1), the frameworks themselves are not explicitly linked. At the workshop there was substantial discussion on whether the Stellenbosch Challenge could be satisfied by the creation of a single all-encompassing framework. However, there was general consensus that the frameworks do not always align, nor should they be forced to do so (cf. the comparison of EICAT and the Red List by Van der Colff et al. 2020, this issue). There was agreement that it is more realistic to aim for a hierarchy of frameworks where important contextual detail is nested within the overarching ideas, rather than aiming for an 'über-framework' that tries to embrace all contexts. The analogy with hypotheses in invasion science is again pertinent. Jeschke and Heger (2018) very elegantly demonstrate the value of the hierarchy of hypotheses approach to organise ideas within invasion science. A similar approach to frameworks in invasion science would help clarify how frameworks constructed to re-



spond to particular needs or contexts are related to each other, how they can share ideas and approaches, and to identify gaps where new frameworks might be valuable. We present a tentative sketch of the inter-connection of existing frameworks in Figure 2.

At a broad scale (Fig. 2A), frameworks in invasion science should link to other drivers of global change (Robinson et al. 2020, this issue, #18 on Fig. 2A), other areas of biological research (7. Hulme et al. 2020, this issue; 13. Paap et al. 2020, this issue), and to societal issues more generally (15. Potgieter and Cadotte 2020, this issue). These linkages can be made within the understanding that biological invasions can be viewed through the prism of pathways, species or sites (4. Essl et al. 2020b, this issue). These linkages can also be made recognising that the phenomenon involves bio-geographical and ecological processes (e.g., the introduction-naturalisation-invasion continuum), that there are environmental and societal impacts (e.g., the ICAT frameworks), and

Figure 1. A citation network of papers within this special issue. Each node represents an article, with the node radius proportional to the number of citations. Citations between papers within the special issue have been excluded, and this editorial was not included at all. Numbered nodes are papers in the special issue (Appendix 1) and lettered nodes are the 15 articles that were cited six or more times in the network. The colours represent different modularity classes of the network (the light green one appears to be related to impact assessments). Of the 1520 papers cited 87.2% were only cited by one paper in special issue, and less than 1% were cited by four papers. This network can thus be seen as indicative of a wide-ranging field linked by a few key frameworks, though the nature of the special issue and the authors involved means there are some significant biases and self-selections occurring (which, we expected, would have biased the network towards being more connected than it would otherwise be). The network was built in Gephi (0.9.2). **A** Bacher et al. (2018), Socio-economic impact classification of alien taxa (SEICAT); https://doi.org/10.1111/2041-210X.12844 **B** Blackburn et al. (2011); A proposed unified framework for biological invasions; https://doi.org/10.1016/j.tree.2011.03.023 **C** Blackburn et al. (2014); A Unified Classification of Alien Species Based on the Magnitude of their Environmental Impacts; https://doi.org/10.1371/journal.pbio.1001850 **D** Evans et al. (2016); Application of the Environmental Impact Classification for Alien Taxa (EICAT) to a global assessment of alien bird impacts; https://doi.org/10.1111/ddi.12464 ental Impact Classification for Alien Taxa (EICAT); https://doi.org/10.1111/ddi.12379 **F** Hulme et al. (2008); Grasping at the routes of biological invasions: a framework for integrating pathways into policy; https://doi.org/10.1111/j.1365-2664.2007.01442.x **G** Latombe et al. (2017); A vision for global monitoring of biological invasions; https://doi.org/10.1016/j.biocon.2016.06.013 **H** McGeoch et al. (2016); Prioritizing species, pathways, and sites to achieve conservation targets for biological invasion; https://doi.org/10.1007/s10530-015-1013-1 **I** Nentwig et al. (2016); The generic impact scoring system (GISS): a standardized tool to quantify the impacts of alien species; https://doi.org/10.1007/s10661-016-5321-4 **J** Richardson et al. (2000); Naturalization and invasion of alien plants: concepts and definitions; https://doi.org/10.1046/j.1472-4642.2000.00083.x **K** Seebens et al. (2017); No saturation in the accumulation of alien species worldwide; https://doi.org/10.1038/ncomms14435 **L** Wilson et al. (2009); Something in the way you move: dispersal pathways affect invasion success; https://doi.org/10.1016/j.tree.2008.10.007 **M** Pyšek et al. (2008); Geographical and taxonomic biases in invasion ecology; https://doi.org/10.1016/j.tree.2008.02.002 **N** Kesner and Kumschick (2018); Gastropods alien to South Africa cause severe environmental harm in their global alien ranges across habitats; https://doi.org/10.1002/ece3.4385 **O** Harrower et al. (2017); Guidance for interpretation of CBD categories on introduction pathways.

that biological invasions pose societal challenges that require political and management responses. These three issues (biogeography, impacts, and interventions) arguably form the core of invasion science (Fig. 2B). However, these issues are not always congruent. For example, while impact, abundance, and geographical distribution are often correlated, alien species can have massive negative impacts without forming a naturalised or invasive population (Ricciardi et al. 2013), and widespread, abundant invaders [‘successful’ as per 10. Latombe et al. (2020, this issue)] might have negative impacts scored as *Minor* or *Minimal Concern* under the ICAT frameworks (Ricciardi and Cohen 2007). Also, while pathways of introduction represent an important elucidation of the first stage of the invasion process, they do not necessarily map neatly on to pathways of spread within a region (6. Faulkner et al. 2020, this issue; 14. Pergl et al. 2020, this issue, 11. Liebhold et al. 2020, this issue). It is important, therefore, to ensure that the domain of applicability and relevance of each framework is clear, and that if linkages are made these are done without compromising the original purpose for which the framework was constructed. As an example, a recent effort to link interventions to the introduction-naturalisation-invasion continuum forces management terms on to invasion stages and barriers, conflates activities, goals, and objectives, and in so doing neglects the primary purposes of the framework, which is to facilitate interventions (Robertson et al. 2020).

Finally, it is important to zoom into on-the-ground management needs to ensure that there are frameworks that can be used to improve our understanding and management of particular issues (one example is shown in Fig. 2C). Context-specific frameworks are needed: for management prioritisation in Italy and Brazil (1. Bertolino et al. 2020, this issue; 24. Ziller et al. 2020, this issue); to support decisions regarding the listing of alien species under South African regulations (9. Kumschick et al. 2020b, this issue); to provide clarity regarding the risks and appropriateness of regulating horticultural cultivars (3. Datta et al. 2020, this issue); and to ensure that the monitoring of alien plant species in Hawai'i is relevant to management (2. Brock and Daehler 2020, this issue). It might be possible to extend such frameworks to similar contexts, but ultimately if those frameworks are not well suited to the problem they were designed to address, then they need to be adapted or abandoned.

The need to zoom in and out to different spatial or thematic scales is currently being developed further by workshop participants with a view to producing a hierarchy of frameworks. Parallel to this work, workshop participants are reviewing the history of frameworks in invasion science and developing a typology to classify them. Finally, participants felt a natural conclusion of the workshop would be to refine and recast some existing frameworks. Specifically, participants suggested that the frameworks used to classify populations according to their stage along the introduction-naturalisation-invasion continuum (Blackburn et al. 2011) and the CBD's introduction pathway classification framework (Box 3) deserved renewed attention. We believe that this special issue provides a necessary precursor to these important products.

Gaps

We could, of course, not address all issues related to invasion frameworks at the workshop or in this special issue. There are notable gaps in the implementation of existing frameworks that deserve much more attention, for example the need for: frameworks to be modified so that they are relevant to different ecological contexts (e.g., freshwater, marine, micro-organisms); a way to incorporate expert opinion in transparent and standardised ways; and methods to apply frameworks when biogeographic and administrative boundaries do not align. There is also a need to consider if existing frameworks can be applied to address broader issues such as invasions at the gene level and range shifts resulting from climate change or other human modifications of the environment (e.g., managed relocation, assisted migrations). These gaps in the ability of frameworks to deal with different contexts impact our ability to monitor and report on invasions [e.g., see Zengeya and Wilson (in press) for South Africa].

Biological invasions are a central factor in global environmental change as they impact, and are impacted by, climate, ecosystem functions and services, and species extinction (Vitousek et al. 1997; Ricciardi et al. 2017). One potential avenue for further work is to try to link frameworks in

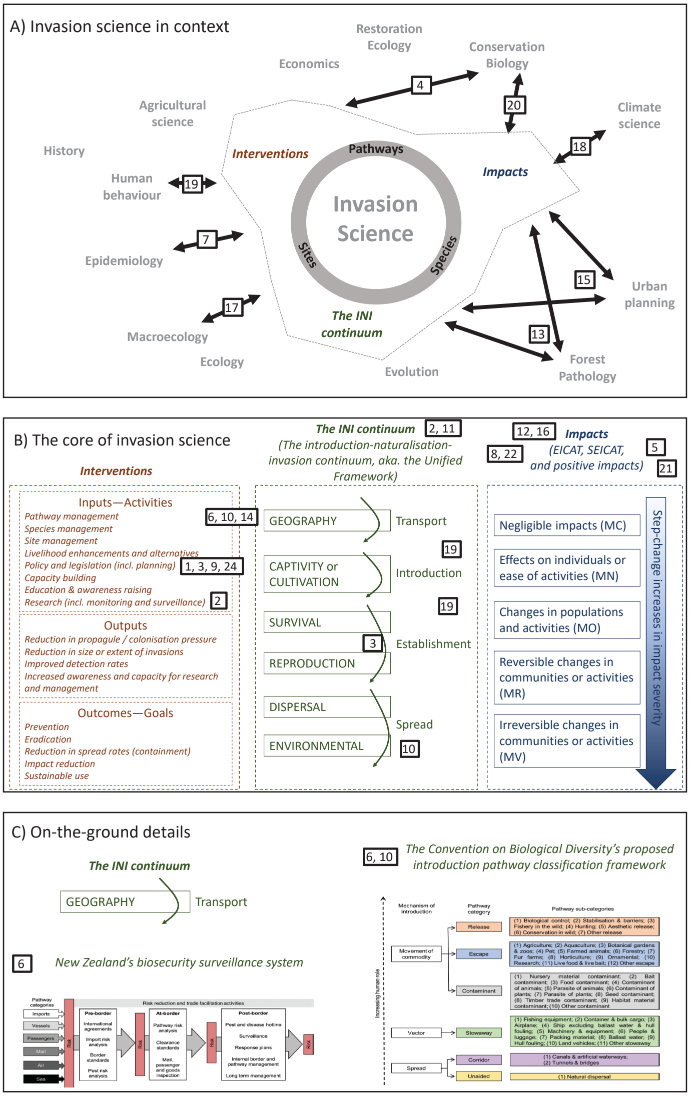


Figure 2. A tentative hierarchical structure linking frameworks in invasion science. Three levels are proposed here, though details at the finest level are only shown for one component—the part of the Unified Framework that addresses transport across the geographic barrier. Numbers represent papers in the special issue as per Appendix 1 and are placed according to how they fit in with the existing frameworks. Papers touch on multiple aspects and different hierarchical levels. However, each paper is only indicated once on the diagram at the place we feel it contributes the most; except for 19. Sinclair et al., which, to highlight how some studies are cross-cutting, is plotted on levels A and B, and, as the paper also discusses how the transport process should be viewed as a coupled-human natural system (CHANS), it could arguably have been plotted on level C as presented here as well. At level B (the core of invasion science), there are well established frameworks for the impacts of species and the introduction-naturalisation-invasion continuum, but there are no equivalent well recognised frameworks for interventions (or the impacts on sites). The intervention activities shown are based on the categories used by the Cambridge Conservation Forum framework for evaluating projects with the addition of a pathway management activity (Kapos et al. 2008).

invasion science more clearly to broader issues within conservation biology, community ecology, evolutionary biology, and global environmental change. Similarly, alien species are now regularly incorporated into foundational ecological and evolutionary science as 'probes' that can effectively test core tenets in these fields (e.g, Strauss et al. 2006; Vellend et al. 2007; Guisan et al. 2014) and 'biological assays' to test dominant paradigms in biogeography (Rouget et al. 2015). If invasion frameworks are to facilitate interdisciplinarity they must be clearly articulated by invasion scientists in collaboration with researchers in other fields to ensure that the definitions and processes that these frameworks capture can be understood and adopted across the various disciplines. However, of the ~110 authors of this special issue, we estimate around 70% would describe themselves as having biological invasions as a main interest or responsibility and about two-thirds are primarily based at a university. All but a handful are ecologists, highlighting the ongoing need for better integration with other disciplines and the social sciences in particular. When invasion frameworks do not successfully bridge disciplines and provide a link between research and implementation, then it seems inevitable that there will be points of confusion and tension (Richardson and Ricciardi 2013), leading to the reinvention or 'creative' use of terminology within allied fields (Essl et al. 2020a; Wilson 2020), and lost opportunities for reciprocal advancement in knowledge (Hulme 2014). We see this articulation between disciplines using invasion frameworks as particularly pertinent given the expected massive shift in species ranges due to climate change and the increasing frequency with which we are confronted with emerging infectious diseases in human and non-human populations (Ogden et al. 2019; Nunez et al. 2020).

Finally, if, as per our working definition, a framework should "…be easily communicated to allow for shared understanding…" then at least some frameworks should also be valuable aids for communicating between invasion scientists and the people and industries that are impacted (negatively and positively) by alien species. Arguably, one of the most effective communication tools in invasion science is the invasion curve [The invasion curve is a roughly logistic shaped curve of 'area infested' or something similar plotted against time. It is split into different stages with different management actions highlighted. It is perhaps best exemplified by the version of the Department of Primary Industries (2010)]. However, this simplifies the issue and so is not useful as a framework in practice. Similarly, the impact equation of Parker et al. (1999) captures the essence of the problem—impact is the product of the range size of a species, its abundance per unit area, and the effect per individual or per biomass unit——but is also not easy to implement in practice (Blanchard et al. 2011). Many frameworks within the field of invasion science might be primarily about facilitating communication between invasion scientists, however it will be valuable to also have frameworks that clarify key aspects of biological invasions in a way that links the 'nuts and bolts' of invasions with societal priorities, and to create or modify frameworks in invasion science so they are easily understood not just by scientists, policy makers, and managers, but also by broader stakeholders.

Conclusion

It appears from the set of articles in this special issue that invasion science is maturing as a distinct discipline. The process of developing, refining, and increasingly implementing frameworks suggests the field is moving from 'storming' to 'norming' [to paraphrase a framework from psychology (Tuckman 1965)]. If we assume that trends in globalisation will continue, as seems almost certain, there is now strong evidence that the taxonomic variety and number of species that have the opportunity to establish as aliens somewhere on Earth will continue to rise (Seebens et al. in press). In this context, frameworks in invasion science should be viewed as tools that are worthwhile only if they are used and are useful. It is important that frameworks are increasingly tested (be it within policy, research or management settings) and any limitations clearly shared with others in and outside the field. We suspect that the overriding importance of context in invasion science will continue to be the rule rather than the exception, and that frameworks will need to adapt to these contingencies to remain useful. We consider this approach to be encompassed by the 'Stellenbosch Challenge for Invasion Science'. We believe the articles within this special issue (Appendix 1) show how responding to this challenge can improve our understanding of, and responses to, biological invasions.

Postscript

The urgent need to reduce carbon emissions meant that several people decided not to attend the workshop in person. Moreover, the review and revision of the articles published in this special issue happened against the backdrop of the COVID-19 pandemic (Nunez et al. 2020). While face-to-face workshops like the one described here might be less common in future, we hope that they will soon be possible again. A beautiful venue, good food, and stimulating company will not resolve biological invasions, but they make the process that bit more enjoyable (Figure 3).

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Figure 3. Workshop attendees benefitting from the shade of an alien *Eucalyptus* sp. on a transformed lawn.

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Supplementary material 1

Details of the workshop, the invitation, list of attendees, the programme, ground rules, form for highlighting case-studies, and the process for compiling the special issue

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Data type: explanatory text

Explanation note: additional information regarding the workshop 'Frameworks used in Invasion Science' held 11–13 November 2019 in Stellenbosch, South Africa, hosted by the DSI-NRF Centre of Excellence for Invasion Biology, and the special issue of NeoBiota on frameworks in invasion science that emerged from it.

Link: https://doi.org/10.3897/neobiota.62.58738.suppl1

Appendix 1

Table A1. The papers in this special issue on 'Frameworks in Invasion Science' with the details of the frameworks they consider, which aims of the special issue they address, and a summary of key findings or recommendations.

	Paper	Frameworks considered[1]	Aims[2]	Findings / Recommendations
1	Bertolino et al. (2020) A framework for prioritising present and potentially invasive mammal species for a national list. https://doi.org/10.3897/neobiota.62.52934	• *CBD pathway classification* • *EICAT* • *SEICAT*	5, 7	• "We developed a prioritisation process for alien mammals already established in Italy…(n = 6 species) and a systematic horizon-scanning procedure to obtain ranked lists for those species that are already introduced worldwide or traded in Italy (n = 213) and which are likely to establish, spread and impact on biodiversity and human well-being." • "…the procedure developed in this study could be used as a blueprint for similar prioritisation initiatives…according to different priorities established by country regulations or policies."
2	Brock and Daehler (2020) Applying an invasion and risk framework to track non-native island floras: a case study of challenges and solutions in Hawai'i. https://doi.org/10.3897/neobiota.62.52764	• *Hawai'i–Pacific Weed Risk Assessment* • *Unified Framework*	1, 4, 5	• The unified framework has limitations as a tracking system for entire alien floras—both too detailed for practical use, and the category 'naturalised but not invasive' can indicate both low and high priority for management. • Propose a revised system for tracking status along the introduction-naturalisation-invasion continuum. • Incorporating information from weed risk assessment frameworks can provide insights for management.
3	Datta et al. (2020) Identifying safe cultivars of invasive plants: six questions for risk assessment, management, and communication. https://doi.org/10.3897/neobiota.62.51635	• None (though follows the generic process of a risk analysis as one composed of risk identification, assessment, management, and communication)	7	• "…clarify the issue of distinguishing 'safe' cultivars from 'risky' relatives by recasting the problem as a set of six questions that align with the risk analysis process" o Has an infra- or inter-specific entity of an invasive entity been proposed as 'safe to use'? o Which traits are different between the non-invasive and invasive entities? o Do the trait differences lead to a significant difference in invasion risk? o Are the differences spatially and temporally stable? o Can the entities be distinguished in practice? o How can the risks and the management of them be best communicated?
4	Essl et al. (2020) The Convention on Biological Diversity (CBD)'s Post-2020 target on invasive alien species – what should it include and how should it be monitored? https://doi.org/10.3897/neobiota.62.53972	• *CBD pathway classification* • *EICAT* • *SEICAT* • *Red List* • *Indicator frameworks*	1, 3, 5, 6	• A target on biological invasions should "…explicitly consider[s] the three main components of the phenomenon of biological invasions, i.e. (i) pathways, (ii) species, and (iii) sites…; (iv) is quantitative…; (v) is supplemented by a set of indicators that can be applied to track progress; and that it (vi) can be evaluated at medium- (2030) and long-term (2050) time horizons". • Proposes the following target: "Halting the loss of biodiversity caused by invasive alien species by 2030, by preventing their impacts in [100% of] the most vulnerable areas, regulating [50% of] the most harmful invasive alien species, and effectively managing [50% of] the most significant pathways of introduction, such that their impacts are reversed through restoration and recovery by 2050." • Provides recommendations for proposed indicators to track progress towards meeting the target.
5	Evans et al. (2020) Application of the Socio-Economic Impact Classification for Alien Taxa (SEICAT) to a global assessment of alien bird impacts. https://doi.org/10.3897/neobiota.62.51150	• *SEICAT*	1, 6	• "…SEICAT can be used effectively to quantify and categorise the impacts of alien species on human well-being." • "The most significant problem… was a lack of impact data." • Most significant threat to human well-being is impacts on aviation safety; most data described agricultural impacts. "No data were found describing disease transmission impacts on humans." Suggests the availability of impact data is biased to developed countries. • Notes that SEICAT is important for stimulating and directing research.

	Paper	Frameworks considered[1]	Aims[2]	Findings / Recommendations
6	Faulkner et al. (2020) Classifying the introduction pathways of alien species: are we moving in the right direction? https://doi.org/10.3897/neobiota.62.53543	• *CBD pathway classification* (main and sub categories) • *New Zealand biosecurity surveillance system*	2, 3, 6	• Identifies five desirable properties for the categories used in an introduction pathway classification framework 'Compatible', 'Actionable', 'General', 'Equivalent', and 'Distinct'. • "…the main categories of the CBD framework have all of the desirable properties…but the sub-categories have few". • Proposes scenarios for improving existing frameworks and recommends "a hybrid model—a few general categories at the global scale and context-specific sub-categories driven by local needs at a regional level".
7	Hulme et al. (2020) The Epidemiological Framework for Biological Invasions (EFBI): an interdisciplinary foundation for the assessment of biosecurity threats. https://doi.org/10.3897/neobiota.62.52463	• *SIR models* • *State-and-Transition model*	7	• "The EFBI approach presents a new biosecurity perspective that takes account of ecosystem status and complements demographic models to deliver clearer insights into the dynamics of biological invasions at the landscape scale." • "The basic epidemiological compartment model can…provide insights… for the monitoring, mapping and management of non-native species."
8	Kumschick et al. (2020) Appropriate uses of EICAT protocol, data and classifications. https://doi.org/10.3897/neobiota.62.51574	• *EICAT*	2, 3, 6	• "Standardising and globalising the process of impact assessment within a framework, such as EICAT, can aid countries…to develop policies and priorities for tackling biological invasions". • "…present guidelines designed to clarify and facilitate the appropriate use of EICAT…as well as to guide research and communication more generally". • "…deviations from the standard process should be adequately described and acknowledged to avoid confusion with the official, standardised process."
9	Kumschick et al. (2020) A framework to support alien species regulation: the Risk Analysis for Alien Taxa (RAAT). https://doi.org/10.3897/neobiota.62.51031	• *EICAT* • *SEICAT* • *CBD pathway classification* • *Unified framework* • *Confidence rating* • *Eradication feasibility*	3, 5, 7	• Proposes a new risk analysis framework for alien taxa: "1) given major recent developments in international frameworks dealing with biological invasions (including the scoring of impacts); 2) so that decisions can be made consistently across taxa, regions, and realms; 3) to explicitly set out uncertainties; and 4) to provide decision-makers with information both on the risks posed and on what can be done to mitigate or prevent impacts." • Outlines how the framework has been tested and applied to support decisions regarding the listing of alien taxa under South Africa's regulations on biological invasions.
10	Latombe et al. (2020) The effect of cross-boundary management on the trajectory to commonness in biological invasions. https://doi.org/10.3897/neobiota.62.52708	• *Categories of commonness*	1, 4	• Proposes an additional two categories to the existing eight categories of commonness: 'dispersed + abundant somewhere' and 'sparse + abundant somewhere'. • Compares the value of improving the efficacy of biosecurity vs. how quickly countries implement biosecurity against a particular threat. • "... [under certain conditions] synchronisation across spatial units will improve the efficacy of management". • "...time lags in population growth…[should] be considered explicitly for management, as they can amplify the efficacy of such measures."
11	Liebhold (2020) Scale invariance in the spatial-dynamics of biological invasions. https://doi.org/10.3897/neobiota.62.53213	• *"stratified diffusion"* • *"bridgehead effect"* • *Unified framework*	7	• "...all [invasion] stages biologically ensue from just two demographic processes—dispersal and population growth" • "...different invasion stages [arrival, establishment, and spread] can be considered manifestations of similar processes operating at different spatial scales". • "...future frameworks may be able to incorporate these similarities in a simpler structure."

	Paper	Frameworks considered[1]	Aims[2]	Findings / Recommendations
12	Measey (2020) The cost and complexity of assessing impact. https://doi.org/10.3897/neobiota.62.52261	• *EICAT* • *SEICAT* • *study designs* (e.g. BACI, randomised control trials)	1, 6	• "…studies that resulted in higher impact scores were more costly…we need to carefully consider whether species with low scores represent true impact, or require more research investment and time." • Suggests the availability of impact data is biased to developed countries. • "…a relatively short period of time (less than four years) is enough to make considerable changes to the global list of EICAT and SEICAT amphibian scores."
13	Paap et al. (2020) Harmonising the fields of invasion science and forest pathology. https://doi.org/10.3897/neobiota.62.52991	• *Unified framework* [cf. Wingfield et al. (2017)] • *CBD pathway framework* • *EID frameworks* • *EICAT*	2, 6	• Invasion frameworks are not widely applied in the study of forest pathology as historically the focus of the field has been on controlling the resulting disease problems rather than understanding how invasions arise. • Advances in molecular technologies increase the "visibility" of microorganisms, and will facilitate productive collaborations between pathologists and other invasion scientists.
14	Pergl et al. (2020) Applying the Convention on Biological Diversity Pathway Classification to alien species in Europe. https://doi.org/10.3897/neobiota.62.53796	• *CBD pathway classification*	1, 4	• "...the CBD Pathway Classification framework offers a robust, hierarchical system suitable for the classification of alien species introduction and spread…However, simple modifications could improve interpretation of the pathway categories ensuring consistent application across databases and information systems at local, national, regional, continental and global scales…[and] in the development of pathway action plans." • The CBD Pathway Classification framework should be used jointly with the guidance of Harrower et al. (2017). • Several specific recommendations, e.g., "…if the contaminated substratum is itself a commodity and a vector, then the assigned pathway should fall in the Contaminant category. However, if the contaminated substratum is only a vector (physical or biological), then the assigned pathway should fall in the Stowaway category".
15	Potgieter and Cadotte (2020) The application of selected invasion frameworks to urban ecosystems. https://doi.org/10.3897/neobiota.62.50661	• *EICAT* • *SEICAT* • *Unified Framework*	1, 6	• "In urban areas, the relative effectiveness of the barriers to invasion is diminished (to varying degrees) allowing a greater proportion of species to move through each subsequent invasion stage, i.e. 'the urban effect' on invasion." • "Impact classification schemes inadequately circumscribe the full suite of impacts (negative and positive) associated with invasions in urban areas." • "We suggest ways of modifying these frameworks to improve their applicability to understanding and managing urban invasions."
16	Probert et al. (2020) Understanding uncertainty in the Impact Classification for Alien Taxa (ICAT) assessments. https://doi.org/10.3897/neobiota.62.52010	• *EICAT* • *SEICAT* • *Uncertainty classification*	2, 4	• "We identify three types of biases…not captured by the confidence score…biases in the existing data, data collection, and data assessment." • "Clarifying uncertainty concepts relevant to [the ICAT frameworks] will lead to more consistent impact assessments and more robust intra- and inter-specific comparison of impact magnitudes".
17	Pyšek et al. (2020) MAcroecological Framework for Invasive Aliens (MAFIA): disentangling large-scale context dependence in biological invasions. https://doi.org/10.3897/neobiota.62.52787	• None though various frameworks are discussed and have elements of MAFIA (e.g., *TEASI* and *PAB*)	3, 6, 7	• Note that as invasion are a result of "Alien species traits, Location characteristics, and Event-related factors", then "For a successful invasion, all factor classes and their interactions need to be favourable (Species × Location × Event)." • Recommend that all these factors and their interactions must be explicitly considered in macroecological analyses of invasions, otherwise spurious conclusions will be reached.

	Paper	Frameworks considered[1]	Aims[2]	Findings / Recommendations
18	Robinson et al. (2020) Double trouble: the implications of climate change for biological invasions. https://doi.org/10.3897/neobiota.62.55729	• *CBD pathway classification* • *Invasion syndromes* • *Unified framework*	6	• Climate change will have varied, and in some cases unpredictable, effects on biological invasions across the introduction-naturalisation-invasion continuum. • Our understanding of the implications of climate change for biological invasions would be improved by: o more foundational research (including on taxonomy); o a greater appreciation of context-dependency and tools to address it explicitly; o data and analytical tools at the appropriate resolution; and o more inter-disciplinary work.
19	Sinclair et al. (2020) Reciprocal human-natural system feedback loops within the invasion process. https://doi.org/10.3897/neobiota.62.52664	• *Propagule pressure as a null model* • *Human Adaptation to Invasive species*	1, 6, 7	• "…invasion frameworks generally do not consider reciprocal interactions between non-native species and people… [but] 'coupled human and natural system' (CHANS) could…play a key role in mitigating…or exacerbating…ongoing and future invasions". • People in source regions (the supply-side) influence which taxa are introduced and how. • The way people interact with non-native species changes over time and can lead to unexpected emergent effects. • The study of CHANS in the context of biological invasions is in its infancy, but CHANS can have important implications for policy and management.
20	Van der Colff et al. (2020) Comparing the IUCN's EICAT and Red List to improve assessments of the impact of biological invasions. https://doi.org/10.3897/neobiota.62.52623	• *EICAT* • *Red List*	1, 2, 5	• "The EICAT and Red List schemes will benefit each other if information underpinning their assessments is made available and shared." • The EICAT and Red List statuses are only closely correlated in special circumstances. In most cases the two frameworks are complementary rather than equivalent, and both should be used to assess impacts.
21	Vimercati et al. (2020) The importance of assessing positive and beneficial impacts of alien species. https://doi.org/10.3897/neobiota.62.52793	• *EICAT* • *Biopollution assessment scheme* • *EICAT* • *GISS* • *impacts of invasive marine species* • *InSEAT* • *Invasive species assessment protocol* • *A prioritisation tool for IAS management* • *SEICAT*	2, 6	• Provides a summary of frameworks assessing beneficial impacts. • Reviews papers arguing for greater inclusion of positive impacts (both from value-free and value-laden perspectives). • Existing frameworks should be extended to include positive impacts.
22	Volery et al. (2020) Improving the Environmental Impact Classification for Alien Taxa (EICAT): a summary of revisions to the framework and guidelines. https://doi.org/10.3897/neobiota.62.52723	• *EICAT*	3, 4	• Details changes made to the EICAT framework and guidelines in response to the IUCN's consultation process in terms of: o definitions (performance rather than fitness; defining population, sub-population, and local population); o impact categories (distinguishing between Major and Massive impacts); o impact mechanisms (to deal with indirect impacts, transmission of disease, and hybridisation); o presentation of overall impact (spatial and geographic scales of assessments, and using maximum ever recorded impact rather than current impact); and o dealing with uncertainty (confounding effects, study design, and temporal scale).

	Paper	Frameworks considered[1]	Aims[2]	Findings / Recommendations
23	Wilson et al. (2020) Is invasion science moving towards agreed standards? The influence of selected frameworks. https://doi.org/10.3897/neobiota.62.53243	• *Hulme et al (2008)* • *CBD pathway classification* (main categories) • *Unified Framework* • *EICAT*	2	• The frameworks are cited by researchers from across the world working on different taxa and in different habitats, and they are increasingly being taken up into invasion policy and management. However, roughly half of all citations might be viewed as frivolous or 'citation fluff'. • A survey of those who cited the frameworks found that while the frameworks are highly regarded, many respondents felt the frameworks have not been rigorously tested yet. • To increase uptake, the frameworks need to be revised or adapted to particular contexts, guidelines for their usage developed, and there should be incentives for their usage.
24	Ziller et al. (2020) A priority-setting scheme for the management of invasive non-native species in protected areas. https://doi.org/10.3897/neobiota.62.52633	• None, though various other prioritisation frameworks are discussed; the definitions used align with those of the *Unified Framework*; and *EICAT* is proposed as a data source	7	• Presents a management prioritisation system for biological invasions that is being applied by managers of protected areas in Brazil. • "Priorities are calculated from…species risk of invasion (R), invasion stage (S), and species frequency for each occurrence (F)". • "As per the prioritisation scheme, the highest priorities for control were attributed to species of high invasion risk in early stages of invasion restricted to one location"

[1] The frameworks / concepts used as cited in the papers are: *Biopollution assessment scheme* (Olenin et al. 2007); *Bridgehead effect* (Lombaert et al. 2010); *Categories of commonness* (McGeoch and Latombe 2016); *CBD pathway classification* (CBD 2014; Harrower et al. 2017), and also *Hulme et al. (2008)*; *Confidence rating* (as cited by Hawkins et al. 2015); *EICAT* (the Environmental Impact Classification for Alien Taxa) (Blackburn et al. 2014; Hawkins et al. 2015; IUCN 2020); *eradication feasibility* (Panetta and Timmins 2004; Wilson et al. 2017); *the Hawai'i–Pacific Weed Risk Assessment* (Daehler et al. 2004) *the Human Adaptation to Invasive Species framework* (Howard 2019); *indicator frameworks for biological invasions* (McGeoch et al. 2010; Latombe et al. 2017; Wilson et al. 2018) see also sTWIST – Theory and Workflows for Alien and Invasive Species Tracking (https://www.idiv.de/en/stwist.html); *invasion syndromes* (Novoa et al. 2020); *Invasive species assessment protocol* (Morse et al. 2004); *INvasive Species Effects Assessment Tool (InSEAT)* (Martinez-Cillero et al. 2019); *impacts of invasive marine species* (Katsanevakis et al. 2014); *the New Zealand biosecurity surveillance system* (Ministry of Agriculture and Forestry (MAF) Biosecurity New Zealand 2008); *a prioritization tool for IAS management* (Kumschick et al. 2012); *propagule pressure as a null model* (Colautti et al. 2006); the *TEASI* (Transport, Establishment, Abundance, Spread, Impact) framework (Leung et al. 2012); the *PAB* (Propagule pressure, Abiotic characteristics, and Biotic characteristics) framework (Catford et al. 2009); *the IUCN Red List* (IUCN Standards and Petitions Committee 2019); *SEICAT* (the Socio-economic Impact Classification of Alien Taxa) (Bacher et al. 2018); *state-and-transition models* (Bestelmeyer et al. 2017); *stratified diffusion models* (Hengeveld 1989); *study designs* (Christie et al. 2019); *SIR models* (Susceptible-Infectious-Resistant compartment model) (Blackwood and Childs 2018); a *classification of uncertainty framework* (Regan et al. 2002); and the *Unified Framework* (for Biological Invasions) (Blackburn et al. 2011).

[2] The aims were adapted and expanded from those of the original advert for the meeting (see Suppl. material 1). As listed here they are: 1) apply the frameworks to new data or contexts; 2) review how the frameworks have been adopted and used; 3) develop useable protocols or guidelines for applying frameworks to different contexts; 4) refine the frameworks; 5) integrate frameworks; 6) identify gaps; and 7) develop new frameworks. Several of the papers addressed multiple aims, but the special issue as a whole addressed all of them fairly evenly (each aim is addressed by between five and eleven papers).

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RESEARCH ARTICLE

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A framework for prioritising present and potentially invasive mammal species for a national list

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Abstract

The European Union (EU) has recently adopted a regulation on invasive alien species that foresees the possibility of developing lists of species of National Concern. We developed a prioritisation process for alien mammals already established in Italy, but not yet included in the EU list (n = 6 species) and a systematic horizon-scanning procedure to obtain ranked lists for those species that are already introduced worldwide or traded in Italy (n = 213). Experts were asked to score these species, by evaluating their likelihood of establishment and spread and the magnitude of their potential impacts on biodiversity, economy, human-health and society. The manageability of each species was also evaluated, both for the proritisation and the horizon-scanning processes. We produced five lists that ranked species according to their potential spread and impacts and their manageability. These will allow policy-makers to select outputs according to a balance between risk assessment and risk management, establishing priorities for alien species management at the national level.

Keywords

Biodiversity, horizon scanning, human well-being, impact, Mammalia, non-native species, prioritisation

Introduction

Establishing a proactive strategy on invasive alien species – i.e. species that are non-native to an area and which may cause environmental or economic harm or adversely affect human health – requires a clear focus on prevention (Simpson et al. 2009). Avoiding the establishment of new species or their spread over large areas greatly reduces the risk that they become invasive (Finnoff et al. 2007). Effective prevention strategies require the identification of those species which are not yet present in a country, but which are likely to enter in the short-medium period, through active pathways (Simpson et al. 2009). This can be done through horizon-scanning protocols. On the other hand, those species which already established could be prioritised for management, through rapid eradication, spatial containment or population control, according to their present spread and manageability.

In 2014, the European Union adopted a regulation (EU Regulation 1143/2014) on the prevention and management of the introduction and spread of invasive alien species. The regulation is based on a list of 'Invasive Alien Species of Union Concern' (hereinafter, Union list), identified through a detailed risk assessment (Roy et al. 2017) evaluated by a Scientific Forum and a Committee with representatives of all Member States. To be included in the list, species have to meet a number of criteria: first, to be alien to the territory of the European Union (excluding the outermost regions); second, to have been assessed as invasive or potentially invasive through a risk assessment. Species included in this list are subject to strict provisions for preventing their introduction into the European Union. The regulation includes a ban on import, trade, breeding, release into the environment and the obligation to produce management plans for already established species (Genovesi et al. 2014). The Union list was based on available risk assessments compliant with the minimum standards (Roy et al. 2017), but subsequently, a horizon-scanning approach was used to rank species to be subjected to risk assessment (Roy et al. 2015).

Horizon scanning is a systematic process aimed at identifying emerging issues which may represent threats or opportunities to society (Sutherland and Woodroof 2009). In the field of biological invasion, horizon scanning allows for the rapid screening of a large number of species through expert opinion and consensus method

(Sutherland et al. 2011). This procedure has already been successfully applied to rank species according to their likelihood of arrival, establishment and impacts (e.g. Roy et al. 2014; Gallardo et al. 2016). In the UK, horizon scanning was able to correctly identify some alien species that subsequently invaded the country, such as *Dreissena rostriformis* or *Vespa velutina* (Aldridge et al. 2014; Roy et al. 2014; Budge et al. 2017). Horizon scanning can thus produce dynamic lists of potential invasive alien species that can be prioritised in regulations.

Within the framework of this EU Regulation, Member states may establish a list of Invasive Alien Species of National Concern, to which provisions and restrictions foreseen for the species of Union Concern may be applied at the national level. Species could be included in national lists only after the evaluation of the same risk assessment procedure used for evaluating species at the EU level (Roy et al. 2017). In 2018, a national legislative decree (no. 230/2017), aimed to adapt national law to EU Regulation 1143/14, entered into force in Italy. The decree provides for the adoption of a national list of invasive or potentially invasive species with the same provisions and restriction foreseen for the Union list.

As a contribution to the development of such a list, the Italian Mammal Society (Associazione Teriologica Italiana: www.mammiferi.org) gathered a group of experts to draw up a proposal for a list of alien mammal species of national concern. This activity was part of a larger initiative promoted by the national Institute for Environmental Protection and Research (ISPRA, identified in the national decree as the governmental agency that technically supports the Ministry of Environment in the application of the EU Regulation at the national level) which addressed the use of a standardised protocol for the assessment many different taxa (e.g. other vertebrates, invertebrates and plants, from terrestrial, freshwater and marine organisms).

Experts tasks: *i*) carry out the horizon scanning to identify species not yet present in Italy, which could potentially enter, establish, spread and produce impacts in the country and *ii*) prioritise the management of alien species already present in the country. The horizon-scanning and prioritisation initiatives were based on the analysis of the invasion process and on the resulting unified framework proposed by Blackburn et al. (2011). The framework breaks down the invasion process into a series of stages (arrival in a new area, introduction, establishment and spread), each one characterised by barriers that need to be overcome by individuals, in order to reach the subsequent stage. Additionally, we also considered the impacts that a species could potentially produce on biodiversity, economy, society and human health.

A comprehensive framework for risk analysis encompasses evaluations regarding both risk assessment and options for management of species (Booy et al. 2017; Kumschick et al. 2020b). Risk assessment evaluates the species based on the likelihood of their successful establishment and spread over large areas, and according to the magnitude of their potential impacts over biodiversity or human well-being. Risk management, on the other hand, accounts for the level of manageability of the species, in terms of the effectiveness of prevention measures and the feasibility of their rapid eradication or control. For instance, species that are difficult to eradicate must be considered a priority for prevention (e.g. through trade restriction), while easy-to-manage species could still be eradicated or controlled after establishment.

Our approach was to develop a support system to help policy-makers establishing national priorities. We thus produced different lists highlighting alien species with a higher likelihood of arrival, establish and spread and that could produce negative impacts on biodiversity or human well-being as a consequence of invasion. These evaluations were then integrated with species manageability.

Methods

Horizon scanning, aimed at producing lists of potentially invasive alien species, was based on: *i*) their likelihood of establishing viable alien populations if imported and released in Italy, *ii*) their potential to impact biodiversity and human well-being and *iii*) their level of manageability, so as to prioritise species for prevention or management. For species already present in the country, the prioritisation process was carried out mainly to rank them for management purposes (Nentwig et al. 2010; Booy et al. 2017). Both processes followed a structured approach that involved five steps (Gallardo et al. 2016; Matthews et al. 2017).

Step 1: Lists of species

The list of species for the horizon scanning included mammals showing at least one alien population worldwide and not yet included in the Union list. The list was built upon information collected from GRIIS (http://www.griis.org/), GISD (http://www.iucngisd.org/gisd/) and CABI (https://www.cabi.org/ISC), and integrated with occasional reports from available scientific literature. Since pet trade is a main pathway of recent mammal introductions (Bertolino 2009; Genovesi et al. 2015), we also scanned the web to identify those species that are traded in Italy and which could potentially escape from captivity. From the resulting list, we then excluded: (*i*) domesticated species, (*ii*) species native to Italy, (*iii*) taxa *incertae sedis* (i.e. potential synonymous to those naturally present in Italy), as well as (*iv*) recently split taxa. Non-native species that were occasionally recorded in Italy, but with no confirmed reproduction events, were also included in this list, for example, the Prevost's squirrel *Callosciurus prevosti*, the Patagonian mara *Dolichotis patagonum* and the Indian crested porcupine *Hystrix indica*. The final list considered for horizon scanning included 212 species (see Suppl. material 1).

The prioritisation list included all non-native species which had been recorded with reproductive populations in Italy (see Loy et al. 2019) and which were not included in the Union list (*sensu* EU Regulation 1143/2014). We did not consider species that had been introduced in Italy before 1500 (i.e. the fallow deer *Dama dama*, the mouflon *Ovis aries*, the wild rabbit *Oryctolagus cuniculus*, the Sardinian hare *Lepus capensis* *mediterraneus*, the black rat *Rattus rattus*), as well as those of uncertain allochthony or for which the introduction date is not defined, i.e. the Norway rat *R. norvegicus* and the crested porcupine *Hystrix cristata*. This decision follows the Italian legislation (Decreto Ministero Ambiente – Ministry of the Environment Decree, 19 January 2015), stating that these species should not be managed as non-native species. The selection ended up with six species retained for the prioritisation list analysis.

For each species in both prioritisation and horizon-scanning lists, we reported the native range following the Taxonomic Database Working Group (TDWG) categories (Europe, Africa, Asia-temperate, Asia-tropical, Australasia, Pacific, North America, South America and Antarctica) and the functional group (predator, herbivore, omnivore).

Step 2: Assessment form

For each species in the lists, we evaluated the following aspects: taxonomy, presence/absence in Italy, likelihood of arrival into the country or escape from confinement, likelihood of establishment and spread, either natural or human aided (with subsequent releases, Hulme et al. 2007), with a scoring system ranging from 1 (low likelihood) to 5 (high likelihood); degree of potential impact on social and economic activities, human health and biodiversity, scoring from 1 (low) to 5 (high), effectiveness and acceptability of prevention and control measures (scoring 1–5, with 5 indicating a species easier to manage). The potential impacts on species and habitats included in annexes of international regulations (Birds Directive 79/409/EEC, Habitats Directive 92/43/EEC) were also added (Table 1).

For horizon scanning, we also reported whether each species was present in zoological gardens or other confined environments in Italy, by checking the zoological garden species lists and the website www.zootierliste.de/en. For both prioritisation and horizon-scanning lists, the main introduction pathways were also reported following the classification provided by the Convention of Biological Diversity (CBD) (Harrower et al. 2018; see also Faulkner et al. 2020 and Pergl et al. 2020 for a discussion of its implementation).

The potential impact on native biodiversity was estimated for both lists, using the evidence-based Environmental Impact Classification of Alien Taxa (EICAT) system (Blackburn et al. 2014; Hawkins et al. 2015; see also Volery et al. and Kumschick et al. 2020a). This protocol scores the progressive severity of the impact produced by an alien species considering if it affects individuals, populations or communities. Ranking from 1 (low) to 5 (high), the EICAT scheme ranges from negligible impacts to a reduction in performance of native individuals, a native population decline and a local extinction, which is naturally reversible or irreversible (IUCN 2020). The EICAT process relies on a complete review of published evidence about the impacts of alien species (Evans et al. 2016). Each expert assessed the potential impact on biodiversity using a simplified EICAT assessment, based on a rapid scan of the main literature. For the same reason, when the impact on biodiversity was classified at

Table 1. Database structure for horizon scanning (HSL) and prioritisation (PL).

Information	HSL	PL
Common and scientific name	×	×
Native range	×	×
Functional group	×	×
Presence/absence in Italy in the wild/occurring in confinement	×	×
Rank 1 – 5: 1 minimum, 5 maximum value		
Likelihood of arrival or escape from confinement	×	
Likelihood of establishment	×	×
Likelihood of natural spread	×	×
Likelihood of human-assisted spread	×	×
Probable main introduction pathway	×	
Likelihood of re-invasion		×
Potential of impact on biodiversity	×	×
Potential of impact on economy	×	×
Potential of impact on human health	×	×
Potential of impact on social aspects	×	×
Likelihood of colonisation and potential impact on habitat and species of European concern, listed in the annexes of Birds or Habitats Directives (yes/no and list)	×	×
Rank 1 – 5: 1 more difficult to manage, 5 more easy to manage		
Effectiveness of prevention measures, including trade regulation, measures related to intentional imports, practicality of carrier treatment etc.	×	
Effectiveness of control measures, including ease of species identification in the field	×	×
Current eradication feasibility		×
Potential eradication feasibility on a small geographical area		×
Eradication potential cost		×
Potential side effects of the eradication		×
Inferred social acceptability of eradication		×
Potential cost of environmental restoration		×
Notes	×	×
References	×	×

the lowest level (i.e. 1), the species was considered a low priority and the remaining fields were not completed. In this way, species that could have a high impact on human well-being, but a low environmental impact, were excluded. This approach was chosen in agreement with ISPRA, following the EU Regulation that specifically addresses species that have or could have adverse impact on biodiversity. We recognise that some species may have been evaluated with a potential low impact simply because they have not yet been studied in their range of introduction. However, we preferred to focus on species with demonstrated, or inferable from similar species (e.g. of the same genus), impacts.

When the impact on native biodiversity was higher than 1, we also estimated their potential for impact on human activities (economic impact), human health and society. These latter evaluations were based on the Socio-Economic Impact Classification of Alien Taxa (SEICAT; Bacher et al. 2017), which evaluates the level of observed changes in peoples' activities. Ranking from 1 (low) to 5 (high), this system is connected to negative effects on peoples' well-being, such that the alien taxon makes it difficult for people to perform their normal activities, to effects leading to changes in the frequency or the local disappearance of an activity, which might be irreversible even if the invasive species is removed. SEICAT is an evidence-based classification system, based on a complete review of literature. Similarly to EICAT, it was applied through a simplified process that considered main references only.

Negative influence on species and habitats protected by EU legislations (Birds Directive 79/409/EEC and Habitats Directive 92/43/EEC) was reported only when clear evidence was detected in scientific literature. For both lists, we also recorded whether species were included in the annexes of other EU regulations and international conventions (e.g. CITES).

The effectiveness of management strategies, for example, eradication, was evaluated, also by taking into account the ease of species identification in the field. The feasibility of eradication was assessed for the prioritisation list only and it was considered low for those species with a wide introduction range and high for localised species (Panetta and Timmins 2004; Robertson et al. 2017; Wilson et al. 2017). Prioritisation was also based on the estimated costs for the management of established species, on potential side effects of eradication methods (e.g. potential impacts on native species), on the social acceptability of eradication and control methods (Booy et al. 2017) and on the estimated costs connected with the environmental restoration following the management intervention.

Step 3: Bioclimatic models

Since climate is one of the main factors limiting the establishment of new species in an area (Redding et al. 2019), we produced suitability maps to help assessors evaluating the climatic similarity between Italy and the native range of each species. Overall, we considered five bioclimatic variables. Four of them described climate conditions: annual mean temperature, temperature seasonality, total annual precipitation and precipitation seasonality. Altogether, these variables explain most of the climatic variation at the global scale (Buckley and Jetz 2008). We also considered the normalised difference vegetation index (NDVI), which is a proxy for vegetation productivity. Climate maps at a resolution of 10 × 10 arc-minutes were obtained from the WorldClim dataset (Fick and Hijmans 2017), while NDVI map was retrieved from the "land cover" project of the climate change initiative of the European Space Agency (Verhegghen et al. 2014). For each species, we extracted its range from IUCN distribution maps (IUCN 2016) and rasterised each range at 10 × 10 arc-minutes resolution. Due to the lack of true absences, we sampled 3,000 pseudo-absences within a radius of 1,000 km from each species' range (Chapman et al. 2019).

Climatic suitability was obtained through an ensemble of species distribution models (Araújo and New 2007), using the package 'biomod2' (Thuiller et al. 2016) within the statistical software R (R Core Team 2020). We ran a total of five different models: boosted regression trees, classification tree analysis, generalised additive models, multivariate adaptive regression splines and random forests. In order to get model evaluations, we performed a 5-fold cross-validation and, for each run of the model, we randomly sampled 67% of the presences for model training and 33% of the presences for testing. The performance of each model was assessed through the True Skill Statistic (TSS), a method for assessing the accuracy of species distribution models, which returns values ranging from -1 to 1, where a value of 0 indicates a performance of a random model, while a value of 1 indicates a perfect agreement between observed data and model predictions (Allouche et al. 2006). Finally, an ensemble model was obtained through the sum of the occurrence probability predicted by each of the five models, weighted by the model's TSS.

For each species, the ensemble model was projected on the Italian and European bioclimatic conditions, in order to obtain a visual representation of the predicted suitability across the country.

Step 4: Expert-based assessment

Eleven mammal experts were involved in three workshops. In the first one, the procedure was discussed with other experts who had previously engaged in at least one horizon-scanning exercise. Subsequently, five species were selected from different taxonomic orders, giving to each mammal expert the task of their independent evaluation, before a second workshop.

In the second workshop, the five species were assessed collectively, by highlighting and resolving differences between assessors' judgements. After the second workshop, each expert assigned the scores to five new species, different from those evaluated previously.

In the last workshop, 1–2 species evaluated by each assessor were scored together, discussing the reasons behind each score. After these workshops, all the species were divided and assigned to experts, each one assessing species belonging to different taxonomic orders, including the previous that were re-evaluated independently.

References on species impacts necessary to fill ICAT Schemes (EICAT and SEICAT) scores were searched in scientific literature (Google Scholar, Scopus and ISI Web of Knowledge) and in GISD and CABI websites. When scientific literature was not available for a certain species, forms were filled using available information on similar, phylogenetically-related taxa, which are expected to have similar ecological requirements and adaptation capabilities (e.g. introduced species of the same genus, see, for example, Lambdon 2008; Bertolino 2009; Gallien and Carboni 2017).

Step 5: Prioritised lists of non-native mammals

From the final database, we compiled five prioritised lists of mammal species, based on their potential impacts on biodiversity and human well-being. Impacts were evaluated first separately and then together and we also assigned a manageability score, reflecting the possibility to effectively manage the species. For the horizon scanning, we first calculated a score for the likelihood of arrival and spread as follows (Fig. 1):

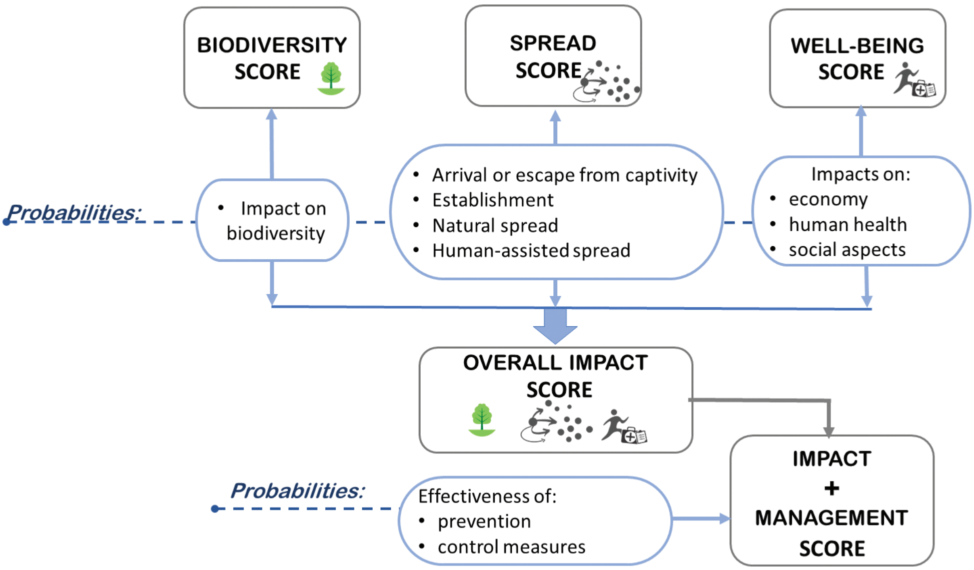

Figure 1. Scores used to produce priority lists from horizon scanning and information on probabilities used to calculate them.

- *SPREAD score* = likelihood of arrival in Italy or escape from captivity if already present × likelihood of establishment × [(likelihood of natural spread + likelihood of human assisted spread)/2] (maximum value = 125);
- *BIODIVERSITY score* = SPREAD score × potential impact on biodiversity (maximum value = 625);
- *WELL-BEING score* = SPREAD score × [(potential impact on economy + potential impact on human health + potential impact on social aspects scores)/3] (maximum value = 1875).

The SPREAD score considered that, at the beginning of the invasion process, a species needs to overcome some natural or artificial barriers, to arrive in Italy and spread and that barriers, like those imposed in captivity (e.g. a fence or a cage) might be effective at preventing a species from becoming an invader (Blackburn et al. 2014). The BIODIVERSITY and WELL-BEING scores considering both the likelihood of spread and the potential of impacts are actually risk scores.

We then combined the three scores into an OVERALL IMPACTS score of the likelihood of impacts. In accordance with EU Regulation, the overall score was calculated with a formula that assigned a higher weight to impacts on biodiversity:

- *OVERALL IMPACTS score* = SPREAD score × [potential impact on biodiversity + (potential impact on economy + potential impact on human health + potential impact on social aspects scores)/6)] (maximum value = 937.5).

An effective strategy aiming at mitigating the impact caused by alien species should consider both the likelihood of prevention and the feasibility and effectiveness of management, once species are established. For this reason, experts were asked to evaluate the manageability of the various species, according to the effectiveness of available prevention measures, including intentional imports and trade regulation, practicality of carrier treatment and the effectiveness of control measures, as well as ease of species recognition in the field. A final score, which considered the likelihood of impacts, feasibility of prevention and effectiveness of control measures was calculated as:

– *IMPACT* + MANAGEABILITY *score* = OVERALL IMPACTS score × effectiveness of prevention measures × (effectiveness of control measures/2) (maximum value = 11718.75),

with an emphasis on prevention rather than control. A TOTAL RANK was then calculated for each species as the sum of ranks in the previous lists.

For the prioritisation of those species that were already present in Italy, scores were similar (Fig. 2), except for the SPREAD score, which did not include the likelihood of arrival or escape and for IMPACT + MANAGEABILITY score which was calculated as:

– *IMPACT* + MANAGEABILITY *score* = OVERALL IMPACT score [((effectiveness of control measures + current eradication feasibility + eradication potential cost + side effects of the eradication + social acceptability of eradication)/5)].

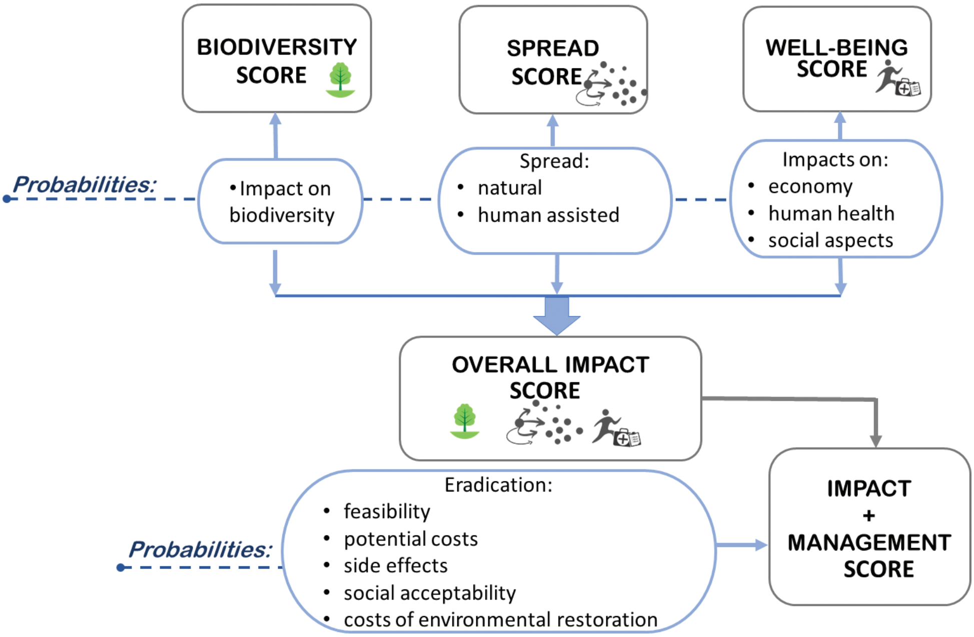

Figure 2. Scores used to produce priority lists from prioritisation and information on probabilities used to calculate them.

Results

Bioclimatic models

Bioclimatic models were produced for all the species that were included in the horizon scanning and prioritisation. Maps, projected at the European level, assisted experts in the assessment of the likelihood that the various species could establish viable populations and spread in Italy. As an example, four maps are reported in Fig. 3: for two species (*Apodemus uralensis*, *Bison bison*) the predicted suitability of Italian territory was considered low, while, for other two (*Sciurus anomalus*, *Sylvilagus floridanus*), it was high.

Prioritisation list

All of the six species that were already present in Italy showed a high likelihood of natural dispersal from their release sites, apart from *Ammotragus lervia*. The first three species, *Sylvilagus floridanus*, *Cervus nippon* and *Callosciurus finlaysonii*, were on top in all the five partial lists that were produced, indicating their high invasibility.

Likelihood of re-invasion was considered high for small-sized species, i.e. those more often traded as pets (*Callosciurus finlaysonii*, *Genetta genetta*), as well as for game species (*Sylvilagus floridanus*) or species farmed for fur (*Neovison vison*). Only *A. lervia* showed an impact on habitats of European interest, i.e. the habitat 4090 (Endemic oro-Mediterranean heaths with gorse). Most species in the prioritisation list showed a medium to high impact on native biodiversity, a medium to low impact on economy and low impact on social aspects and human health (Fig. 4, see Suppl. material 2 for the complete score database).

The prioritisation process highlighted *Sylvilagus floridanus*, *Cervus nippon* and *Callosciurus finlaysonii* as priority species for management actions and, possibly, eradication (Table 2).

Horizon scanning

Amongst the 212 species considered for the horizon scanning, 77 (36.3%) were classified as having an impact score from 3 to 5 and only 18 (8.5%) had major or massive impacts (Fig. 5, see Suppl. material 2 for the complete score database). A total of 164 species had an impact on biodiversity greater than 1 and were identified as relevant for further assessment. The complete list of species is reported in Suppl. material 3.

The first 30 species of the horizon scanning list, ordered according to their *TOTAL rank* are reported in Table 2 with their relative rank position for spread and their different impacts. Notably, in the first ten positions, there are seven rodents, including two rat (*Rattus tanezumi*, *R. exulans*) and three squirrel species (*Callosciurus prevosti*, *Callosciurus notatus*, *Sciurus anomalus*). The first five species (*Rattus tanezumi*, *C. prevosti*, *Mephitis mephitis*, *R. exulans* and *Mastomys natalensis*) are in the first six

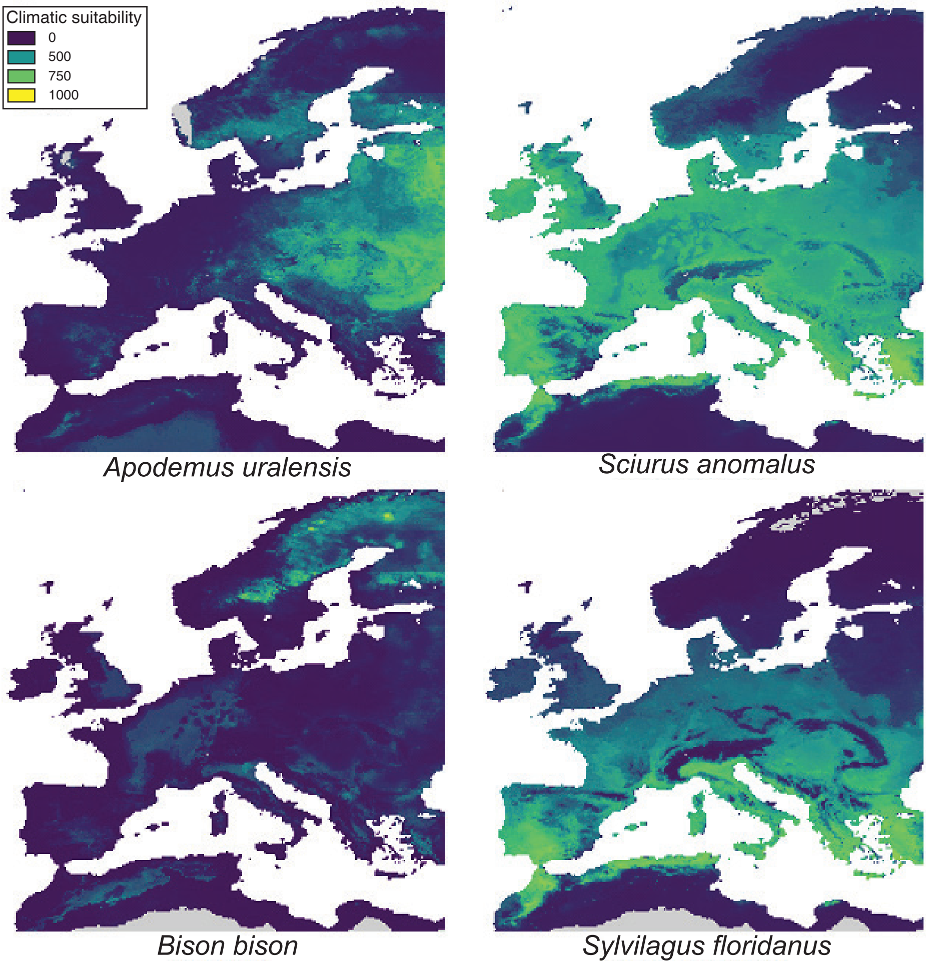

Figure 3. Map produced from bioclimatic models for two species with low (left) and two with high (right) suitability in Italy.

positions in all five partial lists, indicating their high potential for becoming invasive, if arriving in Italy.

The most frequent potential introduction pathway for the species considered in the horizon scanning list was their escape from zoos and aquaria and their escape or release of pets from private houses, followed by intentional releases (Figure 6).

Discussion

Addressing the threats posed by species introductions requires a set of interventions aimed at preventing the arrival of new species and controlling those which are already

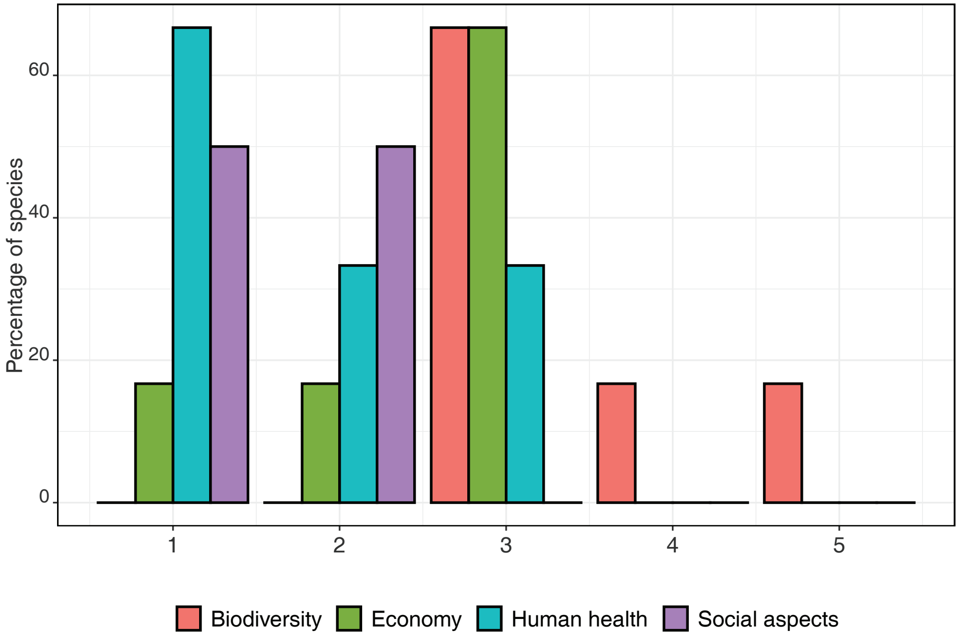

Figure 4. Ranking of impacts of mammalian species listed within the Prioritisation List in Italy.

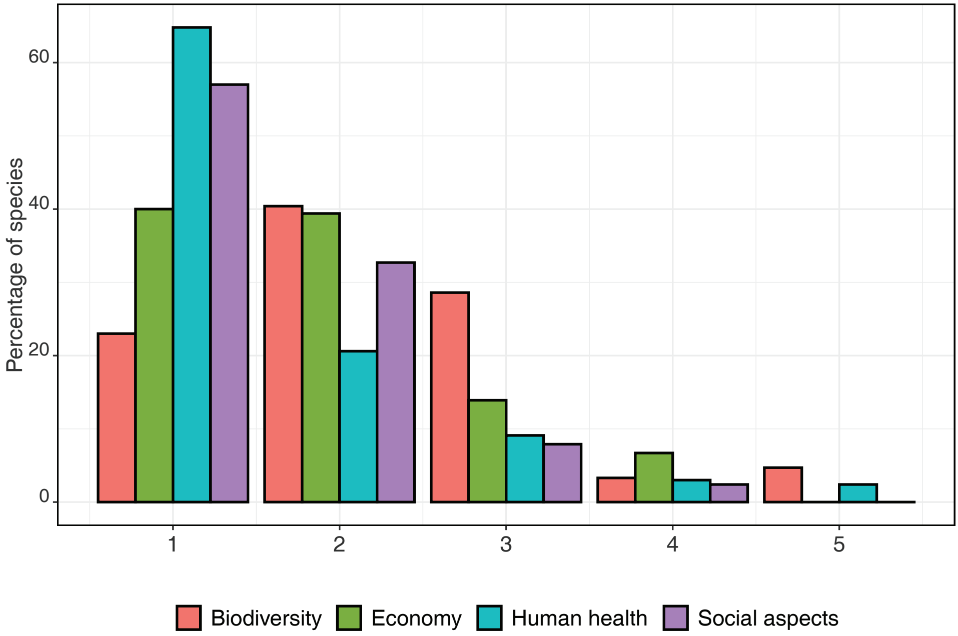

Figure 5. Ranking of impacts of mammalian species listed within the Horizon-scanning List in Italy.

Table 2. Ranked lists of species considered in prioritisation and horizon scanning according to the predicted likelihood of spread, potential impacts on biodiversity and well-being and manageability; the total rank is the sum of the species positions in the previous lists. For horizon scanning, only the first 30 species are reported (for complete lists, see Suppl. material 3).

Species	Spread	Biodiversity	Well-being	Overall impacts	Impacts + manageability	Total Rank
Prioritisation						
Sylvilagus floridanus	1	2	2	1	1	7
Cervus nippon	3	1	1	2	2	9
Callosciurus finlaysonii	2	3	3	3	3	14
Genetta genetta	4	5	5	4	4	22
Neovison vison	5	4	4	5	6	24
Ammotragus lervia	5	6	6	6	5	28
Horizon scanning						
Rattus tanezumi	2	1	1	1	4	9
Callosciurus prevosti	1	2	3	2	1	9
Mephitis mephitis	3	4	4	4	3	18
Rattus exulans	5	3	5	3	6	22
Mastomys natalensis	4	15	2	5	14	40
Microtus levis	5	8	6	6	16	41
Callosciurus notatus	8	6	17	9	2	42
Lepus granatensis	13	5	15	8	5	46
Sciurus anomalus	10	12	8	11	10	51
Genetta pardina	9	10	13	12	12	56
Cervus canadensis	15	7	18	10	7	57
Apodemus uralensis	5	8	7	6	36	62
Capreolus pygargus	17	10	18	13	11	69
Tamiops macclellandi	11	13	25	15	8	72
Mustela lutreola	17	18	18	18	15	86
Funambulus pennantii	11	20	10	19	31	91
Axis axis	27	27	9	21	9	93
Hystrix indica	27	15	18	16	17	93
Tamiasciurus hudsonicus	16	15	28	17	27	103
Herpestes ichneumon	27	27	18	28	22	122
Tamias striatus	26	26	27	27	21	127
Atelerix albiventris	17	20	40	22	30	129
Sciurus lis	17	20	40	22	33	132
Paguma larvata	38	35	11	28	22	134
Mungos mungo	34	20	40	22	19	135
Martes zibellina	34	19	30	20	33	136
Trichosurus vulpecula	34	33	14	31	38	150
Cricetus cricetus	27	46	18	37	24	152
Castor canadensis	38	25	29	28	32	152
Suncus murinus	23	24	30	25	51	153

established. In this study, we prioritised those alien mammal species which are already established in Italy and we used a horizon-scanning approach to highlight the potential risk posed by those species that may arrive or escape captivity in the future.

The prioritisation process ranked *S. floridanus* as the most impacting and easiest to manage alien mammal in Italy. *Sylvilagus floridanus* is an American cottontail introduced in Italy in the 1960s for hunting, which has indirect detrimental effect on native hares through apparent competition mediated by the predator *Vulpes vulpes* (Cerri et al. 2017). The second ranked species was the still localised sika deer *Cervus nippon*, which hybridises with the native red deer *Cervus elaphus* (Smith et al. 2018), followed by the

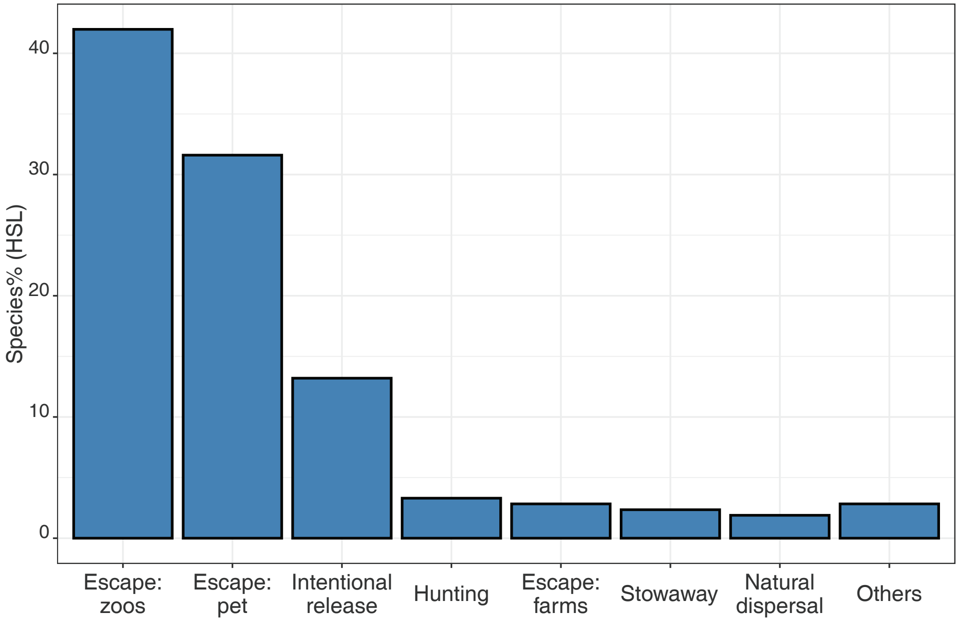

Figure 6. Pathways of introduction of mammal species in Horizon-scanning List.

rapidly spreading Finlayson's squirrel *Callosciurus finlaysonii* (Ancillotto et al. 2018). Notably, four out of 11 (36%) mammal species already listed in the Union list are squirrels. In fact, many squirrel species are highly invasive in Europe (Bertolino 2009; Di Febbraro et al. 2016, 2019) and the Eastern grey squirrel (*Sciurus carolinesis*) is replacing the native Eurasian red squirrel (*Sciurus vulgaris*) in many countries (Bertolino 2008).

Three species, *Sylvilagus floridanus*, *Cervus nippon* and *Callosciurus finlaysonii* were considered a priority for management actions and, possibly, eradication. However, at present only *Sylvilagus floridanus* is irregularly subjected to culling programmes in some areas, besides being a huntable species. *Cervus nippon* and *Callosciurus finlaysonii* are not managed at all, despite their potential impacts on native species and their relatively limited spatial distribution, which would enable successful management actions (Ancillotto et al. 2018; Loy et al. 2019). This denotes a lack of rapid reaction and the need to raise the awareness about the social and ecological impacts that these and other alien species can cause.

As specified in the Methods section, this study does not deal with well-known invasive species, such as rats and mice (e.g. see Capizzi et al. 2014), only for reasons related to the time of their introduction. However, these species can be of great management importance, often higher than most of those listed here and their lack of inclusion in this work does not imply the lack of motivation for their control or eradication.

Horizon scanning for potential alien species traditionally produces a final overall list of prioritised species (e.g. Roy et al. 2014, 2015). In this work, we produced five distinct lists and a final overall ranking, related to the likelihood of adaptation to local landscape and spread, to impacts on biodiversity and human well-being, alone or synergistically, and the feasibility of preventing the introductions and/or to control populations eventually established. These lists could be used to prioritise species for prevention measures, because they are likely to establish and spread over large areas if arriving in Italy, producing relevant impact on biodiversity and human well-being. A strategy aimed at prevention or, at least, rapid removal after introduction, should be particularly in place for those species that are considered difficult to manage, because controlling their populations, once established and widespread, would not be feasible.

The *TOTAL rank* could be used to produce a final list, giving priority to species with the highest values in every partial assessment. At the national level, our assessment will be joined in a process involving the inclusion of assessments for other taxonomic groups, such as other vertebrates, invertebrates and plants, both marine and terrestrial. During the evaluations, experts from different taxonomic groups met in a couple of workshops where the scoring system was discussed in order to use the same scale of reference, for example, when assessing the possibility to eradicate a species, the score was given considering also species from other taxa as comparison. Merging different lists in a unified one is a still an ongoing process; however, the scoring methodology presented here will be applied to all taxa to produce a dynamic list which will include species-specific assessments of spread, impacts and manageability.

The resulting list will assist policy-makers in developing a sound list of alien species of national concern. Such a process will likely lead to the production of a final ranking, based on consensus building between experts and policy-makers, who could assign different weights to the various aspects of the invasion process. Our ranking system highlighted those species characterised by a higher likelihood to overcome different barriers through the invasion process (Blackburn et al. 2011), capable of spreading across large areas and likely to produce negative impacts on species and ecosystems or on human well-being, as well as more likely to be difficult to manage.

The EU Regulation on invasive species was specifically adopted to mitigate the impact of alien species on biodiversity (Genovesi et al. 2014). For this reason, when producing the *OVERALL IMPACTS score*, we weighted more impacts on biodiversity than on human activities. However, our scoring system could be easily adapted to alternative evaluations. For instance, impacts on human activities or the possibility to carry zoonoses may be considered relevant for prioritising the management of alien species. By including the likelihood of spread in calculating the impacts, we also prioritised species that will likely produce a lower impact over larger areas compared to others that will probably have higher impacts, but with a low risk of spread. The reasons behind this choice lies in the easier mitigation of high impacts, through control or eradication when species are still distributed over a restricted area, compared to the mitigation of lower impacts occurring across a vast geographical scale (Panzacchi et al. 2007; Robertson et al. 2017).

Finally, we also produced a list that considers the *OVERALL IMPACTS score* of a species and the feasibility of its management (*IMPACTS score* + MANAGEABILITY *score*), giving more weight to prevention compared to the possibility of control. It is now recognised that an integrated and hierarchical management strategy should act at the different stages of the invasion process, with an emphasis on prevention. The identification of main pathways allows us to prevent many species from entering recipient areas, while control and eradication is generally costly and should be species-specific (Panzacchi et al. 2007; Robertson et al. 2017).

The main pathways of introduction for the mammal species considered in this study are the escape from zoos and from private keepers, followed by intentional releases. This is in accordance with the pathways identified by Genovesi et al. (2009) for mammals already established in Europe. These authors reported that the most frequent pathways for mammal introductions were escapes from fur farms and zoos, intentional releases of animals from captivity and introductions for hunting. However, increasing security systems to captive animals and discouraging hunters from releasing alien mammals have reduced the importance of these pathways, while the release or escape of animals from the pet trade is increasing (Genovesi et al. 2009). In fact, amongst species already established in Italy and here considered for prioritisation, one third have been introduced for hunting (e.g. *S. floridanus*, *A. lervia*), but recently the escape or release of animals from captivity prevailed (e.g. *C. finlaysonii*, *C. nippon*).

Species included in the list of alien species of National Concern might be subject to strict regulation, which includes a ban on import, trade, possession and release (Genovesi et al. 2014). Therefore, we consider that prevention could be an efficient strategy for most of the evaluated species. However, since only a few mammals will probably be included in such a national list, other actions, such as the adoption of voluntary codes of conducts or guidelines for zoos (Scalera et al. 2012), pet trade (Davenport and Collins 2011) and hunting (Monaco et al. 2016), should be encouraged.

ICAT Schemes are two evidence-based classification systems for evaluating the ecological and socioeconomic impacts of non-native species (Blackburn et al. 2014; Bacher et al. 2017). Their assessment requires the collection and evaluation of all the papers reporting data on impacts produced by the target species in its global introduction range and their scoring according to different mechanisms of impact (Volery et al., 2020). Due to the high number of species to assess, we used an expert-based approach where single experts used ICAT Schemes as reference systems for scoring the species after a rapid search of literature and without considering the mechanism of impact. There is the perception that expert-based evaluations overestimate impacts produced by alien species. When mammals are scored worldwide for ICAT Schemes, a comparison with our assessments could be made.

Our work combined a prioritisation process of mammal species already established in Italy and not listed in the EU Regulation 1143/2014, with a horizon scanning of species traded in Italy or recorded as introduced worldwide. This resulted into ranked lists of species, based on their spread capabilities, their potential impacts on biodiversity and human well-being and the feasibility of their management. All these lists could be used to prioritise mammal species for prevention, banning their trade in Italy or for management. The developed database will be integrated with others produced through horizon scanning for invertebrates, vertebrates, plants, marine and terrestrial and will be used to produce a proposal for a list of Invasive Alien Species of National Concern (art. 12, EU Regulation 1143/2014).

In our evaluation, we chose not to consider those species with a low potential of impact on biodiversity (i.e. with a score = 1) and we also calculated the OVERALL IMPACTS score giving a higher weight to potential impacts on biodiversity with respect to potential impacts on economy, human health or on social aspects. This choice was justified by the focus of EU Regulation 1143/2014 on prevention, mitigation and minimisation of adverse impact on biodiversity caused by alien species and the provision to produce a list of 'Invasive Alien Species of National Concern' in accordance with the Regulation. The impacts on human health and the economy were then considered as a secondary aspect. However, the procedure developed in this study could be used as a blueprint for similar prioritisation initiatives (cf. Ziller et al. 2020), as the formulae could be adapted to produce one or more lists of species according to different priorities established by country regulations or policies.

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Supplementary material 1

This is the database produced during the research

Authors: Sandro Bertolino, Leonardo Ancillotto, Paola Bartolommei, Giulia Benassi, Dario Capizzi, Stefania Gasperini, Marco Lucchesi, Emiliano Mori, Laura Scillitani, Giulia Sozio, Mattia Falaschi, Gentile Francesco Ficetola, Jacopo Cerri, Piero Genovesi, Lucilla Carnevali, Anna Loy, Andrea Monaco

Data type: species data

Link: https://doi.org/10.3897/neobiota.62.52934.suppl1

Supplementary material 2

This is the R-script and the output of the analyses

Authors: Sandro Bertolino, Leonardo Ancillotto, Paola Bartolommei, Giulia Benassi, Dario Capizzi, Stefania Gasperini, Marco Lucchesi, Emiliano Mori, Laura Scillitani, Giulia Sozio, Mattia Falaschi, Gentile Francesco Ficetola, Jacopo Cerri, Piero Genovesi, Lucilla Carnevali, Anna Loy, Andrea Monaco

Data type: statistical data

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Supplementary material 3

Complete ranking of the species

Authors: Sandro Bertolino, Leonardo Ancillotto, Paola Bartolommei, Giulia Benassi, Dario Capizzi, Stefania Gasperini, Marco Lucchesi, Emiliano Mori, Laura Scillitani, Giulia Sozio, Mattia Falaschi, Gentile Francesco Ficetola, Jacopo Cerri, Piero Genovesi, Lucilla Carnevali, Anna Loy, Andrea Monaco

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Applying an invasion and risk framework to track non-native island floras: a case study of challenges and solutions in Hawai‘i

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Abstract

Islands are plant invasion hotspots, with some having more non-native than native species. Many plants are recent arrivals, leading to concerns that their full spread and impacts are not yet realised. Given that islands host extraordinary numbers of endemic and threatened species, schemes are urgently needed to track the complex, species-rich but data-poor scenarios typical of islands. This study applies the unified framework by Blackburn et al. (2011) for categorising invasion stages to Hawai‘i's non-native plant checklist and identifies potential uses and complications for species tracking and invasion management. Data deficiencies and ambiguities required lumping Blackburn et al.'s categories to align with Hawai‘i's available data; nonetheless, this coarser categorisation describes invasion phases relevant to managers and could provide the basis for an effective tracking system. However, the unified framework does not accommodate uncertain invasion statuses, which prevents clear categorisation of species that exist outside of cultivation but are not definitely naturalised. In response to this obstacle, scores from the Hawai‘i-Pacific Weed Risk Assessment (WRA) are explored to understand their application for predicting naturalisation, including standard WRA scores as well as alternative scoring methods. We show that this predictive tool may be a promising supplement to on-the-ground monitoring for data-deficient elements of a flora. Finally, a categorisation system for tracking statuses of an entire non-native flora is proposed that requires limited investments in additional data collection while following the rationale of Blackburn et al.'s scheme. This categorisation system may be used to reveal overall invasion patterns and trends in a region, leading to valuable insights into strategies for biodiversity management and conservation.

Keywords

Biodiversity monitoring, flora, invasion framework, invasion tracking, invasive plants, naturalisation, species checklist, weed risk assessment

Introduction

Oceanic islands have long been considered highly invasible, hosting higher ratios of native to non-native richness per area than climatically comparable mainland regions (Lonsdale 1999; Sax and Gaines 2008). Around 40% of island floras are now composed of at least 40% non-native species (Pyšek et al. 2017). These trends are particularly alarming because remote islands are hotspots of endemism, with more than a quarter of all plant species native to islands (Kier et al. 2009). Naturalisations thus far greatly exceed extinctions reported on islands, although many naturalisations are too recent for their impacts to be fully realised and even historical ones are unlikely to have spread throughout their available habitats yet (Sax and Gaines 2008). These trends indicate a potential "extinction debt" that may be paid against island endemics in the future (Kuussaari et al. 2009; Gilbert and Levine 2013).

Uncertainty of impacts from numerous naturalised species, especially on remote islands with unique endemic taxa, severely complicates management strategies. Conservation decision-making is often based on the precautionary principle, a central concept which proposes that actions taken to prevent known negative consequences should also be applied to scenarios where negative consequences are possible, but uncertain (Cooney 2004). In an information-deficient context, the precautionary principle compels conservation biologists to treat all non-native species as if they will inflict negative impacts (a.k.a. "guilty until proven innocent"). Applying this strategy to scenarios where a thousand or more potential invaders exist is unrealistic, as conservation resources are limited; thus, managers are forced to select control targets based on few data and often rely on reports of invasive behaviour elsewhere. Although invasion history is critical for assessing risk, Kueffer et al. (2010) show that problematic species on one island are not necessarily problematic on all, or even most, islands where they are present. Furthermore, invasions of new species without invasive histories continue to be reported worldwide (Seebens et al. 2017). Thus, relying on either a precautionary principle or "bad apple" approach alone could incur high costs, resulting in inefficient and ultimately ineffective conservation of threatened native species and ecosystems.

Given that non-native species are frequently established on islands and that their behaviour over time is uncertain, two approaches are needed to provide the basis for evaluating current and future impacts: 1) tracking non-native species along the introduction-naturalisation-invasion continuum and 2) predicting the likelihood of naturalisation and invasion when field data are sparse or temporally limited (Wilson et al. 2014, 2018). While the latter has attracted significant attention, the former has been tremendously under-appreciated (Hulme 2006), leaving many regions ill-equipped to manage the ever-increasing non-native portion of their floras. Characterising the phase and extent of an invasion is critical for assessing control feasibility. Monitoring already-introduced species is also necessary to fine-tune predictive tools and catch species that invariably defy expectations. For many regions, the monitoring of non-native species begins with checklists of plants that have naturalised, often from data collected for floristic projects (Pyšek et al. 2004). However, some checklists further categorise species, distinguishing between invasive versus naturalised, old versus newer introductions and/or noting species for which data are deficient (Pyšek et al. 2002; Galasso et al. 2018; Imada 2019). Checklists of cultivated species that are not necessarily naturalised have been compiled for some regions, but are rarer (Danihelka et al. 2012). Conservation workers may mistakenly use these checklists as tracking systems, but these lists merely describe snapshots of non-native populations when they were reported. Such surveys may be incomplete and may be several decades old. Given that many introductions are recent and statuses of these plants may change rapidly, supplementing checklists with additional data to track the invasion process is essential (Wilson et al. 2014).

Nearly three decades' worth of work to characterise the invasion process worldwide and across taxa has culminated in a unified framework proposed by Blackburn et al. (2011). The system they proposed, hereon referred to as "the unified framework", uses 11 categories to describe non-native populations by their phase of invasion, thereby providing a method for tracking statuses. These categories describe a population's progress beginning with transport and introduction through establishment and spread, which correspond to six sequential barriers to invasion success: geography, captivity/cultivation, survival, reproduction, dispersal and environment. Furthermore, categories also describe between-barrier details (e.g. B1–B3 refer to explicit, limited and no measures of containment in place, respectively); an inability to breach any one of these barriers amounts to invasion failure (Blackburn et al. 2011). If population statuses are updated frequently enough, this system can be used in conjunction with measures of commonness and distribution to help invasive species managers prioritise targets for control (McGeoch and Latombe 2016; Wilson et al. 2018). Wilson et al. (2014) outlined the unified framework's application for monitoring the status of invasive trees globally and it was successfully applied to assess *Acacia* and *Melaleuca* in South Africa, yielding categories on which to base management decisions (Jacobs et al. 2017; Magona et al. 2018). However, no study has assessed the unified framework's applicability to track an entire non-native flora, including data deficient and cultivated species. Consistent categorisation across species and over time for a region allows assessment of invasion trends, which can then be used to suggest broader scale approaches to invasion management.

The Hawaiian archipelago is an excellent model to assess methods for invasion tracking and prediction as > 55% of the total terrestrial vascular flora is comprised of naturalised species (Imada 2012, 2019; Ranker 2016; Price and Wagner 2018). As such, Hawai‘i offers copious examples of both well-established and newly-naturalised species to test theoretical and practical aspects of applying invasion frameworks. This includes over 1,600 naturalised and possibly naturalised species, with all but 25 thought to be introduced after the year 1778 (European contact) and more than 600 species reported in the last 30 years (Imada 2019). The need to track and mitigate impacts from non-native plants is urgent. The IUCN lists 35% of Hawai‘i's native flora as threatened, although this is very likely an underestimate as less than half of species have been assessed according to these international criteria (IUCN 2020a). Hawai‘i is also an ideal location to evaluate invasion frameworks because an active community of botanists regularly produces reports of new species, contributing to manuals of both flowering plants and ferns that include non-native species (Wagner et al. 1999; Palmer 2003), as well as a periodically updated checklist of naturalised plants (Imada 2019). Moreover, Hawaiʻi utilises a predictive framework known as the Hawaiʻi-Pacific Weed Risk Assessment (WRA) that has evaluated over 2,000 species and is used to discourage the planting of high risk plants and identify low risk alternatives, as well as to inform managers of potential control targets (Kueffer and Loope 2009). A test of this system indicated that it is 95% successful in predicting major pests that were identified by expert opinion (Daehler et al. 2004). The Hawaiʻi-Pacific WRA assigns risk rankings ("Low Risk", "High Risk" and an uncertain "Evaluate" category) by calculating a numerical score based on 49 questions about a plant's biology, which can be divided into 35 questions pertaining to the likelihood that a plant will spread and 14 pertaining to the consequences of their spread (Daehler et al. 2004; Daehler and Virtue 2010). Although weed risk assessment (WRA) is most often highlighted as a tool to prevent harmful introductions, the resulting WRA dataset may also be useful for predicting the progress of already-introduced species along the introduction-naturalisation-invasion continuum.

In this study, we assess the viability of applying the unified framework proposed by Blackburn et al. (2011) to a checklist of non-native plants for the Hawaiian Islands and discuss its applicability for tracking invasions in Hawaiʻi. For data-deficient species whose invasion phase cannot be confidently determined from field data, we assess the potential for the Hawaiʻi-Pacific WRA to infer the naturalisation category to which they might belong. Finally, we propose a modified set of categories based on the unified framework that are relevant for making management decisions and can accommodate data deficiencies, such as those commonly observed in Hawaiʻi.

Methods

Aligning the naturalised species checklist

The Bishop Museum's checklist of naturalised plants (Imada 2019) provided the main list of species for alignment with the population tracking categories outlined in Blackburn et al. (2011). This checklist tallies species that have naturalised or questionably naturalised on any island in the Hawaiian archipelago, including eight main islands (Niʻihau, Kauaʻi, Oʻahu, Molokai, Lānai, Maui, Kahoʻolawe, Hawaiʻi) ranging in maximum elevation from 380–4,200 m above sea level and 11 small, sparsely vegetated islands and atolls, ranging from a few to 259 m above sea level (Kure, Midway, Pearl and Hermes, Lisianski, Laysan, Gardner Pinnacles, French Frigate Shoals, Necker, Nihoa, Kaula Rock, Lehua). The checklist sorts non-native species into five categories describing whether they are a Polynesian or post-European introduction and whether there is uncertainty regarding a species' introduction or naturalisation status.

We additionally reviewed naturalisation reports and herbarium specimen labels, supplementing the checklist by Imada (2019) to include recent naturalisations and re-categorising records that explicitly did not match the definition of naturalised.

We define naturalised as non-native plants that survive and reproduce consistently to sustain populations outside of cultivation over many generations without human aid (Richardson et al. 2000; Pyšek et al. 2004), corresponding to categories C3–onwards in the unified framework (Blackburn et al. 2011). Species not meeting these criteria were downgraded from "naturalised" to the "questionably naturalised" category in the checklist of naturalised plants (Imada 2019), defined as "species not confirmed to be naturalised, including present-day adventive and escaped plants or historical collections not recently vouchered." Ultimately, the compiled checklist used in our analyses included 1,668 species that have been collected outside of cultivation on at least one of the Hawaiian Islands.

For each island, we summed the number of species in each of the following two categories: "naturalised" (including pre-European introductions by Polynesians) and "questionably naturalised" for the remaining species that could not be clearly categorised after considering available data and criteria in the unified framework. We then attempted to align species in these two groups, as well as non-naturalised cultivated species in Hawai'i, with the unified framework categories. We highlighted specific examples of challenges encountered when applying the unified framework across a flora and assessed whether it is valuable for improving non-native plant species tracking and management in Hawai'i and elsewhere. Subsequently, we constructed a modified categorisation scheme that accommodates the data deficiencies found in Hawai'i's non-native flora.

Potential for Weed Risk Assessment scores to predict naturalisation

To determine whether the Hawai'i-Pacific WRA score or components of that score might be useful for inferring the status of "questionably naturalised" species, we examined the distribution of WRA scores amongst known naturalised species versus non-naturalised cultivated species. We also assessed the correlation between WRA score and number of islands where a species is known to be naturalised. The WRA scores were additionally separated into components related to likelihood of spread and potential consequences of impact, creating two independent scores for each species, following Daehler and Virtue (2010). Amongst 2,037 WRAs available for analysis (HPWRA 2019), we tested the hypothesis that the full WRA score or the likelihood-of-spread component of the WRA score (hereon referred to as "likelihood-only score") can predict naturalisation by comparing the scores of plants that have naturalised with those that were introduced, but have not naturalised. The latter species were identified by cross-referencing a list of plants reported from cultivation assembled by Imada et al. (2000), supplemented by approximately 600 species known from cultivation, based on herbarium vouchers. We excluded species that are thought to be very uncommon in cultivation, such as those known from a single collection in a botanical garden, as well as species that are likely held captive in aquaria and have little chance to escape (Staples and Herbst 2005). We also removed possible recent introductions (384 species) first reported in cultivation during the last 20 years because the behaviour of these species is uncertain. A previous study found that lag times averaged less than 20 years between first planting and signs of naturalisation in Hawai‘i (Daehler 2009; see also Schmidt and Drake 2011). Data on time since first cultivation were too unreliable to investigate longer lag periods, but for a few high-scoring species that had not naturalised, we checked herbarium records to make sure they were not first recorded slightly earlier (20–40 years ago).

We conducted statistical analyses with the Python library SciPy 1.0 (Virtanen et al. 2020), visualised with seaborn 0.10.0 (Waskom et al. 2020). We used Welch's *t*-test to determine whether naturalised and non-naturalised species had significantly different WRA scores and likelihood-only scores. Finally, to see if scores are related to a species' potential to spread throughout the archipelago, we compared the WRA and likelihood-only scores to the number of islands naturalised for each plant species. These subsets of the data had non-normal distribution, so we calculated the strength of the correlation with the non-parametric Kendall's τ_b coefficient. The R package mblm (Komsta 2019) enabled us to visualise the linear trend between these variables with the Theil-Sen estimator, which was developed to reflect the strength of Kendall's τ_b (Sen 1968; Wilcox 2010). Kendall's τ_b is rank-based and the associated Theil-Sen estimator is derived from the median slope of pairwise data (Sen 1968). Island counts were restricted to the main Hawaiian Islands minus Ni‘ihau, as these are more frequently surveyed and support more variable habitats in comparison to the low elevation islands in the north-western section of the archipelago (Larrue et al. 2018).

Results

Alignment between the checklist and the unified framework

Cultivated species

More than 7,300 cultivated species have been reported in Hawai‘i, although data describing the circumstances of their containment are often lacking so that they cannot be finely categorised according to the unified framework. Thus, plants that are cultivated in Hawai‘i but are not naturalised were roughly aligned to the lumped categories B1 (in captivity or quarantine) and B2 (in cultivation; Fig. 1). Examples of B1 species may include houseplants that are only planted indoors, which may be less common in Hawai‘i than in temperate areas due to Hawai‘i's tropical climate. Falling into this category are also valuable orchid species grown by hobbyists in controlled environments, such as terraria or greenhouses. We inferred that most common ornamentals and food plants would belong to category B2, where species are planted in suitable conditions with limited intentional measures to restrict their dispersal (e.g. some incidental control or limitation through landscaping activities). No species were thought to match categories B3 or C0, although examples from Hawai‘i likely exist that are not readily added to checklists because they are not currently present. For instance, forestry planting records indicate that *Juglans nigra* (black walnut) was planted to assess its suitability

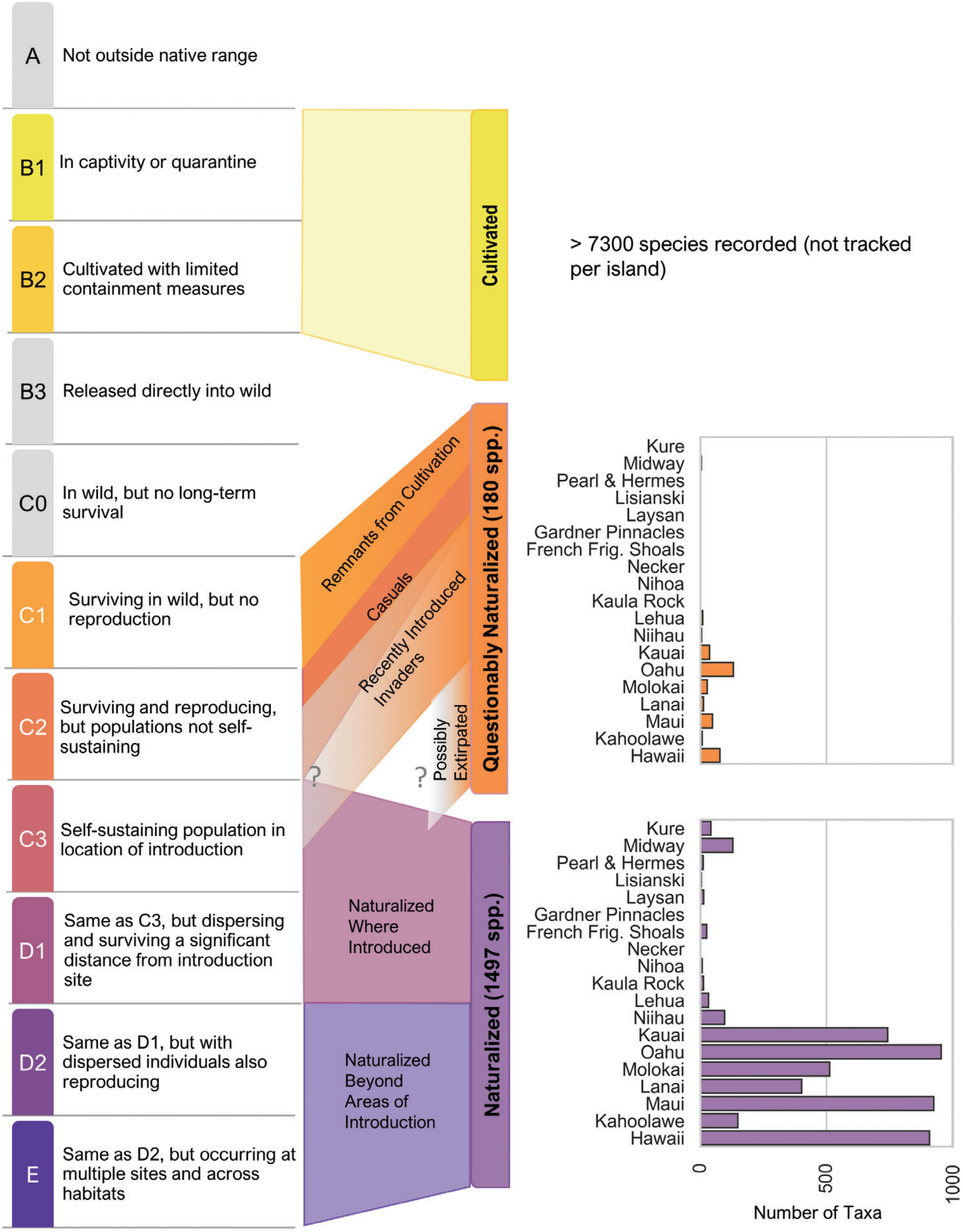

Figure 1. Alignment of Blackburn et al. (2011) scheme with categories in Hawai'i's non-native species checklist. Bar graphs depict counts of species that are considered "Naturalised" (purple) and "Questionably Naturalised" (orange) in Hawai'i per island, with state-wide totals next to checklist status names. Coloured polygons represent alignment or misalignment with the recommended categories. Full descriptions of Blackburn et al. (2011) categories are available in Table 2.

as a timber crop, but growth trials determined that its survivability was very low in Hawai'i (C0) (Nelson and Schubert 1976). Although category B3 is thought to apply to most accidental introductions that are not yet reproducing outside of cultivation (Blackburn et al. 2011), we included contaminants of horticulture in category B2 if some measure of containment is evident (e.g. existing in potting soil imported with an intentionally-cultivated plant).

Questionably naturalised species

We considered 180 species to be "questionably naturalised" at the state-wide level, amounting to 342 per-island introductions being classified in this checklist category. Based on our review of Hawaiʻi's records and recommended terminology for conceptualising plant invasions (Richardson et al. 2000; Pyšek et al. 2004), the "questionably naturalised" category likely contains five distinct classes of species for which there are insufficient data to separate, including: 1) remnants of cultivation, such as long-lived species that were planted some time ago, but where growth of surrounding vegetation masks evidence that the site was formerly cultivated; 2) casual species, where immature or perhaps a few mature individuals originating from cultivated plants may exist outside of cultivation, but for which multiple generations are not produced (i.e. population not self-sustaining); 3) recently introduced invaders that will eventually naturalise, but have not had sufficient time to do so; 4) species that have already naturalised, but only a few individuals have been detected (i.e. current sampling is insufficient to confidently categorise populations that are actually naturalised); and 5) possibly extirpated species, for which historical records indicate that they existed outside of cultivation at one time, but have not been observed for many decades (Fig. 1).

Remnants from cultivation may arise when homesteads or forestry plots are no longer maintained, making it difficult to determine whether a species is a C1 (outside of cultivation, but not reproducing) or a mature individual of a naturalised population, especially if no historical planting data exist. An example of C1 species that may appear as naturalised in the field without prior knowledge of their planting history includes approximately 30 species of *Ficus* that were planted on forest reserves without the introduction of their specific pollinator wasp (Skolmen 1980). Casuals would theoretically align to category C2, but in practice, they are particularly difficult to distinguish from recently-introduced invaders, as was also noted by Wilson et al. (2014) when describing tree invasions. This uncertainty arises because both categories may initially appear in the field as offspring from a single or few age classes, with the distance from the originally-introduced plant dependent on its mode of dispersal (e.g. wind, gravity or bird-dispersed), rather than its potential to naturalise. One example of a species in Hawaiʻi that fits the C2 category is *Sequoia sempervirens* (California redwood), for which more than 130,000 individuals were planted before 1960 (Nelson and Schubert 1976; Skolmen 1980). These plantings have been observed producing seedlings, but they have failed to mature beyond the seedling stage, even after 60+ years and, thus, would likely vanish from the islands if the initial plantings were removed.

Although we currently lack data to distinguish recently introduced invaders from the rest of the "questionably naturalised" group on the checklist, we were conceptually unable to determine to which framework category these species would belong, even if they could be identified. Recently-introduced species do not appear to belong to category C3, as they do not yet form self-sustaining populations with multiple generations, but nor do they align with category C2, for which self-sustaining populations will never be formed.

Naturalised species

Of the 1,668 species in our checklist of plants growing outside of cultivation, 1,473 are considered naturalised in Hawai‘i. However, these species are not uniformly naturalised across all islands, with no island containing naturalised populations of all these species. Considering each naturalisation event separately per island, we counted 4,970 instances by summing the number of naturalisations from all islands. The checklist does not provide information on dispersal and formation of new populations, as needed to distinguish between the last four categories of the unified framework and, thus, the "naturalised" category aligns broadly with C3–E (Fig. 1). On the other hand, the checklist (Imada 2019) does provide information on the number of islands where each species has naturalised. This information is potentially useful for understanding invasions across island regions; however, the unified framework does not provide an additional category for species that have naturalised or invaded across multiple geopolitical boundaries. Thus, these species are lumped in the same category with single-island species.

Relationship between WRA score and naturalisation

The Hawai‘i-Pacific WRA dataset included 828 non-naturalised and 712 naturalised species after questionably naturalised and recently-introduced non-naturalised species were removed (Fig. 2). Differences in likelihood-only scores between naturalised ($\bar{x} = 3.91$, SD = 4.25) and non-naturalised ($\bar{x} = 0.23$, SD = 3.49) plants were significant (Welch's $t = 18.40$, df = 1376.54, $p < 0.001$). Scores were also significantly different between these groups using the standard WRA scoring method (Welch's $t = 27.93$, df = 1303.27, $p < 0.001$), but with more separation between the distributions of scores for naturalised ($\bar{x} = 10.41$, SD = 6.90) and non-naturalised species ($\bar{x} = 1.60$ SD = 5.17) compared to likelihood-only scores. Thus, the standard WRA scoring method differentiates naturalised and non-naturalised species better than likelihood-only scores, making it more useful for inferring the likely status of data-deficient species (Daehler and Virtue 2010).

Only 11% of the 436 species with WRA scores less than 1 are naturalised in Hawai‘i, which is the upper threshold score used by the Hawai‘i-Pacific WRA to designate species as "Low Risk" (Fig. 2). Lowering the scoring threshold from 0 to -3 for predicting non-naturalised species decreases the error rate by only 1% (to 10% out of 201 species). On the other hand, 78% of the 684 species scoring greater than 6 (the threshold used by the WRA to deem a plant "High Risk") were naturalised. Increasing the threshold score to 12 (including 321 species) is required to increase the representation of naturalised species to 90%.

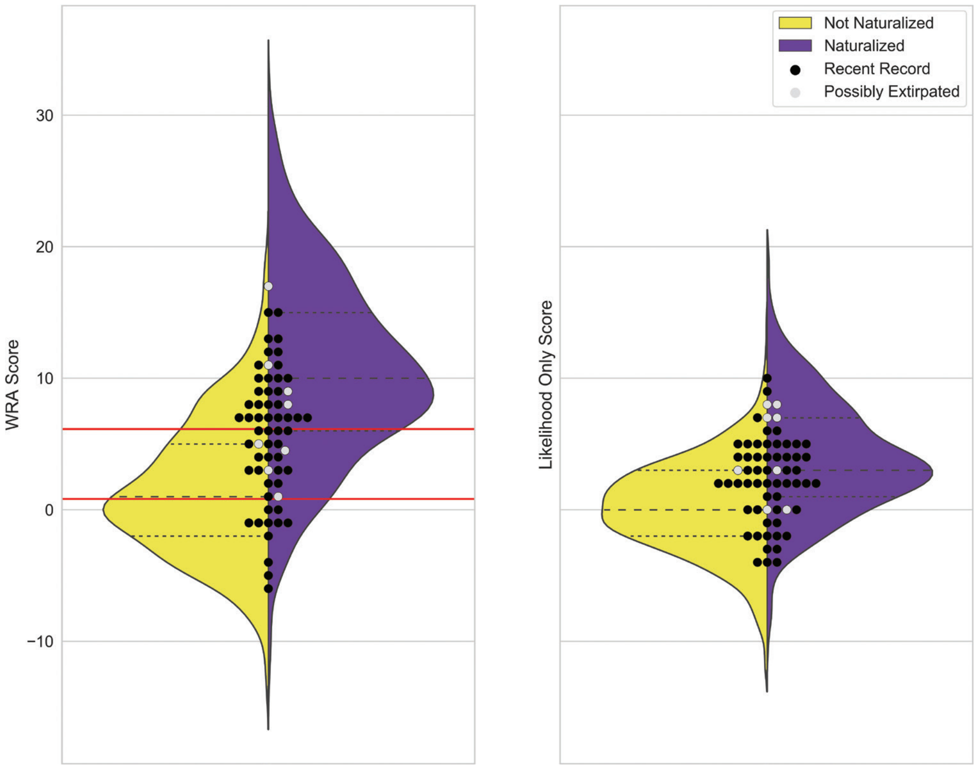

Figure 2. Distribution of non-naturalised (yellow) and naturalised (purple) scores based on WRA (**left**) and likelihood-only scoring (**right**). Dotted lines represent the lower quartile, median and upper quartile while thick solid red lines represent the scoring threshold used by the Hawai'i-Pacific WRA for designating species as high risk (> 6) and low risk (< 1). Dots represent scores for "Questionably Naturalised" species; grey = possibly extirpated, black = recently observed.

The WRA score and likelihood-only score were significantly positively correlated with the number of islands on which a plant has naturalised ($p < 0.001$ for both). The trend was weak in both cases, although we observed a more positive correlation for the standard WRA score than the likelihood-only score (Kendall's $\tau_b = 0.27$ versus 0.14, respectively; Fig. 3).

Predicting the fate of questionably naturalised species

Sixty-three of the 180 "questionably naturalised" species state-wide have been assessed by the Hawai'i-Pacific WRA (Table 1), for which we used WRA scores to infer naturalisation status. We did not consider island-specific "questionably naturalised" species that have definitely naturalised on another island in the archipelago because these species have already demonstrated the ability to successfully naturalise in Hawai'i. After removing eight possibly extirpated species that have not been observed in more than

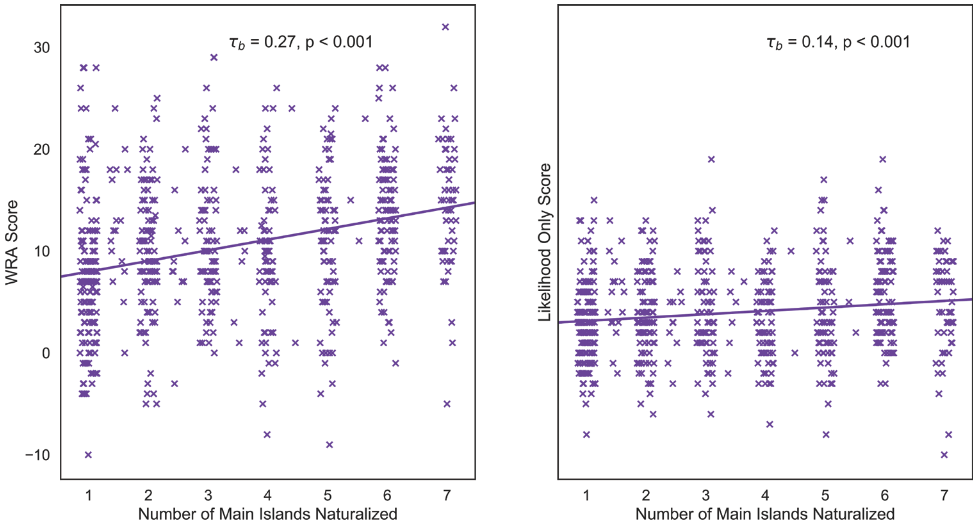

Figure 3. Relationship between the number of Hawaiian Islands naturalised with WRA (**left**) and likelihood-only scores (**right**). The fitted Theil-Sen estimator line is shown with Kendall's τ_b and associated *p*-value.

50 years or whose population declines have been closely monitored (based on herbarium specimens and expert opinion), 55 species remain in the data-deficient "questionably naturalised" category.

Based on the aforementioned relationship between WRA scores and naturalisation, we find that 11 species have scores < 1 and therefore 89% of these are expected to not naturalise (Fig. 2; Table 1). Reducing the threshold to -3 narrows the pool of questionably naturalised species to only three species and there is almost no change in the expected rate of not naturalising amongst the three plant species in this group (90%). Conversely, our data indicate that 78% of the 27 questionably naturalised species with scores greater than 6 (Fig. 2) are either naturalised already or will become naturalised. Raising this threshold to 12 identifies a set of only six species, 90% of which are likely to become naturalised.

Discussion

Our whole-flora analysis identified 342 cases where naturalisation status is currently uncertain, emphasising the need for effective tracking of non-native populations in the Hawaiian Islands. Hawai'i's current checklist (Imada 2019) forms the foundation for a future tracking system, but our attempt to align it to Blackburn et al.'s unified framework (2011) revealed both benefits and drawbacks of the unified framework in handling real-world data. Species listed as "questionably naturalised" proved problematic and, although the Hawai'i-Pacific WRA may assist with categorising these species, adjustments to the unified framework are needed to create a usable system. Based on Hawai'i's non-

Table 1. Species in the "Questionably Naturalised" checklist category alongside their likely status category derived from WRA scores and time since last observation.

Family	Species Name	WRA score	WRA rating	Likely Status*
Fabaceae	*Lespedeza cuneata* (Dum. Cours.) G.Don	17	High Risk	Extirpated
Apiaceae	*Eryngium foetidum* L.	15	High Risk	Naturalised-Unspecified
Asteraceae	*Tithonia rotundifolia* (Mill.) S.F.Blake	15	High Risk	Naturalised-Unspecified
Menispermaceae	*Stephania japonica* (Thunb.) Miers	13	High Risk	Naturalised-Unspecified
Tamaricaceae	*Tamarix aphylla* (L.) H.Karst.	13	High Risk	Naturalised-Unspecified
Cannabaceae	*Cannabis sativa* subsp. *indica* (Lam.) E.Small & Conquist	12	High Risk	Naturalised-Unspecified
Bromeliaceae	*Tillandsia usneoides* (L.) L.	12	High Risk	Naturalised-Unspecified
Asparagaceae	*Asparagus falcatus* L.	11	High Risk	Naturalised-Unspecified
Poaceae	*Lamarckia aurea* (L.) Moench	11	High Risk	Naturalised-Unspecified
Poaceae	*Panicum virgatum* L.	11	High Risk	Extirpated
Acanthaceae	*Barleria lupulina* Lindl.	10	High Risk	Naturalised-Unspecified
Begoniaceae	*Begonia nelumbiifolia* Schltdl & Cham.	10	High Risk	Naturalised-Unspecified
Combretaceae	*Quisqualis indica* L.	10	High Risk	Naturalised-Unspecified
Urticaceae	*Laportea aestuans* (L.) Chew	10	High Risk	Naturalised-Unspecified
Sapindaceae	*Allophylus cobbe* (L.) Raeusch.	9	High Risk	Naturalised-Unspecified
Iridaceae	*Sisyrinchium rosulatum* E.P.Bicknell	9	High Risk	Extirpated
Orchidaceae	*Vanilla planifolia* Jacks.	9	High Risk	Naturalised-Unspecified
Rhamnaceae	*Ziziphus mauritiana* Lam.	9	High Risk	Naturalised-Unspecified
Fabaceae	*Acacia retinodes* Schltdl.	8	High Risk	Naturalised-Unspecified
Apocynaceae	*Allamanda schottii* Pohl	8	High Risk	Naturalised-Unspecified
Primulaceae	*Ardisia virens* Kurz	8	High Risk	Naturalised-Unspecified
Poaceae	*Echinochloa esculenta* (A.Braun) H.Scholz	8	High Risk	Extirpated
Vitaceae	*Tetrastigma voinieranum* (Baltet) Pierre ex Gagnep.	8	High Risk	Naturalised-Unspecified
Fabaceae	*Acacia robusta* Burch. subsp. *clavigera* (E.Mey.) Brenan	7	High Risk	Naturalised-Unspecified
Bromeliaceae	*Aechmea bracteata* (Sw.) Griseb.	7	High Risk	Naturalised-Unspecified
Primulaceae	*Ardisia sieboldii* Miq.	7	High Risk	Naturalised-Unspecified
Scrophulariaceae	*Buddleja paniculata* Wall.	7	High Risk	Naturalised-Unspecified
Poaceae	*Cenchrus elegans* (Hassk.) Veldk.	7	High Risk	Naturalised-Unspecified
Poaceae	*Melinis nerviglumis* (Franch.) Zizka	7	High Risk	Naturalised-Unspecified
Marcgraviaceae	*Norantea guianensis* (Aubl.)	7	High Risk	Naturalised-Unspecified
Pinaceae	*Pinus pinaster* Aiton	7	High Risk	Naturalised-Unspecified
Apocynaceae	*Acokanthera schimperi* (A.DC.) Schweinf.	6	Evaluate	Data Deficient
Polygonaceae	*Homalocladium platycladum* (F.Muell.) L.H.Bailey	6	Evaluate	Data Deficient
Fabaceae	*Platymiscium stipulare* Benth.	6	Evaluate	Data Deficient
Lamiaceae	*Clerodendrum myricoides* (Hochst.) Vatke	6	High Risk	Data Deficient
Bignoniaceae	*Markhamia lutea* (Benth.) K.Schum.	5	High Risk	Data Deficient
Plantaginaceae	*Maurandya antirrhiniflora* Humb. & Bonpl. ex Willd.	5	Evaluate	Extirpated
Aizoaceae	*Mesembryanthemum cordifolium* L.f.	5	Low Risk	Data Deficient
Fabaceae	*Parkia timoriana* (DC.) Merr.	5	Evaluate	Data Deficient
Asteraceae	*Coreopsis tinctoria* Nutt.	4.5	High Risk	Extirpated
Euphorbiaceae	*Synadenium grantii* Hook.f.	4	Low Risk	Data Deficient
Cactaceae	*Peniocereus hirschtianus* (K.Schum.) D.R.Hunt	4	Evaluate	Data Deficient
Bignoniaceae	*Radermachera sinica* (Hance) Hemsl.	4	Evaluate	Data Deficient
Moraceae	*Antiaris toxicaria* Lesch.	3	Evaluate	Data Deficient
Annonaceae	*Cananga odorata* (Lam.) Hook.f & Thoms	3	Low Risk	Data Deficient
Euphorbiaceae	*Euphorbia albomarginata* Torr. & A.Gray	3	Low Risk	Extirpated
Pinaceae	*Pinus jeffreyi* A.Murray bis	3	Evaluate	Data Deficient
Solanaceae	*Solandra maxima* (Sessé & Moç.) P.S.Green	3	Evaluate	Data Deficient
Moraceae	*Ficus pumila* L.	2	Low Risk	Data Deficient
Fabaceae	*Sesbania grandiflora* L. Pers.	2	Low Risk	Data Deficient
Myrtaceae	*Eucalyptus pulchella* Desf.	1	Evaluate	Data Deficient
Plantaginaceae	*Linaria purpurea* (L.) Mill.	1	High Risk	Extirpated
Anacardiaceae	*Anacardium occidentale* L.	0	Low Risk	Not Self-Sustaining
Araliaceae	*Plerandra elegantissima* (Veitch ex Mast.) Lowry, G.M.Plunkett & Frodin	0	Low Risk	Not Self-Sustaining

Family	Species Name	WRA score	WRA rating	Likely Status*
Podocarpaceae	*Afrocarpus mannii* (Hook.f.) C.N.Page	-1	Low Risk	Not Self-Sustaining
Marantaceae	*Calathea zebrina* (Hort. ex Bosse)	-1	Low Risk	Not Self-Sustaining
Boraginaceae	*Cordia sebestena* L.	-1	Low Risk	Not Self-Sustaining
Fabaceae	*Delonix regia* (Bojer ex Hook.) Raf.)	-1	Low Risk	Not Self-Sustaining
Ebenaceae	*Diospyros blancoi* A.DC.	-1	Low Risk	Not Self-Sustaining
Myrtaceae	*Melaleuca styphelioides* (Sol. ex Gaertn.) Sm.	-2	Low Risk	Not Self-Sustaining
Apocynaceae	*Beaumontia multiflora* Teijsm. & Binn.	-4	Low Risk	Not Self-Sustaining
Magnoliaceae	*Magnolia champaca* (L.) Baill. ex Pierre	-5	Low Risk	Not Self-Sustaining
Malvaceae	*Pachira aquatica* Aubl.	-6	Low Risk	Not Self-Sustaining

*Species that have not been observed outside of cultivation for over 50 years are assigned a predicted status of "Extirpated" and, in all cases, they are known from less than three herbarium vouchers. Species having WRA scores > 6 and < 1 were assigned "Naturalised-Unspecified" and "Not Self-Sustaining", respectively, while species with scores from 1–6 were assigned "Data Deficient" (Table 2).

native flora, we propose a 7-category scheme for tracking species' statuses that largely aligns with the unified framework (Table 2). This tracking system includes the minimal number of status categories we think are critical for providing information for management decisions while accounting for common data deficiencies and ambiguities.

Ambiguous alignment of questionably naturalised species

The largest obstacle that arose when aligning the species checklist to the unified framework is that the "questionably naturalised" category contains species on fundamentally different trajectories, from species that have actually died out to those that will very soon become widespread invaders (Fig. 1). Additional field data are needed to accurately categorise them. If such surveys are not possible, an uncertainty variable, which permits categories to be assigned despite some data deficiencies, could avoid pooling species with different trajectories. However, such a scheme would still not account for species that have been introduced very recently and are just beginning to naturalise. These species do not fit into any of the naturalised categories (C3–E) because there is not yet proof that they will form self-sustaining populations in the long-term. Yet, the preceding C2 category implies that these species definitely do not form self-sustaining populations. Unlike species uncertainly aligned to status categories because population data are unknown, additional surveys will not help classify recently-introduced invaders because insufficient time has passed for that data to exist. Placing these data-deficient plants in C2 would remove the urgency to eradicate or at least monitor these species, even though this is precisely the group that concerns early detection and eradication programmes. Contrastingly, assigning these species to the C3 category is not a solution either because, in addition to not meeting the definition of naturalised, it could confound analyses by artificially inflating the number of naturalisations and potentially distract management towards species with less impact.

Hawai'i's checklist is not unique in having questionable status categories (Galasso et al. 2018) and similar problems distinguishing between C2 and C3 have been encountered in other applications of the unified framework to real-world scenarios

Table 2. Practical adaptation of the unified framework requiring minimal additional data collection beyond species checklists.

Categories as per Blackburn et al. (2011), with labels in brackets as per Groom et al. (2019)	Proposed Status Tracking Categories		Category Description
A – Not transported beyond limits of native range.	**Not Present**		No history of introduction, or if previously introduced (e.g. for cultivation or forestry), it was never found outside of cultivation and is no longer present.
Not Included	**No Longer Present** *	**Establishment Failure**	Previously found outside of cultivation at one time, but was purposefully or naturally removed before self-sustaining populations formed (naturalisation).
		Extirpated	Previously forming self-sustaining populations (naturalised) at one time, but no longer existing through purposeful (eradication) or natural means.
B1 (captive) – Individuals transported beyond limits of native range, and in captivity or quarantine (i.e. individuals provided with conditions suitable for them, but explicit measures of containment are in place).	**Contained / Cultivated**		Existing in cultivation or somehow contained. Includes accidental soil contaminants that are contained within pots or aquaria alongside purposefully cultivated species.
B2 (cultivated) – Individuals transported beyond limits of native range and in cultivation (i.e. individuals provided with conditions suitable for them, but explicit measures to prevent dispersal are limited at best).			
B3 (released) – Individuals transported beyond limits of native range, and directly released into novel environment.	Not Included		N/A
C0 (failing) – Individuals released into the wild (i.e. outside of captivity or cultivation) in location where introduced, but incapable of surviving for a significant period.	Re-appropriated into "Establishment Failure" Above		
C1 (casual) – Individuals surviving in the wild (i.e. outside of captivity or cultivation) in location where introduced, no reproduction.	**Not Self-Sustaining**		Plants surviving outside of cultivation with sufficient evidence suggesting that offspring, if produced, do not contribute to a self-sustaining population.
C2 (reproducing) – Individuals surviving in the wild in location where introduced, reproduction occurring, but population not self-sustaining.			
Not Included	**Potentially Naturalising**		Plants apparently surviving and reproducing outside of cultivation, but insufficient time has passed to determine if a self-replacing population exists.
C3 (established) – Individuals surviving in the wild in location where introduced, reproduction occurring and population self-sustaining.	**Naturalised-Unspecified***	**Naturalised Where Introduced**	Plants that form self-sustaining populations without human intervention (e.g. cultivation), but have not dispersed a significant distance from their point of introduction.
D1 (colonising) – Self-sustaining population in the wild, with individuals surviving a significant distance from the original point of introduction.			
D2 (invasive) – Self-sustaining population in the wild, with individuals surviving and reproducing a significant distance from the original point of introduction.		**Naturalised Beyond Introduction Site**	Plants that form self-sustaining populations without human intervention (e.g. cultivation) and have dispersed and established a significant distance from their point of introduction.
E (widespread invasive) – Fully invasive species, with individuals dispersing, surviving and reproducing at multiple sites across a greater or lesser spectrum of habitats and extent of occurrence.			

*Use if data to assign subcategories are insufficient.

(Wilson et al. 2014; Robinson et al. 2016). As discussed above, these mismatches sometimes arise from insufficient population data needed to confidently assign categories, which is common because reports of new species are often opportunistic and thorough surveys to delimit entire populations are rarely conducted. However, misalignments also stem from the unified framework's conceptually discrete barriers along the invasion continuum, when in reality, these boundaries are fuzzy. Moreover, the status of a species will often change over time. For instance, the unified framework acknowledges that several cycles of reproduction are necessary to form a self-sustaining population, thereby surpassing the reproduction barrier, but cannot specify how many are required. Thus, if a recently introduced species is encountered outside of cultivation and only two different life stages are visible (indicating at least one cycle of reproduction after dispersal), the self-sustainability of the population is questionable. Lack of understanding surrounding establishment success has recently been emphasised as an important factor biasing studies on geographical patterns of non-native species richness (Blackburn et al. 2020). Additionally, population sustainability is hard to predict because it depends on numerous interactions between species traits and environmental conditions and, thus, should not be assumed (Duncan et al. 2019). The hundreds of species that have been reported as "questionably naturalised" in our analysis confirm that field botanists are often plagued with uncertainty (Magona et al. 2018). This problem emphasises the need for status tracking frameworks to address uncertainty, but solutions must assess whether that uncertainty arises from insufficient data about an existing population or from insufficient time to assess the behaviour of a new species (see Probert et al. 2020 for addressing impact assessment uncertainty).

WRA scores can assign a likely status for questionably naturalised species

Our data show that the WRA can be a useful tool for predicting naturalisation, with scores obtained from the standard WRA scoring method being more able to distinguish naturalised from non-naturalised species than scores from the likelihood questions only (Fig. 2). This result was surprising because, logically, the likelihood of spread questions should more accurately reflect the propensity for plants to naturalise, whereas impact-related questions seem less relevant to predicting naturalisation. The standard WRA was also more strongly correlated with a species' tendency to naturalise across multiple islands relative to the likelihood-only score (Fig. 3). However, weak correlations for both indicate that other factors besides those accounted for in WRA scores undoubtedly influence the repeated naturalisation of these species across islands. For example, a species' ability to naturalise on multiple islands is more likely explained by deliberate or accidental between-island dispersal by humans (breaching the geographic barrier), rather than factors related to biology that are emphasised in the WRA.

Given that WRA scores appear to be more useful than scores derived from the likelihood questions only, the scoring thresholds currently in use to assess risk of weediness by the Hawaiʻi-Pacific WRA (> 6 = "High Risk", < 1 = "Low Risk") may be sufficient for predicting the likely status of data deficient "questionably naturalised" species (Table 1). Considering that 78% of naturalised species with a WRA score over 6 are naturalised, using this threshold to predict naturalisation could lead to an error rate of up to 22%. Conversely, 89% of plants with scores less than 1 were not naturalised, indicating an error rate of up to 11% when predicting that plants will not naturalise. Our ability to assess the WRA as a predictor of naturalisation depends on accurate categorisation of species in our test data. Undetected naturalisations or species with naturalisation potential could exist in our non-naturalised dataset (e.g. species whose establishment is limited by urban landscaping), even though rarely cultivated plants and introductions less than 20 years old were removed; this may account for the small skew towards higher scores in the distribution of non-naturalised species contributing to this error rate (Fig. 2). However, this error rate may be acceptable to invasive species managers who often err on the side of caution when identifying species likely to naturalise.

By applying the Hawai‘i-Pacific WRA thresholds to “questionably naturalised” species (and accepting their associated error rates), we would infer that the 11 species (~20%) with scores less than 1 are unlikely to naturalise and instead belong to the C1 or C2 categories, while 27 (49%) species with scores greater than 6 would likely belong to, or eventually belong to, the C3 category or higher (Table 1). This leaves 18 species with scores ranging from 1–6 for which we are unable to infer a status category. Interestingly, scores for species not observed for more than 50 years (“possibly extirpated”) ranged from 3–17; although most were predicted to naturalise, they might have existed as very small populations (making them vulnerable to stochastic extinctions) or they might be naturalised at locations rarely visited by botanists.

Accommodating data deficiencies and management needs

Similar to other inventories that reference the unified framework when categorising the status of non-native species (Wilson et al. 2014; Robinson et al. 2016; Henderson and Wilson 2017; Magona et al. 2018; Ansong et al. 2019), we found that the coarse categories typical of species checklists (e.g. cultivated, questionably naturalised and naturalised in Hawai‘i) did not align to all 11 categories in the unified framework. Field surveys would be needed to update existing information and, in some cases, collect new types of data, to apply some framework categories. One interpretation of this problem is that the unified framework’s fine categorisation scheme cannot be realistically implemented as a tracking system for many regions, especially for developing island nations with limited funds for research and conservation (Russell et al. 2017). However, more status categories than are typically used in species checklists are needed to conduct analyses of patterns and trends to provide information for invasive species management. Accordingly, an intermediate approach is needed that avoids unrealistic requirements, such as the need for numerous site revisits over an extended time period and emphasises the use of information commonly available (e.g. occurrence reports, herbarium specimens, general survey data). To establish a tracking system based on this information, we can superimpose the unified framework’s description of the invasion continuum (Blackburn et al. 2011) on to the checklist categories and the most readily attainable data (Table 2). The management goals described in the unified framework, which include prevention, eradication, containment and mitigation, help delineate a broader status categorisation scheme that still assists with management decision-making.

When naming our proposed status categories in Table 2, we avoided the use of alpha-numerics (as are used in the unified framework) in favour of descriptive terms in order to facilitate an intuitive transition from a basic species checklist to a practical tracking system that is usable by non-specialists. To avoid confusion in terminology, our status category names are consistent with terminology used in the unified framework, as well as other publications concerning communication of biological invasions (Richardson et al. 2000; Pyšek et al. 2004; Blackburn et al. 2011). Groom et al. (2019) provide a list of terms that correspond to each of the 11 categories used in the unified framework, although we were unable to directly use those terms because our system required lumping some of the unified framework categories. We avoid using the term "invasive" as a status because it is inconsistently applied and often reserved for species that cause harm (Colautti and MacIsaac 2004; Gbedomon et al. 2020) and, unlike the biological barriers presented in the unified framework to describe a species' journey through the invasion process, harm is context dependent (e.g. impacts to biodiversity versus socio-economic resources) and cannot be conceptualised as a hurdle that must be surpassed (Blackburn et al. 2011, 2014; Bacher et al. 2018; IUCN 2020b)

We combine B1 (measures of containment in place) and B2 (containment limited) into a single category "Contained/Cultivated" because, although information about circumstances preventing dispersal can be informative for management, acquiring this data for an entire flora is difficult. Additionally, plants cultivated under strict containment measures are likely to be far less common than those with limited (or no) attempt to prevent dispersal. We include "Not Self-Sustaining" (aligning to C1–C2) and "Potentially Naturalising", with the latter referring to recently-introduced species that appear to be in the process of naturalising (but have not yet done so), which is not included as a category in the unified framework. The adoption of the latter category provides a list of species in need of careful monitoring and alerts invasive species managers to eradication possibilities without indicating that naturalisation has occurred.

Describing the phase of naturalisation for entire floras provides a unique challenge because distribution data may be insufficient to determine whether individuals are dispersing, surviving and reproducing at locations beyond introduction sites for numerous species (Blackburn et al. 2011). As a result, many checklists do not attempt to further categorise species beyond naturalisation (Uludag et al. 2017). On the other hand, data on the spread of species from known introduction sites (e.g. sites of cultivation or accidental seed contamination) may be available for well-surveyed species, especially for those that are purposefully monitored by invasive species control programmes. Our solution to this data disparity is that species should be sorted into two categories when data are available, including "Naturalised Where Introduced" and "Naturalised Beyond Introduction Site", or placed into a more general status category "Naturalised-Unspecified" (C3–E in the unified framework) if data are insufficient (Table 2). We chose to combine C3–D1 within "Naturalised Where Introduced", including naturalised plants that may or may not disperse beyond their introduction site, but where survival of dispersed offspring is not sufficient (or not yet sufficient) to form new self-sustaining populations. This phenomenon may be observed for plants that are unable to spread beyond their immediate human-disturbed surroundings (Rojas-Sandoval and

Acevedo-Rodríguez 2015), because they are not adapted to conditions where they are dispersed. This status category contrasts with "Naturalised Beyond Introduction Site" (aligning to D2–E), which includes species known to have spread naturally beyond any possible introduction sites. Species of the former status category are likely to have localised impacts and be easier to contain or eradicate, whereas species in the latter category could potentially already have wide-ranging impacts and require substantial intervention to control or prevent further spread.

For the purposes of tracking regional floras, the A category (not transported outside native range) should be adapted to include likely invaders that have not yet arrived in the region of interest, identified via horizon scanning or risk assessment tools. Moreover, the unified framework does not categorise species that were once present in a region and are now absent, but describes the invasion continuum as a unidirectional process, with multiple avenues for invasion failure, making it unclear how species can go backwards in status. Thus, additional categories would be useful for species that were once growing outside of cultivation, but are now absent, with possible sub-categorisation according to whether a species disappeared before (C0–C2) or after naturalisation (≥ C3) if data are available (Table 2). Plant eradication programmes exist on most main Hawaiian Islands, which concentrate on removing species before naturalisation or in the early stages of it (Kraus and Duffy 2010). Furthermore, several previously-naturalised species that were never targeted by weed control programmes have not been observed for numerous decades (Imada 2019) and are presumed to be naturally extirpated. In these examples, it is possible that some species were wrongly reported to be naturalised when, in fact, they failed to surpass the survival and reproduction barriers necessary to form self-sustaining populations (thus aligning to categories C0–C2), but this is now impossible to ascertain. To avoid confusion, a new category for "No Longer Present" is needed for species that were once found outside of cultivation but are not currently present (even if data are not available to accurately assess their historic status) in order to identify re-introductions and re-invasions of species that were previously thought to be extirpated (Panetta 2015).

We found that, although categories B3 (directly released outside of cultivation) and C0 (the same as B3 but no survival) are useful for conceptualising barriers to invasion success, they are not practically applicable as status categories (Table 2). The reason for this is that plant species encountered in the field are assumed to be surviving (and possibly reproducing) and, thus, are assumed to be at least C1. If plants are no longer present when sites are revisited, as would be the case for C0 species, which are released outside of cultivation but fail to survive, then field botanists would assume these species have become extirpated or are present in cultivation only (Table 2).

Implementation and future directions

Classification schemes used in species checklists, such as the three categories used in Hawai'i's checklist, may be converted to our system using typically available information while accommodating more detailed population data when available. To account for uncertainty when assigning categories, we suggest that low, medium and high confidence levels be attached to each status, with guidance available in Suppl. material 1 following previous examples for categorising invasive impacts (Hawkins et al. 2015; Wilson et al. 2018). We additionally suggest that, when possible, statuses assigned with low-medium confidence be given a "likely status" using inferential tools, such as species distribution models and risk assessments (Table 2; Suppl. material 1). The likely status is not intended to be a prediction for a species' future status, but deduces its current reality, which is particularly useful for regions with numerous introductions and insufficient field monitoring, where inference may be the only method for estimating a snapshot of invasion statuses for a region's flora. In our example, analysis of field data for plants in the "questionably naturalised" checklist category can be conducted to reassign as many species as possible into a more informative status category. As we demonstrate here, WRA scores may then be used to assign a likely status of either "Not Self-Sustaining" or one of the naturalised status categories (Tables 1, 2; Suppl. material 1). Nevertheless, it is probable that further analyses and predictive tools will fail to reassign at least a few species. In our example (Table 1), we have labelled these unassignable species as having a "Data Deficient" likely status category to incentivise monitoring of these populations.

Assigning species' statuses along the introduction-naturalisation-invasion continuum is an important first step for developing a biodiversity informatics (rather than species-specific) approach to managing invasions and monitoring status changes over time. Changes in spatial extent and population size could further accompany our proposed status tracking system to strengthen assessments of both impacts and control feasibility. For instance, species that are just beginning to naturalise would be categorised as "Potentially Naturalising", a status potentially assumed to be eradicable, but feasibility may be complicated by the presence of numerous introduction sites. Future efforts towards this goal could refer to frameworks categorising commonness and changes in population size (McGeoch and Latombe 2016; Latombe et al. 2020). Tracking impacts alongside statuses and population extent would be especially useful and could be achieved by integrating the IUCN Environmental Impact Classification for Alien Taxa (EICAT; Blackburn et al. 2014; Hawkins et al. 2015; IUCN 2020b) and its socio-economic equivalent (SEICAT; Bacher et al. 2018).

Our analyses allude to possible uses of the WRA beyond the novel use we describe here, as well as its original goal of identifying potential weeds. High scoring species that have failed to naturalise are priorities for monitoring and prevention (particularly multi-island introductions) and could be compared with similarly-scored species that have naturalised, possibly identifying important traits or conditions inhibiting species otherwise prone to invade. Conversely, investigating low scoring species that have naturalised could reveal possible sources of error during prediction, suggesting location-specific contexts that promote invasion (e.g. remote island ecosystems with low native diversity). While we show that WRAs can help assign naturalised statuses for data-deficient species, future studies could investigate avenues for inferring other positions along the introduction-naturalisation-invasion continuum (Suppl. material 1). For instance, identifying extirpations is challenging because data necessary to establish absence are often insufficient and hence could be made easier with inferential tools. Guidance on declaring extinctions and extirpations for native species is available (IUCN 2019), but a framework that applies these principles to non-native eradications and natural extirpations is sorely needed.

Conclusions

Our attempt to apply the unified framework by Blackburn et al. (2011) to Hawai‘i revealed its limitations as a tracking system for entire non-native floras. Specifically, the unified framework does not address species that have uncertain statuses, which are common surrounding the early stages of naturalisation. However, our findings indicate that this issue can be resolved for many species by predicting a likely status using WRA scores. We therefore demonstrate that species tracking systems and predictive tools like WRA should be integrated to strengthen their ability to inform management of already-introduced plant species. We further propose a system for tracking entire floras that accommodates real-world data while retaining categories relevant to invasive plant managers. Our system is particularly useful for invader-rich floras, such as those common on islands, where a mix of on-the-ground information and methods to address data gaps are necessary to solve real-world biosecurity dilemmas.

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Supplementary material 1

Guidance on the status confidence rating and adapting a regional checklist to track invasion statuses

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Identifying safe cultivars of invasive plants: six questions for risk assessment, management, and communication

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Abstract

The regulation of biological invasions is often focussed at the species level. However, the risks posed by infra- and inter-specific entities can be significantly different from the risks posed by the corresponding species, to the extent that they should be regulated and managed differently. In particular, many ornamental plants have been the subject of long-term breeding and selection programmes, with an increasing focus on trying to develop cultivars and hybrids that are less invasive. In this paper, we frame the problem of determining the risk of invasion posed by cultivars or hybrids as a set of six questions that map on to the key components of a risk analysis, viz., risk identification, risk assessment, risk management, and risk communication. 1) Has an infra- or inter-specific entity been proposed as "safe to use" despite at least one of the corresponding species being a harmful invasive? 2) What are the trait differences between the proposed safe alternative and its corresponding invasive species? 3) Do the differences in traits translate into a difference in invasion risk that is significant for regulation? 4) Are the differences spatially and temporally stable? 5) Can the entities be distinguished from each other in practice? 6) What are the appropriate ways to communicate the risks and what can be done to manage them? For each question, we use examples to illustrate how they might be addressed focussing on plant cultivars that are purported to be safe due to sterility. We review the biological basis of sterility, methods used to generate sterile cultivars, and the methods available to confirm sterility. It is apparent that separating invasive genetic entities from less invasive, but closely related, genetic entities in a manner appropriate for regulation currently remains unfeasible in many circumstances – it is a difficult, expensive and potentially fruitless endeavour. Nonetheless, we strongly believe that an *a priori* assumption of risk should be inherited from the constituent taxa and the onus (and cost) of proof should be held by those who wish to benefit from infra- (or inter-) specific genetic entities. The six questions outlined here provide a general, science-based approach to distinguish closely-related taxa based on the invasion risks they pose.

Keywords

cultivars, hybrids, infra-specific genetic entities, invasive species, non-invasive cultivars, ornamental plants, seedless cultivars, sterility

Introduction

Invasion is a population-level phenomenon (Petit 2004; Zenni et al. 2014). Nonetheless, most regulatory policies focus implicitly or explicitly at the species-level. Consequently, the enormous variation that exists at infra-specific levels is often not considered in regulatory frameworks. The inability to recognise differences below the species rank may lead to serious underestimation or overestimation of invasion risk (Gordon et al. 2016). For example, infra-specific entities can vary in the bioclimatic niches they occupy in their invasive ranges (Thompson et al. 2011; Gotelli and Stanton-Geddes 2015), their host-specificity (Goolsby et al. 2006), and the impacts they cause (Novoa et al. 2018). Likewise, invasions by inter-specific taxa are also very important: hybridisation is one of the major impacts caused by biological invasions (Huxel 1999; Yakandawala and Yakandawala 2011). Therefore, it is vital that policy and regulation can adequately address invasion risk at levels other than the species.

These issues are particularly significant in the context of horticulture. The introduction of plants as ornamentals constitutes a major pathway for invasive plants across the globe (Bell et al. 2003; van Kleunen et al. 2018). Many of the traits that are important for horticultural purposes can also promote invasiveness (Reichard and Hamilton 1997; van Kleunen et al. 2018), for example, the formation of dense thickets, profuse flowering, high fruit set, and wide environmental tolerance (Knight et al. 2011; van Kleunen et al. 2018). In contrast, some horticulturally-desirable traits lead to reduced competitive ability; for example, variegated leaves in plants can have lower photosynthetic performance than non-variegated leaves (Gaskin and Kazmer 2009). Horticulture, therefore, creates very particular ecologically-relevant biases in infra-specific and inter-specific genetic entities. Moreover, many ornamental plants have been subjected to artificial selection and breeding programmes to enhance specific attributes of interest (Reichard and White 2001; van Kleunen et al. 2018), leading, in some cases, to high diversity of genetic entities below and above the species rank. This can have direct consequences for the likelihood of an invasion. For example, above the species rank, hybridisation between two or more species or even genera can promote genetic diversity and increase invasiveness (Culley and Hardiman 2009; Gaskin and Kazmer 2009; Klonner et al. 2017). Below the species rank, cultivars of a species can differ in traits such as allelopathy (Alsaadawi et al. 2012; Al-Bedairy et al. 2013) and herbicide tolerance (Sterling et al. 2004). Horticulture, therefore, creates very particular ecologically-relevant biases in infra-specific and inter-specific genetic entities.

In response to the risks of biological invasions, several countries have enacted legislation to regulate the use and trade of invasive plant species. Many of these regulated species are, however, of great ornamental value, and so such regulations cause economic losses and directly impinge on individual rights (Wirth et al. 2004). Consequently, there has been pressure to either exempt particular genetic entities that are naturally "safe" or "non-invasive" or to develop cultivars that are more environmentally sustainable (Guo et al. 2004; Freyre et al. 2014).

A specific case in point is South Africa's National Environmental Management: Biodiversity Act, Alien and Invasive Species Regulations of 2014 (Department of Environmental Affairs 2014), hereafter referred to as the NEM:BA A&IS Regulations. In an attempt to balance the goal of environmental protection with those of the horticultural industry, the regulations have provision to exempt infra- or inter-specific entities. Out of 379 plant taxa listed in the 2016 revised list, sterile cultivars or hybrids are not listed for 32 taxa, spineless varieties of two cactus species are exempted, and sterile forms of *Pinus elliotti* are regulated differently from fertile forms (Department of Environmental Affairs 2016; Suppl. material 1: Table S1). While excluding sterile cultivars or hybrids is a laudable effort to reduce potential conflicts, the regulations do not provide any guidance on how this is to be implemented, and only in one case, *Duranta erecta* "Sheena's Gold", is an acceptable cultivar specifically named. The regulations also implicitly assume that sterility is a necessary and sufficient condition to reduce invasiveness and impact. However, some of the most damaging invasive plants are predominantly sterile in their invasive range [e.g. water hyacinth (*Eichhornia crassipes*); (Zhang et al. 2010)], conversely, infra- or inter-specific entities might still be fertile, but either the reduction in fertility or changes in other traits mean that they pose an acceptable level of risk. Finally, the risk-reducing trait might not be stable, and so a 'safe' cultivar could revert to an 'invasive' plant [e.g., there is some indication that the spineless non-invasive cacti exempted under the NEM:BA A&IS Regulations might readily revert to spiny invasive forms (Novoa et al. 2019)]. While the consideration of sub-specific entities has been included in a recent risk analysis framework that is being used to provide scientific recommendations for the NEM:BA A&IS Regulations (Kumschick et al. 2020), the framework does not yet include a detailed protocol for how to analyse the relative risk of infra- or inter-specific entities.

Six questions to serve as a guide to differentiate "safe" cultivars from "risky" relatives.

To clarify the issue of how to separate "safe" cultivars from "risky" relatives, we developed a set of six questions (Fig. 1). The questions are framed so they align with the general steps of a risk analysis, i.e., risk identification, risk assessment, risk management, and risk communication.

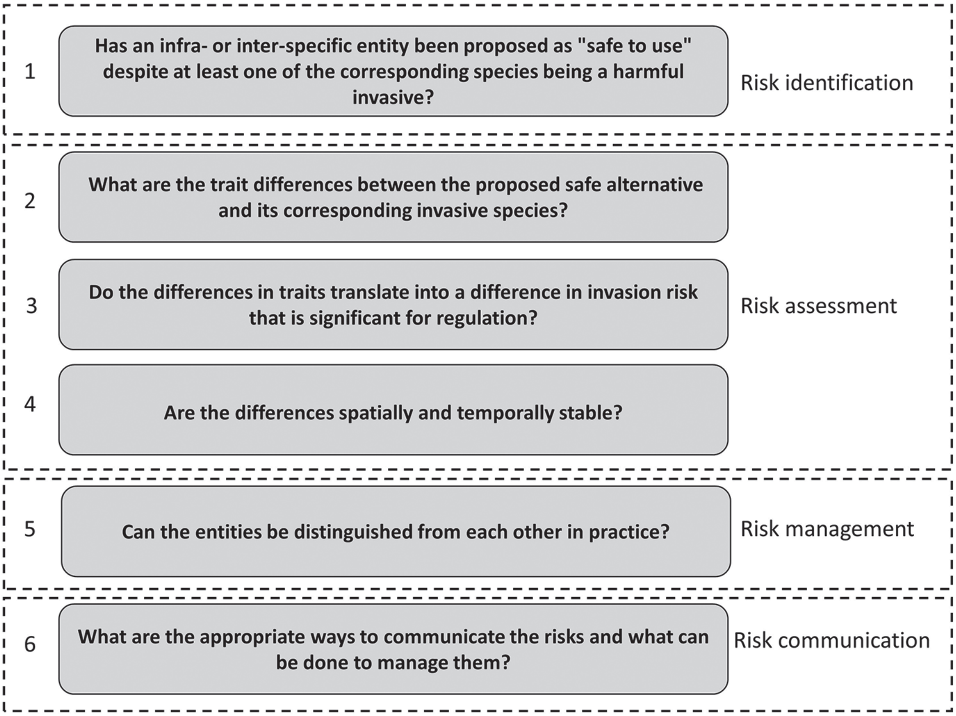

Figure 1. Six questions that should be answered if "safe" cultivars are to be differentiated from "risky" relatives in regulations on biological invasions. The questions align with the constituent parts of risk analysis as indicated by the dotted boxes. Each of the questions is explained in further details in the main text.

Question 1: Has an infra- or inter-specific entity been proposed as "safe to use" despite at least one of the corresponding species being a harmful invasive? To minimise the risk of invasion from known invasive ornamental species, the use of non-invasive and sterile forms has been promoted. Question 1 concerns identifying and specifying this problem. Is there a cultivar of an invasive ornamental species that is deemed to be safe? Is there sufficient demand for this cultivar to warrant answering the other questions? It is essential to assess the invasion risk of a supposedly non-invasive genetic entity in the context of the invasiveness of the closely-related invasive taxa or parent invasive taxa (Table 1). The list of (potentially safe) cultivars can be obtained from published cultivar names (e.g. International Cultivar Registration Authorities), nursery catalogues, and consultation with stakeholders such as plant breeders and wholesale nurseries.

Question 2: What are the trait differences between the proposed safe alternative and its corresponding invasive species? This question refers to measurable differences that could help us to characterise and differentiate between cultivars and the known invasive entity. These differences could either be due to underlying genetic differences or could be induced due to environmental factors. The traits could include vegetative traits (e.g., leaf size, presence of variegated leaves, presence of thorns and spines, height, and growth form) or reproductive traits (e.g., flower colour, phenology or number of fruits

Table 1. Selected case studies in which sterile cultivars and hybrids were specifically generated as an alternative to known invasive stocks. Details of the cultivar name, method used to generate the cultivar or hybrid, biological cause of sterility, and the commercial purpose of generating the sterile cultivar or hybrid are detailed below.

Taxa	Cultivar name(s)	Method	Cause of sterility	Purpose	Reference
Citrus	NA	Cybridisation	Cytoplasmic male sterility	Development of seedless fruits	Guo et al. (2004)
Euonymus alatus	Compactus	Ploidy alternation: Triploid plant generation	Uneven division of chromosomes	Development of sterile ornamental	Thammina et al. (2011)
Lantana camara	UF-T3 UF-T4	Interploid Hybridisation	Highly reduced pollen fertility and seed set (with seed germination highly reduced for UF-T3 and zero for UF-T4)	Development of sterile ornamental	Czarnecki et al. (2012)
Ruellia simplex	R10-102 (Mayan Purple) R10-108 (Mayan White) R12-2-1 (Mayan compact purple)	Interploid hybridisation and induced polyploidy using oryzalin	Fruitless and low pollen viability (R10-102 and R10-108), and both female and male sterility (R12-2-1)	Development of sterile ornamental	Rosanna Freyre et al. (2012)
Verbena x hybrida	SS SC	Mutation by heavy-ion beam	Non functional male and female gametes in SS and self-incompatibility in SC	To halt senescence and increase flowering duration of the plants	Kanaya et al. (2008)

or seeds). In some cases, underlying genetic differences leading to sterility may not be easily detected from phenotypic traits and, therefore, further examination of cytological and genetic differences could be necessary.

Question 3: Do the differences in traits translate into a difference in invasion risk that is significant for regulation? In question 3, we relate the observed differences (seen in question 2) to differences in the level of invasion risk posed and whether any such differences in risk mean that the taxa sit on different sides of a regulatory decision point, i.e., specimens with one set of physical properties pose an acceptable level of risk, while others do not. The observable differences in traits of the related genetic entities may lower the invasion risk only if the fecundity is directly or indirectly lower than the known invasive form. Traits that are directly related to fecundity include pollination, length of flowering time, number of flowers, fertilisation, seed production, germination success, survival rate, and vegetative reproduction. Traits that indirectly affect fecundity include allelopathic potential, mycorrhizal mutualisms, and herbivore deterrence due to the presence of thorns or chemicals. To detect differences in fecundity between different genetic entities, it is necessary to grow them in the same common garden environment and monitor long term. Ideally, the fecundity (or offspring survival) should be so low that population growth rate is negative (Knight et al. 2011).

Question 4: Are the differences spatially and temporally stable? Question 4 concerns whether the changes in the observable traits are stable and no reversal to the parental conditions is likely (see examples in Table 2). The changes should ideally be genetically fixed and not induced by environmental factors or due to short term epigenetic modifications. Even genetic changes could be reversed due to occasional outcrossing with other genotypes. Therefore, long term common garden experiments under differ-

Table 2. Selected examples of cultivar evaluation. Details of the specific method used for evaluation, number of years the evaluation took, and the main result are tabulated below. This Table corresponds to the risk assessment section (questions 2–4) of the conceptual framework proposed (Fig. 1).

Taxa	Method(s) of evaluation	Duration (Years)	Main Results	Reference
Berberis thunbergii	Common garden experiments Seed germination experiments	4–5	Out of 46 cultivars, most cultivars produced seeds. Cultivars that failed to produce seeds initially produced seed after the plants matured for 4–5 years. None of the cultivars can be considered non-invasive.	Brand et al. (2012)
Euonymus alatus	Common garden experiment Open seed germination Establishment experiment	3	None of the cultivars was completely seedless and failed to germinate. Habitat had a strong influence on seed germination and establishment.	Brand et al. (2012)
Lantana camara	Cytology Pollen staining Comment garden experiments	3	All the cultivars produced viable pollen. Almost all cultivars produced viable seeds. Even sterile triploid cultivars produced seeds when allowed to cross pollinate with diploid cultivars. None of the plants were truly sterile.	Spies and du Plessis (1987)
Nandina domestica	Common garden experiments Seed germination	1–2	Large cultivars produced more viable seeds than dwarf cultivars. Seed viability was close to zero for some cultivars which were hence recommended for use.	Knox and Wilson (2006)
Ruellia tweediana	Common garden experiment Seed germination	1–2	All the cultivars were capable of producing viable seeds that germinated. Environmental conditions (light and temperature) influenced the fecundity.	Wilson and Mecca (2003)
Spiraea japonica	Common garden experiments Pollen and seed germination Pollination experiments Flow cytometry	1	Three sterile cultivars were identified that did not produce any viable seeds and had very poor pollen germination. Sterility was not related to polyploidy.	Wilson and Hoch (2009)
Viburnum opulus	Field assessment and germination experiments.	2	All cultivars produced seeds, but varied in amount. Poor germination in open field sites compared to green house	Conklin and Sellmer (2009)

ent experimental conditions should be performed. In order to ensure that fertility does not revert, cross-pollination experiments should be performed between the different non-invasive genetic entities under consideration and the known invasive form. However, ultimately a regulator is interested in whether reversion is likely in the context of where and when (and in what numbers) the entity will be used. If a cultivar is very popular and widely planted, an extremely rare reversion is more likely to happen than for unpopular cultivars, and on-going monitoring might be advisable (see Question 6).

Question 5: Can the entities be distinguished from each other in practice? Question 5 refers to the need that, if the regulation is to be implemented, the safe cultivar must be readily distinguishable from its invasive relatives. This is particularly important for management and regulation so that non-invasive genetic entities can be exempted and monitored. Phenotypic differences might depend on growing conditions, and so other assays (Table 3) should be performed whenever necessary. Molecular markers for specific cultivars could be developed so that they can be readily detected.

Question 6: What are the appropriate ways to communicate the risks and what can be done to manage them? Finally, question 6 requires a mechanism by which recommendations are developed together with stakeholders in a transparent and inclusive manner (e.g., Novoa et al. 2018). This should be based on the results from the previous questions.

Table 3. Selected examples of cultivar identification using different techniques. In order to ensure effective regulation, the cultivar has to be distinguishable from the invasive ones. This Table corresponds to the risk management section of the conceptual framework (question 5) (Fig. 1).

Taxa	Method used	Details of the study	Reference
Castanea sativa	Pollen morphology and germination	Characterisation of sterile and fertile pollen based on pollen morphology.	Mert and Soylu (2007)
Kangaroo Paws: *Anigozanthos* and *Macropidia*	Plastid DNA sequencing	Construction of phylogenetic tree based on plastid DNA confirmed hybrid origin of invasive population and other commercially available cultivars.	Le Roux et al. (2010)
Prunus persica	Molecular markers (RAPDs)	Marker based identification of genes responsible for pollen sterility (Ps/ps).	Jun et al. (2004)
Purple-leaved Japanese barberry: *Berberis thunbergii* var. *atropurpurea* and Green leaved *Berberis thunbergii*	Shade treatments in common garden	The purple leaves of *Berberis thunbergii* var. atropurpurea become green when grown under shade. Therefore, they cannot be easily distinguished from green-leaved *Berberis thunbergii* under shaded conditions.	Lehrer and Brand (2010)

The basis of sterility and how to demonstrate it

Ultimately, the risk posed by a biological invasion is a function of population growth rate, spread rate, and subsequent impacts. Sterility in and of itself is neither a necessary nor sufficient condition to prevent damaging invasions. However, for some taxa (those that do not show asexual reproduction in particular) it is a sufficient condition and one that is particularly relevant to the development of “safe” cultivars from “risky” relatives. In this section, we review the biological bases of sterility and the different methods that have been developed to produce sterile cultivars. Furthermore, we discuss the different methods used to evaluate how “safe” a cultivar is. In each case, we highlight and discuss the links between these issues and how they address the six questions posed in Figure 1.

The biological bases of reduced fecundity and sterility

Fecundity refers to the total number of viable offspring an individual produces over a lifetime. In most plants, fecundity is measured by viable seed production. It is crucial to understand the developmental processes associated with reduced fecundity when studying invasive plants and their apparently less invasive cultivars-in the presented framework, this relates to questions 2–4. In this section, we discuss several mechanisms that can cause low fecundity in plants (viz., cytoplasmic male sterility, pollen – stigma incompatibility, developmental changes, cytological incompatibility, and abortion of embryos) and note the consequence of these for identifying “safe” cultivars.

Cytoplasmic male sterility: The inability of plants to produce functional pollen due to cytoplasmic male sterility is a well-known phenomenon across different groups of angiosperms and is attributed to cytoplasmic factors that are maternally inherited through mitochondria (Schnable and Wise 1988). Specific peptides produced in mitochondria of male-sterile plants are capable of interfering with normal pollen development. These peptides are known to reduce ATP production, enhance the production of reactive oxygen species and cause cytotoxicity (Horn et al. 2014). Interestingly, fertility can be automatically restored (e.g. *Petunia*) in such sterile plants by the action of specific nuclear genes that express proteins which regulate the degradation of mitochondrial proteins responsible for male sterility or by affecting mitochondrial DNA organisation (Gillman et al. 2007, Horn et al. 2014). Therefore, the sterility of pollen may not be a permanent phenomenon and fertility could potentially be restored in male-sterile plants.

Pollen-stigma incompatibility: Fertilisation can occur only when a compatible type of pollen lands on the stigma. Specific proteins are known to mediate the recognition of compatible pollen with the stigmatic papillae (Mattsson et al. 1974; De Nettancourt 1997). For example, in *Brassica* self-incompatibility has been detected due to the presence of specific glycoproteins (Luu et al. 1999). In dioecy (separate male and female plants), reproductive assurance cannot be obtained through the breakdown of self-incompatibility. Interestingly, dioecious species can be as invasive as monoecious species (Daehler 1998). This could be due to leaky dioecy i.e. the ability of a dioecious species to self-fertilise by the presence of flowers of both sexes on a single plant (Venkatasamy et al. 2007). Another mechanism for incompatibility is a physiological incompatibility system that is associated with tristyly. Tristyly is a rare breeding system that ensures optimal seed production and gene flow through cross-pollination since each plant possesses only one of three tristylous morphs (Ornduff 1966). In the tristylous *Pontederia cordata* L. (Pontederiaceae), although self-incompatibility is strongest in the short-styled flowers, it can occasionally break down leading to seed formation. Interestingly, preliminary field observations throughout its invasive range in South Africa have only recorded short-styled morphed flowers and no seed production. A cultivar might appear to be infertile, but will set seed if pollinated by compatible pollen. Multiple introductions of different genotypes increase the chances of restoring fertility in such cases. This suggests that unconditional sterility can only be confirmed conducting outcrossing experiments using a wide diversity of genotypes.

Modifications of floral parts: Differentiation of floral parts is delicately orchestrated by differential gene expression. Mutations in the genes leading to interference with gene expression can lead to the formation of incomplete or defective flowers. However, interestingly, these modifications are sometimes desired traits in the horticultural industry. For example, in some cultivars of petunia, stamens are converted into an additional row of petals or sepals (van der Krol and Chua Nam Hai 1993). Although the intention behind the development of such cultivars might be purely aesthetic, they might lead to reductions in fecundity, thus potentially lowering invasion risk.

Cytogenetic anomalies: Plants can also fail to produce outcrossed seeds for cytological reasons. For example, plants with an odd level of ploidy often fail to produce viable gametes due to abnormal laggard formation during meiosis. However, apomixis can restore fecundity in such cases (Noyes 2007). *Ageratina adenophora* is an example of a highly-invasive triploid Asteraceae that can vigorously reproduce by virtue of its apomictic seeds (Baker 1974; Noyes 2007). Additionally, some instances of successful sexual reproduction in triploid cultivars have been recorded in *Lantana camara* (Spies & du Plessis, 1987). Therefore, the use of triploid cultivars should be advocated with caution.

Abortion of fruits and seeds: is a well-known phenomenon that has been observed in a diverse group of vascular plants (Ganeshaiah and Uma Shaanker 1994; Arathi et al. 1996). Besides cytogenetic anomalies, several other genetic factors might cause abortion of embryos in seed plants. Maternal genotypes in *Pinus sylvestris* determine the seed abortion rate (Kärkkäinen et al. 1999). In *Dedeckera*, accumulation of a lethal genetic load in the populations can lead to developmental abnormalities which, in turn, lead to low viability and low germinability of seeds (Wiens et al. 1989). In the context of invasive ornamental plants, it would be desirable to grow cultivars that have inherent genetic factors that inhibit seed development rather than cultivars in which sterility has been caused by environmental cues.

Exogenous factors: Sub-optimal environmental conditions can reduce the number of seed and fruit set in plants (Lee 1988). Specific chemical triggers are also known to promote selective abortion of seeds in certain plants (Ganeshaiah and Uma Shaanker 1994). Additionally, the absence of favourable biotic interactions such as specialised pollinators in figs and orchids can lead to a seedless condition (Richardson et al. 2000). However, such exogenous factors will only limit invasiveness as long as they are in place and so might require close control if an invasion is to be prevented.

Methods to generate sterile cultivars

Many mechanisms promoting sterility or reduced fecundity discussed above can be induced or enhanced via plant breeding or molecular techniques. A wide array of such techniques to produce cultivars is currently available (see Table 1 for some case-studies). A thorough understanding of these techniques and how they induce sterility or reduce fecundity is important to understand and use questions 2–4 to distinguish between "safe" cultivars and "risky" relatives (Fig. 1).

Traditional breeding: Traditional plant breeding methods are relatively inexpensive, but they require great effort and time to screen for individuals with desired traits. Therefore, recent advances in biotechnology have been explored to produce sterile forms of invasive plants (Vining et al. 2012). Directional natural selection usually prefers the more fecund genotypes over the less fecund genotypes; as a result, the less fecund are often eliminated from the gene pool. For example, sterile triploids in nature are often lost due to natural selection. Traditional breeding methods (i.e., careful observation, artificial selection, and propagation by vegetative means) can, however, still be used to produce sterile or less fecund cultivars.

Induced polyploidy: Induction of polyploidy by the use of antimitotic agents (such as colchicine and oryzalin) has been widely used by plant breeders, as they are relatively inexpensive and technically feasible. Induced polyploidy has often been used in conjunction with hybridisation techniques to produce sterile individuals (Vining et al. 2012, Freyre 2016).

Hybridisation: Hybridisation in plants may be possible between cultivars, species and even genera. Hybridisation between genetic entities with different ploidy levels often leads to sterility due to chromosomal abnormalities leading to interference with normal meiotic cell division. For example, hybridisation between hexaploid and diploid forms can result in the formation of triploid progenies which are generally sterile due to an odd ploidy level. However, in rare cases, reversal of sterility may result from cross-pollination with fertile forms (Spies and du Plessis 1987). Plants with odd chromosome numbers can also be raised from endosperm culture (Vining et al. 2012). Hybridisation experiments can, however, also potentially increase the vigour of the resulting hybrid (Ellstrand and Schierenbeck 2000), thus posing a greater risk if the sterility is accidentally reverted or if fertility is not a requirement for invasiveness. Cybridisation or somatic hybridisation is the process of producing hybrids between two sexually-incompatible individuals by fusing the protoplasm of two cells. This technique allows efficient transfer of cytoplasmic male sterility determined by mitochondrial genes (Guo et al. 2004).

Induced mutation: Mutation breeding using radiation (e.g., from x-rays, ion-beams or gamma-rays) or chemical mutagens [e.g. ethylmethanosulphonate (EMS)] is a popular technique in the toolbox of plant breeders for producing desired traits, including sterile and non-invasive forms (Broertjes and Dejong 1984; Kanaya et al. 2008).

Recombinant DNA technology: Transgenic techniques/recombinant DNA techniques can also potentially be used to transfer the genes of interest, leading to sterility (Vining et al. 2012). Such target genes could be genes responsible for cytoplasmic male sterility such as *cox2* gene (cytochrome c oxidase subunit 2) and T-urf13 gene (Štorchová 2017). However, such techniques should be used with caution, especially while working on invasive species, particularly if there is a risk of hybridisation with related native varieties or species.

Evaluation of sterile cultivars

Different methods have been used to assess the sterility of cultivars or hybrids (some key examples are listed in Table 2). These techniques range from relatively simple and easy to conduct assays (e.g, pollen staining, germination and compatibility tests, and seed viability and germination tests) to more advanced techniques relying on (e.g., molecular markers, cytological examination of chromosomes, long term common garden experiments, and pollination experiments). Here, we discuss some of these.

Pollen viability tests: Pollen staining and germination tests evaluate the quality of pollen produced by the plant. Pollen is stained with cotton blue solution and the number of viable pollen (i.e., that is stained) is counted under a microscope (Czarnecki et al. 2012). Enzymatic induction of fluorescence in viable pollen has also been used to assess the quality of pollen (Heslop-Harrison and Heslop-Harrison 1970). Pollen germination experiments are conducted by allowing the pollen to germinate in a pollen germination media. The emergence of a pollen tube from the pollen grain is then recorded as evidence of pollen viability (Wilson and Hoch 2009).

Cytogenetic tests: Polyploidy levels can be detected by chromosomal staining during cell division or by using more recent techniques, such as flow cytometry (Wilson and Hoch 2009). Individuals with odd ploidy or an abnormal cell division process are likely to be sterile or less fecund.

Sterility genes: Molecular markers linked to genes conferring sterility can be used to screen sterile cultivars. For example, marker-based (RAPD) selection techniques have been applied to facilitate rapid identification of male-sterile cultivars of peach (Jun et al. 2004).

Common garden experiments: Common garden experiments have been used frequently to assess the fecundity of sterile cultivars. Common garden experiments are often coupled with pollination experiments to determine the stability of the sterile cultivars after outcrossing (Spies and du Plessis 1987; Lehrer et al. 2006). Although common garden experiments are crucial for any evaluation procedure, they are time-consuming, and studies confirming long-term sterility are often lacking.

Demographic models: Demographic models are used to estimate the growth rate of populations using data about various life-history stages (Easterling et al. 2000). Data collected from experiments and natural populations can be effectively coupled with demographic models, such as population matrix models and integral projection models to predict population growth rates under different scenarios (Easterling et al. 2000; Geerts 2011; Knight et al. 2011). A population with a negative growth rate might be considered safe for cultivation. However, such models and their parameterisation are often highly context-dependent and caution should be taken when extrapolating results to different habitats or climates.

Conclusions and recommendations

In this paper, we attempted to clarify the issue of distinguishing "safe" cultivars from "risky" relatives by recasting the problem as a set of six questions that align with the risk analysis process (Fig. 1). None of the individual questions is new; however, we hope that this formalisation will be valuable in providing an integrative framework for considering risks of infra- and inter- specific taxa. Although we focussed on ornamental plants, we believe that the set of questions can be extended to other situations (e.g., to breeds of animals), noting there will likely be additional ethical and cultural concerns.

While this set of six questions is, we believe, a useful formulation of the problem, answering the questions remains non-trivial. We highlighted the biological bases of reduced fecundity and sterility, and methods used to achieve and demonstrate this. However, there are many exceptions to each of the mechanisms and situations where particular methods do not work. In many cases, an unequivocal demonstration of sterility, and that any such sterility is stable, requires expensive and long-term field and molecular experiments. Various short-cut proxies of sterility have been proposed. For example, the risk of different *Anigozanthos* spp. cultivars hybridising is a function of the ratio of their genome sizes; therefore, genetic exchange between horticultural and invasive populations can be limited if only taxa with sufficiently different genome sizes are allowed to be planted (Le Roux et al. 2010). However, long-term experiments are often necessary, specifically for woody and perennial species, before any conclusive evidence can be drawn about their invasiveness. Thus, the problem of trying to differentiate "safe" cultivars from "risky" relatives remains.

We hope the six questions outlined here will provide regulators with a basic structure around which a regulatory framework or protocol can be built and provide the horticultural industry with clarity over what needs to be demonstrated if invasions are to be avoided. However, given that the risks of invasion and impact are known from the "risky" relative, we conclude that the precautionary principle should be applied if unwanted consequences are to be avoided. We strongly believe that an *a priori* assumption of risk should be inherited from the closely-related invasive taxa from which the proposed "safe" alternatives are derived. This implies that the onus (and cost) of proof should be held by those who wish to benefit from infra- or inter-specific genetic entities.

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Supplementary material 1

Table S1. Plant taxa listed under South African regulations for which certain sub-specific entities are listed differently from other entities

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Data type: species data

Explanation note: Plant taxa listed under the South African National Environmental Management: Biodiversity Act, Alien and Invasive Species Regulations as amended in 2016, for which certain sub-specific entities are listed differently from other entities. There is no published account as to why these taxa were selected.

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Advancing research on alien species and biological invasions

The Convention on Biological Diversity (CBD)'s Post-2020 target on invasive alien species – what should it include and how should it be monitored?*

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Abstract

The year 2020 and the next few years are critical for the development of the global biodiversity policy agenda until the mid-21st century, with countries agreeing to a Post-2020 Global Biodiversity Framework under the Convention on Biological Diversity (CBD). Reducing the substantial and still rising impacts of invasive alien species (IAS) on biodiversity will be essential if we are to meet the 2050 Vision where biodiversity is valued, conserved, and restored. A tentative target has been developed by the IUCN Invasive Species Specialist Group (ISSG), and formally submitted to the CBD for consideration in the discussion on the Post-2020 targets. Here, we present properties of this proposal that we regard as essential for an effective Post-2020 Framework. The target should explicitly consider the three main components of biological invasions, i.e. (i) pathways, (ii) species, and (iii) sites; the target should also be (iv) quantitative, (v) supple-

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* The opinions given herein belong solely to the authors and do not represent the views or policies of IUCN nor do they replace IUCN's evolving position on the Post-2020 Global Biodiversity Framework.

mented by a set of indicators that can be applied to track progress, and (vi) evaluated at medium- (2030) and long-term (2050) time horizons. We also present a proposed set of indicators to track progress. These properties and indicators are based on the increasing scientific understanding of biological invasions and effectiveness of responses. Achieving an ambitious action-oriented target so that the 2050 Vision can be achieved will require substantial effort and resources, and the cooperation of a wide range of stakeholders.

Keywords

biological invasions, conservation policy, Convention on Biological Diversity (CBD), policy targets, sustainable development

Introduction

Invasive alien species (IAS, see Box 1 for definitions used in this manuscript) are one of the main drivers of global change (Lockwood et al. 2007; Simberloff et al. 2013). They are a major cause of biodiversity loss (Maxwell et al. 2016; Díaz et al. 2019; IPBES 2019), especially on islands (e.g. Bellard et al. 2016; Spatz et al. 2017; Butchart et al. 2018), and cause substantial negative impacts on human health (Mazza et al. 2014, Mazza and Tricarico 2018), livelihoods (Vilà et al. 2010; Pratt et al. 2017), and economies (Bradshaw et al. 2016).

The number of new introductions of species to areas outside their natural range is growing at an unprecedented pace, among all taxonomic groups, and on all continents, with no sign of saturation (Seebens et al. 2017). A high proportion of recent introductions are species that have never been recorded as alien before, meaning that the number of IAS is forecasted to increase in the future among all taxonomic groups and regions (Seebens et al. 2018). In addition, climate change will cause many regions to become more suitable for a greater number of IAS (Bellard et al. 2013), and an increase in extreme weather events will likely facilitate their spread (Diez et al. 2012). Given that there is a close correlation between numbers of established alien species and those causing impacts (Essl et al. 2019), the impacts caused by IAS are expected to continue to increase.

In 2010, Parties to the Convention on Biological Diversity of the United Nation (CBD) adopted the Strategic Plan for Biodiversity 2011–2020, with 20 targets ("Aichi Targets"), including one on IAS: Aichi Target 9 aims that "*By 2020, invasive alien species and pathways are identified and prioritized, priority species are controlled or eradicated and measures are in place to manage pathways to prevent their introduction and establishment*". The evidence so far shows that while there has been some progress, for example on eradications and pathway management (CBD 2018), overall efforts to meet this target have been largely inadequate (Tittensor et al. 2014). Parties to the CBD are now negotiating a Post-2020 global biodiversity framework and targets, which will aim to bring about a fundamental change in societies' relationships with nature.

Here, we discuss properties that we regard as essential for a new target on IAS for the Post-2020 Framework. A proposed target based on these properties was developed by the IUCN Invasive Species Specialist Group (ISSG), and submitted in 2019 to the CBD as a contribution to the discussion on the Post-2020 targets (Box 2).

Box 1. Definitions of terms used.

The definitions used in this manuscript and the wording of the targets are, wherever possible, aligned with the terminology used by the CBD, noting that some of the terms are used slightly differently in different contexts. For example, biological invasions are a population level phenomenon, though such invasions are often referred to as "invasive alien species", rather than invasive alien populations; a commonly used definition of "invasive alien species" does not require impact (Blackburn et al. 2011); and "introduction" is often defined in terms of the human-mediated process of moving propagules to a site where the species to which they belong is not native, without specifying whether there is evidence that such a species has escaped or been released from captivity or cultivation. There is uncertainty in each of the definitions, and it is important that this is specified (e.g. for whether something is alien or native see Essl et al. 2018).

– ***Control*** refers to management measures that are applied to established IAS over the long term that successfully reduce the impacts from the IAS to desired (and measurable) levels.

– ***Effectively managed*** pathways of introduction refer to measures that are put in place that successfully prevent the introduction of IAS that cause significant impacts. For example, treatment of ballast water, biosecurity, and rapid detection and eradication capacity.

– ***Effectively preventing impacts in vulnerable areas*** refers to the establishment of effective management programs that control, or where feasible eradicate IAS, and prevent their introduction.

– ***EICAT and SEICAT*** are the Environmental Impact Classification of Alien Taxa (EICAT) and the Socio-economic Impact Classification of Alien Taxa (SEICAT) schemes developed by the IUCN ISSG (as requested by Parties to the CBD). The schemes use current known records of impact to develop a standardised impact score for each IAS.

– ***Eradicate*** refers to management measures that are applied to established IAS that remove all individuals from an area, where there is no chance of re-introduction.

– ***Harmful IAS*** refers to IAS that cause, or have the potential to cause, substantial environmental and/or socio-economic impacts within the boundaries of a country. Substantial impacts can be defined as those that cause moderate, major or massive impacts under the EICAT or SEICAT schemes.

– ***Invasive Alien Species (IAS)*** refer to species introduced to areas outside their native range that have become successfully established and cause substantial impacts on the new environment (CBD 2002).

– ***Introduction*** refers to the introduction of alien species to sites outside of captivity or cultivation and does not include species that may already be alien and introduced within a country but are only found in captivity or in gardens etc.

– ***Regulated*** refers to the adoption and enforcement of national or regional legislation that results in the prevention and effective management of IAS, in particular through: the development of lists of IAS whose import, transport, possession, and trade are restricted; the establishment of a biosecurity framework; and the introduction of an obligation to control and/or eradicate priority IAS.

– ***SEICAT*** (see ***EICAT***)

– ***Significant pathways of introduction*** are those pathways that facilitate the introduction of known and potentially harmful IAS within national or subnational boundaries.

– ***Vulnerable areas*** are geographically defined areas that are important for the persistence of biodiversity and sensitive and susceptible to impacts from IAS. For example, islands, protected areas, and Key Biodiversity Areas.

Box 2. ISSG initial proposal for an invasive alien species target in the Post-2020 biodiversity framework.

The IAS target initially proposed by the IUCN Invasive Species Specialist Group (ISSG) in 2019 was (Figure 2):

Halting the loss of biodiversity caused by invasive alien species by 2030, by preventing their impacts in [100% of] the most vulnerable areas, regulating [50% of] the most harmful invasive alien species, and effectively managing [50% of] the most significant pathways of introduction, such that their impacts are reversed through restoration and recovery by 2050.

This proposal was incorporated, with some changes, in the draft discussed by the CBD's Open Ended Working Group on the Post-2020 Global Biodiversity Framework (WG2020) (https://www.cbd.int/doc/c/efb0/1f84/a892b98d-2982a829962b6371/wg2020-02-03-en.pdf). The WG2020 met in February 2020 in Rome and several proposals for improvement of the target have been proposed (https://www.cbd.int/doc/c/9a1b/c778/8e3ea4d851b7770b59d5a524/wg2020-02-l-02-en.pdf). IUCN views and suggestions for amendments to the 'zero draft' IAS target have been transmitted to the CBD, including with the option to replace the numerical thresholds with "*to the extent necessary for achieving the Goals*", in order to set the level of ambition for the target at the extent necessary for delivering the Goals, and to highlight "priority" invasive alien species and reduction of their "harmful" impacts. The discussion on the post-2020 targets is still ongoing, and the ISSG will continue to engage in the process using the principles set out in this paper. However, the political discussion so far conducted confirms the general agreement that the Post-2020 Framework shall include a target on IAS, which should be consistent with the key principles summarised in this article.

We also provide further justification for the continuing process of developing the IAS target, based on scientific evidence and extensive policy experience (Figure 1). The properties we regard as essential for such a target are that it:

(i–iii) explicitly considers the three main components of the phenomenon of biological invasions, i.e. (i) pathways, (ii) species, and (iii) sites (McGeoch et al. 2016);
(iv) is quantitative, i.e. numerical goals and timelines are provided;
(v) is supplemented by a set of indicators that can be applied to track progress; and that it
(vi) can be evaluated at medium- (2030) and long-term (2050) time horizons.

Policy background

The recent global assessment on biodiversity and ecosystem services by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES)

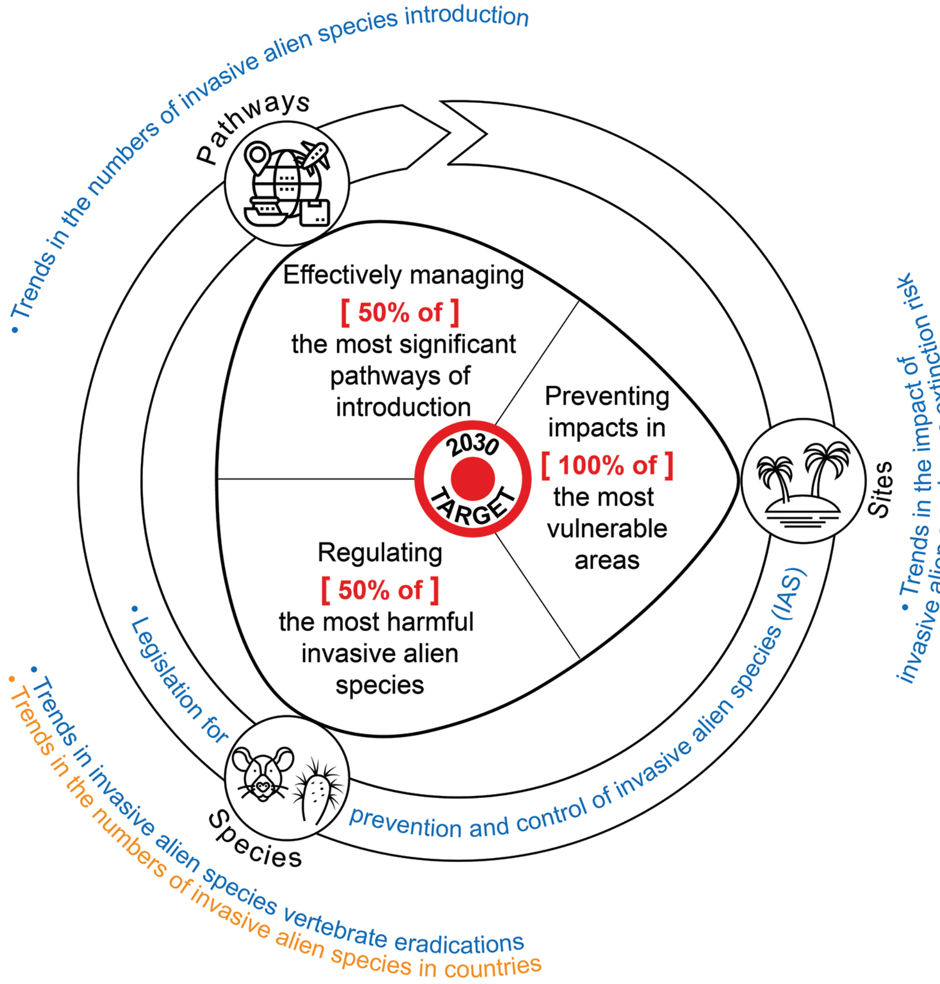

Figure 1. Proposed key components for an IAS target as part of the Post-2020 CBD framework. The components address the three inter-related components of pathways, species, and sites. Tentative quantitative targets are provided in brackets for 2030 [based on the proposal of the IUCN Invasive Species Specialist Group (ISSG), see Box 2], as a necessary step to achieve the management, regulation and protection of 100% of the most harmful IAS, the most significant pathways and the most vulnerable sites, by 2050 (Table 1). Bullet points indicate indicators for monitoring progress towards these targets. The text in blue indicates indicators used for the 2020 targets, and the text in orange indicates additional new indicators for the Post-2020 targets. Two icons made by Eucalyp from www.flaticon.com.

has documented that conservation efforts are inadequate to stop the loss of biodiversity and that IAS are one of the five major drivers of the current biodiversity crisis (Díaz et al. 2019). A 'zero draft' of the Post-2020 framework was published in early 2020, and carries forward the 2050 Vision "Living in Harmony with Nature" from the previous 2010–2020 strategy, which aims to reduce the rate of biodiversity loss, while securing food production and climate change mitigation (Leclere et al. 2018). The 'zero draft'

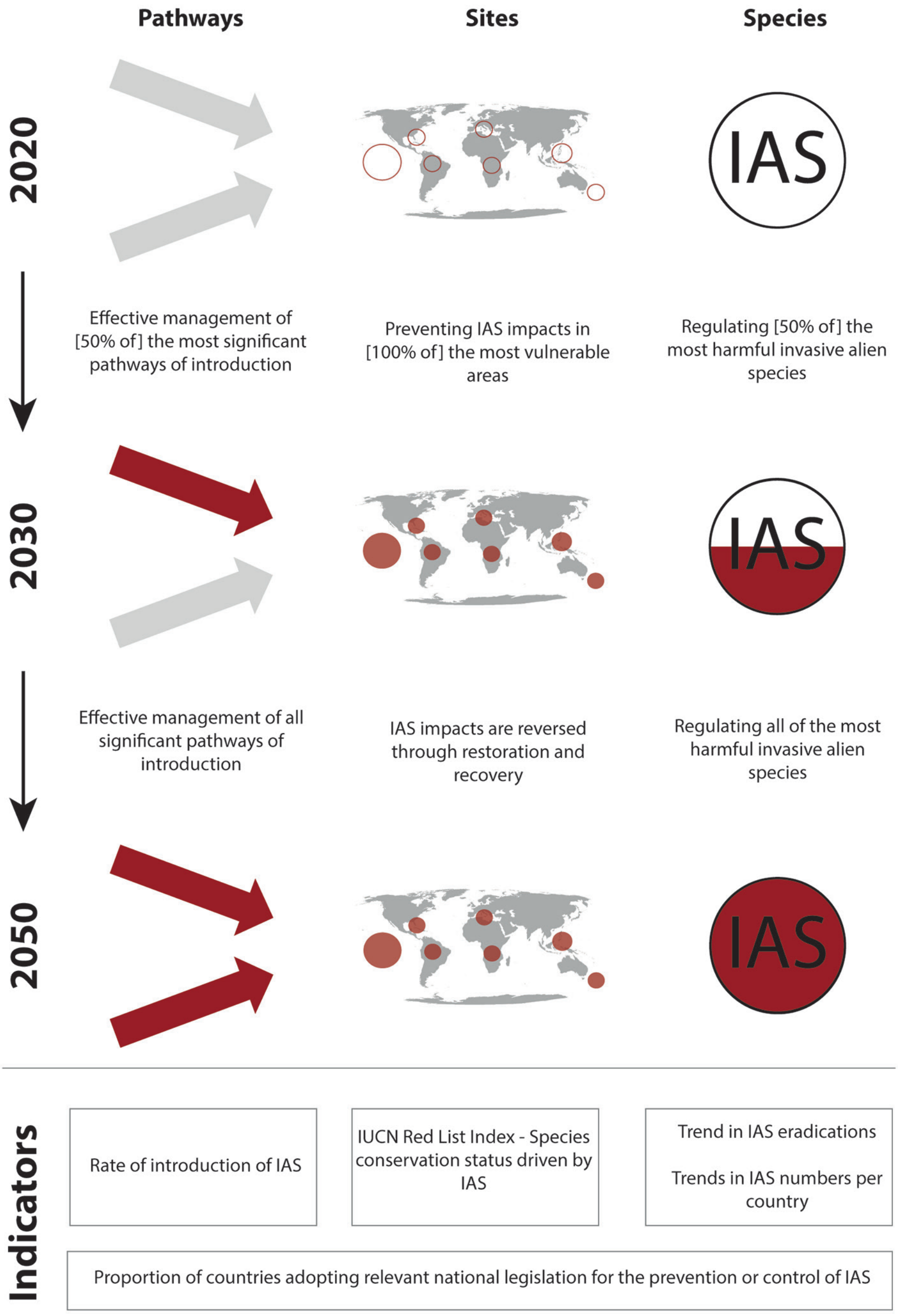

Figure 2. Schematic representation of the IUCN Invasive Species Specialist Group (ISSG) initial proposal of a post-2020 IAS target and the associated timeline. The target focusses on three key components – pathways, sites, and species (left to right) – and provides mid-term (2030) and long-term (2050) quantitative targets (cf. Table 1). For pathways, red arrows represent IAS pathways that are managed (50% in 2030 and 100% in 2050). For species the red area in the circle indicates the proportion of the most harmful IAS that are managed (50% in 2030 and 100% in 2050). For sites, filled red circles indicate priority sites that are managed (100% in 2030 and 2050). The proposed indicators to monitor progress are indicated at the bottom of the figure.

also sets out five goals for 2050, each with associated action-oriented targets for 2030 (CBD 2020). Target 3 is on IAS, and calls to '*Control all pathways for the introduction of invasive alien species, achieving by 2030 a [50%] reduction in the rate of new introductions, and eradicate or control invasive alien species to eliminate or reduce their impacts by 2030 in at least [50%] of priority sites*' (CBD 2020). The exact formulation of this Target is likely to change due to ongoing discussions, and new drafts will be produced before being adopted at the 15th Conference of Parties to CBD.

In addition to Aichi Target 9 of the 2010–2020 Strategy, reducing the impacts caused by IAS has been recognised as a priority field of action by other global environmental policies. The United Nations Sustainable Development Goals (SDGs) contain a target on IAS which aims to "*prevent the introduction and significantly reduce the impact of IAS in terrestrial and water ecosystems and control or eradicate the priority species*" by 2030 (SDG 15.8). Progress is measured by the proportion of countries enacting relevant legislation and adequately resourcing IAS management and control (United Nations 2015, Egoh et al. 2020). Calls to action on IAS have been issued by the Intergovernmental Panel on Climate Change (IPCC) in its 5th Assessment Report (IPCC 2014). Following the first global assessment on biodiversity and ecosystem services (IPBES 2019), IPBES started a thematic assessment of IAS and their control in 2019, in response to the increasing recognition of the relevance of IAS to global biodiversity, ecosystem services and human livelihoods (https://ipbes.net/sites/default/files/ipbes-6-inf-10_en.pdf; final report due May 2023). The findings will be a highly relevant synthesis for future biodiversity policies of the state of knowledge of biological invasions and their impacts.

Essential properties of an IAS target

(i) It should consider the most significant pathways of introduction and their management

The paramount role of international trade and introduction pathways in shaping biological invasions and the impacts they cause is well understood (Essl et al. 2015; Seebens et al. 2015; Sardain et al. 2019). The transport and introduction of IAS can be intentional, e.g. for the pet trade or for ornamental horticulture, or unintentional, e.g. as stowaways on ships, planes, and vehicles or in the commodities carried by them (Hulme et al. 2008). The effective management of these pathways of introduction is critical to reduce future introductions. Intentional movements of species can be managed by regulating trade, import, possession, and transport; whereas unintentional (and to a large extent illegal intentional) movements first require the identification of their most important pathways of introduction. Prevention by managing pathways of unintentional introduction is particularly critical for marine and freshwater species and invertebrates, both because most such IAS arrive via unintentional transport (such as in ballast waters, as biofouling, and as soil contaminants), and because they are very difficult to control or eradicate once introduced. Managing key pathways of introduction for such IAS is feasible. For example, the International Convention for the

Control and Management of Ships' Ballast Water and Sediments (IMO 2014) which entered into force on 8 September 2017 includes targets (e.g. full global implementation by 2024) whose fulfilment would make significant progress towards stopping introductions via shipping (e.g. Bailey et al. 2011). Progress on biofouling, such as the GloFouling Project launched in 2018 (http://www.imo.org/en/mediacentre/pressbriefings/pages/20-biofouling.aspx), could permit additional significant advances in the prevention of marine IAS introductions.

Similarly, several of the International Standards for Phytosanitary Measures (ISPM) developed by the IPPC (International Plant Protection Convention) specify measures to prevent the spread of pests and pathogens, including ISPM 03 (guidelines for the export, shipment, import and release of biological control agents and other beneficial organisms), 11 (pest risk analysis for quarantine pests), 15 (regulation of wood packaging material in international trade), 38 (international movement of seeds (as a commodity class)), 39 (quarantine pests associated with the international movement of wood, in particular those that infest trees), 40 (growing media in association with plants for planting), and 41 (used vehicles, machinery and equipment utilised in agriculture, forestry, horticulture, earth moving, surface mining, waste management and by the military) (FAO 2020). However, efforts on a similar scale are still largely lacking for most other pathways such as the illegal pet trade or eCommerce.

Pathway management and relevant targets and reporting are increasingly based on the pathway classification scheme adopted by the CBD (see Harrower et al. 2018 for guidance on its application). This scheme has, however, been criticised (e.g. Faulkner et al. 2020a), and it might be more appropriate to have tailored systems in place for particular contexts. For example, the traditional medicine trade has recently been highlighted as a potentially important introduction pathway for South Africa (Burness 2019). Such a pathway requires specific management interventions developed with the affected stakeholders, however it corresponds to three to four separate pathways in the scheme adopted by the CBD.

There is also a need to apply and adapt existing methods to monitor and control pathways after the initial introduction (secondary spread) (e.g. USDA APHIS, https://www.aphis.usda.gov/aphis/home/) in countries that do not yet have such systems in place (Zengeya and Wilson 2020), and between countries when intra-continental spread is important (Faulkner et al. 2020b). This secondary spread of IAS causes significant challenges as, in contrast to inter-continental movements of IAS which often rely on a few specific vectors, movements within a land mass can happen in many different ways, including by natural dispersal. Rapid response is therefore a major challenge for biosecurity.

(ii) It should take into account which species are the most harmful IAS

If the impact of IAS is to be reduced efficiently, it is essential to prioritise both the management of IAS that are currently most harmful, and those that are predicted to become the most harmful in the future. Recently, substantial progress has been made in understanding the global patterns and underlying causes of biological invasions, and in developing globally applicable tools for assessing their environmental and socio-economic impacts (Blackburn et al. 2014, Bacher et al. 2018, IUCN 2020). This was aided by recent compilations and analyses of global databases on the spatial distribution of alien species of various taxonomic groups (e.g. van Kleunen et al. 2015; Dyer et al. 2016; Capinha et al. 2017; Dawson et al. 2017; Pagad et al. 2018) and by analyses of the temporal trajectories of alien species accumulation (Seebens et al. 2017, 2018). However, predicting the impacts of IAS remains challenging (e.g. due to time lags, boom and bust-phenomena, and context specificity), and requires more research on understanding the processes leading to such impacts (e.g. Rouget et al. 2016; Strayer et al. 2017).

(iii) It should consider which sites (areas) are the most vulnerable to IAS

There is a need to identify and prioritise sites for management that are pivotal for biodiversity conservation (McGeoch et al. 2016). We believe that focusing global policy targets on regions that are particularly vulnerable to biological invasions is appropriate, as the largest biodiversity benefits can be accrued there. Islands and freshwater systems are particularly important as they often contain unique and highly threatened biota. Further, they are highly sensitive to invasions and IAS are the main cause of extinctions on islands (Bellard et al. 2013). Distant islands with high proportions of endemic and threatened species are the most invaded ones (Moser et al. 2018). IAS management on islands brings substantial biodiversity gains and ecosystem regeneration (Brook et al. 2007; Jones et al. 2016; Graham et al. 2018). For instance, eradicating invasive mammals from 100–200 high priority islands around the world would improve the survival prospects of many threatened species (e.g. Brooke et al. 2007; Dawson et al. 2015; Holmes et al. 2019). Recently, New Zealand has committed to eradicate by 2050 five highly invasive mammal species (three rat species, stoats, and possums) that are estimated to consume up to 26.6 million eggs and juveniles of native birds every year (Russel et al. 2015). Freshwater systems are similar in that they were historically isolated and are highly susceptible to invasions, such that IAS are a major threat to freshwater biodiversity (Dudgeon et al. 2006; Gallardo et al. 2015; Reid et al. 2019). However, the eradication of established freshwater IAS is often unfeasible, making prevention, pathway management and long-term population management critical.

Well-managed networks of protected areas are crucial for biodiversity conservation (Watson et al. 2014, Visconti et al. 2019) but biological invasions have substantial impacts in protected areas (Gallardo et al. 2017), which appear to be accelerating (Foxcroft et al. 2017). Consequently, IAS are a leading driver of biodiversity loss in terrestrial and aquatic protected areas worldwide (e.g. Bax et al. 2003; Kannan et al. 2013; Spear et al. 2013; Kearney et al. 2018). It is therefore essential to integrate IAS management into protected area management (Bax et al. 2003) such as it has been successfully done in the Kruger National Park (Foxcroft et al. 2008); however, dedicated resources are currently often insufficient (Braun et al. 2016).

(iv) It should contain quantitative policy targets

Several global environmental policy targets lack quantitative goals. Aichi Target 9 (along with the majority of Aichi Targets) does not include any quantitative scale of the desired reduction of impacts by IAS. The absence of quantitative targets can be detrimental for policy implementation and monitoring. Clear quantitative targets enable the development of policy options and actions that can be taken to reach or stay below the assigned thresholds (van Vuuren et al. 2012; IPBES 2016). In addition, quantitative targets can ease the communication of conservation goals to decision-makers and the general public. Thus, it has been increasingly recognised that quantitative policy targets are often preferable over qualitative ones. As an example in climate policy, a consensus was reached to keep global warming within specific boundaries of maximum mean annual temperature increase (e.g. 1.5 °C above pre-industrial times), which has been enshrined in the Paris Accord (UNFCC 2015). Quantitative targets are therefore proposed within the 'zero draft' of the Post-2020 Framework, expressed as percentages of pathways, species, sites or other quantities to manage, including within the five overarching goals (CBD 2020). The significant progress in invasion science during the last decade now permits establishing evidence-based quantitative targets to be developed for the Post-2020 framework, that are scientifically sound, politically attainable, and for which progress can be assessed by monitoring existing or new IAS indicators (Burgman et al. 2014; Pergl et al. 2019; Latombe et al. 2017; Wilson et al. 2018). Furthermore, it will be important to recognise that the quantitative targets are global. Depending on the resources available, the risks faced, and the status of current invasions, the target that is achievable will likely vary significantly between countries and regions (cf. Box 3).

(v) It should define indicators to track progress

Standardised and accepted indicators on pathways, species, and sites are essential for monitoring the effectiveness of management with respect to the proposed target and for communicating progress to stakeholders and decision-makers. Indicators must assess changes of the status of interest over time. They should be easy to calculate, transparent, reproducible, robust, and meaningful, and they should not be restricted to a certain spatial scale. Indicators have been developed and used for specific functions, e.g. to track eradication campaigns (Holmes et al. 2019), measure the effectiveness of biological control programs (e.g. Klein 2011; Schwarzländer et al. 2018), and assess the status of biological invasions in World Heritage Sites (Shackleton et al. 2020). However, accepted indicators are needed to track progress towards the proposed target itself. Initiatives such as the sTWIST project (https://www.idiv.de/de/sdiv/arbeitsgruppen/pool-of-working-groups/stwist.html) are currently working on this issue.

Box 3. Reflections on the zero draft of the IAS target.

While the authors recognise that the IAS target in the 'zero draft' of the Post-2020 Framework is going to change based on ongoing negotiations, it is encouraging to see that the three main components of biological invasions – pathways, species, and sites – are reflected. However, we would stress the need to focus eradication and control upon **priority** IAS (based on their impacts), and that it is their **harmful** impacts that need to be reduced, especially in priority sites (e.g. islands, freshwaters) but also across continental habitats.

Importantly, the current target includes a clause that "impacts are reversed through restoration and recovery". It is not clear, as yet, how this will be measured or monitored.

Many concerns were raised during the construction of the draft target. Here, we summarise some of the ideas based on comments raised by the ISSG members list server, and e-mail discussion with the IUCN ISSG. They are not comprehensive, but indicative, and have been rephrased as questions for consistency.

- Basic information on impact and pathways is not available for many countries / regions, perhaps gathering or collating this should be specified?
- Is there a need for an explicit call for data access and data sharing, particular between countries in a given region?
- Much of the problem is down to information and communication, so why are these not explicitly required in the target? Biosecurity often comes down to people's behaviours.
- How do the targets incentivise proactive responses (contingency planning, early warning systems, and capacity to deal timeously with incursions)? Do priority species include both those that are currently widespread and those that will be threatening in future?
- Are researchers/scientists proposing interventions that can never be implemented? Maybe there is a need to be realistic about the target given that many of the necessary conditions, e.g. for effective biosecurity, are much broader than just IAS?
- Can managers be consulted as to the feasibility of these targets (financial, human capacity, infrastructure), and in terms of determining what factors are limiting their effectiveness? Currently, isn't this rather a top-down approach?
- The targets might be appropriate for some countries and contexts, but are they right for others? Can targets better reflect the differences required to achieve them?
- For regulations to be effective, enabling conditions need to be in place. How can these be incentivised?
- Can the target be linked to the UN SDG goals? And the concept of "One Health"?
- Should trends in the spread of infectious diseases (for humans, plants and animal health) be included?
- Climate change will not just increase IAS incursions but also the trajectories of existing IAS (e.g. by changing the location of the climatically suitable ranges). How can shifts regarding which IAS are a priority be taken into account?
- How will we measure and monitor the extent to which impacts are reversed through restoration and recovery?
- What is the best way to focus eradication and control upon priority IAS (based on their impacts), and reducing their harmful impacts?
- How will we get the balance right between focussing on both priority sites (e.g. islands, freshwaters) and invasions of continental habitats?

Table 1. The components of the initially proposed IAS post-2020 target, and the proposed goals for the mid-(2030) and long-(2050) term perspective.

Element	Proposed activity	2030	2050
Pathway management	Managing the most significant pathways of introduction	50 %	100 %
Species prioritization	Regulating the most harmful IAS	50 %	100 %
Spatial prioritization	Preventing impacts in the most vulnerable sites	100 %	100 %
Restoration and recovery	Restoring degraded or heavily invaded ecosystems	To be decided	To be decided

(vi) It should be applicable to medium- (2030) and long-term (2050) time horizons

Quantitative targets are needed for 2030, although they might need refinement over time based on new data, and alignment with other targets. However, they should be seen as a ‘stepping stone’ for 2040 and 2050 where more visionary targets are included. Examples might be that by 2040 ***all*** harmful invasive alien species are regulated and ***all*** significant pathways of introduction effectively managed, and that IAS impacts are being reversed through restoration and recovery by 2050 (Table 1).

Potential indicators for measuring progress towards the proposed IAS target

Trends in the number of IAS introduction events

For monitoring the rate of introductions of alien species, the time series of IAS numbers now available for various taxonomic groups (Seebens et al. 2017, 2018) and regions (i.e. countries, islands) greatly assist the development of global indicators of alien species accumulation (McGeoch and Jetz 2019), although further research is needed to reduce existing sampling biases in space and time. Indicators should also cover aspects of invasion dynamics such as spatial extent, invasiveness, and impacts as well. Currently, new global indicators of biological invasions are under development (McGeoch et al. in prep.), which aim to obtain unbiased estimates of global and national introduced and invasive alien species richness, spatial extent, and degree of impact. These indicators ideally need datasets that follow the FAIR (Findable, Accessible, Interoperable, and Reusable) data principle (Wilkinson et al. 2016) to ensure comparability across regions and long-term availability. A restricted IAS dataset for just 21 countries was used as an indicator for Aichi Target 9 (GBO 2014).

Trends in the impact of IAS on extinction risk

The IUCN Red List Index on impacts of IAS is used as an indicator for Aichi Target 9. It shows trends in the conservation status (IUCN Red List, https://www.iucnredlist.org) of all birds worldwide driven only by the negative impacts of IAS or the positive impacts of their control (McGeoch et al. 2010, Genovesi et al. 2013). For a 2030 target, this indicator should be broadened to include additional taxonomic groups (e.g. mammals, amphibians) that have now undergone multiple IUCN Red List assessments (Regan et al. 2015).

Trends in invasive alien vertebrate eradications

The Database of Islands and Invasive Species Eradication (DIISE, https://www.islandconservation.org/diise-database) compiles all known historical and current invasive bird and mammal eradications on islands, and should be used to track progress on IAS eradications.

Legislation, policy and regulations for prevention and control of invasive alien species (IAS)

This indicator should encompass the "Trends in policy responses, legislation and management plans to control and prevent spread of invasive alien species" and the "Proportion of countries adopting relevant national legislation and adequately resourcing the prevention or control of invasive alien species" (www.cbd.int/invasive). More specifically, it should measure a) national adoption of IAS-relevant international policy, b) percentage of countries with national legislation and policy relevant to IAS, c) national strategies for preventing and controlling IAS, d) national commitment (mandate and legal authority, cf. Fox et al. 2015) to key IAS related themes, and e) resourcing by national governments for the prevention and control of IAS as identified by the Sustainable Development Goals indicator 15.8.1 (https://sdg.data.gov/15-8-1).

Proposed new indicator: Trends in the numbers and impacts of invasive alien species in countries

The IUCN SSC Invasive Species Specialist Group working with partners under a mandate provided by Parties to the CBD, has developed the Global Register of Introduced and Invasive Species (GRIIS, http://www.griis.org), which will form a global baseline for trends in the numbers of IAS in countries, and their impacts where demonstrated impact has been recorded. The IUCN has endorsed the Environmental Impact Classification of Alien Taxa (EICAT) scheme (IUCN 2016), and developed a protocol for its implementation (IUCN 2020), see also Kumschick et al. (2020) for a discussion on its usage. EICAT provides an impact level category for each species based on its maximum impact globally and promises to complement information from the Red List (Van der Colff et al. 2020). Development of regional applications of the EICAT scheme (or of comparable risk schemes), regularly updated, would provide a tool to assess trends in impact of IAS. A framework has also been developed to address socio-economic impacts, the Socio-Economic Impact Classification of Alien Taxa (SEICAT) (Bacher et al. 2018), which is still to be extensively tested and proposed to the IUCN as a tool, but will hopefully be used in concert with EICAT to broaden the consideration of the negative impacts of an IAS.

Relationship of the proposed IAS target with other policies

Relationship with other proposed Post-2020 Framework targets

Efforts to prevent and mitigate the impacts caused by IAS will also affect other goals and targets of the Post-2020 Framework; these goals include stopping the loss in the area and integrity of freshwater, marine, and terrestrial ecosystems, and reducing the percentage of species threatened with extinction. Considering the major effects of IAS on ecosystem degradation and species extinction, the IAS target should be ambitious enough to lead to the fundamental changes required to support the attainment of these goals and the 2050 Vision. The proposed measures should do this, and should also contribute to other targets, such as those aimed at retaining and restoring ecosystems of particular importance for biodiversity.

Relationship with existing regional and national policies

The new IAS target will only be achieved if subnational, national, and international policies are adequately implemented. Among such existing policies, the European Union (EU) Regulation 1143/2014 on Invasive Alien Species (EU 2014) fulfils Action 16 of Target 5 of the EU 2020 Biodiversity Strategy, as well as Aichi Target 9. It is accompanied by a set of implementation support documents targeting three aspects to promote its implementation: 1) prevention (introduction pathways and action plans), 2) management (measures and costs), and 3) early detection and rapid eradication (surveillance and identification). Relevant policies can also target specific, vulnerable regions, such as protected areas or Key Biodiversity Areas, as do the Council of Europe's guidelines on protected areas and IAS (Monaco and Genovesi 2013).

Biodiversity policies will only be efficient if supported by adequate resources. For example, the LIFE programme in Europe funds climate and environment actions, including many projects aimed at controlling IAS (https://ec.europa.eu/environment/life/project/Projects/index.cfm?fuseaction=home.getProjects&themeID=96&projectList). Other funding initiatives, such as the EU's Horizon 2020, will be essential for the acquisition and sharing of data.

Conclusions and outlook

During the writing of this article, negotiations on the nature and content of the Post-2020 Framework have continued with the goal that parties to the CBD will agree on its key components at their upcoming conference in Kunming, China, but the outcome of the negotiations is unpredictable. While the socio-economic and political context is volatile, the key components that should be in the centre of global IAS policy will not change. Substantial progress in invasion science during the last decade allows, for the first time, the formulation of quantitative IAS targets that are informed by solid data, and which can be tracked by appropriate indicators. Measureable quantitative targets are also pivotal for developing targeted IAS management and policies.

The proposed properties that are essential for an IAS target are based on these advances, and they must be complemented by further instruments such as risk analysis, prioritization tools, decision support tools, cost-effective management tools, and efficient monitoring and evaluation systems. Further, community engagement and effective policy instruments are essential for successful implementation. We hope that these instruments, along with the list of proposed indicators, will support the negotiations towards finalizing an IAS target for the Post-2020 CBD framework. Whatever the final Target text is, achieving the fundamental changes necessary to prevent and mitigate impacts from IAS successfully over the coming decades will require substantial efforts and resources, and the cooperation of a wide range of stakeholders. The prevention of IAS impacts by precautionary measures and early response will avoid post-invasion costs and damages that are in many cases much – often by an order of magnitude – higher (Leung et al. 2002; Diagne et al. 2020).

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Application of the Socio-Economic Impact Classification for Alien Taxa (SEICAT) to a global assessment of alien bird impacts

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Abstract

We use a recently proposed framework, the Socio-Economic Impact Classification for Alien Taxa (SEICAT) to undertake the first global assessment of the impacts of alien birds on human well-being. A review of the published literature and online resources was undertaken to collate information on the reported socio-economic impacts of 415 bird species with self-sustaining alien populations worldwide. These data were then categorised following the SEICAT guidelines. Impact data were found for 57 (14%) of the 415 alien bird species in this study. All but two of these species were found to have minor impacts on human well-being. The most significant threat to human well-being posed by alien birds may be associated with their impacts on aviation safety. About two-thirds of the impact data found described agricultural impacts. No data were found describing disease transmission impacts on humans. We lack data for developing regions of the world: this is of concern as alien species can threaten livelihoods in developing countries, particularly by affecting agricultural production and hence food security. Most assessments were allocated a 'Low' confidence score. This may be because SEICAT is a new framework, requiring data on the way in which alien species affect human well-being, as measured by changes to human activities: even where we do have data describing an alien bird impact, information on how profoundly this impact affects people's activities is currently rarely available.

Keywords
Aviation safety, biological invasions, common starling, Canada goose, Eurasian blackbird, frugivory, grape damage, human well-being

Introduction

The socio-economic impacts of alien species can be severe, affecting human health and livelihoods across the globe. For example, in the Mediterranean, the silver-cheeked toad-fish (*Lagocephalus sceleratus*) impacts commercial and recreational fishing activities by predating upon fish caught in nets and damaging fishing gear. It is also highly toxic and has little economic value, but represents 4% of the total weight of artisanal catches, resulting in reduced incomes (Coro et al. 2018). In 2005, the tiger mosquito (*Aedes albopictus*) caused an outbreak of chikungunya fever on Reunion Island, which resulted in approximately 255,000 infections and more than 200 deaths (Josseran et al. 2006). The cumulative (present-value) costs of the golden apple snail (*Pomacea canaliculata*) invasion to rice agriculture in the Philippines in 1990 were between US$ 425 million – 1.2 billion/year (€ 380 million – 1.1 billion/year) (Naylor 1996).

While there are many examples of alien species having socio-economic impacts, systematic assessments of these impacts for a given alien higher taxon are rare. Here, we address this with an analysis of the socio-economic impacts of an entire alien taxon, birds, the alien populations of which are relatively well documented (Dyer et al. 2017a). Alien birds can impose a substantial financial burden: in just six countries (the UK, USA, Australia, South Africa, India and Brazil), they have been estimated to cause combined economic losses of US$ 2.4 billion/year (€ 2.2 billion/year) (Pimentel et al. 2001). In Australia, the Eurasian blackbird (*Turdus merula*) and common starling (*Sturnus vulgaris*) cause significant damage to vineyards and orchards (Tracey and Saunders 2003): should the common starling establish in Western Australia, the estimated cost to the region resulting from agricultural damage would be AU$ 43.7 million/year (€ 26.2 million/year) (Campbell et al. 2016). In the UK, Canada geese (*Branta canadensis*) are a significant threat to aviation safety: in 1998, a Boeing 767 struck a flock of Canada geese on landing at Heathrow Airport in London, causing extensive damage to the plane (Civil Aviation Authority, no date). In Florida, monk parakeets (*Myiopsitta monachus*) build nests on electrical utility facilities, including distribution poles, transmission line towers and electrical substations. The nests cause regular power outages, pose a health and safety concern and result in lost revenue for utility companies (Avery et al. 2002). On Haiti, the village weaver (*Ploceus cucullatus*) is a significant pest to rice agriculture (Fitzwater 1973). Given the wide-ranging socio-economic impacts of alien birds, an analysis that categorises, scores and compares species based on the mechanism and severity of their impacts (as has been done for the environmental impacts of alien birds (Evans et al. 2016) using a related framework, the Environmental Impact Classification for Alien Taxa (EICAT: Blackburn et al. 2014)), would provide useful insights regarding the most damaging species. It would also enable the identification of regions sustaining the most severe impacts, potentially informing management interventions to protect human health and livelihoods.

To date, four studies have used scoring systems to quantify the socio-economic impacts of alien birds (Shirley and Kark 2009; Kumschick and Nentwig 2010; Kumschick et al. 2013; Evans et al. 2014). Shirley and Kark (2009) scored alien bird impacts under two broad categories: economic impacts resulting from damage to agricultural crops and human health impacts resulting from disease transmission, noise disturbance and threats to aviation safety. They found alien birds from three families (true parrots (Psittacidae), pheasants (Phasianidae) and ducks, geese and swans (Anatidae)) to have the most severe economic impacts and pigeons and doves (Columbidae) and true parrots to have the most severe human health impacts. The other three studies used the Generic Impact Scoring System (GISS: Nentwig et al. 2010) to quantify the severity of alien bird impacts using six categories: agriculture, animal production, forestry, human infrastructure, human health and human social life. Kumschick and Nentwig (2010) found four alien bird species to have the most severe economic impacts in Europe: the Canada goose, rose-ringed parakeet (*Psittacula krameri*), monk parakeet and the African sacred ibis (*Threskiornis aethiopicus*). Kumschick et al. (2013) found that most alien birds generally have relatively minor economic impacts in Europe, with the exception of the Canada goose. Evans et al. (2014) found the economic impacts of alien birds in Australia to be more frequently documented than their environmental impacts, that there are more species with recorded economic impacts in Australia than in Europe (14 vs. 7) and that these impacts tend to be more severe in Australia than in Europe. The species with the most severe economic impacts in Australia included the common starling, common myna (*Acridotheres tristis*) and house sparrow (*Passer domesticus*). These regional studies have provided useful insights regarding the types of alien birds that have the most severe impacts on a range of socio-economic activities in Europe and Australia. However, these studies did not adopt a common metric with which to determine the severity of socio-economic impacts generated by alien birds: this means they are less useful when trying to directly compare the severity of impacts caused by different alien bird species and sustained across different regions of the world.

The recently proposed Socio-Economic Impact Classification for Alien Taxa (SEICAT: Bacher et al. 2018) has been developed to provide a standardised method to quantify and categorise the broad range of socio-economic impacts generated by alien species. Crucially, it differs from previous scoring systems (e.g. D´hondt et al. 2014; Nentwig et al. 2016), because it uses changes in human activities that result from the impacts of an alien species as a common metric for assessing the severity of these impacts. In so doing, SEICAT enables direct comparisons to be made across alien taxa and regions regarding the severity of the impacts caused by alien species. Here, we apply SEICAT to undertake the first global assessment of the impacts of alien birds on human well-being. Based on the results of previous studies, we expect to find variation in the severity of these impacts across alien bird orders and geographic regions, with impacts in Europe being generally minor. We also expect to find a lack of data describing the socio-economic impacts of many alien bird species. By undertaking this assessment, we aim to further our understanding of the global threat posed by alien birds to human well-being and to identify knowledge gaps, directing future alien bird impact studies. When combined with the recently produced global dataset on the environmental impacts of alien birds (Evans et al. 2016), the data generated by this study will form the first complete, global dataset on the impacts of alien species from an entire taxonomic class.

Methods

Data

A list of 415 alien bird species with self-sustaining populations worldwide (i.e. established breeding populations that can persist without further human intervention) was taken from Evans et al. (2016). A review to identify literature on the socio-economic impacts of these species was undertaken following the approach adopted in Evans et al. (2016) as summarised in the Suppl. material 1: Appendix A. Using the information gathered during the literature review, each alien bird species was allocated to one of five SEICAT impact categories, depending on its most severe impacts to human well-being. In order of severity, these categories are: Minimal Concern (**MC**), Minor (**MN**), Moderate (**MO**), Major (**MR**) and Massive (**MV**).

The impact categories have been designed to reflect an increase in the order of magnitude of a particular impact caused by an alien species to human well-being. Impacts of **MC** do not affect human well-being; **MN** impacts make it difficult for people to participate in their normal activities and individuals suffer in at least one constituent of human well-being (e.g. security, material assets, health); **MO** impacts result in a reduction in the size of an activity, with fewer people participating in it (e.g. the partial abandonment of an activity); **MR** impacts result in the local disappearance of an activity from all or part of an area invaded by an alien taxon (e.g. people switch to other activities), but this impact is considered to be reversible within a decade if the alien species is controlled or removed; **MV** impacts result in the local disappearance of an activity and this change is likely to persist for at least a decade, even if the alien species is controlled or removed.

A series of impact descriptions were used to guide the assessment process, as shown in the Suppl. material 3: Table S1. As an example, on Easter Island, the chimango caracara (*Phalcoboenus chimango*) feeds on insects on the backs of cattle and horses. This feeding can damage the skin of the livestock, which reduces the value of the hides, and results in lost income for livestock owners (Johnson et al. 1970). However, there is no evidence to show that this impact has resulted in a reduction in the number of people buying and selling cattle and horses on Easter Island. As such, recorded impacts for the chimango caracara match the impact description relating to **MN** under the SEICAT guidelines (Bacher et al. (2018): see Suppl. material 3: Table S1). The scoring of impacts was undertaken by one assessor (T.E.), and it is therefore possible that the results of the assessment were influenced by subjectivity. However, the impact descriptions used to guide the assessment process (Suppl. material 3: Table S1) have been developed in order to minimise subjectivity. The impact descriptions are analogous to those used for the IUCN EICAT protocol, which has been used by individual assessors to undertake global assessments of the environmental impacts of alien species (e.g. Canavan et al. 2019).

SEICAT does not include formal alien species impact mechanisms with which to categorise the type of impacts caused by alien species: this is because any such mechanisms are likely to vary depending on the impacting alien species and the people/communities affected. For this assessment, and based on the findings of previous studies (Shirley and Kark 2009; Kumschick and Nentwig 2010; Kumschick et al. 2013; Evans et al. 2014), we identified six broad mechanisms through which alien birds may affect human well-being: damage to agriculture (for example, by grazing and trampling on growing crops or by spoiling harvested crops with droppings); damage to public facilities, buildings and utilities (for example, by spoiling public spaces and recreational areas with droppings, damaging ornamental trees in public parks though herbivory, and by nesting on buildings and pylons, which blocks gutters and causes power outages); being a public nuisance (by being noisy, aggressive and spreading rubbish); posing a risk to aviation safety (through collisions with aircraft); transmitting diseases to animals; and transmitting diseases to humans. To reflect any uncertainty over the accuracy of the assessments, including the correct classification of an alien bird species using the SEICAT impact categories, a confidence score of ‘High’, ‘Medium’ or ‘Low’ was allocated to each assessment using the EICAT guidelines (IUCN 2020) which are also applicable to SEICAT assessments. For example, the data describing the impacts caused by the Eurasian blackbird on the grape growing industry in Tasmania were published and peer-reviewed, but the report expressed some uncertainty over whether these impacts caused a reduction to the scale of grape growing operations on Tasmania (Guiler 1989). Consequently, a confidence score of ‘Medium’ was allocated to the SEICAT assessment for this species (see Probert et al. (2020) for a broader discussion on the classification of uncertainties in EICAT and SEICAT). Where insufficient data was available to assess the socio-economic impacts of an alien species, it was categorised as Data Deficient (**DD**).

Analysis

Contingency table tests (unconditional exact tests: the FunChisq package (Zhong and Song 2019)) were used to analyse the actual and expected distribution of: (i) the severity of impacts across alien bird orders and geographic regions; (ii) alien bird species that have and do not have reported socio-economic impacts, that also have and do not have reported environmental impacts; and (iii) impact data availability across regional alien bird species richness scores.

Regional alien bird species richness scores (the number of alien bird species with established populations in a region) were calculated using the Global Avian Invasions Atlas (GAVIA: Dyer et al. 2017a). Analysis of regions was undertaken at the continental scale using the following groups: Africa, Asia, Australasia, Europe, North and Central America, South America and Oceanic Islands. Following Evans et al. (2016), due to the relatively small size of our impact dataset, impact severity data were converted into a two-level response variable: 'less severe impacts' being those categorised as **MC** or **MN** under SEICAT, and 'more severe impacts' being those categorised as **MO**, **MR** or **MV** (these three impact categories are analogous to the 'harmful' categories as described in the IUCN EICAT guidelines (IUCN 2020)). We excluded the rock dove (*Columba livia*) from our study, as there is some uncertainty as to the extent of its native and alien range. All analyses were carried out in R version 3.5.3 (R Core Team 2019).

Results

We found 128 impact reports for 57 (14%) of the 415 bird species with self-sustaining alien populations worldwide (see Suppl. material 2: Appendix B for a summary). These 57 species are from six orders of alien birds (Figure 1): Passeriformes (perching birds: 25 species, 44% of all species with impact data), Psittaciformes (parrots: 13, 23%), Galliformes (gamebirds: 9, 16%), Anseriformes (waterfowl: 5, 9%), Columbiformes (pigeons and doves: 4, 7%) and Falconiformes (falcons and caracaras: 1, 2%). No impact data were found for 358 species, which were categorised as Data Deficient (**DD**) under SEICAT. Furthermore, no impact data were found for 20 of the 26 orders of birds containing species with self-sustaining alien populations worldwide: these 20 orders are therefore entirely **DD**. Impact data availability is randomly distributed across the six orders for which impact data were available (unconditional exact test: chi-square value = 1.071, degrees of freedom = 4, $P = 0.841$, estimate = 0.054) (Suppl. material 1: Table S2). There are more alien bird species with reported socio-economic impacts that also have reported environmental impacts than would be expected by chance (unconditional exact test: chi-square value = 38.7, degrees of freedom = 1, $P < 0.001$, estimate = 0.305) (Table 1).

Several alien bird species were found to have equally severe impacts through more than one impact mechanism: for example, the Canada goose consumes crops, fouls public parks and poses a risk to aviation safety. The majority (98%) of the impacts reported were classified as being 'less severe' (**MC** impacts = 9; **MN** impacts = 117), with the remainder being classified as 'more severe' (**MO** impacts = 2; **MR** and **MV** impacts = 0) (Figure 2). Impact magnitudes are randomly distributed across orders (unconditional exact test: chi-square value = 0.214, degrees of freedom = 4, $P = 0.958$, estimate = 0.041) (Suppl. material 3: Table S3).

Impacts on agriculture was the most frequently reported impact mechanism (83 impact reports, 65% of all reported impacts), followed by damage to public facilities,

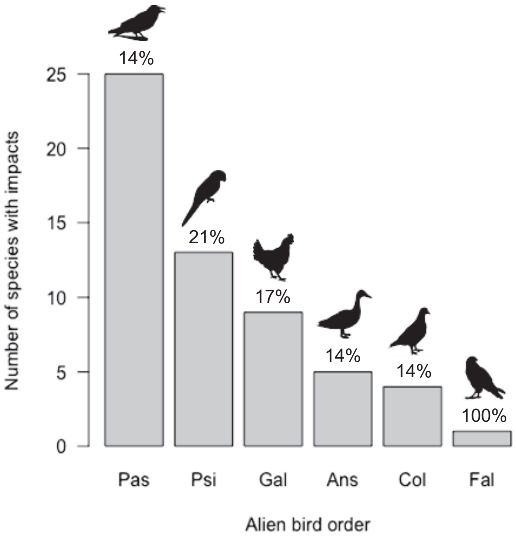

Figure 1. The number of alien bird species with recorded socio-economic impacts from each of six orders. Pas: Passeriformes; Psi: Psittaciformes; Gal: Galliformes; Ans: Anseriformes; Col: Columbiformes; Fal: Falconiformes. Total species with impacts = 57. A further 358 species were categorised as being Data Deficient (**DD**) under SEICAT. % = proportion of bird species in each order with impact data.

Table 1. Contingency table (unconditional exact test) showing actual and expected numbers of alien bird species that have or do not have reported socio-economic impacts that also have or do not have reported environmental impacts. Expected values are displayed in italics.

	Alien bird species with reported environmental impacts	**Alien bird species without reported environmental impacts (DD species)**	**Total**
Alien bird species with reported socio-economic impacts	45 *16.34*	12 *40.66*	**57**
Alien bird species without reported socio-economic impacts (DD species)	74 *102.66*	284 *255.35*	**358**
Total	**119**	**296**	**415**

Chi-square value = 38.7, degrees of freedom = 1, $P < 0.001$, estimate = 0.31.

buildings and utilities (26 impacts, 20%) (Figure 2). One report described disease transmission impacts on animals; no reports were found describing disease transmission impacts on humans. Impact magnitudes are randomly distributed across impact mechanisms (unconditional exact test: chi-square value = 0.922, degrees of freedom = 3, $P = 0.66$, estimate = 0.085) (Suppl. material 3: Table S4). Impact mechanisms are non-randomly distributed across alien bird orders (unconditional exact test: chi-square value = 31.7, degrees of freedom = 12, $P = 0.003$; estimate = 0.29): there are fewer parrot species with impacts on agriculture than would be expected by chance, and more parrot and waterfowl species and fewer perching bird species with impacts on public facilities, buildings and utilities than would be expected by chance (Table 2).

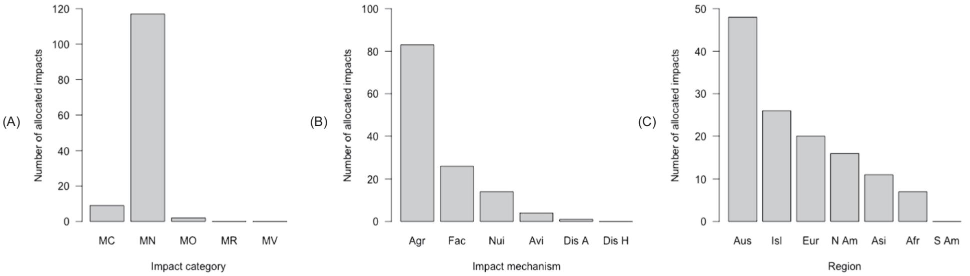

Figure 2. The severity and type of socio-economic impacts caused by alien birds, and the regions in which they are sustained. This figure shows the number of impact records for each of: (**A**) five impact categories; (**B**) six impact mechanisms; and (**C**) seven regions of the world. MC: Minimal Concern; MN: Minor; MO: Moderate; MR: Major; MV: Massive. Agr: Damage to agriculture; Fac: Damage to public facilities, buildings and utilities; Nui: public nuisance; Avi: risk to aviation safety; Dis A: transmission of diseases to animals; Dis H: transmission of diseases to humans. Aus: Australasia; Isl: Oceanic Islands; Eur: Europe; N Am: North (and Central) America; Asi: Asia; Afr: Africa; S Am: South America. Total impact reports = 128.

Table 2. Contingency table (unconditional exact test) showing actual and expected numbers of impact allocations to each impact mechanism for each order of alien birds. Expected values are displayed in italics. Data for impacts by Falconiformes and disease transmission were removed from the dataset for the test, due to low sample sizes (one **MN** impact each).

	Damage to agriculture	Damage to public facilities, buildings and utilities	Nuisance	Aviation safety	Total
Passeriformes	38	3	5	1	**47**
	30.59	*9.7*	*5.22*	*1.49*	
Psittaciformes	12	12	5	2	**31**
	20.17	*6.4*	*3.44*	*0.98*	
Galliformes	12	1	2	0	**15**
	9.76	*3.1*	*1.67*	*0.48*	
Anseriformes	10	8	2	1	**21**
	13.67	*4.33*	*2.33*	*0.67*	
Columbiformes	10	2	0	0	**12**
	7.81	*2.48*	*1.33*	*0.38*	
Total	**82**	**26**	**14**	**4**	**126**

Chi-square value = 31.7, degrees of freedom = 12, $P = 0.003$, estimate = 0.29.

The greatest number of impacts were recorded in Australasia (48 impacts, 38% of all impacts), followed by Oceanic Islands (26 impacts, 20%). No impact data were found for South America (Figure 2). Impact data availability is non-randomly distributed, given regional alien species richness (unconditional exact test: chi-square value = 23.8, degrees of freedom = 5, $P < 0.001$, estimate = 0.167), a result driven by the larger number of impact reports for Australasia than would be expected by chance (Table 3). Impact magnitudes are randomly distributed across regions (unconditional exact test: chi-square value = 0.208, degrees of freedom = 5, $P = 0.98$, estimate = 0.04) (Suppl. material 3: Table S5). Impact mechanisms are also randomly distributed across regions (chi-square value = 9.318, degrees of freedom = 15, $P = 0.812$, estimate = 0.156) (Suppl. material 3: Table S6).

Table 3. Contingency table (unconditional exact test) showing actual and expected numbers of impact reports and regional alien species richness scores. Expected values are displayed in italics.

	No. of alien bird species (alien species richness)	No. of impact reports	Total
Africa	50	7	**57**
	48.48	*8.52*	
Asia	121	11	**132**
	112.26	*19.74*	
Australasia	99	48	**147**
	125.02	*21.98*	
Europe	112	20	**132**
	112.26	*19.74*	
North and Central America	156	16	**172**
	146.28	*25.72*	
Oceanic Islands	190	26	**216**
	183.7	*32.3*	
Total	**728**	**128**	**856**

Chi-square value = 23.8, degrees of freedom = 5, $P < 0.001$, estimate = 0.17.

The majority of recorded impacts were allocated a 'Low' confidence score (121 impacts, 95% of all impacts); five impacts were allocated a 'Medium' confidence score and two were allocated a 'High' confidence score. Confidence scores are randomly distributed across impact mechanisms (unconditional exact test: chi-square value = 1.7, degrees of freedom = 6, $P = 0.86$, estimate = 0.082) (Suppl. material 3: Table S7). Confidence scores are also randomly distributed across regions (chi-square value = 1.4, degrees of freedom = 10, $P = 0.98$, estimate = 0.074) (Suppl. material 3: Table S8). Confidence scores are non-randomly distributed across impact magnitudes (chi-square value = 8.17, degrees of freedom = 2, $P = 0.01$, estimate = 0.206) (Suppl. material 3: Table S9), with higher confidence being placed in impacts of higher magnitude.

Discussion

As far as we are aware, this study represents the first global assessment of the socio-economic impacts of alien birds. Our literature search identified data on socio-economic impacts for just 14% of the 415 alien bird species with self-sustaining populations worldwide. This paucity of impact data reflects the findings of other studies on the socio-economic impacts of alien species, including SEICAT assessments undertaken for amphibians (Bacher et al. 2018; Measey et al. 2020) and gastropods (Kesner and Kumschick 2018). Taken together, this suggests that the socio-economic impacts of most alien species are unknown.

There are at least four reasons why we may lack data on the socio-economic impacts of alien birds. First, some species may have, or be perceived to have, socio-economic impacts that are minor and do not cause problems for human beings, and hence do not warrant socio-economic impact research. Research on the environmental impacts of alien species tends to focus on species that have the most damaging environmental impacts (Pyšek et al. 2008), and for alien birds, we are likely to lack data on the environmental impacts of many species because their impacts are minor (Evans et al. 2018). If this is also true for alien species socio-economic impact research, the results of this study suggest that the socio-economic impacts of alien birds are generally minor and unlikely to pose a severe threat to human well-being.

Second, the impacts of some species may be going unnoticed because they occur in regions of the world with limited capacity to study their impacts or in remote regions where those impacts are not easily recorded. Consistent with this hypothesis, we find more data on the socio-economic impacts of alien birds in developed regions: 66% of impacts occur in Australasia, Europe and North America; 14% occur in Asia and Africa; no impact data were found for South America (Figure 2). Of the 26 impacts occurring on islands, approximately 70% relate to developed nations or overseas territories thereof (e.g. Hawaii, New Caledonia, Bermuda, St Helena, Netherlands Antilles). This pattern is also evident for alien bird environmental impact research (Martin-Albarracin et al. 2015; Evans et al. 2018; Evans and Blackburn 2020), alien amphibian impact research (Measey et al. 2020), and for alien species research more generally (Bellard and Jeschke 2015), and suggests we may have much to learn about the impacts of alien birds on human well-being in developing regions. This is of concern as the impacts of alien species can be a major threat to human livelihoods in developing countries, particularly by affecting agricultural production and hence food security (Perrings 2005).

Third, the tendency for impacts to be recorded in developed regions may also reflect the global distribution of alien bird species, which tends to show high species richness in Europe, former European colonies such as the USA, Australia and New Zealand, and economic hotspots such as Singapore, Hong Kong and Taiwan (Dyer et al. 2017b). Nevertheless, Australasia has more impact reports deriving from the region than would be expected by chance given the number of alien bird species established there (the region also has many more impact reports than would be expected if alien species richness is ignored) (Table 3). This suggests that impacts in Australasia may be over-reported, lending support to our previous hypotheses that impacts are less frequently reported in developing regions.

Fourth, research on socio-economic impacts may be biased towards species with existing environmental impacts. Of the 57 alien bird species with reported socio-economic impacts, approximately 80% (45) also have reported environmental impacts; of the 358 species that are **DD** for socio-economic impacts, approximately 80% (284) are also **DD** for environmental impacts (Table 1). This implies that in general, alien bird species with environmental impacts have socio-economic impacts. Indeed, across taxa (and regions), the environmental and socio-economic impacts of alien species are highly correlated (Vilà et al. 2010). If this is the case, predicting which species are likely to have socio-economic impacts may be informed by determining whether they have environmental impacts. However, this result may also arise because alien bird species with damaging environmental impacts are noticed and studied, and these assessments also include a review of their socio-economic impacts. Indeed, several alien species impact scoring schemes require consideration of both the environmental and socio-economic impacts (e.g. the Generic Impact Scoring System (GISS) (Nentwig et al. 2016), Harmonia+ (D´hondt et al. 2014) and the UK risk assessment scheme for all non-native species (Baker et al. 2008)). If this is true, the impacts of alien bird species that have socio-economic impacts, but do not have environmental impacts, may be going unnoticed (the fact that there are more data on environmental than socio-economic impacts suggests this direction of causation, rather than vice versa). This may be why the same five orders that account for 90% of species with environmental impact data (Evans et al. 2016) also account for almost 90% of species with socio-economic impact data.

The socio-economic impacts of alien birds are generally minor (Figure 2), with all but two of the 128 recorded impacts being either **MC** (i.e. no deleterious impact was identified) or **MN** (i.e. whilst the impacts of an alien bird may make it difficult for humans to participate in an activity, they did not lead to a decline in the size of an activity). Two species were found to have **MO** impacts. First, frugivory by the Eurasian blackbird contributed to the decline of the small-fruit growing industry across Tasmania in the 1800s (Guiler 1989). Second, a collision with a flock of common starlings at Boston Airport in 1960 resulted in an aeroplane crash that killed 62 people (Dolbeer 2013). Although this event is unlikely to have caused a reduction in aviation activities and airline passenger numbers in the USA, under SEICAT, any impact resulting in a human fatality automatically qualifies as an **MO** impact (see Suppl. material 1: Table S1).

The prevalence of **MC** and **MN** impacts may support our hypothesis that we lack impact data for many alien bird species because their socio-economic impacts are negligible and do not attract research. However, a ‘Low’ confidence score was assigned to 95% of SEICAT alien bird impact assessments because, whilst adequate data were available to ascertain that an alien bird was exerting an impact, there were inadequate data to determine how severely this impact affected human well-being (in particular, to distinguish between an **MN** impact (where an alien bird makes an activity difficult) and an **MO** impact (where it causes a decline in the population participating in an activity)). This may be because whilst these studies identified socio-economic impacts, they did not go on to quantify how they affected the scale of the impacted activities. For example, by eating rice grown for duck feed, the Eurasian tree sparrow (*Passer montanus*) causes economic losses for duck farmers in the Philippines (Libay et al. 1983). Whilst empirical evidence is available to confidently determine that the sparrows cause economic losses (an **MN** impact under SEICAT), there is inadequate information to determine whether these impacts have resulted in some people abandoning duck farming activities in the region (an **MO** impact). Consequently, rice predation by sparrows on duck farming in the Philippines is classified as an **MN** impact with a ‘Low’ confidence score. SEICAT is a new framework that requires specific data on the level of impact on human activities, which as yet is unavailable for many alien bird impacts. The adoption of SEICAT may therefore foster a broader approach to future alien species socio-economic impact assessments, which will not only describe impacts, but also consider their wider implications for human well-being. We recommend that future studies on the socio-economic impacts of alien species go beyond the identification of impacts, by attempting to quantify how these impacts reduce the scale of affected activities. We also recommend that these assessments are not based on anecdotal evidence, as this would most likely improve the level of confidence allocated to future SEICAT assessments.

From the data that are currently available, the most severe impacts on human well-being caused by alien birds are associated with aviation safety (an air strike with a flock of common starlings having caused the deadliest bird-induced plane crash in history (Dolbeer 2013)). Collisions with birds (both native and alien) have resulted in the loss of at least 190 lives and 52 aircraft, and cost the global aviation industry approximately US$ 1.2 billion/year (€ 1.1 billion/year) in damage and delays (Allan 2000). Three alien bird species continue to be adjudged to pose a significant threat to aviation safety: the Canada goose, rose-ringed parakeet and common starling. Of these species, the Canada goose may represent the most serious threat, due to its large body size, flocking nature and attraction to managed grasslands as found at airports (Bradbeer et al. 2017). It is present in large numbers at Heathrow Airport in the UK, where it has caused at least one serious safety incident: in 1998, a Boeing 767 collided with a flock of Canada geese when coming in to land, damaging the nose, wing and left engine of the plane (Civil Aviation Authority, no date). In its native range in North America, air strikes with Canada geese have caused several serious safety incidents, including a crash in which 24 people died (Bradbeer et al. 2017) and an emergency landing on the Hudson River in New York City (Marra et al. 2009; Dolbeer 2011). The rose-ringed parakeet is also present at Heathrow Airport: between 2005 and 2006, three of the 98 reported airstrikes at the airport involved this species (Avery and Shiels 2017). The common starling poses a growing threat to aviation safety across the USA: between 1990 and 2001, there were 852 reported strikes that involved common starlings, and over that time-period the annual strike rate more than doubled. Together with airstrikes involving native blackbird species, these incidents cost approximately US$ 1.6 million (€ 1.4 million), although damage to aircraft was only reported in approximately 6% of strikes (Barras et al. 2003). Alien birds may continue to contribute disproportionately to bird strikes because of their greater tendency to be found in anthropogenic environments, in both their native and alien ranges (Cardador and Blackburn 2019).

Impacts on agriculture account for approximately two-thirds of all recorded impacts (Figure 2). Nearly 40% of these impacts occur in Australasia. This may be for a number of reasons: Australia and New Zealand are developed countries with the capacity to undertake and publish research on the impacts of alien species; both countries have been subject to many deliberate alien bird introductions (McDowall 1994; Dyer et al. 2017a), including several frugivorous species (e.g. common myna, common starling, Eurasian blackbird, house sparrow); and both countries have economically important fruit-growing industries that have been affected by pest birds (Tracey et al. 2007). Damage to the fruit-growing industry in Australia is estimated to cost AU$ 300 million (€ 180 million) annually. Together, these reasons may explain why there are many more impact reports than would be expected by chance in Australasia, given its alien species richness score (Table 3). However, this impact is not caused by alien birds alone, as more than 60 bird species (the majority being native) are known agricultural pests in Australia (Tracey et al. 2007). While these agricultural impacts may be financially costly, there is little evidence to indicate that they reduce the scale of agricultural activities in Australia (or have done recently, at least; Guiler 1989). Thus the large financial losses that may be incurred only rate as a Minor (**MN**) impact under SEICAT.

There are few data on the spread of diseases by alien birds and the subsequent socio-economic impacts (Figure 2) or environmental impacts (Evans et al. 2016). This may be because disease assessments are complex: it is often difficult to confirm whether a specific species has transmitted a disease (see Tompkins and Jakob-Hoff 2011), although exotic parakeets kept as pets in the UK were associated with disease scares that may have contributed to their unplanned introduction (Heald et al. 2019). Almost half of the 26 impacts on public facilities are generated by parrot species (Table 2). This is likely to be because parrots often possess high levels of urban tolerance (Maklakov et al. 2011), facilitating their establishment in urban areas (e.g. Diamond and Ross (2019)). This may explain the general prevalence of parrot species in our dataset (Figure 1). Examples include the monk parakeet (see Introduction); the sulphur-crested cockatoo (*Cacatua galerita*) and Alexandrine parakeet (*Psittacula eupatria*) which damage ornamental trees in public parks in Australia and Iran, respectively (Khaleghizadeh 2004; Department of Environment and Conservation 2009); the rose-ringed parakeet which disturbs residents and tourists on Hawaii with its loud calls (Shiels and Kalodimos 2019); and the long-billed corella (*Cacatua tenuirostris*) and little corella (*Cacatua sanguinea*) which damage grass sports pitches in Western Australia (Department of Environment and Conservation 2009). The prevalence of waterfowl species with impacts on public facilities (Table 2) is primarily caused by the Canada goose, which has a rapidly expanding population across northwest Europe (Banks et al. 2008), where it fouls public spaces such as parks, sports pitches and swimming ponds with droppings (see van Haam et al. 2013).

We have more confidence in the accuracy of SEICAT assessments where the impacts on human well-being are more severe (Suppl. material 3: Table S9**)**. This may be because one of the two 'more severe' impacts in our dataset resulted in human fatalities which meant it automatically qualified as an **MO** impact, and was thus assigned a 'High' confidence score. As there are only two 'more severe' impacts in our dataset, we do not place much emphasis on this result.

Conclusions

This study represents the first large-scale application of the SEICAT protocol, and the first global assessment of the socio-economic impacts of alien birds. It demonstrates that SEICAT can be used effectively to quantify and categorise the impacts of alien species on human well-being. The most significant problem encountered during this assessment was a lack of impact data: we only know about the socio-economic impacts of a small proportion of the alien birds with self-sustaining populations worldwide. This study may therefore help to focus research regarding the impacts of alien birds on human well-being, particularly in developing regions of the world, where impact data are scarce. Birds are well-studied in comparison to many other taxonomic groups, and thus the problem of data paucity may extend to SEICAT assessments for other groups yet to be assessed, such as invertebrates. Nevertheless, completion of these assessments would reveal the global taxonomic distribution of impact data availability (see Evans and Blackburn 2020), and hence inform future socio-economic impact research.

SEICAT is a new framework, requiring data on the way in which alien species affect human well-being, as measured by changes to human activities: even where we do have data describing an alien bird impact, data on how profoundly this impact affects people's activities are often unavailable. As a result, the confidence assigned to most SEICAT classifications is 'Low'. The adoption of SEICAT may encourage a more holistic approach to future socio-economic impact assessments which not only describe impacts, but also consider their wider implications for human well-being.

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Supplementary material 1

Appendix A

Authors: Thomas Evans, Tim M. Blackburn, Jonathan M. Jeschke, Anna F. Probert, Sven Bacher

Data type: (measurement/occurrence/multimedia/etc.)

Explanation note: Alien bird SEICAT assessment: literature review protocol.

Link: https://doi.org/10.3897/neobiota.62.51150.suppl1

Supplementary material 2

Appendix B

Authors: Thomas Evans, Tim M. Blackburn, Jonathan M. Jeschke, Anna F. Probert, Sven Bacher

Data type: (measurement/occurrence/multimedia/etc.)

Explanation note: Alien bird SEICAT assessment (species summary).

Link: https://doi.org/10.3897/neobiota.62.51150.suppl2

Supplementary material 3

Nine additional tables

Authors: Thomas Evans, Tim M. Blackburn, Jonathan M. Jeschke, Anna F. Probert, Sven Bacher

Data type: Tables

Explanation note: **Table S1.** Impact descriptions used to guide the SEICAT assessment process (from Bacher et al. 2018). **Table S2.** Contingency table (unconditional exact test) showing actual and expected numbers of alien bird species for each order, with and without recorded impacts. **Table S3.** Contingency table (unconditional exact test) showing actual and expected numbers of impact allocations to less severe (MC & MN) and more severe (MO) impact categories for each alien bird order. **Table S4.** Contingency table (unconditional exact test) showing actual and expected numbers of impact allocations to less severe (MC & MN) and more severe (MO) impact categories for each impact mechanism. **Table S5.** Contingency table (unconditional exact test) showing actual and expected numbers of impact allocations by region, to less severe (MC & MN) and more severe (MO) impact categories. **Table S6.** Contingency table (unconditional exact test) showing actual and expected numbers of impact allocations by region, to each impact mechanism. **Table S7.** Contingency table (unconditional exact test) showing actual and expected numbers of impact allocations by confidence score, to less severe (MC & MN) and more severe (MO) impact categories. **Table S8.** Contingency table (unconditional exact test) showing actual and expected numbers of impact allocations by confidence score, to each region. **Table S9.** Contingency table (unconditional exact test) showing actual and expected numbers of impact allocations by confidence score, to less severe (MC & MN) and more severe (MO) impact categories.

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DISCUSSION PAPER

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Classifying the introduction pathways of alien species: are we moving in the right direction?

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Abstract

Alien species are introduced to new regions in many different ways and for different purposes. A number of frameworks have been developed to group such pathways of introduction into discrete categories in order to improve our understanding of biological invasions, provide information for interventions that aim to prevent introductions, enable reporting to national and international organisations and facilitate the prediction of threats. The introduction pathway classification framework proposed by the Convention on Biological Diversity (CBD) as a global standard is comprised of six main categories and 44 sub-categories. However, issues have arisen with its implementation. In this position paper, we outline five desirable properties of an introduction pathway classification framework – it should be compatible (i.e. the level of detail of the categories is similar to that of the available data), actionable (i.e. categories link to specific interventions), general (i.e. categories are applicable across the contexts that are of interest (e.g. taxa, habitats and regions)), equivalent (i.e. categories are equivalent in their level of detail) and distinct (i.e. categories are discrete and easily distinguished) – termed the CAGED properties. The six main categories of the CBD framework have all of the CAGED properties, but the detailed sub-categories have few. Therefore, while the framework has been proposed by the CBD as a global standard and efforts have been made to put it into practice, we argue that there is room for improvement. We conclude by presenting scenarios for how the issues identified could be addressed, noting that a hybrid model might be most appropriate.

Keywords
biological invasions, biosecurity, Convention on Biological Diversity, framework, introduction effort, invasion biology, mode of introduction, propagule pressure

Introduction

Information on how and why alien species are introduced to new regions provides the foundation for pre- and at-border management strategies that aim to prevent the introduction of harmful species (Hulme et al. 2008; Hulme 2015). However, alien species can be introduced through a vast number of introduction pathways and, as there are limited resources available to manage introductions, important pathways must be identified and prioritised (Hulme et al. 2008; Essl et al. 2015; Essl et al. 2020). A number of frameworks have been developed to aggregate the immense number of introduction pathways into discrete categories (Essl et al. 2015). These introduction pathway classification frameworks (hereafter simply frameworks) are used in analyses that improve our understanding of biological invasions, provide information for interventions that aim to prevent introductions, enable reporting to national and international organisations and facilitate the prediction of threats. The different frameworks were developed for use in different contexts and they differ with respect to the way in which they were developed and in their level of detail. For example, there are six main categories and 20 sub-categories in the framework used by the European Alien Species Information Network (EASIN), which supports European states by providing information for policy and management (Tsiamis et al. 2017); the framework developed by Wilson et al. (2009) comprises six categories and aims to improve understanding of the underlying properties of pathways and the consequences for invasion success; and the framework developed by Hulme et al. (2008) has six categories and was developed to provide information for decisions on existing regulatory instruments.

Based on the framework of Hulme et al. (2008), a hierarchical framework was developed to assist countries to achieve Aichi Biodiversity Target 9 of the Convention on Biological Diversity (CBD), specifically the requirement to identify and manage pathways of introduction (https://www.cbd.int/sp/targets/, CBD 2014; Essl et al. 2015; Scalera et al. 2016; Harrower et al. 2018). This framework (hereafter referred to as the CBD framework) was proposed by the CBD as a global standard (CBD 2014). With six main categories and 44 sub-categories, the CBD framework is very detailed (Fig. 1). The six main categories of the CBD framework, which were adopted from the framework of Hulme et al. (2008), were developed by classifying pathways, based on three shared attributes: the degree of human involvement, the means of transport and the means of subsequent introduction (Hulme et al. 2008). In contrast, the 44 sub-categories of the CBD framework were developed by comparing and incorporating existing frameworks [including those used by the Global Invasive Species Database (GISD), the Centre for Agriculture and Bioscience International's (CABI) Invasive Species Compendium and the Delivering Alien Invasive Species Inventories for Europe (DAISIE) consortium].

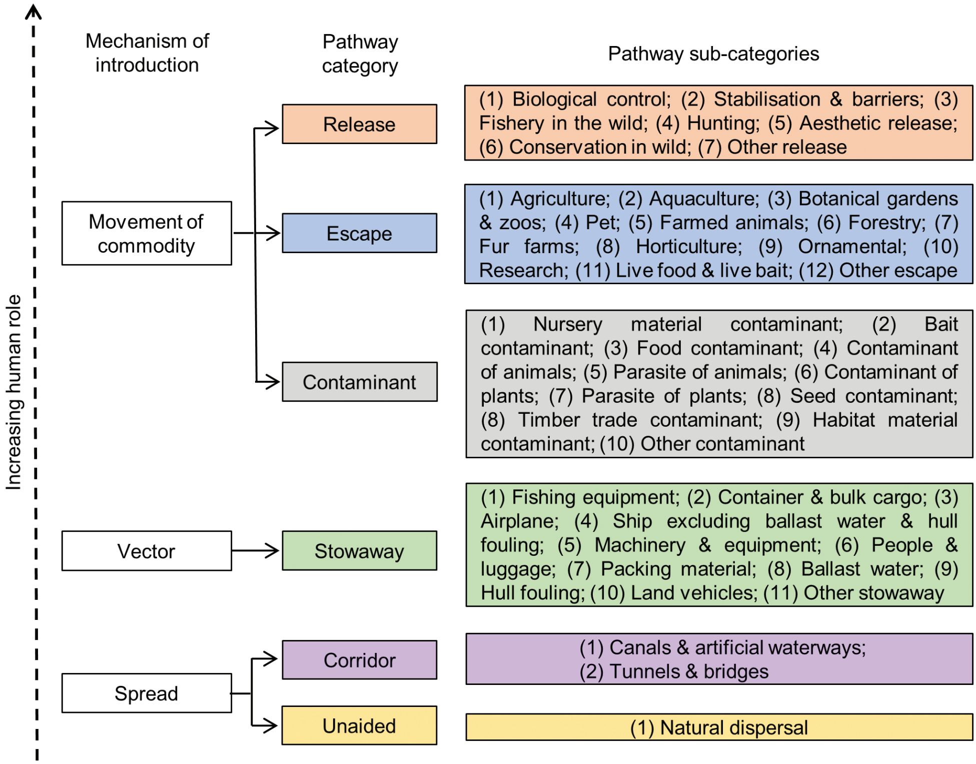

Figure 1. The introduction pathway classification framework proposed by the Convention on Biological Diversity (CBD 2014). The nomenclature proposed in Harrower et al. (2018) has been implemented. The mechanisms of introduction and main categories were adopted from the framework developed by Hulme et al. (2008).

Assessments that have attempted to apply the CBD framework have highlighted implementation issues (Saul et al. 2017; Tsiamis et al. 2017; Zenetos 2017; van Wilgen and Wilson 2018; Pergl et al. 2020). For instance, the sub-categories cannot accommodate all data and some sub-categories overlap and are indistinguishable. Subsequent to the launch of the CBD framework, guidelines were produced which clarified the definitions of the framework's main categories and sub-categories and proposed small adjustments to the framework's nomenclature and structure to address some of the areas of confusion and uncertainty (Harrower et al. 2018, for details see Appendix I: Fig. A1). To date, the guidelines and the proposed changes do not appear to have been officially recognised by the CBD.

Despite these issues, the development of the framework and its recognition by the CBD was an important step towards the global implementation of a shared terminology and classification framework for pathways (Rabitsch et al. 2016, but see Paap et al. 2020). Parties to the CBD have been encouraged to make use of the framework (Essl et al. 2015) and efforts have been made to implement it. Data in existing databases have been re-classified using the CBD framework (Saul et al. 2017; Tsiamis et al. 2017; van Wilgen and Wilson 2018; Pergl et al. 2020), its terminologies have been included in the vocabularies of global data standards (Groom et al. 2019), it has been used in national

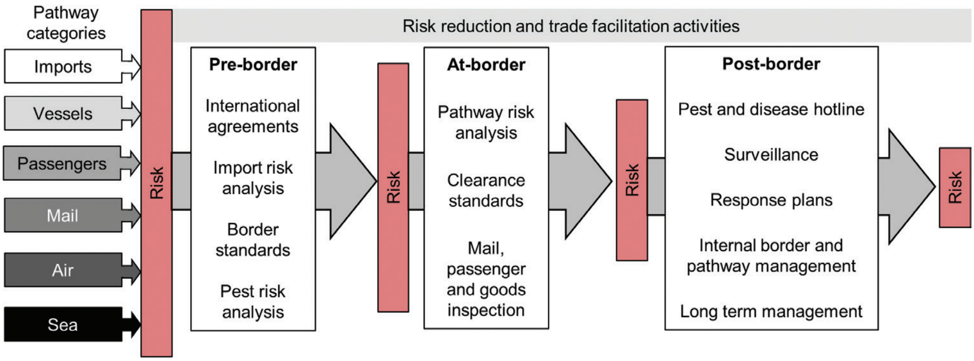

Figure 2. The six pathway categories recognised by New Zealand's biosecurity surveillance system. These categories are linked to the location of biosecurity pressures and interventions (see Suppl. material 1: Fig. S1). Figure redrawn from Ministry of Agriculture and Forestry (MAF) Biosecurity New Zealand (2008).

level reporting (Wilson et al. 2018) and is employed in the system (NOTSYS) used by member states of the European Commission to report new observations of invasive species that are of Union concern (https://easin.jrc.ec.europa.eu/notsys). However, some countries still make use of their own frameworks. For example, New Zealand's biosecurity surveillance system uses a framework that comprises six pathway categories (Fig. 2). This framework, unlike others, does not consider the degree of human involvement when classifying introductions into pathway categories, but introductions are instead classified based on the location of biosecurity interventions. This approach means that intentional and accidental introductions can be classified into the same pathway category.

In this position paper, we discuss why introduction pathway classification frameworks are needed and identify the desirable properties that these frameworks should have in order to achieve their stated purpose. Based on these properties, we assess the main categories and sub-categories of the CBD framework and the framework used by New Zealand's biosecurity surveillance system. We conclude by presenting scenarios for how frameworks might be improved in future.

The purpose of introduction pathway classification frameworks and their desirable properties

An ideal framework should aim to: improve our understanding of biological invasions, provide information for policy and management interventions that aim to prevent introductions, enable reporting to national and international organisations and facilitate the prediction of threats. Unfortunately, existing frameworks differ in terms of their structure and in the context for which they were developed and, thus, rarely address all four of these aims.

Frameworks have been used in retrospective analyses, whereby historical introduction data are categorised and the frequency of introductions through each of the pathways is assessed. These analyses improve our understanding of how and why alien species have been introduced in the past. Additionally, when information is included on invasion success and impacts, these analyses can be used to explore the link between the pathway through which an organism was introduced and its likelihood of becoming invasive and causing harm (Wilson et al. 2009; Pyšek et al. 2011; Faulkner et al. 2016; Pergl et al. 2017). Many of these retrospective analyses have been performed and they have answered a wide range of questions, including how the pathways vary in their importance geographically and over time, as well as across taxonomic groups, habitats and spatial scales (Hulme et al. 2008; Pyšek et al. 2011; Katsanevakis et al. 2013; Faulkner et al. 2016; Zieritz et al. 2017). A variety of frameworks have been used for this purpose; however, frameworks with broad, inclusive categories are most useful for cross-cutting analyses, as introductions that occur in a variety of contexts can be classified within the same categories. Although such frameworks are particularly suitable for studies at a global scale (e.g. Hulme et al. 2008; Saul et al. 2017), they have also been used successfully in cross-cutting analyses at regional- (Pergl et al. 2017) and national-scales (e.g. Pyšek et al. 2011; Faulkner et al. 2016).

Frameworks are also used to direct or provide information for policies, legislation and pre- and at-border management strategies that focus on either preventing the introduction of specific priority species or managing specific pathways or vectors of concern (to reduce propagule and colonisation pressure (Lockwood et al. 2005, 2009)). Examples of these interventions include inspections at ports of entry that aim to prevent the introduction of potentially harmful species (Liebhold et al. 2006; McCullough et al. 2006) and policies that require foreign vessels entering a region to exchange and/or flush their ballast tanks with mid-ocean saltwater (Bailey et al. 2011). As it would be impossible to create different legislative instruments for the vast number of pathways that exist, frameworks with broad, inclusive categories are most useful for legislation and policy (Hulme et al. 2008). However, to provide information for direct interventions, more detailed categories that are explicitly constructed with interventions in mind may be required.

Another important role of frameworks is to assist with the standardised monitoring and reporting of biological invasions at different scales (Latombe et al. 2017; Wilson et al. 2018; Groom et al. 2019). Indeed, the CBD framework has been proposed as an explicit component of global monitoring for biological invasions and its vocabulary has been proposed as part of the Darwin Core biodiversity standards (Latombe et al. 2017; Groom et al. 2019). As pathways of introduction vary across regions and countries (Essl et al. 2015), it would be difficult to create a detailed framework that comprises the introduction pathways that are important for all regions and, therefore, frameworks with broad, inclusive categories are likely to be most useful for monitoring and reporting, particularly at the global scale.

Finally, frameworks can be incorporated in risk analyses (Kumschick et al. 2020) and horizon-scanning exercises (Matthews et al. 2014, 2017; Tsiamis et al. 2020) to make predictions concerning future invaders and their pathways of introduction and to determine what can be done to prevent future introductions. Frameworks with detailed categories are likely to be most useful for this purpose and, indeed, the detailed sub-categories of the CBD framework have been used in horizon-scanning exercises (e.g. Tsiamis et al. 2020).

In order for a framework to achieve all of these purposes, we suggest that it should have five properties, that we have termed the CAGED properties. Frameworks must be: Compatible, Actionable, General, Equivalent and Distinct (CAGED) (Table 1).

Table 1. The proposed five desirable properties that introduction pathway classification frameworks should have in order to achieve their purpose, the rationale for why each is important and examples of where the property is missing.

Property	Definition	Rationale	Examples of where the property is missing
Compatible	The level of detail of each category should be compatible with that of the available data so that it is possible to classify the available data into the categories. The level of detail of the categories must be similar to (or coarser than) that of the available data, so that pathways do not match to multiple categories.	Facilitates the classification of available data, ensures that all introductions can be classified and included in analyses and that introductions are not classified into multiple categories (which could artificially inflate the relative importance of some pathways).	It is often unclear whether a marine species has been introduced through the 'hull-fouling' or 'ballast water' sub-categories of the CBD framework. Therefore, these sub-categories are not compatible with the available data and, consequently, introductions are often classified into both sub-categories or the sub-categories are merged.
Actionable	The links between the categories and interventions need to be clear, with each category aligning with a specific intervention.	If the primary purpose of a framework is to facilitate interventions, then the structure of the framework should be based on the interventions themselves. Actionability ensures that knowledge on the pathways can be easily translated into appropriate action. If multiple pathways are managed using the same tool, then data will need to be re-interpreted to provide information for management.	Multiple sub-categories of the CBD framework pertain to the introduction of contaminants of imported plants or plant products (e.g. 'nursery material contaminant', 'contaminant of plants' and 'parasite of plants' sub-categories). These sub-categories are managed using the same tools and so data will need to be re-interpreted in order to provide information for management.
General	The framework and individual categories should be applicable across whatever contexts are of interest (e.g. regions, taxa, habitats and time periods).	Frameworks that are generalisable across taxa, habitats and regions, allow for the classification of available data in a comparable way, which enables cross-cutting analyses and reporting at global scales. It also means that the categories will likely be able to accommodate data from a wide range of pathways that will change in importance and possibly become more diverse over time. Furthermore, it is inappropriate for countries/regions to manage pathways that are not applicable to them, as this would be a waste of resources. Reporting on pathways that are not applicable could lead to the success of management being overstated.	The framework used by New Zealand's biosecurity surveillance system does not make provision for introductions where alien species spread through natural dispersal over land borders. In the New Zealand context, few alien species have arrived from other regions without human intervention (Hulme 2020), but this is one reason why the framework does not have generality at a global level. Note that species that disperse naturally through the air (e.g. seeds blown over from Australia) or sea are classified into the 'air' or 'sea' categories of the framework.
Equivalent	Categories should be equivalent in their level of detail (i.e. pathways on the same level of a framework should not be subsets of each other).	Ensures that the categories are comparable, which is vital for analyses that explore the relative importance of pathways and that inform management. If categories are not equivalent, the relative importance of some pathways could be underestimated.	The 'mail' category of the framework used by New Zealand's biosecurity surveillance system is a subset of the 'imports' category, which is on the same level of the framework. Therefore, the importance of 'imports' could be underestimated.
Distinct	Categories should be easily distinguished and discrete.	Ensures consistent interpretation by stakeholders and, therefore, the consistent classification of data. If categories are not distinct, they could be misinterpreted, data will be inconsistently classified and ultimately cross-cutting analyses will be precluded.	The difference between the 'horticulture' and 'ornamental' sub-categories of the CBD framework is uncertain since some species can be of both ornamental and horticultural value. As these sub-categories are not distinct, it is likely that classifications are inconsistent.

We have not attempted to rank or weight these properties as their relative importance will vary depending on the context for which the framework is developed, but we argue that all are required for a framework to be effective. Whether a framework possesses the CAGED properties could also vary, based on the context of interest; for instance, a framework developed for regional use could possess the CAGED properties within that context, but not at a global level. Note these properties are, we believe, discrete. For example, if introductions are described by more than one category, then the framework is too detailed and is not compatible with the available data. Nonetheless, the categories might still be applicable across different taxonomic groups, habitats, regions and time periods and so the framework has generality. In contrast, a category could be compatible with the available data, but will not be general if it is only applicable to one type of organism, habitat or region.

Assessment of introduction pathway classification frameworks

Based on the CAGED properties, we evaluated the framework used by New Zealand's biosecurity surveillance system, the six main categories of the CBD framework and the 44 sub-categories of the CBD framework (Table 2 and for details on each framework, see Figs 1, 2). We aimed to assess whether a diverse set of frameworks exhibited the CAGED properties at a global level and so these frameworks were selected as they vary in their level of detail, in the approach followed for their development and in the political level for which they were developed (Table 2). The main categories and sub-categories of the CBD framework were assessed separately as they were developed separately, using different methods. Furthermore, assessing the levels separately meant that the usefulness of each level could be determined, and issues that are specific to each level of the framework could be identified.

Introduction pathway classification framework used by New Zealand's biosecurity surveillance system

The framework used by New Zealand's biosecurity surveillance system (Fig. 2) has some of the CAGED properties (Table 2 and, for further details, Suppl. material 1: Table S1). In particular, it was developed explicitly with biosecurity in mind and so is positioned in the context of at-border interventions (Suppl. material 1: Fig. S1). However, the categories are not equivalent in their level of detail as some categories are subsets of others (see Table 1 for an example), their compatibility with the available data will vary across regions and the framework is not general as the categories do not include introductions where alien species spread through natural dispersal over land borders (see Table 1). The framework was developed from first principles, but due to the political level for which it was developed (an island country) and the approach used (which focused on the location of biosecurity pressures and interventions), it does not have all the CAGED properties (including for the context for which it was developed).

Main categories of the CBD introduction pathway classification framework

The main categories of the CBD framework, which were adopted from the framework of Hulme et al. (2008), have all of the CAGED properties (Table 2 and, for further details, Suppl. material 1: Table S3). The links between the main categories and existing regulations are clear (Suppl. material 1: Fig. S2) and the inclusive nature of the main categories means that it is likely that it will be possible to integrate data for current and historical pathways, as well as those that will develop in the future. Furthermore, pathways from many different regions (e.g. Pyšek et al. 2011; Faulkner et al. 2016), taxonomic groups (Faulkner et al. 2016; Padayachee et al. 2017; Pergl et al. 2017) and habitats (Padayachee et al. 2017) have been successfully classified according to the main categories and they have been used to assess changes over time (Pyšek et al. 2011; Faulkner et al. 2016). Hulme et al. (2008) is widely cited and the framework has been used by researchers from across the world working on many different issues (Wilson et al. in 2020b). The stimulus for the framework of Hulme et al. (2008) was that there was a critical need for an approach that balanced comprehensiveness with utility, in terms of both understanding the drivers of invasion and guiding the development of overarching legislation. It is, therefore, likely that the main categories of the CBD framework have the CAGED properties as they were developed from first principles and as they were specifically designed to provide information for regulations, assess risks in a variety of contexts and facilitate comparative analyses across habitats, regions and taxonomic groups (Hulme et al. 2008).

Sub-categories of the CBD introduction pathway classification framework

The sub-categories of the CBD framework (Fig. 1) have few of the CAGED properties (Table 2 and Table 3 for further details). Assessments that have used the CBD framework have highlighted that the differences between the sub-categories are unclear (Tsiamis et al. 2017; van Wilgen and Wilson 2018; Pergl et al. 2020), the information available is often not detailed enough for classification at the sub-category level (i.e. introductions match to more than one sub-category) (Tsiamis et al. 2017; Zenetos 2017; van Wilgen and Wilson 2018) and many of the sub-categories are only appropriate for specific taxonomic groups or habitats (Matthews et al. 2014; Padayachee et al. 2017). The sub-categories of the framework are also not equivalent in their level of detail as some sub-categories are subsets of others (Harrower et al. 2018). While an ef-

Table 2. Assessment of the introduction pathway classification frameworks, based on the CAGED properties. For each framework the method of development, the political level for which it was developed and level of detail is presented, together with an assessment indicating which of the five properties it possesses. As the main categories of the CBD framework were developed separately and using different methods, they were assessed separately from the sub-categories. Frameworks were partially compatible or actionable if some categories possessed the property, but not all. It is uncertain if the sub-categories of the CBD framework are distinct, as the definitions in the proposed guidelines have not been widely tested. See Table 3 for details of the scoring of the CBD framework's sub-categories.

Framework	Method of development	Political level	Number of categories	Property				
				Compatible	Actionable	General	Equivalent	Distinct
New Zealand biosecurity surveillance system	Based on the location of biosecurity pressures and interventions	Country	Six	Partially	Yes	No	No	Yes
Main categories of the CBD framework	Three pre-determined criteria	Global	Six	Yes	Yes	Yes	Yes	Yes
Sub-categories of the CBD framework	Compared and incorporated existing frameworks	Global	44	Partially	Partially	No	No	Uncertain

fort has been made to link the sub-categories to existing regulations and international management tools, for most sub-categories, pathway-specific management tools were not identified (CBD 2014) and a number of the sub-categories are managed using the same tools (see Table 3 for details). If many sub-categories are managed using the same tools, then the results from analyses using the framework will need to be re-interpreted to provide information for management (the data from various sub-categories would have to be merged) and this puts into question why such a high level of detail is required. Therefore, while the sub-categories were developed to inform specific, tailored management (Essl et al. 2015), there is little evidence that they do.

Despite their high level of detail, the sub-categories are also not likely to be appropriate for all regions. Geographically biased datasets (largely European and global datasets (e.g. GISD) that contain few data from developing regions) were used to develop the sub-categories. Consequently, it is likely that some pathways that are important in under-studied or developing regions will not fit into the detailed sub-categories of the framework. Furthermore, the data that are available will often not

Table 3. The evidence used to assess the sub-categories of the CBD introduction pathway classification framework. Presented are the CAGED properties, the outcomes of an assessment indicating which of the five properties the xsub-categories possess and the evidence.

Property	Outcome	Evidence
Compatible	Partially	The level of detail of some of the sub-categories is suitable for the classification of the available data, but published assessments have highlighted that, for some of the sub-categories, the information available is often not sufficiently detailed for classification and, consequently, pathways map on to more than one sub-category (see Tsiamis et al. 2017, Zenetos 2017, van Wilgen and Wilson 2018). For example, the level of detail required to determine whether a marine species was introduced through hull fouling or the release of ballast water is often not available (Tsiamis et al. 2017, Zenetos 2017).
Actionable	Partially	In a technical note, an effort was made to link the sub-categories of the framework to interventions (see CBD 2014). Existing international tools that are pathway-specific were only identified for 14 of the 44 sub-categories, with no pathway-specific tools identified for, for example, 'fur farms', 'contaminated bait' and 'stowaways on land vehicles' (CBD 2014). Furthermore, a number of the sub-categories are managed using the same tools. For example, the multiple sub-categories that pertain to the introduction of contaminants of imported plants or plant products are managed using the standards developed under the International Plant Protection Convention and the pre- and at-border management for all of these pathways would be similar.
General	No	Published assessments have highlighted that many of the sub-categories are only appropriate for specific taxonomic groups or habitats (see Matthews et al. 2014, Padayachee et al. 2017, Saul et al. 2017). For example, the 'horticulture' sub-category is specific to plants, while the 'airplane' sub-category is specific to the terrestrial habitat. Consequently, variations across taxonomic groups and habitats have only been assessed at the main category level (e.g. Padayachee et al. 2017, Saul et al. 2017). The sub-categories are not applicable to all regions. For South Africa, 8% of known introductions with a recorded pathway did not fit into any of the detailed sub-categories and had to be classified into the 'other' sub-categories (Suppl. material 1: Fig. S3). For some regions, introductions are often due to a few, highly prominent sub-categories, with no introductions through others (see Suppl. material 1: Fig. S3 and Matthews et al. 2014). The sub-categories are very specific and so may not be able to incorporate data for new pathways.
Equivalent	No	Sub-categories of the framework are subsets of others. For example, four sub-categories ('nursery material contaminant', 'seed contaminant', 'timber trade contaminant' and 'parasite of plants') are subsets of the 'contaminant of plants' sub-category, while the 'fur farms' sub-category is a subset of the 'farmed animals' sub-category (Harrower et al. 2018).
Distinct	Uncertain	Published assessments have highlighted that the differences between the pathway sub-categories are unclear (Saul et al. 2017, Tsiamis et al. 2017, Grousset et al. 2018, van Wilgen and Wilson 2018). For example, the difference between the 'horticulture' and 'ornamental' sub-categories is uncertain (Tsiamis et al. 2017). Consequently, in some instances, species have been assigned to pathways which are indirectly associated with introduction (although, in some cases, this is due to differing opinions on how classifications should be done (Harrower et al. 2018)), for example, pathogens introduced as contaminants of agricultural products assigned to the 'agriculture' sub-category (Qongqo 2018). Recently produced guidelines for the framework (Harrower et al. 2018) provide detailed descriptions of the main categories and sub-categories and define the pathways in relation to one another. Therefore, the differences between the sub-categories should now be clear. However, as the guidelines have not been widely tested, it is uncertain as to whether the sub-categories are distinct.

be of sufficient detail for classification. Pathways that will pose a challenge include the traditional medicine trade, which is an important pathway of introduction in South Africa (Byrne et al. 2017; Burness 2019). The traditional medicine trade in South Africa largely occurs in informal markets and it is highly unlikely that the details that are required to classify these introductions, according to the sub-categories of the CBD framework, will be available (e.g. whether the species was imported and released to be harvested later, whether it was imported in a form that is ready to be processed/consumed or whether it was farmed in controlled situations from which some individuals escaped). Even if these details were available, most of these introductions would be classified within the catch-all 'other' sub-categories of the framework, while the remaining introductions, those species that are 'farmed' for this purpose, would be classified within the 'horticulture' sub-category. This classification is not useful, as the traditional medicine trade is often informal and it would be inappropriate/ineffective to regulate and manage it in the same way as commercial horticulture. Therefore, the sub-categories of the CBD framework are not general enough to be applicable to this pathway, but they are also not compatible with the available data. While some studies have highlighted that some of the sub-categories are too detailed to be compatible with the available data (e.g. van Wilgen and Wilson 2018), further testing is required to determine the extent to which this is an issue, especially for developing regions.

The reason that the sub-categories of the CBD framework have few of the CAGED properties might be because they were not developed from first principles and were informed by geographically restricted or biased datasets. The guidelines for the framework (Harrower et al. 2018) should reduce the ambiguity of the sub-categories; however, this needs to be widely tested (see Pergl et al. 2020). It is important to note that the definitions proposed by Harrower et al. (2018) highlight that there are often subtle differences between the sub-categories. Therefore, while the proposed definitions could reduce the ambiguity of the sub-categories, for introductions to be consistently and correctly classified, users of the framework will need to invest a considerable amount of time to understand the differences between them. It remains to be seen how many countries will invest the time required.

A way forward

An introduction pathway classification framework will likely be an important tool in efforts to track progress towards meeting the Convention on Biological Diversity's post-2020 target on invasive alien species (Essl et al. 2020). However, the current CBD framework, or at least the framework's sub-categories, has few of the properties that such a framework should have (i.e. the CAGED properties). The relative importance of the CAGED properties will vary depending on the context for which a framework is developed. However, all the CAGED properties are required if frameworks that are developed in a global context (like that proposed by the CBD) are to be effective. We present four scenarios for how the identified issues could be addressed, with the aim of ensuring the development of a global level framework that has categories that are compatible, actionable, general, equivalent and distinct (i.e. CAGED).

1 Refine the current CBD framework: make adjustments as required and create a process for updating and adapting the framework so that it can better respond to the needs of the users. As the framework was developed within the last six years, there may not have been sufficient time for the framework to be adequately tested and for wrinkles to be identified and ironed out. The framework has already been put into practice and so, this would be the simplest way to move forward. As a start, the adjustments and recommendations proposed by Harrower et al. (2018) and Pergl et al. (2020) could be widely tested and adopted and the terminologies could be better aligned with those used in related fields (see Paap et al. 2020). The effort that would be required to implement any changes (i.e. the re-assignment of data) would also need to be considered. Furthermore, before being put into effect, the changes would need to be tested and widely accepted, ideally published in a peer-reviewed journal, recognised by the CBD and maintained as a standard (Wilson et al. 2020-a).

2 Develop a new framework: design a new framework that has categories that are CAGED at a global level. The development of a new framework should ideally be based on first principles and there would have to be a process to obtain consensus from the global community on interpretations of categories and their definitions (Tsiamis et al. 2017). Before adoption, the framework would need to be thoroughly tested using data from a wide range of regions, taxonomic groups and habitats. This test should involve a number of individuals from all groups of stakeholders that would apply the framework (i.e. more than one person should classify pathways using the framework) and the consistency of their classifications should be assessed. This would require a considerable amount of work and records in existing databases that have been classified using the CBD framework would have to be re-classified. This new framework would ideally be backwardly compatible with the CBD framework, though this would be undesirable if it came at the expense of the CAGED properties.

3 Develop context-specific frameworks: biological invasions are not managed at a global scale and so a single global framework may not be appropriate. For example, in South Africa, most known introductions for which a pathway was recorded have been assigned to only four of the CBD framework's sub-categories (‘horticulture’, ‘biocontrol’, ‘agriculture’ and ‘other escape’) and there were no introductions through ten of the 44 sub-categories (Suppl. material 1: Fig. S3). Therefore, in the South African context, it is inappropriate to manage many of the pathways in the CBD framework and reporting on them could be misleading. For example, there has only been one known introduction to South Africa for fur farming and so, while technically one can report that this pathway is managed, this is misleading (Table 1). The CBD framework may also not be appropriate in the context of secondary dispersal (i.e. dispersal of an alien species after introduction; but see Pergl et al. 2020) and so, a separate framework may be required to monitor and report on the movement of alien species post-border. Therefore, context-specific frameworks could be more valuable. As context-specific frameworks would make data exchanges and cross-cutting research more difficult and labour intensive, they should ideally align.

4 Use a hybrid model: Use the six main categories of the CBD framework (possibly with the recommendations of Pergl et al. (2020) and Paap et al. (2020) incorporated

following testing), but encourage countries to develop their own sub-categories (e.g. that are explicitly relevant for local management) or adapt the sub-categories so that they meet their needs. Countries could report to international organisations at the main category level, but context-specific variation would be accommodated at lower levels of the framework. This would additionally allow countries or regions (e.g. Europe) that have adopted the CBD framework to continue to use it in its entirety.

In conclusion, the main categories of the CBD framework have all of the desirable properties of an introduction pathway classification framework, but the sub-categories have few and so there is a need for improvement. Whether one of the four scenarios listed above is the best way to move forward or whether a different approach is preferable, will require further discussion. Even in the absence of most CAGED properties, all current frameworks can help to improve our understanding of biological invasions. However, to facilitate cross-cutting analyses, provide information for policy and enable reporting to national and international organisations, a classification at a higher level using a few, inclusive categories that fulfil the CAGED properties appears most appropriate. While higher level categorisation can also provide information for management interventions that aim to prevent introductions and facilitate the prediction of threats, detailed, context-specific categories may be more effective in these instances. Thus, our view is that, while it is possible to refine or fundamentally recast the CBD framework, a universal framework may simply be too general to ever be useful in specific applied contexts. As such, we believe a hybrid model – a few general categories at the global scale and context-specific sub-categories driven by local needs at a regional level – may be the most appropriate.

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Supplementary material 1

Evidence used to assess the introduction pathway classification frameworks

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Data type: Additional information

Explanation note: Evidence not included in the paper that was used to assess whether three introduction pathway classification frameworks are fit for purpose.

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Appendix 1

	Introduction pathway classification framework	Proposed revisions to the introduction pathway classification framework	
RELEASE IN NATURE	Biological control	Biological control	**RELEASE**
	Erosion control/dune stabilisation	**Stabilisation and barriers**	
	Fishery in the wild	Fishery in the wild	
	Hunting	Hunting	
	Landscape/flora/fauna "improvement" in the wild	**Aesthetic release**	
	Introduction for conservation purposes or wildlife management	**Conservation in wild**	
	Release in nature for use other than above	**Other release**	
	Other intentional release		
ESCAPE FROM CONFINEMENT	Agriculture	Agriculture	**ESCAPE**
	Aquaculture/mariculture	**Aquaculture**	
	Botanical garden/zoo/aquaria	**Botanical gardens & zoos**	
	Pet/aquarium/terrarium species	**Pet**	
	Farmed animals	Farmed animals	
	Forestry	Forestry	
	Fur farms	Fur farms	
	Horticulture	Horticulture	
	Ornamental purpose other than horticulture	**Ornamental**	
	Research and ex-situ breeding	**Research**	
	Live food and live baits	Live food and live bait	
	Other escape from confinement	**Other escape**	
TRANSPORT-CONTAMINANT	**Contaminant nursery material**	**Nursery material contaminant**	**CONTAMINANT**
	Contaminated bait	**Bait contaminant**	
	Food contaminant	Food contaminant	
	Contaminant on animals	**Contaminant of animals**	
	Parasites on animals	**Parasites of animals**	
	Contaminant on plants	**Contaminant of plants**	
	Parasites on plants	**Parasites of plants**	
	Seed contaminant	Seed contaminant	
	Timber trade	**Timber trade contaminant**	
	Transportation of habitat material	**Habitat material contaminant**	
	NA	**Other contaminant**	
TRANSPORT-STOWAWAY	**Angling/fishing equipment**	**Fishing equipment**	**STOWAWAY**
	Container/bulk	**Container/bulk cargo**	
	Hitchhikers in or on airplane	**Airplane**	
	Hitchhikers on ship/boat	**Ship excluding ballast water or hull fouling**	
	Machinery/equipment	**Machinery & equipment**	
	People and their luggage/equipment	**People & luggage**	
	Organic packing material, in particular wood packaging	**Packing material**	
	Ship/boat ballast water	**Ballast water**	
	Ship/boat hull fouling	**Hull fouling**	
	Vehicles	**Land vehicles**	
	Other means of transport	**Other stowaway**	
CORRIDOR	**Interconnected waterways/basins/seas**	**Canals and artificial waterways**	CORRIDOR
	Tunnels and land bridges	**Tunnels and bridges**	
UNAIDED	**Natural dispersal across borders of invasive alien species that have been introduced through pathways 1 to 5**	**Natural dispersal**	UNAIDED

Figure A1. The introduction pathway classification framework developed for the Convention on Biological Diversity and changes, shown in bold, to the framework as recommended in guidelines produced by Harrower et al. (2018). The guidelines were written specifically to avoid making major changes to the framework. The proposed structural changes were that two overlapping sub-categories be merged and that a catch-all sub-category (called 'other contaminant') be added for contaminant introductions that do not fit into any of the detailed sub-categories.

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RESEARCH ARTICLE

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The Epidemiological Framework for Biological Invasions (EFBI): an interdisciplinary foundation for the assessment of biosecurity threats

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Abstract

Emerging microparasite (e.g. viruses, bacteria, protozoa and fungi) epidemics and the introduction of non-native pests and weeds are major biosecurity threats worldwide. The likelihood of these threats is often estimated from probabilities of their entry, establishment, spread and ease of prevention. If ecosystems are considered equivalent to hosts, then compartment disease models should provide a useful framework for understanding the processes that underpin non-native species invasions. To enable greater cross-fertilisation between these two disciplines, the Epidemiological Framework for Biological Invasions (EFBI) is developed that classifies ecosystems in relation to their invasion status: Susceptible, Exposed, Infectious and Resistant. These states are linked by transitions relating to transmission, latency and recovery. This viewpoint differs markedly from the species-centric approaches often applied to non-native species. It allows generalisations from epidemiology, such as the force of infection, the basic reproductive ratio R_0, super-spreaders, herd immunity, cordon sanitaire and ring vaccination, to be discussed in the novel context of non-native species and helps identify important gaps in the study of biological invasions. The EFBI approach highlights several limitations inherent in current approaches to the study of biological invasions including: (i) the variance in non-native abundance across ecosystems is rarely reported; (ii) field data rarely (if ever) distinguish source from sink ecosystems; (iii) estimates of the susceptibility of ecosystems to invasion seldom account for differences in exposure to non-native species; and (iv) assessments of ecosystem susceptibility often confuse the processes that underpin patterns of spread within -and between- ecosystems. Using the invasion of lakes as a model, the EFBI approach is shown to present a new biosecurity perspective that takes account of ecosystem status and complements demographic models to deliver clearer insights into the dynamics of biological invasions at the landscape scale. It will help to identify whether management of the susceptibility of ecosystems, of the number of vectors, or of the diversity of pathways (for movement between ecosystems) is the best way of limiting or reversing the population growth of a non-native species. The framework can be adapted to incorporate increasing levels of complexity and realism and to provide insights into how to monitor, map and manage biological invasions more effectively.

Keywords
Alien, climate change, COVID-19, eradication, exotic, metapopulation, SEIR; state-and-transition models, vectors

Introduction

Emerging microparasitic diseases and biological invasions by non-native species represent two of the most significant biological threats to the survival of endangered species, the ecological integrity of ecosystems, the economic productivity of agriculture and the quality of human health (Early et al. 2016; Halliday et al. 2017; Ogden et al. 2019; Paini et al. 2016). There are fundamental differences between microparasites (e.g. viruses, bacteria, protozoa and fungi) and non-native species (e.g. plants, invertebrates and vertebrates) in their life-history and epidemiology (Table 1, Morand et al. 2015). However, invasions by microparasites and non-native species can be similarly conceptualised as comprising a minimum of two interacting components: an agent (e.g. microparasite or non-native species) and one or more receptors (e.g. host or ecosystem). They also share commonalities in that they both require an agent to be introduced into a new area, for it then to establish and reproduce and subsequently spread over large spatial scales (either naturally or via a vector) when it may have an impact on the environment, as well as human, plant or animal health. The similarity in the process of invasion is such that the threats these different classes of invader pose to the environment, human, plant or animal health are often assessed using the same risk assessment tools (Baker et al. 2008; Ireland et al. 2020). Indeed, when non-native species act as hosts, their spatial dynamics often play an important role in the introduction, establishment and spread of microparasites (Bufford et al. 2016; Hulme 2014).

Epidemiologists have highlighted the crucial importance in disease management of integrating the population dynamics of the agents, as well as the states and transitions amongst receptors (Diekmann et al. 2013; Loker and Hofkin 2015; Wilson et al.

Table 1. Differences between microparasites and non-native species that are considered in the Epidemiological Framework for Biological Invasions.

Characteristic	Microparasites (e.g. virus, bacteria, fungus) infecting animal or plant hosts	Non-native species (e.g. plant, invertebrate, vertebrate) invading ecosystems
Agent demography	Demography of the agent within a host is rarely quantified and is assumed to play a limited role in disease epidemiology	Non-native species population dynamics within ecosystems are important in invasion dynamics
Agent distribution	Distribution of parasites amongst hosts is rarely modelled apart from whether infected or uninfected	Density varies amongst individual ecosystems and will influence demography and dispersal
Agent specificity	Usually one or a few closely-related hosts	Can often be generalists found in many different ecosystem types
Host distinctiveness	Usually easily defined (e.g. a particular species such as *Homo sapiens*) for which individuals can be distinguished	Ecosystems are more problematic to define as hosts, since they can sometimes grade into each other
Host heterogeneity	Low heterogeneity amongst susceptible hosts arising from similarities in physiology and immunology within a species	High heterogeneity amongst susceptible hosts due to differences in abiotic conditions and biotic communities within each class of ecosystem
Host immunity	Hosts, especially vertebrates, may naturally acquire short- or long-term immunity following infection	Ecosystems do not normally acquire natural immunity to further invasion by a species following its initial colonisation
Host mobility	Animal hosts are often mobile and host movements can be critical in the dynamics of disease	Ecosystems are, to all intents and purposes, immobile and thus, as hosts, may be better captured by plant epidemiological models
Host scale	With the exception of age-related variation, the size of a particular host species is similar across individuals	For a single ecosystem type, the area of individual localities can vary considerably
Host vital rates	Hosts can die as a result of infection and can be born	Ecosystem are not usually viewed as having vital rates
Vectors	Usually a living organism (e.g. mosquito, aphid) that carries microparasites from one host individual to another	Often a physical vehicle (e.g. train, car, boat) that transports a non-native species but can include living organisms (e.g. birds, humans)

2019). Invasions by microparasites and non-native species are inherently spatial processes, frequently affected by the distribution of receptors and the extent to which the (meta)populations of receptors are subdivided into networks of smaller, partly isolated, subunits (Briscoe et al. 2019; Seabloom et al. 2015; Tadiri et al. 2018). However, with the exception of plants, most hosts of microparasites are mobile and host movements can be critically important in the dynamics of disease. In contrast, ecosystems are, to all intents and purposes, immobile. Thus the spatial structure of ecosystems, particularly the extent of spatial clustering and the connectivity of the landscape, will likely play a more important role in biological invasions. Therefore, in many respects, the dynamics of agents and receptors in the invasion of ecosystems will have greater parallels with the epidemiology of plant than animal diseases.

Progress in understanding the dynamics of biological invasions has largely been agent-centred (Hui and Richardson 2017; Jeschke and Heger 2018; Liebhold et al. 2020). Given the important contribution of receptor-centred approaches in disease epidemiology, extending this perspective to biological invasions may similarly deliver considerable insights if ecosystems can be classified in terms of their susceptibility and exposure to non-native species, their contribution to the spread of invasions (i.e. their infectivity) and the likelihood and duration of any recovery. Furthermore, a more aligned approach to the study of biological invasions that builds on ideas developed within disease epidemiology will facilitate cross-fertilisation between the disciplines and, as a result, may deliver more comprehensive biosecurity policies (Crowl et al. 2008; Ogden et al. 2019).

Current understanding and management of emerging diseases has benefited from the progressive development of a multitude of epidemiological models (Diekmann et al. 2013; Kleczkowski et al. 2019; Rock et al. 2014). Yet despite a rich tradition of theory underpinning biological invasions (Hengeveld 1989; Lewis et al. 2016; Shigesada and Kawasaki 1997), epidemiological perspectives in this field have largely focused on the analysis of introduced microparasites of humans (Li et al. 2019; Sun et al. 2018), animals (Orsel et al. 2009; Samuel et al. 2011) or plants (Cunniffe et al. 2016; Soubeyrand et al. 2018). Underlying all dynamical system models of epidemiological processes is the basic SIR framework (Fig. 1A) in which receptors (e.g. hosts) are categorised into three compartments: Susceptible, Infectious and Resistant (sometimes classed as Removed or Recovered), based on their infection status (Blackwood and Childs 2018; Gilligan 2008; Kleczkowski et al. 2019). Some infections do not provide long-lasting acquired immunity (e.g. HIV), which may parallel ecosystems for which resistance from invasion is either impossible or short-lived and, in these circumstances, an SIS model (Susceptible-Infectious-Susceptible) may be more appropriate (Diekmann et al. 2013). The independent variable in compartment disease models is time t and the rates of transfer between compartments is described by a series of ordinary differential equations that capture transmission and recovery rates (Brauer and Castillo-Chavez 2010). Simple SIR compartment disease models have provided important insights into disease epidemiology and can be readily expanded to capture more complex phenomena through the inclusion of additional compartments. However, these complex models often exhibit types of behaviour that are qualitatively similar to the simplest SIR model (Brauer and Castillo-Chavez 2010). Could such an approach also provide insights into biological invasions by species that are not pathogens or parasites?

Some might argue that, unlike hosts which are discrete entities (individual animals or plants), many ecosystems have far less clear-cut and temporally-stable boundaries (Evans and Brown 2017; Oliveras and Malhi 2016). The difficulty of the ecosystem concept is not exclusive to the field of biological invasions and it is understood to be an ad hoc construct on the part of an observer for a particular purpose (Gignoux et al. 2011). An important difference from the hosts of microparasites is that ecosystems show much greater heterogeneity, both amongst different ecosystem types (e.g. tallgrass prairie, deciduous temperate forest, heathland), but also within a particular ecosystem type as a result of variation in biotic and abiotic conditions. Similarly, within a single ecosystem type, the areas of different localities can vary across many orders of magnitude (e.g. 0.1 to > 10,000 km^2), as in the case of lake ecosystems (Downing et al. 2006). Nevertheless, there is a long history of compartmentalising ecosystems into representative units. State-and-Transition Model (STM) approaches have long been used to define a discrete ecosystem, identify alternative ecosystem states and quantify the abiotic (e.g. drought, fire, eutrophication) and biotic (e.g. grazing, insect outbreaks) drivers that lead to transitions from one ecosystem state to another (Bestelmeyer et al. 2017). The STM framework has increasingly been used to model shifts in ecosystem state as a result of biological invasions by non-native plants, pathogens and animals (Cobb et al. 2017; Jarnevich et al. 2019; Perry et al. 2015; Stein et al. 2016). Furthermore, STMs are also one of the most widespread modelling techniques in clinical decision analysis to capture transitions in disease status of individual patients (Siebert et al. 2012). While STMs are superficially similar in structure to SIR models (Fig. 1B), the rates of transfer between compartments (states) is usually described by linear models that capture the effect of combinations of biotic and abiotic drivers (Bestelmeyer et al. 2017). Thus progressive deterioration of an ecosystem due to human activities can be captured by flows from a pristine ecosystem to one that is disturbed as a result of anthropogenic fire regimes that, if not restored, would further degrade under the pressure of overgrazing (Fig. 1B).

The foregoing discussion of SIR and STM approaches highlights a sufficient number of parallels between microparasitic diseases and non-native species invasions to suggest that the bringing together of these different compartment perspectives may provide a valuable framework to further the current understanding of biological invasions. Indeed, epidemiological compartment models have been applied to describe the status of farms as Susceptible or Infectious in the analysis of foot-and-mouth disease (Rossi et al. 2017) and, thus, it is only a small step to extend this perspective to ecosystems. Compartment models have provided the basis for key epidemiological insights including: thresholds for disease persistence, rate limiting functions for microparasite population growth, criteria for stable dynamics, impact of different transmission functions on disease spread and optimal control strategies (Kleczkowski et al. 2019; Rock et al. 2014). Similarly, STMs have been used to detect thresholds, identify positive and negative feedbacks, as well as indicate the reversibility of change in ecosystem properties (Bestelmeyer et al. 2017). By linking together these different modelling perspectives, the opportunity therefore exists to:

1. Construct an epidemiological framework that captures the fundamental components of a compartment disease model for non-native species and invaded ecosystems.
2. Assess the relevance of the framework to non-native invasion dynamics in relation to the large body of theory that has addressed microparasite infections.
3. Examine the implications of the compartment disease model perspective for the management of biological invasions at the ecosystem level.

Given that epidemiological studies on non-native species have only been undertaken on those species that are pathogenic or parasitic (Lewis et al. 2016), there are currently insufficient data to build an epidemiological model for biological invasions by non-native plants, invertebrates or vertebrates. Nevertheless, by outlining a structure and the necessary parameters, a framework can provide a robust foundation for future modelling approaches.

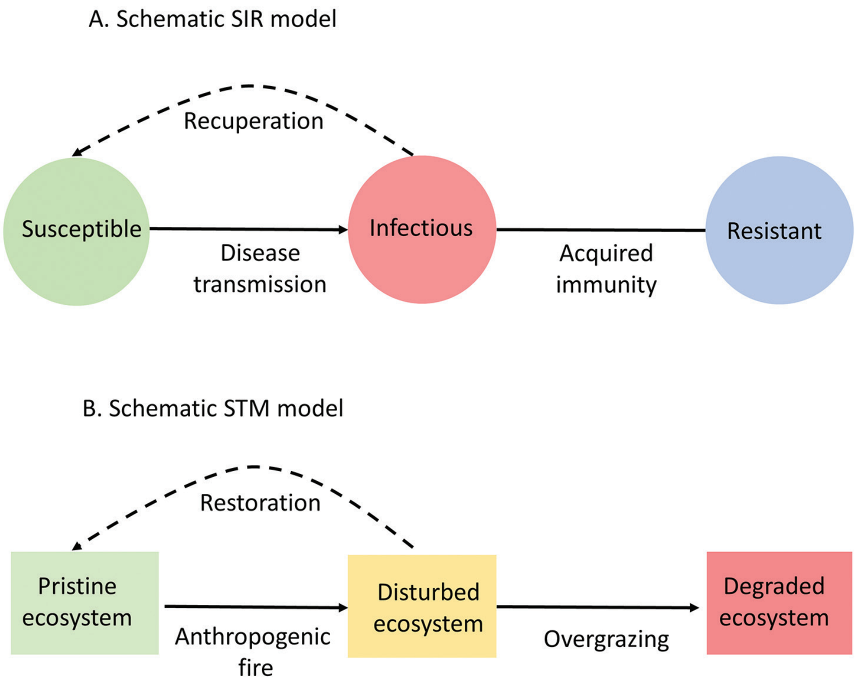
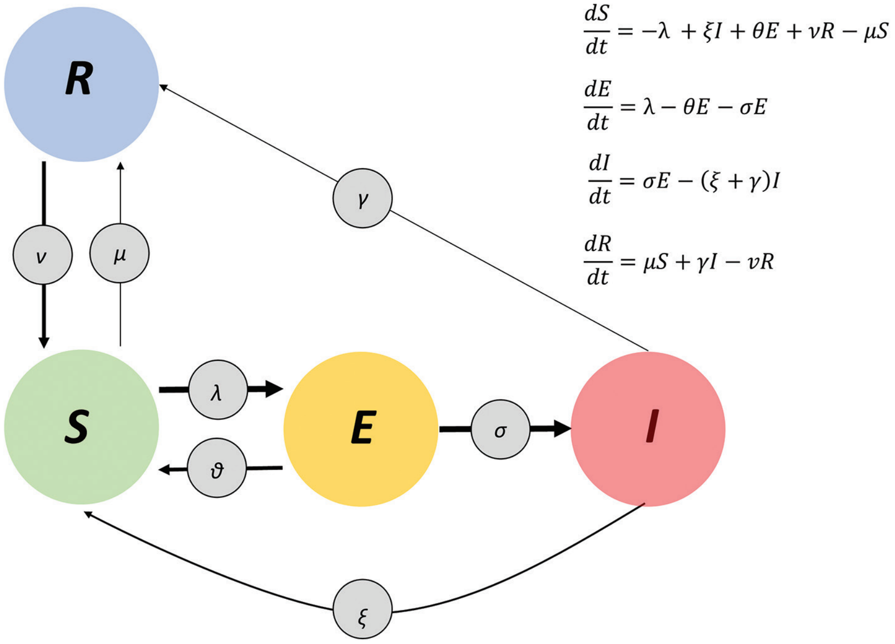


Figure 1. Similarities between a simple Susceptible-Infectious-Resistant compartment model for a microparasitic disease and a state-and-transition model describing progressive ecosystem degradation. Both types of model show transitions between different states (solid arrows) with potential for reversal (dotted arrows).

Components of an Epidemiological Framework for Biological Invasions

The SIR model (Fig. 1A) has been widely adapted to include greater complexity including additional compartments, such as Exposed but not Infectious (capturing latency in infectiousness), cryptic Infectious (infectiousness prior to the onset of symptoms), Immunised (as a result of vaccination) and Quarantine (temporally isolated), as well as subdividing individual compartments by age-class or behaviour (Brauer and Castillo-Chavez 2010). The proposed framework for non-native species combines elements of both SEIR (Susceptible - Exposed – Infectious – Resistant) and SEIS (Susceptible – Exposed – Infectious – Susceptible) models of microparasite infections to characterise the ecosystem states and transitions that are more appropriate for the management of biological invasions (Fig. 2). Within the framework, an ecosystem can also be considered to exist in one of four different states in relation to a non-native species: Susceptible (S); Exposed (E); Infectious (I); and Resistant (R). The key flows linking the four states are the force of infection (λ) between Infectious and Susceptible ecosystems, the probability of transition from Exposed to Infectious (σ), the rate of natural recovery of Infectious ecosystems (ξ), the rate of recovery of Infectious ecosystems following management (γ), the rate at which Exposed ecosystems revert to the Susceptible state (θ), the rate at which Resistant ecosystems enter the Susceptible state (ν) and the rate



$$\frac{dS}{dt} = -\lambda + \xi I + \theta E + \nu R - \mu S$$

$$\frac{dE}{dt} = \lambda - \theta E - \sigma E$$

$$\frac{dI}{dt} = \sigma E - (\xi + \gamma)I$$

$$\frac{dR}{dt} = \mu S + \gamma I - \nu R$$

Figure 2. Schematic compartment model illustrating how ecosystems may be classified into four invasion states (Susceptible, Exposed, Infectious and Resistant) linked by transitions relating transmission of non-native species amongst ecosystems, exposure and recovery. The characteristic dynamics within a receptor will exhibit three phases: a period prior to colonisation; growth as the local population increases; followed by fluctuations around the steady state. These phases can be identified with the epidemiological categorisations of Susceptible (no non-natives present), Exposed (low numbers of non-natives with essentially no dispersal) and Infectious (a viable population of non-native species contributing to dispersal). Termination of the Infectious state corresponds to the collapse of the meta-stable population due to stochastic events or some externally driven change (e.g. in the birth or death rates) or intervention which removes the local population and results in the receptor returning to either being Susceptible again or Resistant. Transitions between the four different states are: λ = the force of infection between Infectious and Susceptible ecosystems; θ = the rate at which an Exposed receptor reverts to become Susceptible; σ = the latency between initial exposure and infectivity; ξ = the rate of natural recovery of Infectious ecosystems to the Susceptible state; γ = the rate recovery of Infectious ecosystems following management to the Resistant state; ν = the rate which Resistant ecosystems enter the Susceptible state; μ = the rate which Susceptible ecosystems become Resistant. The total number of ecosystems (N) is given by the sum of the number of ecosystems in each state. Different weights for each arrow are for illustration only to highlight that transition rates between compartments differ and illustrate the probable importance of different transitions in biological invasions.

at which Susceptible ecosystems become Resistant (μ). The total number of ecosystems (N) is given by the sum of the number of ecosystems in each state.

The overall framework proposed is simpler than compartment disease models since sex-structure, maternal effects and vertical transmission do not have clear equivalents when applied to ecosystems. Although ecosystems can be created and destroyed by humans (e.g. creation of water reservoirs *versus* the draining of lakes), the model does not include any processes that increase or reduce the numbers of ecosystems. A further difference is that many ecosystems, either inherently or through human activities, may be entirely unsuitable for occupation by a particular non-native species. These ecosystems are described as Resistant since the growth rate of a non-native population is likely to be negative and extinction will be an inevitable consequence of any colonisation event. Resistant ecosystems are only included in compartment models if they can become Susceptible through some external agency (e.g. climate change, anthropogenic disturbance), otherwise they play no part in the epidemiology of invasion. Resistant ecosystems may be transformed into Susceptibles (at a rate ν) by a range of external pressures (e.g. fire, grazing, climate change, eutrophication). Similarly, Susceptibles can be transformed into the Resistant state (at a rate μ) by the reversal of many of those pressures. In contrast to SEIR models, this can occur without having to pass through the Exposed state. Thus, unlike standard SEIR models, at the beginning of any simulation, the Resistant state will contain ecosystems that have never been Exposed, but are capable of being transformed to become Susceptible.

The characteristic dynamics of non-native species within an ecosystem will exhibit three phases: a period associated with early colonisation; growth of the non-native population; followed by fluctuations around a steady state. These phases correspond to the following states: Susceptible (no agent present), Exposed (low numbers of agents with no dispersal outside of the ecosystem) and Infectious (a viable population of agents contributing to dispersal). Transition from the Exposed (at a rate θ, Fig. 2) or Infectious (at a rate ξ, Fig. 2) states to Susceptible or from Susceptible (at a rate μ, Fig. 2) or Infectious (at a rate γ, Fig. 2) states to Resistant corresponds to the collapse of the population due to stochastic events or some externally-driven change, such as the eradication of the non-native population from the ecosystem. The following sections use examples drawn from both the epidemiological and invasion literature to illustrate the utility of the Epidemiological Framework for Biological Invasions and highlight similarities in the factors that determine the different states and the flows that link them. These similarities emphasise how epidemiological perspectives can advance current understanding of biological invasions.

Relevance of an Epidemiological Framework for Biological Invasions

By examining the similarities and differences between microparasitic diseases and non-native species invasions for the different compartments of an SEIR disease model, it may be possible to identify the key parameters of an Epidemiological Framework for Biological Invasions that will facilitate cross-fertilisation between disease and invasion biology.

Susceptibility

Certain ecosystems are known to be inherently more susceptible to the colonisation by a non-native species than others. At any one time within a population of N ecosystems (which could be different ecosystem types or different areas of a single ecosystem type), the rate of change in the number of Susceptible ecosystems (*S*) will be a function of the rate at which Susceptibles become infected and move to the Exposed class (λ, the force of infection), become resistant and move to the Resistant class (μS), as well as the rates at which Infectious (ξI), Exposed (θE) and Resistant (vR) classes become Susceptible (Fig. 2, Eqn 1).

$$\frac{dS}{dt} = -\lambda + \xi I + \theta E + vR - \mu S \tag{1}$$

Susceptibility can be viewed at two levels: amongst different types of receptors (e.g. woodlands, grasslands and wetlands) and within a single receptor type (e.g. coniferous forest). Intriguingly, the balance of effort has differed between disease and invasion studies: the former have focused more strongly on intra-host variability (Fellous et al. 2012; Tack et al. 2014; Vale 2013), whereas the latter have largely addressed why some ecosystems are more vulnerable to invasion than others. This is understandable since many microparasites have a relatively-narrow host range (Loker and Hofkin 2015), but a single non-native species can often colonise a wide range of different ecosystem types (Affre et al. 2010). Nevertheless, similarities exist in the factors influencing the relative susceptibility of different host species to microparasites and ecosystems to non-native species. For example, the absence of specific tissue or cellular receptors for colonisation of hosts by microparasites (Doran et al. 2016; Toruno et al. 2016) is equivalent to the absence of suitable resources (e.g. diet, habitat, symbiont) for a non-native species (Gioria and Osborne 2014). Temperature of the host may limit microparasite growth (Fang et al. 2016), just as it can limit the establishment of poikilothermic non-native animals and frost-intolerant plants (Hulme 2017). A lack of the exact nutrient requirements to support microparasite growth or development (Johnson et al. 2010; Smith 2007) corresponds with the scarcity of non-native plants in nutrient-poor habitats. Even the dynamic nature of a host's immune response through phagocytic defences may have its counterpart in the role of natural enemies in limiting non-native species to certain ecosystems (Schulz et al. 2019). External drivers of susceptibility, such as ecosystem fragmentation and land-use change, can similarly affect invasions by non-native species (Riitters et al. 2018), as well as the spread of infectious diseases (Gottdenker et al. 2014).

Analogous factors also exist that influence susceptibility to microparasites and non-native species within a specific host or ecosystem. Host age, homeostatic disturbance, intercurrent disease, microbial antagonism and MHC diversity have all been proposed to influence host susceptibility to microparasites (Casadevall and Pirofski 2018). A similar list can be generated for the susceptibility to non-native species of an individual ecosystem type that includes successional age, habitat disturbance, the presence of other non-native species, competition with resident species and native species diversity (Guo et al. 2015). The concept of "invasional meltdown", where one non-native species facilitates the invasion by other species (Simberloff 2006), has similarities in the multiple opportunistic bacterial infections of individuals with HIV (Joos et al. 2007). Susceptibility is not necessarily an immutable characteristic of a receptor and external drivers, such as climate change, increases or decreases in resource supply, pollution etc., can lead to previously Resistant receptors becoming Susceptible (Guo et al. 2015; Johnson et al. 2010).

However, an important issue when examining ecosystem vulnerability to invasion is the need to control for variation in exposure to colonisation by non-native species (e.g. propagule pressure), because this is rarely independent of the type of ecosystem. When this has been taken into account, emerging hypotheses are that ecosystems that naturally experience recurrent disturbances and are rich in available nutrients are most susceptible to invasion (Aikio et al. 2012; Chytrý et al. 2008). The receptor-centred framework presented here requires that inherent susceptibility is assessed independently of exposure (e.g. propagule pressure and force of infection), since it provides the basis for clearer prioritisation of the ecosystems most at risk from biological invasions (Catterall et al. 2012).

Force of infection and transmission

The transitions between the Susceptible and Exposed and Infectious states have received considerable empirical and theoretical attention with reference to the factors shaping disease transmission (Johnson et al. 2019). The force of infection (λ) depends on the number of Susceptible receptors (S), the proportion of Infectious receptors (I/N) and the transmission rate (β) which is a function of the rate of contact between receptors and a per-contact probability of infection (Kleczkowski et al. 2019).

$$\lambda = \frac{\beta St}{N} \tag{2}$$

Epidemiological approaches have tended to focus on the spread of a disease following its establishment in the host population (Diekmann et al. 2013), whereas the study of biological invasions has stressed the role of propagule pressure (i.e. the number and frequency with which individuals of a particular non-native species are introduced) in determining whether or not the agent will establish itself in a specific ecosystem (Simberloff 2009). However, estimation of propagule pressure has largely focused on the raw numbers of individuals of a particular non-native species arriving into an ecosystem (equivalent to the contact rate) and less on the likelihood of establishment per contact (equivalent to the per-contact probability of infection). Vectors often facilitate the transmission of agents of disease and non-native species. Yet, although the terminology is the same, the processes by which vectors transmit microparasites and spread non-native species are often quite different. In epidemiology, a vector is usually an alternative host, whose demography and status (Susceptible, Exposed, Infectious etc.) is a fundamental component of disease dynamics. Furthermore, living vectors may exhibit specific host-seeking behaviour that will increase transmission rates (Wynne et al. 2020). In contrast, the most important vectors of non-native species are humans and human-driven instruments (e.g. boats, trains, cars) that may provide passive transport between locations (Hulme et al. 2008). The extent to which such passive vectors link similar ecosystems and facilitate transmission has yet to be explored in detail. There are, of course, exceptions to this dichotomy, such as the role played by unclean needles in the spread of HIV amongst intravenous drug users (Smith et al. 2005), the deliberate mailing of anthrax spores to unfortunate victims (Arora et al. 2012)), the role of frugivores in the dispersal of non-native plants (Dawson et al. 2011) and the many occasions where humans have selected, bred and deliberately released non-native species for hunting, fishing or biological control. It is becoming increasingly clear that, just as in the case of non-native species, complex vector components and multiple hosts are often involved in the transmission of emerging zoonotic diseases (Engering et al. 2013; Hulme 2014).

In the case of local direct transmission or spread of diseases, the simplest model assumes that exposure is a product of the numbers of Susceptible and Infectious receptors linked by a transmission function (Diekmann et al. 2013; Kleczkowski et al. 2019). Epidemiological SEIR models often assume homogenous mixing of Susceptible and Infectious receptors as a result of random movement of the receptors, but ecosystems cannot be assumed to “mix” in the same way as mobile hosts. The assumption of homogeneous mixing can provide general insights once an epidemic is well established, but can lead to errors if incorrectly assumed at the earliest stages (Del Valle et al. 2013). Instead, invasion models have focused on the agents’ dispersal kernel (Sullivan et al. 2017). Models of the dispersal of non-native species have moved from simple diffusion processes to explore stratified dispersal (multiple functions) and integro-difference equation approaches in order to capture the importance of rare long-distance dispersal events (Kot et al. 2012). Such dispersal models may be equally appropriate for microparasites, as in the case of foot and mouth disease in the UK, where local spread was from aerial plumes and typically modelled via a transmission kernel, based on Euclidean distance, but long distance movement occurred via vehicles (Keeling et al. 2003). Indeed, there is an increasing push to model microparasite transmission and non-native species dispersal in similar ways (Lindström et al. 2011).

Where mixing is known to be non-random but the variation in individual contact rates is poorly known, lattice models, in which random connections between neighbouring sites facilitate transmission, have been used to assess the role of connectivity and spatial heterogeneity in disease epidemics (Liccardo and Fierro 2015). However, when the movement of agents is facilitated by human activity (e.g. shipping, airfreight, railroads) and the origins and destinations of the activity are known, gravity models can be used to assess the potential spread of disease (Charu et al. 2017) and non-native species (Drake and Mandrak 2014). These models estimate rates of transmission as a function of the distance between receptors. Where additional data are available on contact rates between receptors, network models are appropriate to predict future disease and non-native threats (Silk et al. 2017). Receptors have transmission contacts only along the links in a specified network of hosts or ecosystems. The existence of a connection predisposes the receptors to infection, but does not guarantee it. The number of connections each receptor has with others can be modelled by choosing a particular degree distribution for the network (e.g. a power-law would describe most receptors having few connections but a small number having many). In these models, the agent usually originates in one or more randomly-selected Infectious nodes in a population that is otherwise made up of Susceptible receptors. For discrete time models, in every time-step, all the Susceptible neighbours of the Infectious nodes become infected with probability β (the transmission rate) per Infectious neighbour (Enright and Kao 2018).

Network models have been used to model the connections between individuals linked to the spread of sexually-transmitted diseases (Beyrer et al. 2012), the spread of COVID-19 in cities (Xue et al. 2020), the global movement of shipping that enables the spread of non-native species (Seebens et al. 2019), the dissemination of plant pathogens through international horticultural trade (Moslonka-Lefebvre et al. 2011) and parasite transmission in wildlife (White et al. 2017). Different network topologies have a significant impact on disease dynamics and can have a stronger impact on outbreak magnitude than fundamental microparasite features such as transmission rate, infection duration and immunisation ability with important implications for management and control (Strona et al. 2018). In both gravity and network models, key considerations underpinning the likelihood of transmission include the life-history traits of the agent, such as how likely it is to survive and/or increase in prevalence during transport, the ease of detection of the agent or its symptoms, as well as attributes of the pathways (or connections) themselves. These attributes include the duration and condition of transport and the probability of transfer to suitable receptors on arrival. As the importance of landscape and spatial heterogeneity in the transmission and dispersal of disease and non-native species is recognised, so it is likely that these fields will increasingly converge on common modelling approaches (Claflin et al. 2017; de la Fuente et al. 2018; Kirby et al. 2017).

Exposure and latency

Once it has been infected or colonised by an agent and assuming there is growth of the agent population, a Susceptible receptor enters the Exposed state. The transition of Exposed receptors to the Infectious state is determined by the latent period or lag-phase (determined by $1/\sigma$), that reflects the time elapsed before the emergence of symptoms of disease or noticeable impacts of the non-native species. For many diseases, the "latent period" is so brief that the Exposed state is not incorporated into compartment models, although the human prion disease, kuru, has an incubation period of between 40 and 60 years (Collinge et al. 2006). In contrast, the temporal dynamics of many non-native species show a marked "lag-phase" between initial colonisation and subsequent spread that can span several decades (Aikio et al. 2010; Coutts et al. 2018; Rouget et al. 2016). Drake (2005) compared the latent-period of bovine tuberculosis (*Mycobacterium bovis*) infection and the lag-phase in the spread of coypu (*Myocastor coypus*) in the UK and concluded that their different durations may be explained by the demographic stochasticity associated with small founder populations. Thus, the transition from the Exposed state reflects the turnover of agents within the receptor, which is determined by their rates of immigration, establishment, reproduction and mortality. In contrast to most microparasite SEIR models, epidemiological invasion models require knowledge of the population dynamics of the agent within the receptor. These mathematical models will need to track the population size of the non-native species within each particular ecosystem that has become Exposed, rather than simply their presence or absence. Allee dynamics, where populations experience low or negative per capita growth rates at low densities can result in longer lag-phases, slower spread and decreased establishment likelihood of both non-native species and microparasites (Tobin et al. 2011). During this phase, the agent may become extinct as a result of demographic stochasticity, in which case the receptor will revert to the Susceptible state (Fig. 2). The latent-period or lag-phase may also result from genetic processes including: selection and adaptation of agent genotypes to the receptor environment, purging of genetic load responsible for inbreeding depression, accumulation of additive genetic variation and recovery from loss of genetic diversity (Pysek and Hulme 2005; Vieira et al. 2019). Under these circumstances, the duration of the Exposed state may reflect the strength of selection pressures, generation time of the agent and the genetic diversity of the inoculum.

Infectivity

Once exposed and possibly following a latent period or lag-phase, a receptor may become Infectious. Whether or not an Exposed receptor transitions to the Infectious state will depend on the ability of the agent population to produce migrants or propagules that can colonise other receptors. This ability will be affected by the nature of density-dependence (including Allee effects) and the generation time of the agent (Cassey et al. 2014; Drake and Lodge 2006). Transmission of agents from one receptor to another may be passive (e.g. virus shedding, oocytes in faeces, wind-dispersed seeds) or via a vector (e.g. mosquito, frugivore, vehicle). For microparasites, the length of the infectious period, during which migrants or propagules are generated, can range from only a few days (e.g. COVID-19) to a decade or more (e.g. HIV). In contrast, without intervention, many non-native species can persist in ecosystems for centuries (Hulme 2020) and which therefore remain Infectious almost indefinitely. It might be expected that the likelihood of transmission to other receptors will be a function of local (within-receptor) population size, as it is in many macroparasites (Hollingsworth et al. 2015). Nevertheless, population size is only one factor influencing transmission rates since agents need to be dispersed and make contact with Susceptible receptors. Contact rates will reflect the attraction of receptors to agents or their vectors. This attraction and the availability of suitable vectors will influence both the spread of disease and non-native species. This is equally true for the host feeding preference of mosquitoes (Takken and Verhulst 2013) or the suitability of lake ecosystems for recreational anglers (Oh et al. 2018). In addition, the ultimate probability of transmission should increase as the duration of the infectious period lengthens.

While metapopulation models have been used to understand the spatial dynamics of disease (Grenfell and Harwood 1997; Parratt et al. 2016; Wang and Wu 2018) and non-native species (Pichlmueller and Russell 2018; Tamburello et al. 2019), attention has primarily focused on the demographic attributes of the agent rather than the infectivity of receptors. Within the Epidemiological Framework for Biological Invasions, Infectious receptors are those within which an agent can reproduce and from which it can disperse, either naturally or with human assistance. Not all receptors are equally likely to play a role in the spread of an agent, a number will act as sources (where agent population growth is positive) and others as sinks (where agent population growth is negative or dispersal is prevented) of varying strengths (Geoghegan et al. 2016). The importance of an Infectious receptor to the spread of an agent will be a function of its connectivity (e.g. existence of invasion corridors, proximity to Susceptible receptors) and of the agent's life-history.

The minimum evidence for classifying a receptor as Infectious is the persistence of the microparasite or non-native species. Such evidence is usually obtained through expression of symptoms or impacts on the receptor or detection of a persistent population of the agent using serological techniques or field surveys. Nevertheless, not all receptors classified as Infectious in this way may actually be capable of infecting Susceptible receptors. Furthermore, not all Infectious receptors will be symptomatic. As has been seen with COVID-19, asymptomatic hosts can contribute to the spread of disease, but go largely undetected and can therefore undermine efforts to control transmission (Gandhi et al. 2020). Although the ability to distinguish the occurrence of symptoms from an Infectious status has proved invaluable in the management of disease, such a classification of ecosystems remains in its infancy with respect to biological invasions. Non-native species may occur in an ecosystem without having a significant impact on native biodiversity or ecosystem function, yet that ecosystem may still contribute to the spread of the species. An "asymptomatic" Infectious state may also occur where non-native species possess covert resting stages (e.g. seeds, rhizomes, spores, cysts and eggs) that remain viable in the receptor without developing into adults, but may be dispersed passively by the transport of soil between ecosystems.

Recovery and resistance

In microparasitic diseases, the Infectious state comes to an end through the recovery or death of the host. Recovery may result from a natural acquired immune response and may render a receptor Resistant to further infection, either permanently (e.g. measles) or temporarily, in which the receptor becomes Susceptible at some time in the future (e.g. common cold). Alternatively, human intervention such as chemotherapy (e.g. antiviral drugs, antibiotics, fungicides, pesticides etc.) can lead to recovery, but only to the Susceptible rather than Resistant state. Evidence for natural recovery of ecosystems following invasion is scarce, although several cases of boom and bust dynamics of non-native species, where formerly widespread populations collapse, have been documented (Strayer et al. 2017). However, there is no general equivalent of acquired immunity to non-native species. While there is evidence that native insects and pathogens may adapt to non-native plant hosts and may even inflict severe damage, there is limited evidence that these natural enemies impede invasions or result in ecosystems no longer being Susceptible (Crous et al. 2017). In most cases, ecosystem recovery is the result of human intervention. Evidence of interventions resulting in successful recovery from biological invasions is mixed with about half of all non-native arthropod eradications being successful, while for non-native plant species most programmes have failed to deliver eradication (Hulme 2020) or promote ecosystem recovery (Prior et al. 2018) due to re-invasion. Nevertheless, possibly with the exception of a few classical biological control programmes, there are no studies suggesting that, even where eradication is completely successful, the ecosystems concerned are subsequently more resistant to future invasion. Therefore, it is likely that, for non-native species invasions, the rates at which Susceptible (μ) or Infectious (γ) receptors become Resistant will be negligible (Fig. 2).

In the case of microparasites, a high rate of transition to the Resistant state shortens the duration of the Infectious state, thus lowering the opportunities for transmission (Diekmann et al. 2013). To ensure the spread of disease under such circumstances, agents require a high transmission rate and short latent period. This points to a major difference from biological invasions in that, without a significant scope for ecosystem recovery, non-native species can persist even in the face of low transmission rates and long lag-phases. An understanding of the role of the Resistant state in the dynamics of disease is essential to the design of effective immunisation programmes. Therefore, more effort should be invested in research on ecosystem resistance to invasion and the development of tools that could be used to increase the resistance of ecosystems following the eradication on a non-native species.

Vital rates

The incorporation of host vital rates (births and deaths) into microparasite models can have dramatic implications for disease dynamics (Gallos and Fefferman 2015), but it is difficult to conceive of birth and death processes for entire ecosystems. Non-native species can dramatically impact species diversity and ecosystem functions following invasion and they may even transform ecosystems from one state to another (e.g. non-native rabbits impeding woody succession), but the spatial unit itself does not usually disappear (Vilà and Hulme 2017). Even if it is transformed to another ecosystem state (Cobb et al. 2017; Jarnevich et al. 2019; Perry et al. 2015; Stein et al. 2016), the receptor may remain Susceptible to further colonisation by non-native species and it may even continue to be Infectious. Human activities can, of course, create and destroy entire ecosystems. For example, the establishment of new forest plantations or their harvest can influence the spread and persistence of phytophagous non-native arthropods (Be et al. 2017); and newly-created reservoirs (Smith et al. 2015) or coastal marinas (Floerl et al. 2009) may act as stepping stones for the spread of non-native aquatic species. The potential importance of the addition or removal of ecosystems from a landscape for the spread of non-native species has received relatively little attention. but it may be a powerful driver of biological invasions, as well as a useful tool for management (Alharbi and Petrovskii 2019).

The value of the Epidemiological Framework for Biological Invasions

The foregoing sections have shown that, just as hosts may be viewed as ecosystems (Rynkiewicz et al. 2015), ecosystems can be viewed as hosts. One of the aims of the Epidemiological Framework for Biological Invasions is that it is designed to transfer the insights from compartment models of microparasitic diseases to the management of non-native species. The potential of this framework can be illustrated using three examples: (i) basic reproductive ratio for invasions; (ii) super-spreaders vs. sinks; and (iii) ring eradication and herd immunity.

Towards a basic reproductive ratio R_0 for biological invasions

The Epidemiological Framework for Biological Invasions is receptor-focused and, although complementary to more traditional agent-focused demographic models, it provides new opportunities to understand biological invasions. The agent-centred approach to biological invasions assumes the probability of successful invasion is a function of the intrinsic rate of population increase when a non-native species is rare (Grainger et al. 2019). However, the receptor-centred approach suggests that an estimate of the mean number of Susceptible receptors likely to be colonised from the first Infectious receptor may be a better indicator of invasion risk, since it explicitly includes both population growth and spread. This parameter is equivalent to the basic reproductive ratio (R_0) which is defined as the expected number of secondary infections in a population of Susceptible receptors arising from a single individual during their entire infectious period and it often serves as a threshold parameter that predicts whether an infection will spread. The basic reproductive ratio (R_0) is the product of the transmission rate and the average amount of time a receptor spends in the Infectious state and, the larger its value, the harder it will be to eradicate the microparasite or non-native species (Blackwood and Childs 2018). For non-native species, the duration of the Infectious state can be many decades so even if transmission rates are low, R_0 will be much greater than 1.0 and the invasion will persist. Therefore, the rate at which a non-native species is eradicated from ecosystems must be higher than the rate at which new ecosystems are colonised. If, as is likely, there are often few options for creating Resistant ecosystems and once a non-native species has been eradicated from an Infectious ecosystem, it reverts to being Susceptible, then the proportion of ecosystems from which invasion must be prevented will be close to 1.0 (Fine et al. 2011). This undoubtedly explains why, once a non-native species is widely established, it becomes almost impossible to eradicate. Perhaps the primary application of R_0 is not in predicting the difficulty of eradicating an established non-native species, but in assessing the potential risk posed by species that have yet to be introduced. Under this scenario, rather than derive an arbitrary score or probability on invasion likelihood, risk assessment tools could be designed to estimate $R_{0.}$

Identifying sources, super-spreaders and sinks

In models of biological invasions, Infectious receptors act as sources that are capable of infecting Susceptible receptors, but can also maintain non-native species populations in Exposed receptors that would otherwise become extinct without immigration. Sink ecosystems have been observed for non-native fish (Dauphinais et al. 2018) and plants (Seipel et al. 2016) while microparasites in dead-end hosts are unable to achieve further transmission (Geoghegan et al. 2016). Similarly, measles in small rural villages is often sustained by the influx of infectious individuals from neighbouring major urban centres (Grenfell and Bolker 1998). In many disease systems, < 20% of Infectious receptors may be involved in 80% of transmission (Stein 2011). The receptors that make up this 20% are usually referred to as super-spreaders and their identification and subsequent targeting is a fundamental goal in disease management. It is unclear if the same 80/20 rule holds for non-native species, but identifying Infectious receptors that are super-spreaders could be an important component of the management of biological invasions. How can managers identify these super-spreaders? Managers surveying the distribution of non-native species may face difficulties in distinguishing between the stochastic population dynamics that may occur during the latent/lag phase in source receptors and the transient dynamics of agents in sink receptors where populations are maintained by immigration. The former scenario requires greater vigilance from managers to ensure the Exposed state does not progress to become Infectious (Fig. 2 σ). In contrast, sink receptors play little further part in invasion dynamics, but may divert management resources away from more important targets. The stochastic population dynamics that occur during the lag-phase following infection makes it difficult for managers to distinguish sources from sinks. However, Runge et al. (2006) provide some useful guidance on how this may be done. Transient populations of non-native species are frequently recorded (e.g. as casual alien plants), but the dynamics of these populations are rarely documented (Iles et al. 2016; Brock and Daehler 2020). Distinguishing between sources and sinks is an essential component in managing diseases and biological invasions (Hulme 2020). Unfortunately, data relating to biological invasions tend to score ecosystems as invaded (i.e. Exposed or Infectious) or uninvaded (i.e. Susceptible or Resistant), but rarely quantify the distribution of agents amongst receptors or address the equivalent of the infectivity of a receptor. This issue could be addressed if epidemiological states and transitions were incorporated into spatio-temporal models representing the spread of non-native species through heterogeneous landscapes (Catterall et al. 2012; Mang et al. 2018).

Ring eradication and herd immunity

A much-debated approach for the management of microparasitic diseases is "ring vaccination" that targets immunisation to particular groups of Infectious receptors in order to prevent the spread of disease agents (Deen and von Seidlein 2018; Merler et al. 2016). A similar approach, which might be called "ring eradication" has been put forward for biological invasions, whereby non-native species eradication programmes may initially target small, isolated "satellites" first, rather than a single large core population, since many satellites will contribute disproportionally more to population expansion in a homogeneous environment (Hulme 2006; Kovacs et al. 2011; Panetta and Cacho 2014). However, in contrast to the management of diseases, quantitative assessments of the likelihood of containment of invasion through the targeted control of satellite populations through ring eradication have yet to be undertaken.

A more dramatic form of intervention is the establishment of a cordon sanitaire where locations containing high risk hosts are almost sealed from the outside world with severe restrictions placed on the movement in or out of the cordon sanitaire (Gostin et al. 2020). A dramatic example, recognised as the largest quarantine in history, was the cordon sanitaire imposed on Wuhan, a city of 11 million residents, with closure of all transport in and out of the city for 76 days to limit the spread of COVID-19 (Wan et al. 2020). Similar approaches have been used to prevent the spread of non-native species, including the establishment of movement controls, such as the Fruit Fly Exclusion Zone in Australia (Dominiak and Mapson 2017) and buffer zones around protected areas to prevent the spread of non-native weeds (Foxcroft et al. 2011).

The concept of "herd immunity" in which there may be a critical community size, beneath which persistence of metapopulations is not possible, has been influential in microparasitic disease management, since it suggests that only a proportion (albeit often high) of receptors needs to be managed (immunised) to prevent the persistence of disease (Metcalf et al. 2015). If applicable to non-native species, the concept of herd immunity could significantly assist control efforts. If a non-native species exhibited a metapopulation structure and was confined to a specific ecosystem type that was patchily distributed (e.g. lake ecosystems), then population persistence would depend on local dynamics and connectivity (Hastings 2014). In theory, reducing local population growth and eradicating the non-native species from a progressively greater proportion of patches to reduce connectivity could lead to the collapse of the metapopulation. Unfortunately, such an approach, while fine in theory, appears difficult to achieve in practice (Garcia-Diaz et al. 2019). Given that for many biological invasions, R_0 is much greater than 1.0, herd immunity would require most ecosystems to be or become Resistant which is unlikely since there is limited knowledge on what makes an ecosystem Resistant. Taken together this suggests that, for most biological invasions, it is currently impractical to attempt the equivalent of herd immunity for ecosystems.

Applying the Epidemiological Framework to Invasions in Lakes

There appear to be opportunities to apply a more epidemiological perspective to the spatio-temporal dynamics of non-native species, but the real test of the value of the Epidemiological Framework for Biological Invasions will be in its application to a specific case study. Lake ecosystems (including ponds and impoundments) are widely recognised as being discrete units in the landscape and, while connectivity amongst lakes can often

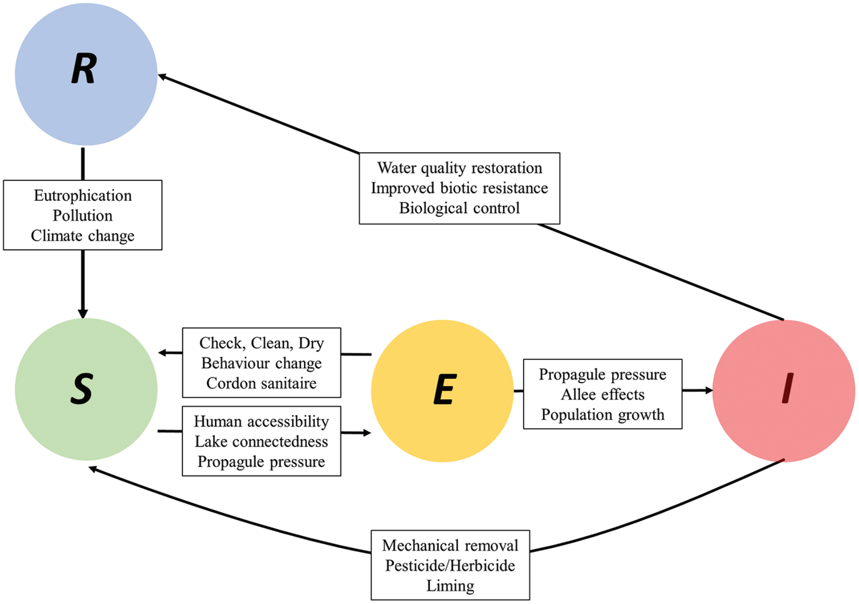


Figure 3. Schematic diagram based on a disease compartment model applied to invasions of lake ecosystems (lakes, ponds and impoundments) to illustrate the different variables that could influence the flows between Resistant, Susceptible, Exposed and Infectious compartments.

occur through natural watercourses or anthropogenic canals, the boundaries between lake ecosystems and surrounding ecosystems are often clear cut (Likens 2010). This discrete nature, combined with the fact that they represent one of the ecosystems most vulnerable to invasion by plants, invertebrates and vertebrates (Carpenter et al. 2011), make lake ecosystems particularly suitable for exploring the value of the Epidemiological Framework for Biological Invasions (Fig. 3). Despite their inherent vulnerability to biological invasions, the extent to which different lake ecosystems are Susceptible to non-native species colonisation can differ quite markedly even within the same landscape (June-Wells et al. 2013). Water chemistry, in particular the specific conductance and pH, is an important determinant of whether a particular non-native species can establish in a lake ecosystem and can be a significant barrier to invasion, effectively rendering the ecosystem Resistant (Karatayev et al. 2015). Coldwater temperatures may also act as a filter that prevents warmwater-adapted species from establishing self-sustaining populations in lake ecosystems (Rahel and Olden 2008). Thus, for a particular non-native species threat, it may be possible to distinguish Susceptible and Resistant lake ecosystems *a priori* and so establish the starting conditions for an epidemiological approach to understanding future invasions. Resistant lake ecosystems can become Susceptible when runoff from urban or agricultural land or pollution from domestic or industrial sources alters water conductivity and pH. Similarly, a warming climate may reduce the cold temperature limits that prevent some non-native taxa establishing in a lake ecosystem. However, even when Susceptible, invasion will not occur unless lake ecosystems enter the Exposed class and the likelihood of exposure to non-native species has been successfully modelled using environmental parameters that point to metrics capturing accessibility to the human population and connectivity to other lake ecosystems as being critically important (Compton et al. 2012; Leathwick et al. 2016; Tamayo and Olden 2014). The progression of lake ecosystems from the Exposed to the Infectious class will be a function of the propagule pressure (the number and frequency of introductions into a lake ecosystem) and specific attributes of the non-native species of concern, particularly Allee effects and the population growth rate (Gertzen et al. 2011; Leung et al. 2004). For lake ecosystems in the Infectious class, two routes exist for interventions that either result in a shift to the Susceptible or Resistant class. In the former, mechanical or chemical removal of the target non-native species can be successful (Rytwinski et al. 2019), but lake ecosystems often simply return to the Susceptible class and, depending on the unintended side effects of these treatments (e.g. disturbance, mortality of non-target native species), can become more prone to invasion. If lake ecosystems were initially Resistant, but have been converted to Susceptible as a consequence of environmental degradation and then subsequently become Infectious, then the potential exists for reversing the process through restoration of water quality or improving biotic resistance amongst resident species, particularly predators that might feed on non-native species. These interventions could, of course, be implemented before a lake ecosystem enters the Exposed class. Although classical biological controls do not usually remove the target non-native species completely, they have been used successfully to reduce the abundance of specific aquatic weeds and prevent their subsequent re-invasion over several years (Martin et al. 2018). Interventions can also be effective in limiting the transition from Susceptible to Exposed and include deterring or preventing boaters from accessing Susceptible lake ecosystems (e.g. by using a cordon sanitaire), targeted education including the prevention of inadvertent introductions through Check, Clean and Dry campaigns, as well as large-scale education efforts directed towards users of lake ecosystems (Morandi et al. 2015). Intriguingly, there is evidence that lake invertebrates (Freeland et al. 2000), fish (Murphy et al. 2012; Wilberg et al. 2008), waterfowl (Regehr 2011) and aquatic plants (Purves and Dushoff 2005) may exist as metapopulations and, in some cases, exhibit source-sink dynamics. If such a population structure is found for a non-native species, then there may be scope for coordinated interventions at the landscape scale. Of course, identifying the key variables underlying the transitions between different classes in compartment models is only the first step in parameterising an epidemiological model of lake-ecosystem invasions. As yet, the data required to undertake such parameterisation is not available for any non-native species invading lake-ecosystem networks, but the potential for applying the Epidemiological Framework for Biological Invasions appears promising.

Conclusions

The wide range of insights, tools and approaches, arising from over a century of work in modelling disease dynamics (Rock et al. 2014) has great relevance to the understanding of biological invasions. The basic epidemiological compartment model can be adapted to incorporate increasing levels of complexity and realism (Diekmann et al. 2013) and the concepts at its core can, in most cases, be generally applied to the spread and management of non-native species. While models may be translated from diseases to biological invasions with relative ease, the greatest insights will come if they are used to provide information for the monitoring, mapping and management of non-native species. Initial attempts to use statistical techniques, developed in epidemiology to estimate dispersal and receptor properties from spatio-temporal data on biological invasions, are promising (Catterall et al. 2012; Mang et al. 2018). Such an interdisciplinary approach should allow the field of biological invasion modelling to provide the same benefits that epidemiological compartment models have brought to the management of disease.

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DISCUSSION PAPER

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Advancing research on alien species and biological invasions

Appropriate uses of EICAT protocol, data and classifications

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Abstract

The Environmental Impact Classification for Alien Taxa (EICAT) can be used to classify alien taxa according to the magnitude and type of their environmental impacts. The EICAT protocol, classifications of alien taxa using the protocol (EICAT classification) and the data underpinning classifications (EICAT data) are increasingly used by scientists and practitioners such as governments, NGOs and civil society for a variety of purposes. However, the properties of the EICAT protocol and the data it generates are not suitable for certain uses. Therefore, we present guidelines designed to clarify and facilitate the appropriate use of EICAT to tackle a broad range of conservation issues related to biological invasions, as well as to guide research and communication more generally. Here we address common misconceptions and give a brief overview of some key issues that all EICAT users need to be aware of to take maximal advantage of this resource. Furthermore, we give examples of the wide variety of ways in which the EICAT protocol, classifications and data can be and have been utilised and outline common errors and pitfalls to avoid.

Keywords
Biological invasions, Environmental Impact Classification for Alien Taxa, management, policy-making, prioritisation

Introduction

A range of scoring schemes have been developed to enable the assessment and comparison of diverse impacts caused by biological invasions among taxa, sites and mechanisms (e.g. Blackburn et al. 2014; Nentwig et al. 2016; Bacher et al. 2018). Such comparisons are needed for a variety of applications, for example, to prioritise management actions to minimise the impacts of alien species (e.g. Kumschick et al. 2016; Nentwig et al. 2018), to study patterns of impacts across regions and taxa (e.g. Evans et al. 2014; Nkuna et al. 2018) and to underpin predictions regarding the types of species that have potentially damaging impacts currently or in the future (Evans et al. 2018). To this end and at the invitation of Parties to the Convention on Biological Diversity (CBD 2014), the Environmental Impact Classification for Alien Taxa (EICAT) has been developed to compare the severity and type of environmental impacts of alien taxa in a simple, transparent and evidence-based manner (Blackburn et al. 2014; Hawkins et al. 2015). EICAT assesses the severity of the impact caused by an alien taxon through its effects on individuals or populations of native species. EICAT has been well received by the invasion biology community [as evidenced by a high number of citations: Blackburn et al. 2014 is considered a highly-cited paper, i.e. within the top 1% in terms of citations for its age and field (Wilson et al. 2020)], as well as by policy-makers (e.g. CBD 2018; Wilson et al. 2018) and has been adopted as an official Standard by the International Union for the Conservation of Nature (IUCN; IUCN 2020a, b).

Given its function as a standard classification scheme for alien taxa and its potential widespread application, there is a need to ensure that current and future users of EICAT are aware of its appropriate application and the ways in which it should, and should not, be used. Here, we first briefly summarise how EICAT works, including how it is applied and its outputs and also clarify the terminology used in this study. Guidelines for applying EICAT have been described comprehensively (IUCN 2020a, b) and we, therefore, mainly refer to relevant documents here and add some points not previously explicitly addressed in detail. Second, we focus on the use and misuse of EICAT. To this end, we provide a table with examples of applications, including descriptions of appropriate and inappropriate uses of EICAT. These guidelines will hopefully encourage and facilitate the use of EICAT for purposes such as management, conservation, research and communication with stakeholders on biological invasions.

Note that this document does not address inconsistencies in the application of EICAT itself, which could lead to ambiguous outcomes and ultimately, data that are difficult to interpret (Kumschick et al. 2017; Gonzalez-Moreno et al. 2019). These issues should be addressed through the full and proper application of the EICAT protocol as documented by the EICAT Categories and Criteria and the Guidelines for application of EICAT Categories and Criteria (see IUCN 2020a, b; Volery et al. 2020).

Application of EICAT

The EICAT process relies on published evidence of impacts of the alien taxa under assessment; what counts as evidence in this case has been described elsewhere (e.g. Hawkins et al. 2015; Evans et al. 2016; IUCN 2020a, b; Volery et al. 2020). To summarise, the first step is a thorough and exhaustive literature search to identify all published (including grey) literature on the impacts of an alien taxon. Then, the EICAT protocol is applied to organise all this information in the standardised EICAT format and to classify each impact record for an alien taxon using the EICAT Categories and Criteria and the Guidelines (see also IUCN 2020a, b). The result is a compilation of all impact records available for a certain alien taxon, including the mechanisms of impact, the magnitudes of impact associated with those mechanisms, an EICAT assessment confidence score of 'Low', 'Medium' or 'High' for each record and additional information, such as where the impact took place and which native species were impacted (for details, see

Box 1. The EICAT categories.

EICAT classifies taxa into eight categories based on: whether they have been assessed using EICAT; their alien status; impact data availability; and impact magnitude (IUCN 2020a, b). The EICAT categories are:

Not Evaluated (**NE**): Taxa which have not been assessed using the EICAT protocol.

No Alien Populations (**NA**): Taxa which have not been introduced to areas outside of their native range.

Data Deficient (**DD**): Alien taxa which have been assessed using the EICAT protocol, but for which no data were available to classify them.

Minimal Concern (**MC**): Alien taxa which have been assessed using the EICAT protocol and that do not affect the performance of native taxa (i.e. their impacts to native taxa are negligible).

Minor (**MN**): Alien taxa which affect the performance of native taxa, but for which there is no evidence to suggest that they lead to decreased population sizes of any native taxon.

Moderate (**MO**): Alien taxa which have been shown to adversely affect native taxa population size, but which have not caused the local disappearance of any native taxon.

Major (**MR**): Alien taxa which have caused the reversible local population extinction of at least one native taxon.

Massive (**MV**): Alien taxa which have caused the irreversible local population extinction of at least one native taxon.

MC, **MN**, **MO**, **MR** and **MV** are the EICAT impact categories. The three highest magnitudes (**MO**, **MR** and **MV**) are termed "harmful" under EICAT.

Box 2. Terminology.

The three fundamentals of an EICAT assessment are: 1) the protocol used to perform EICAT assessments (EICAT protocol), 2) the data collected and assessed using the EICAT protocol (EICAT data) and 3) the resulting classification of an alien taxon using the data collected with the EICAT protocol (EICAT classification) (Fig. 1).

EICAT protocol: The protocol used to classify alien taxa according to the magnitude of their environmental impacts on native species, as described in detail in the Categories and Criteria and Guidelines documents (see also IUCN 2020a, b; Volery et al. 2020).

EICAT data: The evidence collected during EICAT assessments and provided as supporting information for EICAT classifications, including all records of impact for the taxon under assessment and their categories and criteria. The type of data and the standardised process in which it is collected is governed by the EICAT protocol.

EICAT classification: The classification of any alien taxon (mostly species) according to the EICAT Categories and Criteria and Guidelines (IUCN 2020a, b), i.e. the maximum impact recorded for the taxon and associated mechanism and confidence score.

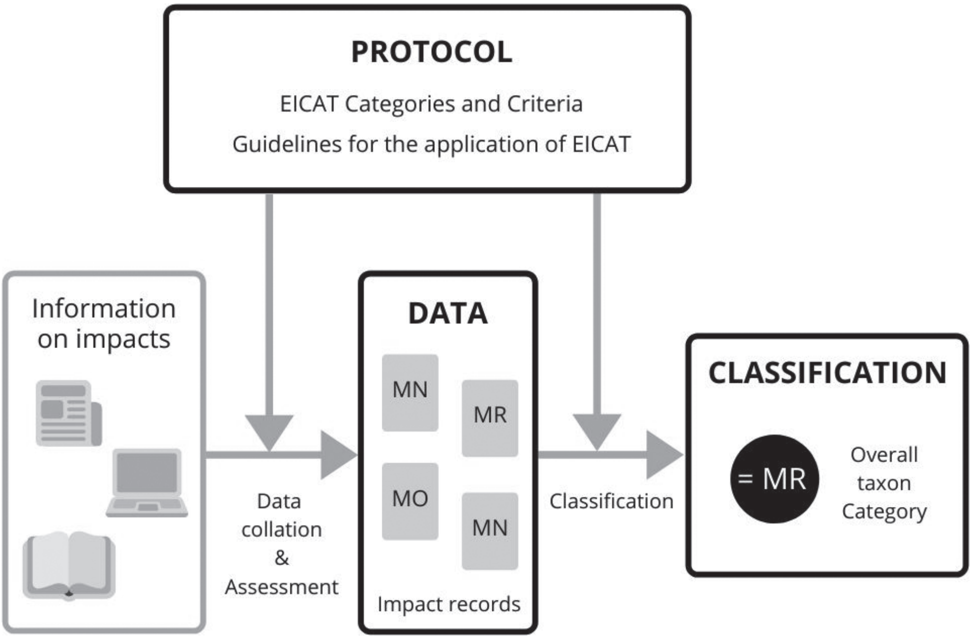

Figure 1. The three elements of EICAT (black boxes). Details on the terms can be found in Boxes 1 and 2. This will be followed by submission to the IUCN EICAT Authority and review. Once approved, results will be published online. For details on these later steps, see IUCN 2020a, b. **MN** = Minor; **MO** = Moderate; **MR** = Major.

https://www.iucn.org/theme/species/our-work/invasive-species/eicat; IUCN 2020a, b). The final step is the allocation of the maximum recorded impact across all the different impact records, which becomes the overall EICAT category for the taxon (Fig. 1).

Unlike the Red List (IUCN 2016), EICAT does not include information on potential impacts (Van der Colff et al. 2020). Furthermore, it distinguishes taxa with no impacts detected, but research on impacts available (classified as Minimal Concern **MC**) from species for which no data are available (Data Deficient **DD**).

EICAT categories and criteria

EICAT categories are distinct from each other, as they target different levels of organisation in the native species affected (e.g. individuals and populations, see IUCN 2020a, b; Box 1). However, within an impact category, impacts can vary in severity: for example, two alien species classified as having Major (**MR**) impacts are not necessarily equally as harmful to native species and the environment as a whole. To have **MR** impacts, both of these alien species would have, at least, caused the local disappearance of a subpopulation of a native species (but this disappearance would be reversible if the alien species were no longer present in the affected site, as per IUCN 2020a, b). However, EICAT does not specify, for example: (i) how abundant the native species was before the arrival of the alien species, (ii) what function the lost native species had in the environment and (iii) to what extent this function can be replaced by the alien species or other natives. Furthermore, EICAT classifications do not directly make it obvious how many native species are affected – sometimes only one native species declines due to an alien species, in other cases whole communities change their structure. Data on which, and consequently how many, native species are affected can be extracted from the EICAT data (at least, if records for these impacts are available). On that note, we would like to encourage authors of primary impact studies to publish the list of affected species to aid this process.

Taxa assessed

The EICAT protocol has been applied to a broad variety of taxonomic groups, mainly for research purposes. This includes the following: birds (e.g. Evans et al. 2016), amphibians (Kumschick et al. 2017), reptiles (Kraus 2015), some gastropods (Kesner and Kumschick 2018), some marine fish (Galanidi et al. 2018), bamboos (Canavan et al. 2019) and some mammals (Hagen and Kumschick 2018). These studies demonstrate that EICAT is applicable across a wide range of taxa and habitats. To date, none of these assessments has been reviewed and approved by the EICAT Authority (the body established to govern EICAT assessments; IUCN 2020a, b), as these formal processes are still being developed. This step will be a necessary requirement for EICAT assessments to be accepted and published by IUCN and to ensure consistent application of the protocol. Furthermore, many taxa have not yet been formally assessed with EICAT at a global level.

EICAT assessments for all alien taxa, not only taxa with harmful impacts [Moderate (**MO**) or higher], will be made available through an online database linked with the IUCN Global Invasive Species Database (GISD). This means that assessments of alien taxa, for which there are no impact data (**DD**; Box 1), taxa for which the evidence available shows they do not affect the performance of native individuals (**MC**) and taxa with very low impacts (**MN**), will also all be made available. Taxa classified as having No Alien Population (**NA**) and Not Evaluated (**NE**) will not be included in the EICAT database. Despite the intended use for alien species and populations, the categories and criteria can, with small adaptations, also be applied to native taxa in their native ranges (see, for example, Canavan et al. 2019). Even though assessments on native species impacts will not be accepted by IUCN as part of EICAT, they can nonetheless provide important information for conservation managers and policy-makers.

Geographic scale of assessments

A taxon's EICAT classification may differ depending on the geographic scale under consideration. Sub-global (e.g. regional, national or habitat-specific) EICAT assessments only include information on impacts from a specific region or habitat, as opposed to global EICAT assessments which should include information from anywhere in the global alien range. Examples of completed sub-global assessments include alien grasses (Visser et al. 2017) and alien fish (Marr et al. 2017) in South Africa and mammals, amphibians and reptiles on Cuba (Borroto-Paez et al. 2015; Borroto-Paez and Manica 2017). Assessments can also be undertaken at smaller scales if data availability allows, as for terrestrial invasions on Marion and Prince Edward Islands (Greve et al. 2017) and for the black locust tree (*Robinia pseudoacacia*) in Europe, where habitat-specific EICAT assessments were produced (Branquart et al. 2016). For example, such classifications can be useful to provide information for local management actions or reporting on the status of an invasion in a region (e.g. van Wilgen and Wilson 2018 for South Africa), but will not be reviewed by IUCN or displayed on the EICAT website. However, country-specific data on impacts and their associated EICAT classifications are planned to be included in the Global Register for Introduced and Invasive Species (GRIIS; http://www.griis.org/about.php; Pagad et al. 2018). These data can complement global assessments as country assessors might have access to local grey literature like reports and databases which are often written in local languages. Such assessments might unlock these data which can subsequently be added to the global EICAT data on the IUCN EICAT platform.

Appropriate use of EICAT

There are many contexts in which EICAT can be used, ranging from policy-making and conservation planning, to research, education and communication with the public. In Table 1, we outline some specific uses. These are all based on a standardised application of EICAT, as described in previously-published guidelines and standards (IUCN 2020a, b) or else the (potential) modifications are specified. In the following paragraphs, we provide background on some major uses as outlined in Table 1 and previous applications and uses of EICAT.

Policy and legislation

One of the responses to threats by alien species globally has been the development of local, national and international policies (Turbelin et al. 2017). The development of regulations on alien species, in most cases, includes lists of species to be regulated, for example, to implement control actions or trade restrictions (e.g. Essl et al. 2011; García-de-Lomas and Vilà 2015). Such lists need to be developed in a manner that adheres to international agreements, such as the International Plant Protection Convention (IPPC; FAO 1996), the World Organisation for Animal Health (OIE 2011) and the World Trade Organisation (Shine et al. 2000) and need to follow best practices including, for example, transparency and evidence-based decision-making (Roy et al. 2018). EICAT has been used to contribute to processes leading up to policy-making and the development of lists and regulations as a transparent and evidence-based tool (Pergl et al. 2016; Roy et al. 2019). It is also an integral part of the risk analysis framework used to underpin the listing of alien taxa under South African national regulations (DEA 2014; Kumschick et al. 2020a, b). Furthermore, it is used in Europe as a reference to select species that will undergo full risk assessment for inclusion in the list of Invasive Alien Species of Union Concern (Regulation 1143/2014) and related national lists (Bertolino et al. 2020).

However, it must be stressed that EICAT, in itself, does not constitute a risk assessment and should not be used as one. Impact assessment tools like EICAT provide useful information on environmental impacts which may provide information for the process of risk assessment. However, risk assessments require additional information on the likelihood of the hazard occurring, such as the probability that the alien taxon will enter, establish and spread at a certain site. For policy-making and legislative decisions, additional information on benefits, costs and efficiency of management options are required (Kumschick et al. 2020; Vimercati et al. 2020; Bertolino et al. 2020).

Conservation planning

Many of the processes feeding into policy-making and the regulation of alien taxa also apply to conservation planning and the setting of management priorities, i.e. there is a large overlap between the two as priority setting is also needed for policy-making (e.g. McGeoch et al. 2016; Booy et al. 2017; Kumschick et al. 2020a). In each case, impact is an important factor to be taken into account for decision-making and EICAT has been put forward as a suitable protocol for this purpose (McGeoch et al. 2016). For example,

Table 1. Ways in which the EICAT protocol, data and classification can be used, with selected, not exhaustive examples on appropriate and inappropriate applications for those uses. The structure and content of this table are based on the Guidelines for appropriate uses of IUCN Red List data (IUCN 2016). “Additional information recommended” presents examples only and is not a comprehensive list of factors to be considered. **MC** = Minimal Concern; **MN** = Minor; **MO** = Moderate; **MR** = Major; **MV** = Massive; **DD** = Data Deficient (see Box 1 for descriptions).

Types of uses	Appropriate uses	Inappropriate uses	Additional information recommended
Policy and legislation			
International/ national/ sub-national legislation and policy	EICAT can provide information for the development of: – International and national strategies to manage biological invasions – International, national, regional and local regulations on alien and invasive species	Putting an alien taxon on a regulated list just because of its EICAT classification	– invasion potential – management options – local conditions
International agreements	Guiding and providing information for decisions in international conventions and agreements, including: – Convention on Biological Diversity (CBD) – Sustainable Development Goals (SDG) – International Plant Protection Convention (IPPC) – World Organisation for Animal Health (OIE)	Automatically banning an alien species from trade because of its EICAT classification (e.g. assuming a high global impact category mean this impact will occur anywhere in its alien range)	– likelihood of the impact occurring – mechanism of impact, taxa and habitats affected
Development planning and environmental review			
Regional and national resource management and development	Using EICAT data to provide information for natural resource management at various scales in conjunction with other information	Relying solely on information from EICAT for local planning (e.g. using EICAT for deciding which trees to plant for forestry)	– other properties of the resource – economic considerations – demand for resource
Site-level planning and Environmental Impact Assessment (EIA)	EICAT can be used to feed into site level evaluation and EIA (e.g. using or adapting EICAT protocol to assess magnitude of impacts at site)	Relying solely on information from EICAT for site-level planning (e.g. assuming the level of impact at the site is currently that of the global or national EICAT category)	– presence and abundance of the alien taxa at the site – native taxa at risk – vulnerability of the habitat at the site – resources to be protected – other pressures
Conservation planning			
Providing information for conservation action for native species	EICAT data can provide important information on impacts to native species by alien taxa	Managing an alien taxon solely based on its impact on a specific native species.	– other pressures on native species – potential impact of native species
Risk assessment of alien species	EICAT data and classifications can be used to provide information for risk assessment procedure	EICAT classification alone should not be used to evaluate the level of risk posed by an alien species. A global classification as “harmful” (**MO** or higher) of a taxon does not necessarily imply a risk for the target region	– likelihood of the alien taxon to enter, establish and spread in the risk area
Providing information for management of alien species	EICAT data and classifications can feed into prioritisation of alien taxa for management	EICAT classification alone should not be used to justify management actions against an alien taxon. A classification as “harmful” (**MO** or higher) of a taxon does not necessarily warrant or require action	– practicality and cost of management – likelihood of the taxon to cause impacts at the management site
Prioritising management of regions threatened by biological invasions	EICAT data and classifications can feed into site prioritisation	The presence of an alien taxon classified as “harmful” (**MO** or higher) at a site does not necessarily warrant action.	– site-specific conditions with regards to the alien taxon – local impact (actual and potential) – features of the region to be protected – local management options
Geographic priority setting: site-level, landscape/seascape level and global level	Using EICAT protocol, data and classifications to support site priority setting by providing information on the impacts to native species (both current and potential) within sites of conservation importance	Using EICAT data and classifications (especially global EICAT classifications of an alien taxon) on their own to prioritise sites	– site-specific conditions – local impact (actual and potential) – features of the site to be protected

Types of uses	**Appropriate uses**	**Inappropriate uses**	**Additional information recommended**
Monitoring and evaluation			
Evaluating the state of invasion and monitoring changes in the state of invasion	EICAT can be used as an indicator for biological invasions	Using EICAT as the only indicator of the state of invasion	– area occupied – number of alien taxa present
Measuring the effectiveness and impact of control activities	The EICAT protocol can be used to assess information on impacts of a certain population of an alien species before and after control measures have been implemented at a site. The resulting data can show the effectiveness of control measures and the resilience of a system with regards to the impacts caused	Management at a local scale does not necessarily lead to a decrease in the impacts of a species at a global scale. Furthermore, the global impact classifications, as supported by IUCN, are not suitable to reflect changes in impacts due to management actions, as they consist of the maximum impact ever recorded	– local impacts – native taxa affected
Documenting species with low impacts	EICAT does not only allow for the classification of severe impacts, but it ranges from classifying evidence on no and low impacts on native species (**MC** and **MN,** respectively) up to high impacts. This should encourage the publication of results of taxa which had low impacts on the recipient systems.	Species which are classified as causing impacts that are of **MC MN** should not automatically be considered as safe or to pose no risk. These low impacts could be found for several reasons, for example: i) the alien species does not and will not have high impacts, ii) the introduced populations have not had the opportunity to cause high impacts due to, for example, lag times or low abundance, iii) there is a lack of data on impact such that the scored impact is lower than the actual impact	– time since introduction – abundance of alien taxon
Documenting ecosystem recovery after control (e.g. extirpation or eradication)	The EICAT protocol can be used to classify studies on impacts or legacy effects after an alien taxon has been removed and can facilitate the understanding of whether these impacts are reduced after removal	EICAT data should not be used as sole evidence for successful restoration	– native taxa recovery – other stressors on the site
Scientific research			
Providing information for species-specific studies	Use gaps identified in the information on impacts of species or lack thereof (e.g. species classified as **DD**), to guide research	EICAT classifications do not replace field studies: field studies are needed to populate EICAT	– detection of a new alien taxon at a site
Providing information for research on multiple species and invasion processes	Using EICAT data to show patterns and trends related to alien species impacts, including potential future threats	Assuming a change in EICAT score means a change in impact without considering the likelihood of the change being observed due to improved knowledge	– pathways transporting alien taxa – sites vulnerable to alien taxa
Predicting impacts of alien species	EICAT data can feed into trait-based, mechanistic and species interaction studies and can generate testable hypotheses	EICAT classifications cannot – in isolation – predict impacts of a taxon in a new region	– traits of alien taxa – invasion history
Education, communication and awareness raising			
Education	Providing information for academic work across educational levels, for example, school assignments, undergraduate essays and dissertations	Use EICAT data as only information about risks of alien species	– invasion history – vulnerable habitats
Media and awareness raising	Promoting knowledge and awareness on alien species, their impacts on native biodiversity, biodiversity conservation issues, risks to biodiversity	A high EICAT category does not imply an alien species has no benefits and that control and regulation should not take stakeholders into account	– benefits of taxa – conflicts of interest
Fund-raising	Providing a solid evidence-base for funding proposals to engage in work on alien species and conservation of native biodiversity		project dependent

Katsanevakis et al. (2016) adapted and used EICAT to aid prioritisation of conservation actions in the Mediterranean Sea. The principles of EICAT – adapted to a questionnaire – have also been used as part of a decision-support scheme for alien species management in cities and been applied in Cape Town, South Africa (Gaertner et al. 2017).

Ideally, EICAT should not be used in isolation to set management priorities (as also outlined in Branquart et al. 2016), especially for already established alien taxa. However, EICAT can be useful as an early warning system for taxa which have been shown to cause harmful impacts in other areas to which they were introduced and so could be considered a "rapid response" tool. When resources are limited and decisions need to be taken without delay, EICAT can provide useful information on potentially harmful taxa, allowing prioritisation of their interception at borders or rapid management actions for new incursions. EICAT shows the maximum impact ever recorded for certain populations of an alien taxon and collates all records of impact for the taxon. It is, therefore, a useful reference to select the most harmful taxa, providing an overview of how they impact native species and ecosystems. To set management priorities for alien taxa most effectively, their current and potential future local impact should be considered and EICAT can clearly contribute to assessing the former, but could also be used for prioritising species for the latter. Nevertheless, where possible, additional information should be taken into account, including, for example, the distribution and the invasion potential of the taxon in the region to be managed, management options available and their costs and effectiveness. The same applies when setting priorities for site and pathway management. EICAT data can be useful to assess which pathways facilitate the movement of more harmful taxa (Pergl et al. 2017) or which regions are more at risk due to high-impacting aliens being present there (Nentwig et al. 2010). However, managing a pathway is not necessarily needed just because it contains harmful taxa (**MO**, **MR**, **MV**) and a taxon with a high impact elsewhere does not necessarily have the same impact in the region of interest. Nevertheless, EICAT provides important information feeding into prioritisation processes for alien taxa, especially considering that the main justification for management, in many cases, is their negative impacts (e.g. McGeoch et al. 2016; Roy et al. 2019).

Monitoring and evaluation

Simple and understandable indicators can be produced from EICAT to track changes in the magnitude of environmental impacts from alien species over time. This can provide information for policy processes at the global level, such as the CBD Strategic Plan, UN Sustainable Development Goals and the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) or at the national level to support the monitoring of management measures. For example, EICAT has been recommended as a tool to monitor biological invasions globally and is listed as one of three essential variables to report on when monitoring biological invasions at country level (Latombe et al. 2017). The number and identity of taxa in each impact category, for example, can give an indication of how many (potentially) harmful taxa are present in the country and, if collected over time, can be used to track trends in the impacts of these taxa. Furthermore, impact is one of the main indicators used to provide information for reports on the status of alien taxa in a country (Wilson et al. 2018).

Scientific research

Aside from the availability (or lack) of data on impacts, the sky is the limit for the uses of EICAT for research. The questions which EICAT can help to answer are diverse, but due to the nature of the system are focussed around topics related to the magnitude and type of alien species' environmental impacts and the availability of impact data.

The most basic application of EICAT enables alien species with severe impacts to be distinguished from those which are less harmful, at least on the basis of available data. This allows comparisons of species with different reported levels of impact, which have been made within taxonomic groups, including birds (Evans et al. 2016), amphibians (Kumschick et al. 2017), fish (Galanidi et al. 2018) and bamboos (Canavan et al. 2019). EICAT data can also be used to compare impact magnitudes between taxonomic groups (similarly to Kumschick et al. 2015). Comparisons need to be interpreted with caution, as the absence of evidence of impacts does not mean that no impacts are occurring (see, for example, Hulme et al. 2013); however, empirical studies can only ever proceed on the basis of what data are available (Blackburn et al. 2015).

The ways in which alien taxa affect native species can differ between taxonomic groups or habitats. EICAT has been used to show that the importance of mechanisms can differ between groups of insects (McGeoch et al. 2015), amphibians and reptiles (Kraus 2015), birds (Evans et al. 2016) and gastropods (Kesner and Kumschick 2018). Some impact mechanisms are associated with more harmful impacts (Evans et al. 2016; Rockwell-Postel et al. 2020). Furthermore, the available data suggest that certain regions are more highly impacted by alien species than others. Assessing which regions are more highly impacted and improving our ability to understand why, can aid in setting priorities for management and resource allocation (e.g. Evans et al. 2016), albeit that spatial biases in the literature (e.g. Evans and Blackburn 2020) should be considered when interpreting such findings. Similarly, certain habitats could be more vulnerable to impacts by certain taxa, as in the case of *Robinia pseudoacacia*, which affects open habitats like grasslands more severely than closed, forested habitats (Branquart et al. 2016).

Theory suggests that species traits should play a role in their invasiveness and impacts. EICAT can be useful to study patterns related to the traits of alien species with and without harmful impacts (e.g. Evans et al. 2018a). It has also been used to test general invasion hypotheses related to the severity of impacts of alien taxa, such as the island susceptibility hypothesis (Hagen and Kumschick 2018). Additionally, studies indicate that we lack information on the environmental impacts of many alien species (Simberloff et al. 2013; Kumschick et al. 2015; Evans et al. 2016). EICAT provides a structured way to identify data gaps and can, therefore, help to set priorities for future impact research (Evans et al. 2018b; Evans and Blackburn 2020).

Education, communication and awareness raising

EICAT provides a solid base for communicating the breadth and diversity of impacts which alien taxa can cause on the environment and the range in magnitude of those impacts. Other communication tools have been put forward to achieve the same goal, including the "100 of the world's worst invaders" list compiled by experts of the IUCN Invasive Species Specialist Group (Lowe et al. 2004) or the "100 worst list" of the European Union (Vila et al. 2009) and more recently using a similar impact scoring approach for European aliens (Nentwig et al. 2018). One of the main advantages of the EICAT approach compared to a "100 worst list" is that it showcases not only species with high impacts, but also gives the range in known magnitudes of impact caused by different alien taxa.

One particular communication value of EICAT is that it translates a complex issue – the magnitude of environmental impacts from alien taxa – into a simple but well-defined set of categories. It has been repeatedly used for this purpose in scientific papers studying certain organisms, for example, giant African land snails (*Achatina fulica*) on Christmas Island (O'Loughlin and Green 2017), crayfish spp. in parts of the USA (DiStefano et al. 2015), the anole lizard (*Anolis porcatus*) in Brazil (Prates et al. 2016) and red king crab (*Paralithodes camtschaticus*) on the Euro-Arctic shelf (Christiansen et al. 2015). It is also a standardised tool that can be used to assess alien taxa from any taxonomic group, making it applicable across the globe. This lends itself to becoming a powerful communication tool, in much the same vein as the IUCN Red List, which shares the same characteristics, but categorises species based on their risk of extinction. As with the IUCN Red List, EICAT can be used to communicate and engage with a wide variety of audiences for different purposes.

EICAT classifications can be converted into info-graphics, or even art, to help communicate information on impacts from alien species (e.g. as done for the IUCN Red List data, https://www.sharktrust.org/shark-science or https://infowetrust.com/endangeredsafari/), making the messages and results more attractive to print, online and on social media. EICAT can also be used by civil society organisations in supporting them in funding applications and communicating and engaging with stakeholders to raise awareness and change behaviour or support them in undertaking action on the ground. In addition, as it is an IUCN 'global standard', it is also more likely to be a known and 'trusted' information source for policy-makers, supporting scientists in bridging the science-policy interface at a national and global level.

Conclusions

EICAT has a wealth of uses and, if the protocol is correctly applied (i.e. applying the EICAT Categories and Criteria and following the Guidelines in full), can feed into a wide range of processes. EICAT provides a platform for sharing data on the impacts of alien species in a standardised way, which comes with several benefits. First, the capacity to act upon and control invasions differs greatly amongst countries (Early et al. 2016; Latombe et al. 2017). Standardising and globalising the process of impact assessment within a framework such as EICAT, can aid countries with less financial or technical capacity to develop policies and priorities for tackling biological invasions, as it provides a resource on impacts of invasions to tap into. It also highlights priorities for regional biosecurity (Faulkner et al. 2020). Second, it is a versatile protocol which allows for the regular updating of information. Since all the sources considered for each classification are provided in the EICAT data, anyone can, and should be encouraged to, add relevant missing information. This is also an opportunity for less accessible sources of information to be added to the impact database.

That said, for some uses, it might be beneficial to deviate from the EICAT protocol or to extract only certain information from the EICAT data. For example, the use of expert opinion on impact magnitudes, in addition to or instead of written reports, can be justified for feeding into local management recommendations (e.g. Zengeya et al. 2017; Carboneras et al. 2018; Bertolino et al. 2020). This can be legitimate and reflects the original authors' intent to develop a broadly applicable and versatile system (Blackburn et al. 2014), but these deviations from the standard process should be adequately described and acknowledged to avoid confusion with the official, standardised process as established and administered by IUCN. Furthermore, data and classifications produced during such non-standardised exercises will not be accepted by IUCN for incorporation into the official EICAT process or displayed on the website. Nevertheless, they can, in some cases, provide a starting point for, or feed into, standardised assessments.

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METHODS

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A framework to support alien species regulation: the Risk Analysis for Alien Taxa (RAAT)

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Abstract

Human livelihoods and well-being in almost all regions of the world depend on taxa which are alien. Such taxa also, however, threaten human health, sustainable development, and biodiversity. Since it is not feasible or desirable to control all alien taxa, decision-makers increasingly rely on risk analyses to formalise the best available evidence of the threats posed and whether and how they can be managed. There are a variety of schemes available that consider the risks of alien taxa, but we argue a new framework is needed: 1) given major recent developments in international frameworks dealing with biological invasions (including the scoring of impacts); 2) so that decisions can be made consistently across taxa, regions and realms; 3) to explicitly set out uncertainties; and 4) to provide decision-makers with information both on the risks posed and on what can be done to mitigate or prevent impacts. Any such scheme must also be flexible enough to deal with constraints in capacity and information. Here we present a framework to address these points – the Risk Analysis for Alien Taxa (RAAT). It outlines a series of questions related to an alien taxon's likelihood of invasion, realised and potential impacts, and options for management. The framework provides a structure for collating relevant data from the published literature to support a robust, transparent process to list alien taxa under legislative and regulatory requirements, with the aim that it can be completed by a trained science graduate within a few days. The framework also provides a defensible process for developing recommendations for the management of assessed taxa. We trialled the framework in South Africa and outline the process followed and some of the taxa assessed to date.

Keywords

Biological invasions, policy, regulations, risk analysis, risk assessment, risk management

Introduction

Species are being moved around the world by humans, both accidentally and deliberately, with the rate of introduction of new species showing few signs of declining (Seebens et al. 2017). Once introduced, some of these species establish and spread without further human assistance. There are also numerous species that have already been introduced and that will likely become invasive in future. While many alien taxa are highly beneficial, some can have significant negative impacts on the recipient environment and human livelihoods (Pimentel 2011; Blackburn et al. 2014). This makes management of the most problematic alien taxa a necessity. However, it is not feasible, desirable or necessary to manage all aliens and prioritisation is needed (McGeoch et al. 2016).

International agreements under the World Trade Organisation (WTO) require the assessment of risks before certain activities involving an alien taxon, especially trade, can be restricted, or before a new taxon should be allowed for import. These agreements recognise the standards set by the International Plant Protection Convention (IPPC; FAO 1996) and the World Organisation for Animal Health (OIE 2011). Such risk assessments are aimed at distinguishing potentially harmful taxa from those that are benign.

We argue that for successful management and the development of efficient regulations, three components are required, namely, risk assessment, risk management, and risk communication. While elements of each have been developed in different cases separately (see for example Branquart et al. 2016; Booy et al. 2017), regulatory decisions regarding biological invasions rest on all three components: (i) risk assessment consists of the likelihood and consequences of an alien taxon causing negative impacts (Daehler and Virtue 2010); (ii) risk management deals with options to reduce the risk, including due consideration of potential benefits; and (iii) risk communication details how the information is made accessible (Branquart et al. 2016). Therefore, besides the mandatory risk assessments prescribed by the international agreements, regulatory decisions need also to take risk management into account, i.e., management feasibility, benefits of the taxon, and potential conflicts between/amongst stakeholders [see van Wilgen and Richardson (2012) for examples of the costs of ignoring such considerations]. Furthermore, decisions are often only successful and implementable if stakeholders understand the risks associated with the taxon. To gain the support from the general public and other stakeholders, engagement and clear communication regarding risks is crucial and this is where risk communication has its place. Therefore, to support decision-makers, the broader process of risk analysis is required (Convention on Biological Diversity 2002). There is a plethora of frameworks that have been developed to address particular parts of the problem, but they are mostly taxon-specific (Leung et al. 2012) and often do not link to probabilities or are not mathematically consistent (Holt 2006). Furthermore, risk analyses need to be transparent and repeatable and align with national and international agreements, policies, and best practice (e.g. Verbrugge et al. 2010; Essl et al. 2011; Heikkilä 2011; Kumschick and Richardson 2013; Roy et al. 2018).

Much progress has been made in recent years in the way we analyse risks and aspects thereof. For example, impact scoring schemes have been developed which enable the comparison of a wide range of impacts between taxa and habitats – most notably the Environmental Impact Classification for Alien Taxa (EICAT; Hawkins et al. 2015, IUCN 2020a, b) and its socioeconomic equivalent, SEICAT (Bacher et al. 2018) (more detail in Consequences section below). More thought has also been given to the management aspect of the decision-making and prioritisation processes (e.g. Booy et al. 2017).

Decisions often have to be made on the basis of limited evidence. Therefore, risk analyses should explicitly highlight uncertainties and flag where recommendations are based on projections. Moreover, consideration should be given as to when the precautionary principle is appropriate. As set out by the Convention on Biological Diversity in their guiding principles related to alien species that threaten ecosystems, habitats or species: "… The precautionary approach should also be applied when considering eradication, containment and control measures in relation to alien species that have become established. Lack of scientific certainty about the various implications of an invasion should not be used as a reason for postponing or failing to take appropriate eradication, containment and control measures" [guiding principle 1 (Convention on Biological Diversity 2002)].

In order to deal with undesirable consequences and to mitigate future impacts, policy frameworks for the regulation of alien taxa have been developed for many countries (McGeoch et al. 2010; Early et al. 2016). For example, the European Union (EU) has developed new legislation to ensure a consistent response to the threat of alien taxa by all member states (EU Regulation 2014). Such regulations often include lists of species for which certain activities like trade, propagation and movement are prohibited or restricted and which require mandatory management interventions (Garcia-de-Lomas and Vilà 2015). Decisions on the categorisation of alien taxa in these lists require a transparent and evidence-based analysis of risk.

Here we present a practical framework for the analysis of risks associated with alien taxa and provide a structure for collating scientific evidence. We provide detailed information on the framework including how and why it was developed and its structure and content. Lastly, we provide some results from applications of RAAT and outline how the framework can aid and support the regulation and listing of alien taxa, using the South African legislative background as an example.

The Risk Analysis for Alien Taxa (RAAT) framework

We first outline how and why the framework was developed and tested, provide general guidance on how risk is scored and confidence estimated, and present the overall structure of the framework followed by a detailed description of each section.

Development and testing of the RAAT

The risk analysis framework presented here was specifically designed for the purpose of listing alien species under the regulatory framework of the South African National

Environmental Management: Biodiversity Act (NEMBA, Act 10 of 2004) Alien and Invasive Species Regulations (hereafter called the NEM:BA A&IS Regulations; Department of Environmental Affairs 2014; for details of how the framework aligns with the regulations, see Suppl. material 1). The development of the RAAT framework was initiated in 2015, in response to the promulgation of the NEM:BA A&IS Regulations. The regulatory lists of 2014 were informed by expert opinion, but the decisions taken and recommendations made were not clearly documented (see Kumschick et al. 2020a for a discussion). As the regulatory lists specify taxa which need to be controlled and for which other restrictions are in place, it has social and economic implications and has been contested in a number of cases [van Wilgen and Wilson (2018); see also Novoa et al. (2015) for a discussion on listing alien Cactaceae]. A framework was therefore required to (retrospectively) provide evidence for listing in a consistent transparent manner (e.g. Woodford et al. 2017).

During the development of this framework, regular meetings with decision-makers [mainly representatives from the Biosecurity Division of what was, at the start of the process, the South African Department of Environmental Affairs (DEA), but became the Department of Forestry, Fisheries and the Environment (DFFtE) in 2020] were held to ensure their needs were taken into account and the framework was relevant for the intended purpose. The first version of the framework was used by graduate students at the Centre for Invasion Biology at Stellenbosch University (CIB) to assess taxa from a wide range of taxonomic groups and feedback from this exercise was used to refine it, providing additional clarification and guidance. The second version was reviewed by the Alien Species Risk Analysis Review Panel (ASRARP), a panel of South African experts set up by the South African National Biodiversity Institute (SANBI) to review risk analyses for alien taxa [both those performed in relation to the import of species not yet present in the country and those performed in relation to the regulation and listing of alien taxa under the NEM:BA A&IS Regulations (Kumschick et al. 2020a)]. The panel includes independent experts on biological invasions and risk analyses, with representatives from private and public entities and experts on a wide range of taxonomic groups. The issues raised by the ASRARP on the framework were mainly related to details in the wording which could lead to misunderstandings. These were subsequently addressed, and a new draft was reviewed by representatives from different organisations, including the DEA, members of the ASRARP, the SANBI, and the CIB. Finally, RAAT was signed off by the ASRARP before submission as a report to the DEA in March 2017. A revised version was subsequently uploaded to a pre-print server to make it widely accessible (Kumschick et al. 2018).

Initially, several risk analyses were piloted by ASRARP members, but after the first three risk analyses were approved, subsequent risk analyses were submitted by SANBI staff, students, and post-docs not affiliated with ASRARP to ensure a separation between the review panel and the assessors. The risk assessors (who had various backgrounds and levels of education, including alien species managers, taxonomists, post-graduate students, and researchers), were trained to use the framework during five courses that were run over 2018–2019 (Table 1, several additional courses were held in 2020 based on an accepted draft of this paper). The courses provided valuable feedback in terms of how the framework should be worded to avoid inconsistencies and to clarify the calculations of likelihood and risk specifically. Moreover, as the risk analyses were submitted for review at the meetings of the ASRARP and reviewed by independent experts, the framework has been further refined by adding sections on management that could help clarify specific issues on sub-specific entities. The framework presented here has thus been tested and refined in practice over two years (Suppl. material 2).

RAAT is yet to be either formally adopted in South African legislation or included as an official guiding document, but it is being used by officials to justify applications to revise the listing of taxa under their mandate. Even though RAAT was initially designed for the purpose of listing alien species under the NEM:BA A&IS Regulations, the intention was always to create a system that can be used more generally to aid decisions regarding management prioritisation and the listing of taxa under policy frameworks. Therefore, throughout the framework, the questions posed and options for answers were designed to be generic and applicable across regions. However, in the Suppl. material 2, these are worded specifically with the South African context in mind for local decision-makers and managers to determine the appropriate categories as referenced in the NEM:BA A&IS Regulations.

Scoring risk and confidence

RAAT consists of a series of questions which need to be answered by the person assessing an alien taxon of interest. The accuracy of an analysis relies, amongst other factors, on ensuring that a thorough literature review on the taxon under assessment is conducted. Some information can be extracted from national and international databases on native and alien species, such as the Global Invasive Species Database (http://www.iucngisd.org/gisd/), CABI's Invasive Species Compendium (https://www.cabi.org/isc/), Global Biodiversity Information Facility (https://www.gbif.org/), and the Red List of Threatened Species (http://www.iucnredlist.org/). However, primary literature should preferably be consulted and included. Information from the native range can be useful, including indigenous knowledge.

If insufficient information is published on the taxon, closely related taxa should be considered, for example, congeners (e.g. Bomford 2008). However, it needs to be clearly stated when such information is used, and which species was selected as a surrogate and why. Species with similar life history traits and behaviour are preferred. All information must be documented and referenced to be able to review how recommendations were developed and when assumptions were made and to facilitate updating the analysis as suitable information becomes available.

Taxonomists and other experts should be consulted for the risk analysis process to fill gaps in literature, especially for sections initially scored data-deficient for a given taxon. Expert opinion is beset with biases that are well understood and described (Burgman 2016). To minimise such biases, all information sources need to be documented, includ-

Table 1. Taxa analysed using the Risk Analysis for Alien Taxa (RAAT) framework under the South African NEM:BA A&IS regulatory lists of 2014 as revised 2016 with recommendations approved by the Alien Species Risk Analysis Review Panel up until end March 2020. Details of permit conditions (including cases where the listing varies depending on specific conditions, for example, for *Oreochromis niloticus*) are not shown. Listing categories are as follows: 1a – Nation-wide eradication target; 1b – Control target; 2 – Control target with permits; 3 – Control targets with certain exemptions. As species listed as 1b can also have exemptions, category 3 is redundant and is not considered as an option in the RAAT framework. All species assessed so far are known to be present in South Africa, except *Myocastor coypus* which was recommended to be listed as "prohibited". LIK is likelihood; CON is consequence; and MAN is management (see Figure 1).

Type of organism	Scientific name	LIK	CON	Risk	MAN	Current listing	Recommended listing
Arthropod	*Acarapis woodi* (Rennie, 1921)	Probable	MO	High	Difficult	1b	1b
Plant	*Acacia stricta* (Andrews) Willd.	Probable	MO	High	Medium	1a	1a
Plant	*Ailanthus altissima* (Mill.) Swingle	Fairly probable	MR	High	Medium	1b	1b
Bird	*Anas platyrhynchos* (Linnaeus, 1758)	Probable	MV	High	Medium	2	1b (with exemptions)
Plant	*Ageratina adenophora* (Spreng.) R.M.King & H.Rob. (= *Eupatorium adenophorum* Spreng.)	Probable	MR	High	Medium	1b	1b
Arthropod	*Carausius morosus* Sinety, 1901 [listed under Phasmatodea species (Jacobson & Blanchi, 1902)]	Fairly probable	MO	High	Difficult	1b (all Phasmatodea)	1b (*Carausius morosus* Sinety, 1901)
Plant	*Chondrilla juncea* L.	Probable	MV	High	Difficult	1a	1a
Plant	*Coreopsis lanceolata* L.	Probable	MO	High	Difficult	1a (Sterile cultivars or hybrids are not listed)	1b (the appropriateness of exemptions for sterile cultivars or hybrids was not assessed)
Mollusc	*Crassostrea gigas* (Thunberg 1793)	Probable	MR	High	Difficult	2	2
Plant	*Eugenia uniflora L.*	Probable	MO	High	Medium	1b	1b (with exemptions)
Plant	*Iris pseudacorus* L.	Probable	MR	High	Difficult	1a	1b
Plant	*Jatropha curcas* L.	Fairly probable	MO	High	Medium	2	1b
Plant	*Lilium formosanum* Wallace (= *L. longiflorum* Thunb. var. *formosanum* Baker)	Probable	MO	High	Difficult	1b	1b
Plant	*Melaleuca hypericifolia* Sm.	Probable	MN	High	Easy	1a	1b
Mammal	*Myocastor coypus* (Molina, 1872)	Unlikely	MR	High	Medium	2	Prohibited
Mollusc	*Mytilus galloprovincialis* Lamarck, 1819	Probable	MV	High	Medium	2	2
Fish	*Oreochromis niloticus* (Linnaeus, 1758)	Fairly probable	MV	High	Difficult	2	2
Plant	*Paspalum quadrifarium* (Lam 1791)	Fairly probable	MO	High	Medium	1a	1b
Arthropod	*Penaeus indicus* H. Milne-Edwards, 1837 [listed as *Fenneropenaeus indicus* (H. Milne-Edwards, 1837)]	Fairly probable	MC	Medium	Difficult	2	Delist
Plant	*Psidium cattleianum* Afzel. ex Sabine	Probable	MO	High	Medium	1b	1b
Bird	*Psittacula krameri* (Scopoli, 1769)	Probable	MV	High	Medium	2	1b
Bird	*Pycnonotus cafer* (Linnaeus, 1766)	Probable	MR	High	Easy	2	1a
Plant	*Ricinus communis* L.	Probable	MO	High	Medium	2	2
Plant	*Robinia pseudoacacia* L.	Fairly probable	MV	High	Difficult	1b	1b
Plant	*Sagittaria platyphylla* (Engelmann) J.G Smith	Probable	MO	High	Difficult	1a	1b
Plant	*Sasa ramosa* (Makino) Makino & Shibata	Very unlikely	MO	Low	Easy	3	Delist
Plant	*Senna bicapsularis* (L.) Roxb	Probable	MO	High	Medium	1b	1b
Plant	*Sphaeropteris cooperi* (F. Muell.) R.M. Tryon	Fairly probable	MR	High	Medium	Not listed	1b
Plant	*Syzygium jambos* L. Alston	Probable	MO	High	Easy	3	1b (with exemptions)
Arthropod	*Vespula germanica* (Fabricius, 1973)	Probable	MV	High	Medium	1b	1b

ing listing which experts were consulted and their expertise in the respective topic. It is also possible, and preferable in many cases, that taxa are assessed in working groups rather than by a single assessor to minimise bias (Burgman et al. 2011). In the South African case, and based on international best practice (e.g. Defra 2015), review of analyses through the ASRARP provides another mechanism to avoid bias (Kumschick et al. 2020a).

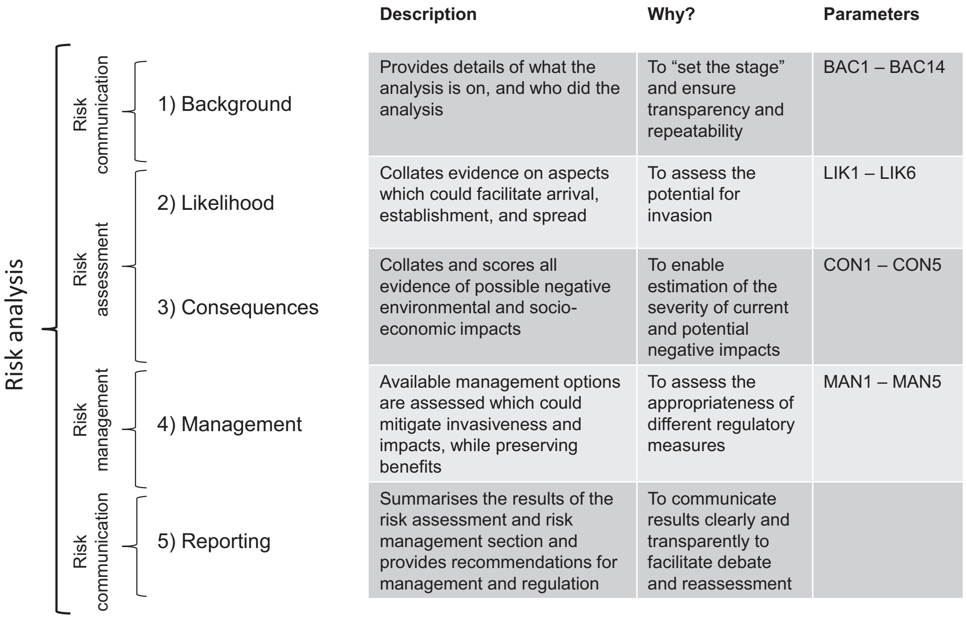
Assessors can also, of course, be biased and there is often considerable uncertainty when interpreting data (McGeoch et al. 2012; Vanderhoeven et al. 2017) and which is difficult to avoid. Clear guidance on how to respond to each question in the RAAT and formalised descriptions of each response option is provided in the form of scenarios to minimise assessor bias. It is important to indicate how confident the assessor is in the response provided (Carrington and Bolger 1998). The confidence score should give an indication on how confident the assessor is that the answer provided is correct. This generally depends on the amount and quality of data available on the taxon. We followed the guidelines as described in the European Plant Protection Organisation (EPPO) pest risk assessment decision support scheme and as published in Hawkins et al. (2015) for confidence ratings (see also Suppl. material 5).

Structure of the RAAT

The RAAT is divided into five sections and includes all aspects of risk analysis, namely risk assessment (sections 2 and 3), risk management (section 4), and risk communication (sections 1 and 5) (Fig. 1). The sections are abbreviated with three-letter acronyms: 1) Background (BAC) provides information on the assessor, the taxon under consideration, and information needed to perform the analysis; 2) Likelihood (LIK) assesses biological, ecological, and behavioural traits of the taxon that could lead to its arrival, establishment, and spread; 3) Consequences (CON) include the recorded and potential impacts of the taxon; 4) Risk management (MAN) includes questions related to the ability to control a taxon, whether the taxon is beneficial in some situations, and provides recommendations for management and/or listing of taxa; 5) Reporting provides guidance on how to communicate the outcomes of the analysis. This last section does not consist of questions, but is a compilation of the results of the previous four sections and provides an easily digestible summary for the communication of recommendations to stakeholders. Each section is discussed below.

1) Background

It is important to clearly outline the scope of the analysis to clarify what is assessed, for which region, and by whom. This section therefore includes the region of interest, the taxon for which the analysis is performed, and information on the taxon, as this forms the basis for data collection (Table 2).



	Description	Why?	Parameters
1) Background	Provides details of what the analysis is on, and who did the analysis	To "set the stage" and ensure transparency and repeatability	BAC1 – BAC14
2) Likelihood	Collates evidence on aspects which could facilitate arrival, establishment, and spread	To assess the potential for invasion	LIK1 – LIK6
3) Consequences	Collates and scores all evidence of possible negative environmental and socio-economic impacts	To enable estimation of the severity of current and potential negative impacts	CON1 – CON5
4) Management	Available management options are assessed which could mitigate invasiveness and impacts, while preserving benefits	To assess the appropriateness of different regulatory measures	MAN1 – MAN5
5) Reporting	Summarises the results of the risk assessment and risk management section and provides recommendations for management and regulation	To communicate results clearly and transparently to facilitate debate and reassessment	

Figure 1. A schematic of the Risk Analysis for Alien Taxa framework described here. For each section a number of parameters need to be assessed (more detail in Table 2).

The region for which the risk analysis is performed is referred to as the *Area* (developed from the concept by D'Hondt et al. 2015). In most cases, analyses will be undertaken at a national level (e.g. South Africa), but the structure of the framework allows the analyses to be undertaken for different spatial units (e.g. for a national park or for the southern African region). However, the *Area* must be clearly specified and all questions referring to the *Area* specifically consider information with respect to the region chosen.

The taxon under assessment is referred to as the *Taxon*. The *Taxon* can be a species, sub-species, infra-specific entity, genus or any other taxonomic level. Risk analyses are mostly carried out on individual species as a standard taxonomic entity as, mostly, this is the level at which information is available, but this is not always appropriate, feasible or desirable. For example, different taxonomic levels are preferable: if the taxonomy of a group is not well resolved (e.g. some genera within the family Cactaceae, Novoa et al. 2015); if species are difficult to distinguish but the whole group (i.e. genus or family) poses a significant threat (e.g. certain taxa of mites or plant pathogenic rust fungi); and if there are important differences between sub-species or infra-specific entities (e.g. varieties and cultivars; see Datta et al. 2020 and Gordon et al. 2016). Ideally the analysis should consider whatever taxonomic grouping for which the risk is the same (e.g. Wilson et al. 2011), though in practice, this is very hard to achieve and species level assessments are therefore most common.

Table 2. A list of the parameters and information needed to complete the Risk Analysis for Alien Taxa.

Section	Parameter	Description	Definition and purpose
Background	BAC1	Name of assessor(s)	To identify the person who performed the assessment.
	BAC2	Contact details of assessor(s)	For means of contacting the assessors in case of questions, further information required or if the assessment needs revision.
	BAC3	Name(s) and contact details of expert(s) consulted	Identifies experts which were consulted.
	BAC4	Scientific name (including the authority) of *Taxon* under assessment	Gives information on the species, sub-species, variety, genus or other taxonomic entity under assessment.
	BAC5	Synonym(s) considered	Information on which synonyms were considered for the assessment.
	BAC6	Common name(s) considered	Information on which common names were considered for the assessment.
	BAC7	What is the native range of the *Taxon*?	Information on the distribution range of the taxon is important for the assessment as the framework is designed for alien species specifically.
	BAC8	What is the global alien range of the *Taxon*?	This is crucial as, for some questions, only information in the alien range is considered.
	BAC9	The *Area* under consideration	Delimits the geographic scope of the assessment area.
	BAC10	Is the *Taxon* present in the *Area*?	Crucial for management recommendations (e.g. prevention vs. control).
	BAC11	Availability of physical specimen	To link the identification of the taxon to a physical sample, as it is important to be able to refine the identity (BAC 4) in the light of new information and following taxonomic revision or the detection of errors in identification.
	BAC12	Is the *Taxon* native to the *Area* or part of the *Area*?	Important for management as this framework only deals with alien species.
	BAC13	What is the *Taxon's* introduction status in the *Area*?	Knowing the introduction status of populations (e.g. as per the Unified Framework of Biological Invasions, Blackburn et al. 2011) can aid with management decisions.
	BAC14	Primary (introduction) pathways	This information will be used to answer questions on likelihood of entry.
Likelihood	LIK1	Likelihood of entry via unaided primary pathways	The probability of the T*axon* to arrive and enter an area without human assistance.
	LIK2	Likelihood of entry via human aided primary pathways	The probability of the *Taxon* to arrive and enter an area human aided.
	LIK3	Habitat suitability	Forms part of the likelihood of a *Taxon* to establish.
	LIK4	Climate suitability	Forms part of the likelihood of establishment.
	LIK5	Unaided secondary (dispersal) pathways	Assesses spread potential.
	LIK6	Human aided secondary (dispersal) pathways	Assesses spread potential aided by humans.
Consequence	CON1	Environmental impact	Includes impacts caused by the *Taxon* on the environment through different mechanisms, based on EICAT (Hawkins et al. 2015).
	CON2	Socio-economic impact	Includes impacts caused by the *Taxon* on human well-being and livelihood, based on SEICAT (Bacher et al. 2018).
	*CON3	Closely related species' environmental impact	If no data on the *Taxon* itself are available, this includes impacts caused by related taxa on the environment through different mechanisms.
	*CON4	Closely related species' socio-economic impact	If no data on the *Taxon* itself are available, this includes impacts caused by related taxa on different socio-economic sectors.
	CON5	Potential impact	Assesses the potential impact of the T*axon* in the A*rea*, if invasive.
Management	#MAN1	What is the feasibility of stopping future immigration?	Important for effectiveness of control, as new influx of propagules needs to be stopped to control the *Taxon* effectively and sustainably.
	#MAN2	Benefits of the *Taxon*	Socio-economic and environmental benefits are included to assess the need of stakeholders for the *Taxon*.
	#MAN3	Ease of management	To provide indication of how easy the *Taxon* is to manage in the *Area* as this will influence risk management decisions.
	#MAN4	Has the feasibility of eradication been evaluated?	Indicates whether the feasibility of eradicating the *Taxon* from the *Area* has been formally evaluated. Note the evaluation of eradication feasibility is a separate process to the risk analysis framework.
	#MAN5	Control options and monitoring approaches available for the Taxon	Provides an overview of control options available.
	#MAN6	Any other considerations to highlight?	Can aid the development of management plans, permit conditions and exemptions.

* not assessed if CON1 and CON2 can be filled in respectively, i.e. information on impact is available for the *Taxon*; # not assessed if risk is low for the *Taxon*

2) Risk assessment: Likelihood

The section on likelihood assesses the probability of the *Taxon* to arrive, establish, and spread in the *Area*, with two questions for each process (arrival, establishment, and spread), resulting in six questions in total (LIK1–LIK6 in Suppl. material 2). These include questions on habitat and climate suitability and likelihood of entry and spread via aided and unaided pathways. Each answer is expressed as a probability value p, with all the levels and scenarios described in the narrative section and each level representing an order of magnitude difference. If the answer is not known after consulting literature and experts, following a precautionary principle, the answer is treated as p = 1 for the rest of the assessment, though noting that no answer was supplied and so highlighting an obvious area where more research is needed (Hulme 2012). For each probability level, we give general examples to provide guidance. These are structured as follows:

- Extremely unlikely (p = 0.000001): as likely as winning the lottery, if you play it once.
- Very unlikely (p = 0.0027): as likely as a new person you meet having their birthday on the same day as yours.
- Unlikely (p = 0.027): as likely as rolling two sixes when playing dice.
- Fairly probable (p = 0.5): as likely as getting heads when flipping a coin, i.e. fifty-fifty.
- Probable (p = 1 for calculation purposes): more likely to happen than not.

The probability levels of all the questions in this section are combined to calculate the likelihood of an invasion occurring. The final likelihood is calculated as the product of the maximum scores for each stage, i.e. p(arrival) [= max(LIK1, LIK2)] × p(establishment) [= max(LIK3, LIK4)] × p(spread) [= max(LIK5, LIK6)] (Suppl. material 2)].

RAAT thus incorporates some basic considerations of probabilities by multiplying the likelihoods of a taxon to cross the barriers in the invasion process, i.e., if the taxon cannot cross a certain barrier, the likelihood of establishment is decreased (Suppl. material 2: Fig. S2).

3) Risk assessment: Consequence

As it is important to get a comprehensive understanding of the potential harm caused by an alien taxon, it has been suggested that both environmental and socio-economic impacts should be included in risk assessments (e.g., Kumschick and Richardson 2013; Roy et al. 2018). The assessment of current and potential impacts, or consequences, is based on recent developments of impact scoring schemes (Blackburn et al. 2014; Nentwig et al. 2016; Bacher et al. 2018). EICAT is used for the assessment of environmental impacts (Blackburn et al. 2014; Hawkins et al. 2015). It was adopted by the International Union for the Conservation of Nature (IUCN) as a standard for the classification of alien taxa (IUCN 2020a, b), to be used alongside the Red List for the conservation of biodiversity. For socio-economic impacts, we initially used parts of the Generic Impact Scoring System (GISS) (Nentwig et al. 2016; see Kumschick et al. 2018). Since then, a new scoring scheme, more similar to EICAT and more consistent in the way impact levels are assigned, was published, namely the SocioEconomic Impact Classification of Alien Taxa (SEICAT) (Bacher et al. 2018). The version of the framework presented here therefore uses SEICAT instead of the GISS (Suppl. material 2), although all approved risk analyses reported in Table 1 are based on the GISS.

These impact scoring schemes have been shown to be intuitive to use, robust (Kumschick et al. 2017a, b), and transparent, and have proven to be applicable for a wide range of taxa (e.g., Kumschick et al. 2015; Evans et al. 2016; Kumschick et al. 2017a; Rumlerova et al. 2017; Hagen and Kumschick 2018; Kesner and Kumschick 2018; Nkuna et al. 2018). This makes them suitable for use as a component in a risk analysis framework. Another common feature of these impact assessment schemes is that all available evidence of impacts in the global alien range (including the *Area*) of the *Taxon* is collated and used for scoring (Hawkins et al. 2015; Nentwig et al. 2016; Bacher et al. 2018; see also Table 3 for an overview of the different impact levels). The guidelines cover each mechanism and sector through which alien taxa can affect the recipient regions, including competition, herbivory, and hybridisation for environmental impacts; and safety, material assets, and health for socio-economic impacts.

Table 3. Impact levels for the assessment of consequences in the risk assessment, based on Hawkins et al. (2015) and IUCN (2020a, b); Environmental impact), Bacher et al. (2018; Socio-economic impact), and this study (Potential impact).

Impact levels	Massive (MV)	Major (MR)	Moderate (MO)	Minor (MN)	Minimal Concern (MC)
Environmental impact (CON1 & CON3)	Causes at least local extinction of native species, and irreversible changes in community composition; even if the alien taxon is removed the system does not recover its original state.	Causes changes in community composition, which are reversible if the alien taxon is removed.	Causes local population declines in native species, but no changes in community composition.	Causes reductions in individual performance, but no declines in native population sizes.	No effect on performance of individuals of native species.
Socio-economic impact (CON2 & CON4)	Local disappearance of an activity from all or part of the area invaded; change is permanent and irreversible for at least a decade after removal of the alien taxon.	Local disappearance of an activity from all or part of the area invaded; change can be reversible within a decade after removal or control of the alien taxon.	Negative effects on well-being leading to changes in activity size; fewer people participating in an activity, but the activity is still carried out.	Alien species make it difficult for people to participate in their normal activities although the number of participants in any activity does not change.	No deleterious impacts reported despite availability of relevant studies with regard to its impacts on human well-being.
Potential impact (CON5)	The *Taxon* is a transformer in its native range, has ecosystem engineering properties or possesses other traits which suggest irreversible impacts on the community composition in the *Area* to occur. The *Taxon* is a pest of agricultural production in the native range and/or has the potential to cause high losses.	The *Taxon* has traits which suggest major impacts on native communities in the *Area*, but these impacts are likely to be reversible. The *Taxon* has traits which can lead to high losses to economy.	The *Taxon* possesses several undesirable traits. Due to the traits of the *Taxon* and/or its behaviour, it is expected to reduce population sizes of at least one native species. Economic loss is expected to be medium.	The *Taxon* does not possess any traits which could lead to effects on native species population sizes, but reduction in native individuals' performance is expected. Minor economic loss is possibly widespread.	Due to the traits of the *Taxon*, no effect on native individuals' performance is expected. No socio-economic loss is expected. The *Taxon* does not possess any undesirable traits.

These impact classification schemes, however, only consider impacts for which evidence is available (see also Kumschick et al. 2020b). Due to the lack of comprehensive impact studies for most species in most regions (e.g. Pyšek et al. 2008; Evans et al. 2016; Bacher et al. 2018; Kumschick et al. 2017a), the impact of alien species is likely under-reported. We therefore included the possibility to use data from congeners or other closely related species with similar life history traits to the RAAT framework (similar to Bomford 2008). Furthermore, to estimate potential and currently unrecorded impacts of the *Taxon* in the *Area*, we include considerations on the *Taxon*'s traits, behaviour, ecology, and impacts recorded in the native range (Table 3). This results in three to five questions related to impact – depending on data availability for the *Taxon* itself (Table 2). As we are interested in what the worst that could happen is, the maximum of the different impact scores is used as the consequence score.

The consequence score, together with the final probability from the Likelihood section, calculated as described above, are used to assess the level of risk (low, medium, high; as shown in Table 4). If the risk is low, no prioritised management or regulations are recommended and there is no requirement to complete the risk management section of the framework. If the risk is medium or high, however, the risk management section must be completed.

4) Risk Management

Generally, the distinction between whether or not (as opposed to how) to regulate a *Taxon* relies on the risks it poses to the recipient environment and economy. For taxa that are not yet present in an area and for which decisions on importation are required, this can be a relatively straightforward process: if the *Taxon* poses a high risk, it should not be allowed for import, but if it is low risk, it can be considered safe for import (e.g. Keller and Kumschick 2017). However, decisions regarding taxa that are already present and potentially well established in an area and are in use for various purposes, also depend on how easily they can be managed. Since management does not happen in isolation from the rest of society, social perceptions and benefits provided by the *Taxon* need to be assessed and accounted for in these cases (e.g., Zengeya et al. 2017). Unlike in the risk assessment section of the framework, where clear answers and probabilities are provided to determine the level of risk, the inclusion of benefits is dependent on the agenda of various stakeholders, priorities of decision-makers and the influence

Table 4. Table on how to determine the risk score from the likelihood and consequence assessments.

		Consequences				
		MC	MN	MO	MR	MV
Likelihood	Extremely unlikely	low	low	low	medium	medium
	Very unlikely	low	low	low	medium	high
	Unlikely	low	low	medium	high	high
	Fairly probable	medium	medium	high	high	high
	Probable	medium	high	high	high	high

of key stakeholders (e.g. Kumschick et al. 2012; Woodford et al. 2017). To keep the process transparent, we make provision for these aspects to outline how the inclusion of benefits influences management decisions and which benefits were included (Suppl. material 2).

Furthermore, once a taxon has been identified as posing a medium or high risk, one needs to consider what can be done to manage the risk. For taxa already present in the *Area* (i.e., for which prevention is no longer an option), this will often require a detailed evaluation of management options, the development of management plans, an assessment of financial resources, and a process of prioritisation of potential interventions (Wilson et al. 2017). Such detailed assessments are beyond the intended scope of the RAAT framework, as they also depend on political decisions and the allocation of resources. However, the RAAT framework provides for some basic management considerations which allow for a broad classification of how to treat certain risks. Therefore, the aim of this section is to provide some guidance as to which broad management goals should be investigated and what information is required in order to prioritise management actions.

The assessment of risk management is more open-ended, but needs to be documented in detail to assure transparency of decisions. In the RAAT framework, this includes socio-economic and environmental benefits, the feasibility to stop future immigration of the *Taxon,* and basic considerations regarding management feasibility (Suppl. material 2). The latter are based on Wilson et al. (2017) and Panetta and Timmins (2004) and include: a) accessibility of populations, b) whether detectability is time-dependent, c) time to reproduction, and d) propagule persistence of the *Taxon*. A scoring approach leads to a basic assessment of the ease of management.

Further to the assessment of these traits, it is important to note that for an assessment of eradication feasibility, a detailed study including, for example, the delimitation of all alien populations of the *Taxon*, population estimates, management trials, and some estimate of the return on investment of different competing strategies, should be conducted (Wilson et al. 2017). Eradication should not be set as a target if not evaluated in detail, as this could lead to a waste of limited resources (e.g., Cacho et al. 2007). To aid this process, there is a question in the framework asking if an eradication feasibility study has been performed for the *Area* (MAN4 in Suppl. material 2) and a further question on control options available (MAN5 in Suppl. material 2).

The answers provided in the risk management section feed into Fig. 2, which leads to broad recommendations on how to manage a *Taxon*. These differ, based on whether the *Taxon* is already present in the *Area*, whether prevention or eradication are feasible goals, and whether the *Taxon* has benefits to the *Area*, such that it might be a conflict species that could be allowed with a permit under certain conditions (Fig. 2).

5) Risk communication

Once the level of risk has been determined and options for management and benefits evaluated, it is crucial to clearly communicate the outcomes of the analysis to stakehold-

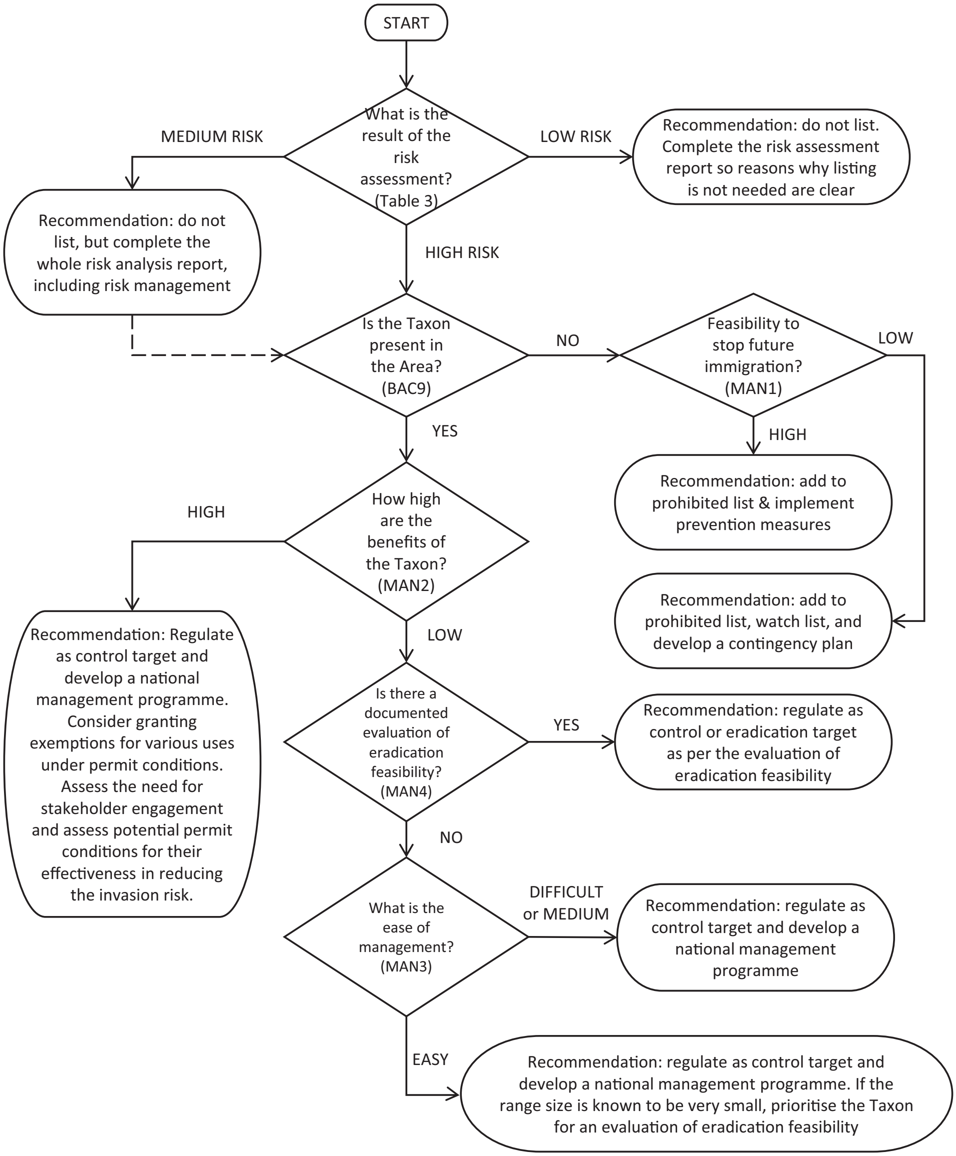


Figure 2. A decision tree for determining the appropriate regulatory response for species which are considered to be of medium or high risk during the risk assessment process. The information in brackets refers to question numbers in the RAAT framework (Table 1 and Suppl. material 2).

ers, including the general public, policy-makers, traders, and users of the *Taxon*. We identify two important components of risk communication. First, stakeholders need to be engaged during the risk analysis process for assessors to obtain information on the *Taxon* and to gain the support of stakeholders in the process (e.g., Novoa et al. 2018). There are often formal regulatory processes of stakeholder engagement and, in contentious cases, an independent scientific assessment might be needed (Scholes et al. 2017), but if conflicts are to be avoided, engagement should happen close to the outset of the process. Second, risk communication is important to provide stakeholders with sufficient information to understand the recommendations and be in a position to know under which circumstances decisions would change, for example, how new information will influence risk. Therefore, communication needs to be simple enough to reach understanding, but needs to provide enough information to underpin the decision.

In the RAAT framework, we incorporated several communication strategies to reach these goals. We provide a decision tree which uses information from the analysis to make recommendations on the management strategy for the *Taxon.* Fig. 2 describes how to arrive at recommendations for the management and regulation from the answers provided in the risk analysis. This depicts a simplified decision-making process which can be easily understood by policy-makers and stakeholders, while the details to feed into the flow diagram are documented and provided in detail in the full analysis. Furthermore, in addition to providing all details of the risk analysis with information on each parameter, we provide a template for an easy-to-digest summary and reporting sheet, including the conclusions from each section, with short descriptions on the *Taxon* itself, impacts, risks, ease of management, and benefits. An example of a summary sheet is given in the Suppl. material 3.

Application in South Africa

As discussed previously, the RAAT framework was tested and applied by different groups. This process has helped us to significantly refine (and we believe improve) the framework over time. It has also highlighted that, while the RAAT framework is fairly straightforward, some scientific experience is needed and assessors must be able to obtain a certain level of knowledge on alien taxa and the processes related to their invasion and impacts. Access to literature and experts is, therefore, also crucial. In South Africa for example, many employees of government agencies who initially tested the framework only had limited access to scientific literature and they therefore initially could not appropriately fill in some of the information required, even though relevant literature was available on the taxon (but not accessible to them).

To date, most taxa analysed with RAAT are of high risk (Table 1), which does not represent an ideal sample of taxa for a test of the applicability of the framework. This bias is due to the mandate of SANBI to analyse species which are currently regulated under the NEMBA A&IS Regulations, but for which no risk analysis had been performed to date. In addition, most taxa analysed so far are already present in South Africa (which was defined as the assessment area for all analyses). Ideally, species with different invasion statuses and risks should be analysed to test the RAAT framework further.

Notably for 13 of the 29 listed species that were assessed, a change in the listing category was recommended (Table 1). This is, again, likely due to the biased selection of taxa – in some cases, taxa were selected for analysis as they were contentious or it was felt the current category was inappropriate. However, it is clear that the listing of taxa, as determined during the original process, will be substantively different from the recommendations obtained by the process outlined here (i.e., completing the RAAT framework with the results reviewed and approved by ASRARP). The RAAT/ASRARP process (see Kumschick et al. 2020a) produces recommendations that are based on the best available scientific evidence, are peer-reviewed, and are transparent. The decision to list taxa, however, is the prerogative of the relevant government departments subject to a mandated requirement for public consultation. As of August 2020, the DFFtE was still in the process of establishing a cross-governmental decision-making panel on the risks of biological invasion. It is anticipated that ASRARP recommendations will be discussed at the meetings of such a panel.

Another lesson learnt was that it was important to train assessors in the application of the RAAT framework if uncertainties and misunderstanding in the questions, answer levels, and verbal descriptions were to be minimised (as also suggested by Sutherland and Burgman 2015). Such training ensures that the assessors applying the framework have a basic level of knowledge on risk analysis, alien taxa, and related processes. The training courses we ran also highlighted some important considerations to be made regarding the application of the RAAT framework. Firstly, there were some insights into the level of prior experience needed to complete a risk analysis. A BSc Hons degree in a relevant field (natural sciences) was mostly sufficient to understand the concepts provided after training, but a postgraduate degree (e.g. Masters) in a relevant field and experience in having authored a scientific publication (and specifically the experience of having responded to critical review comments) is very valuable in order to successfully complete a risk analysis and be able to respond appropriately to ASRARP reviews. Secondly, after training, the time to perform a risk analysis is 4–6 days, excluding the review by ASRARP and external reviewers, with the bulk of the time usually spent reviewing literature on a taxon. This is often increased due to the initial lack of access to primary literature.

While the RAAT framework strives to be objective, there is no guarantee that ASRARP and the assessor conducting the risk analysis agree on the outcome. During ASRARP deliberations it was decided that, if an assessor does not agree with changes requested by the ASRARP, an assessor can withdraw their risk analysis report and their report cannot subsequently be used by ASRARP or a third party. This has only happened once so far, but the issue of recognising potential biases is important – assessors who are knowledgeable on a taxon are likely to have specific views and motivations, while ASRARP members also have their own predilections.

Ideally, several experts should assess the same species and working groups and workshops held to reach final decisions on which species to list under national regulations (Sutherland and Burgman 2015). However, this was not an option in the South African case due to budgetary and time constraints. Increasingly, risk analyses are discussed at appropriate national working groups before submission to ASRARP [e.g., national working groups on alien Cactaceae, alien grasses, and a working group on alien animals in the Cape Floristic Region (Kaplan et al. 2017; Visser et al. 2017; Davies et al. 2020)]. The intention is that the risk analyses, once approved, represent both the best available scientific evidence and are also a consensus of those working on the species.

Dealing with risks that vary significantly with context

Beside the need to set appropriate management goals after risk analysis, there are some other considerations to be made specifically in the South African context. The NEMBA A&IS Regulations set out four potential listing statuses, all linked to specific conditions (Department of Environmental Affairs 2014; Kumschick et al. 2020b): Category 1a: eradication targets; Category 1b: control targets (potentially with exemptions); Category 2: control targets for which certain activities are allowed under permits with conditions; Category 3: control targets with exemptions. During the development and testing of the RAAT framework, it became clear that, with a desktop study (such as the RAAT framework) alone, these categories cannot always be conclusively determined. We therefore recommend that many of the management specific recommendations should be developed on a case by case basis for the species regulated. This includes, for example, suitable permit conditions for category 2 species, management goals for category 1b species (e.g., containment or asset protection, and the need for area-specific management), and the situations under which species can be exempt from conditions (this included category 3 species which are effectively listed the same as category 1b species with some specified exemptions according to the NEM:BA and its A&IS Regulations). Such exemptions could include trees declared as national monuments and protected as "heritage" (e.g., Dickie et al. 2014) should they prove not to contribute to the invasion. A related issue is that of subspecific entities – certain cultivars or varieties could be considered safe for cultivation even if the "parental stock" is invasive (e.g. Datta et al. 2020; Gordon et al. 2016). There is provision within the RAAT framework to assess sub-specific entities separately, but often data on underlying traits are missing (e.g., proof of sterility).

We believe that the RAAT framework is not the place to develop the details of such risk management issues in depth. This should rather be an integral part of the development of national management programmes for particular taxa that can elucidate where and when control should be targeted and when, perhaps, control will be ineffective (for South African examples of such plans, see, for example, van Wilgen et al. 2011; Le Maitre et al. 2015; Terblanche et al. 2016; and the discussion in van Wilgen and Wilson 2018).

Discussion and Way Forward

Biological invasions pose a variety of threats and risk analysis frameworks are needed to explicitly assess and help co-ordinate efforts to manage these. Many decision-support tools for the management of alien taxa have been developed (reviewed by Heikkilä 2011; Leung et al. 2012; Kumschick and Richardson 2013). The RAAT framework takes advantage of the lessons learnt from the application of previous schemes (e.g. Roy et al. 2018) and, therefore, has several key advantages: it provides a comprehensive structure, it addresses all the aspects of risk analysis in one framework, and it is applicable across taxa and regions. RAAT therefore provides a transparent and evidence-based tool to underpin policy decisions and to assist in the prioritisation of alien taxa for management.

Threats posed by biological invasions include not only individual alien taxa, but also invasion pathways and threats posed collectively to specific sites (CBD 2002; McGeoch et al. 2016; Essl et al. 2020). While the RAAT framework focuses on species-based assessments (Kumschick and Richardson 2013), it can feed into pathway and area-based approaches. By formalising risk in a practical and mathematically sound manner, we believe the RAAT framework provides a valuable additional tool for decision-makers, both to assess and manage the threat posed by alien species that are proposed to be deliberately and legally introduced, and to provide a co-ordinated way of providing the evidence base to justify regulating alien species already present in a country.

Ideally, a risk analysis framework for alien species would recommend the most appropriate management goal for an alien species to be regulated (e.g., see Booy et al. 2017). However, the RAAT framework is not exhaustive in terms of making decisions on which management goal is the most suitable for any taxon. Such decisions often need detailed consideration of political and budgetary constraints. In particular, the RAAT framework in isolation does not provide recommendations as to whether a taxon can be eradicated, but rather relies on detailed analysis of eradication feasibility (e.g., Panetta and Timmins 2004; Wilson et al. 2017). Our framework can, however, prioritise taxa for which more information should be gathered for this purpose.

More generally, the RAAT framework does not provide management plans for any taxon recommended for regulation as a control target (Fig. 2). There are several additional considerations that will need to be made when drafting management plans, for instance: Will stakeholders be opposed to management (e.g. access to land)? Are control efforts ethical? Might it be feasible to contain populations? Or should asset protection be the main goal of management? Should resources be spent to develop new control measures, for example, biological control? Such issues are important when attempting management and to reduce and mitigate the risks caused, but need to be considered explicitly outside of the RAAT framework and in many cases need practical considerations outside the realms of a desktop analysis.

In the next phase of development, the RAAT framework will be calibrated to adjust the preliminary cut-off levels set to assign risk categories (e.g. Kumschick and Richardson 2013). The questions, answer levels, and written descriptions as outlined in the Suppl. material 2 will not be affected by this process, but the levels of risk assigned, as shown in Table 3, might change according to the outcome. Generally, the RAAT framework allows for risk analyses to be updated if and when more information becomes available. Cut-off levels for low, medium, and high risk can be adapted if needed or as appropriate, however justification needs to be provided. It will also be important to assess the degree to which a risk analysis performed in South Africa on a given taxon can be used as the basis for a risk analysis of a given taxon in a different country or even a specific part of South Africa. As currently formulated, we suspect information on the likelihoods are context-specific, the potential consequences are more general and management considerations are a mix of the two, but this remains to be tested.

As more taxa in South Africa are analysed, new issues with the RAAT framework will undoubtedly arise. However, we feel that it represents a significant advance in making the process of regulating alien taxa more transparent, defensible, and more clearly linked to international protocols.

Accessibility of data

An updated version of the RAAT framework is appended here (Suppl. material 2, dubbed v1.2), but we plan to maintain the most recent version on the Zenodo server [DOI 10.5281/zenodo.3760907] and would encourage readers to check there for the latest version.

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Supplementary material 1

How the Risk Analysis Framework covers Section 6, Regulation 14-17, in the NEM:BA A&IS Regulations of 2014 (Appendix S1)

Authors: Sabrina Kumschick, John R. U. Wilson, Llewellyn C. Foxcroft

Data type: List of parameters and link to regulations

Explanation note: Questions in the Risk Analysis Framework and the aspects in the NEMBA A&IS Regulations (DEA 2014) they cover (Table s1.1) and aspects not covered in the Risk Analysis Framework which deal with the restricted activity regarding the permit application and are suggested to be requested for permit applications in a separate document (from NEMBA A&IS Regulations; DEA 2014) (Table S1.2).

Link: https://doi.org/10.3897/neobiota.62.51031.suppl1

Supplementary material 2

Risk Analysis for Alien Taxa framework, adapted to South African NEMBA A&IS Regulations (v.1.2) (Appendix S2)

Authors: Sabrina Kumschick, John R. U. Wilson, Llewellyn C. Foxcroft

Data type: Detailed guidelines for RAAT

Explanation note: Detailed guidelines for applying the Risk Analysis for Alien Taxa (RAAT) framework, including the reporting template.

Link: https://doi.org/10.3897/neobiota.62.51031.suppl2

Supplementary material 3

Example of RAAT (Appendix S3)

Authors: Sabrina Kumschick, John R. U. Wilson, Llewellyn C. Foxcroft

Data type: Example risk analysis

Explanation note: Example of a reporting sheet for the risk analysis of Psittacula krameria in South Africa. Note: this has been updated to the most recent format and is slightly different from the approved version.

Link: https://doi.org/10.3897/neobiota.62.51031.suppl3

Supplementary material 4

List of contributors to the risk analysis process in South Africa 2018, 2019 (Appendix S4)

Authors: Sabrina Kumschick, John R. U. Wilson, Llewellyn C. Foxcroft

Data type: List of assessors, reviewers and experts

Explanation note: Only people involved in risk analyses where the recommendation has been approved are noted here; there are many others who are currently involved as assessors, experts or reviewers, but they have not yet been involved in an approved risk analysis. Many other people were involved prior to 2018 (in particular the panel was set up and initially chaired by Philip Ivey), but the risk analysis framework had not been implemented at that stage. A 'Member' is someone who served on the Alien Species Risk Analysis Review Panel (with ex-officio members indicated with an asterisk); an 'Assessor' is someone who conducted a risk analysis; an 'Expert' is a person who is an Assessor and listed as someone who was formally consulted during the development of their risk analysis report; a 'Reviewer' is someone who reviewed a risk analysis report at the bequest of an ASRARP member (i.e. independent from the Assessor). In addition, Khensani Nkuna and Viwe Balfour assisted as part of the ASRARP Secretariat. It is intended that an updated list will be published annually on SANBI's website, but it can also be provided on request.

Link: https://doi.org/10.3897/neobiota.62.51031.suppl4

Supplementary material 5

Guidance regarding the use of the confidence rating (Appendix S5)

Authors: Sabrina Kumschick, John R. U. Wilson, Llewellyn C. Foxcroft

Data type: Guidance on confidence ratings

Explanation note: Guidance regarding the use of the confidence rating (taken from Hawkins et al. 2015, modified from the EPPO pest risk assessment decision support scheme (Alan MacLeod 09/03/2011; revised 28/04/2011; copied from CAPRA, version 2.74; 2)).

Link: https://doi.org/10.3897/neobiota.62.51031.suppl5

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RESEARCH ARTICLE

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The effect of cross-boundary management on the trajectory to commonness in biological invasions

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Abstract

The number of alien species introduced and undergoing range expansion in novel environments is steadily increasing, with important consequences for native ecosystems. The efficacy of management planning and decision making to limit such invasions can be improved by understanding how interventions will impact the population dynamics of recently introduced species. To do so, here we expand on a typological framework that enables the classification of populations over time into 10 categories of commonness, and apply it to a spatially discrete metapopulation with heterogeneous abundance across spatial units (patches). We use this framework to assess the effect of cross-boundary management on the capacity of a metapopulation with different demographic and dispersal characteristics, including time lags in population growth, to become common. We demonstrate this framework by simulating a simple theoretical metapopulation model capable of exploring a range of environments, species characteristics, and management actions. Management can vary in the efficacy of propagule interception between patches, and in the synchronisation of the implementation of these measures across patches (i.e. if management is implemented simultaneously across patches). Simulations show that poor interception efficacy that only modestly reduces the number of propagules entering a given spatial unit cannot be compensated for by strong management synchronisation between spatial units. Management synchronisation will nonetheless result in a reduction in rates of spread once a critical threshold of interception efficacy has been met. Finally, time lags in population

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growth that may result in delayed spread are an important aspect to be considered in management as they can amplify the efficacy of management. Our results demonstrate how a typological framework of categories of commonness can be used to provide practical insights for the management of biological invasions.

Keywords
Abundance, alien species, allee effect, biosecurity, occupancy, simulation model, spread, time lags

Introduction

The number of species becoming established in regions outside their native range is rapidly increasing as a result of human trade and transport (Seebens et al. 2017). This rapid accumulation of alien species is troublesome as biological invasions constitute a major threat to biodiversity, local economies and human welfare (McGeoch et al. 2010; UNEP CBD 2010; Bellard et al. 2016). Cross-border biosecurity measures focussed on prevention of introductions are most effective at limiting invasions (Hulme 2009; Hulme et al. 2009; Scalera et al. 2016; IUCN 2018), in combination with the management of populations of alien species that are already established (Martin et al. 2020). A combination of both approaches can also be used to prevent the secondary spread of an introduced species across spatial units, such as water bodies or conservation areas (Vander Zanden and Olden 2008). Cooperation between countries is also crucial to control biological invasions and prevent efforts from one country to control a given species to be undermined by the lack of action of others where the species is present (Genovesi 2011; Faulkner et al. 2020). The resources and self-interests of different countries can nonetheless affect the degree of cooperation.

Quantifying both the local abundance and area of occupancy of alien populations is important to assess and track how a species newly introduced into a novel environment may spread (Catford et al. 2016; McGeoch and Latombe 2016). Considering local abundance separately from the distribution is crucial to implement appropriate management responses, as different actions will be more or less efficient over large regions and small or large populations. For alien species that have recently been introduced, the residence time is also of utmost importance, as it will influence the urgency and efficacy of management actions, with species spreading rapidly being of particular concern (McGeoch and Latombe 2016). Residence time also provides important information on management feasibility (Brock et al. 2020). Taken together, these three dimensions (local abundance, area of occupancy, residence time) can be combined following a typological approach into eight discrete categories of commonness for alien species (Fig. 1; see also table 1 in McGeoch and Latombe 2016). In this typology, local population size can be small or large, geographic range can be narrow or wide, and residence time can be short or long. A newly introduced alien species with low abundance over a narrow range (‘Newly established’) can become more common, i.e. being abundant over a wide region after some time (‘Successful’), by transiting over time through different categories of commonness (e.g. by first increasing its abundance locally before a)

Category	Local Population Size		Geographic Range	Residence Time
	Local Mean Abundance	Maximum Local Abundance	Area of Occupancy	
Newly established	Small	Small	Narrow	Short
Incipient	Large	Large	Narrow	Short
Dispersed	Small	Small	Wide	Short
Dispersed + Abundant somewhere	Small	Large	Wide	Short
Highly successful	Large	Large	Wide	Short
Not common	Small	Small	Narrow	Long
Constrained	Large	Large	Narrow	Long
Sparse	Small	Small	Wide	Long
Sparse + Abundant somewhere	Small	Large	Wide	Long
Successful	Large	Large	Wide	Long

b)

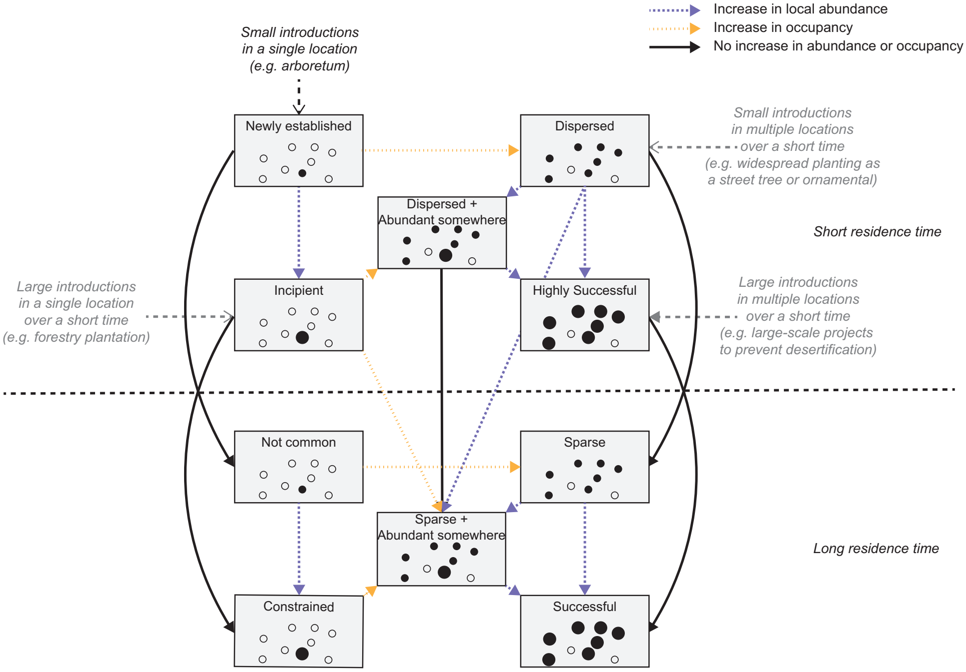

Figure 1. Schematic showing the different trajectories to commonness for alien species described by a typological approach based on ten categories. **a** For a metapopulation in a network of discrete patches, abundance can be spatially heterogeneous, and both local mean abundance (LMA) and maximum local abundance (MxLA) must be used to capture all the potential trajectories to commonness (see text explanation). Using LMA only to quantify local population size can underestimate the commonness of a metapopulation. This results in the creation of two new categories in addition to the original eight categories from McGeoch and Latombe (2016): 'Dispersed + abundant somewhere' and 'Sparse + abundant somewhere'. **b** A population can transit from one category to another by increasing its abundance (blue arrows – large circles) or range (yellow arrows) rapidly, or by remaining at similar abundance and range levels over a long period of time (black arrows). When both abundance and range increase rapidly at the same time, some categories may be skipped (e.g. transit directly from 'Newly established' to 'Dispersed + abundant somewhere'). Arrows that cross or are under the dashed line indicate changes in abundance or occupancy that occur after a time lag.

dispersing). The sequence of categories will depend on the species' demographic and dispersal characteristics, but also on stochastic effects, lag phases, etc. It is important to note that these categories should not be seen as having hard boundaries for species or populations in space or time. Rather, they are a useful typological approach to better understand and conceptualise the variable ways in which species expand their ranges (and in some situations eventually contract them), and potentially identify management strategies that are more or less effective in each case.

The potential for a newly introduced alien species to become abundant will be determined mostly by its local population growth rate, whereas its capacity to become widespread will be determined primarily by its dispersal rate, and both can be influenced by humans. Newly introduced populations are often assumed to exhibit logistic growth, although many factors can affect population growth, from the relationship between density and per capita population growth to the influence of the local spatial structure on encounters between organisms (Law et al. 2003; Mistro et al. 2012). Population growth can also be reduced by multiple mechanisms associated with small population size leading to time lags caused, for example, by Allee effects (Courchamp et al. 1999; Stephens et al. 1999; Berec et al. 2007), or the time required for genetic or phenotypic adaptations to the new environment (Pérez et al. 2006). Such time lags in population growth imply that newly introduced populations may remain at low density and have a restricted range for some time, before growing and spreading across regions (Mistro et al. 2012; Essl et al. 2015; Rouget et al. 2016; Hui and Richardson 2017).

Species dispersal, the mechanism directly responsible for range expansion, is affected by a wide variety of factors, from species' physical traits, behaviours and movements to the presence of natural and human-mediated vectors, as well as properties of the local environment (e.g. connectivity) (Nathan et al. 2012). At a given spatial scale, dispersal can be considered to range from (1) diffusion processes (usually natural), (2) dispersal involving long-distance dispersal events (either through natural processes or human mediation), and (3) stratified diffusion explicitly representing two different spatial scales (Wilson et al. 2009; Lewis et al. 2016; McGeoch and Latombe 2016). Even human-mediated dispersal can encompass a wide variety of vectors with different dispersal characteristics within a network of connected locations (e.g. Seebens et al. 2013; Banks et al. 2015). Long-distance dispersal, either natural or by human agency, is a key factor responsible for dramatic increases in the spread and invasion success of alien species (Lewis et al. 2016; Hui and Richardson 2017). Abundance and dispersal are not independent phenomena, thus understanding how the combination of different growth and dispersal rates affect the abundance and range of species is necessary to capture the complexity of the different ways in which a species can become more common (McGeoch and Latombe 2016).

Here, we simulate the effect of cross-boundary management of a theoretical species on a network of discrete, interconnected patches randomly distributed in space, exchanging propagules with each other through human mediation (i.e. a metapopulation). We analyse (1) how variations in interception efficacy (the proportion of propagules from the simulated species that get intercepted when migrating from one patch to another) and (2) management synchronisation between patches affects the trajectories of how alien species become more common under different demographic and dispersal characteristics. Here management synchronisation represents the simultaneity in the implementation of management measures across patches. Once these measures start being implemented in a patch, low synchronisation therefore corresponds to a delay before they start being implemented in other patches. In real systems, lack of synchronisation can be driven by differences in priorities, for example if different countries consider an alien species to be more or less harmful. Practical limitations also play a role when, for example, resources to implement management measures across, for example, water bodies, are logistically difficult or costly. We focus on cross-boundary management, and do not consider within-patch management of alien populations in the model. We first outline the categories of commonness constituting the typological approach, and the mechanisms through which a population can transit from one category to another, i.e. the trajectory to commonness (*sensu* McGeoch and Latombe 2016). We show how the original classification into eight categories must be extended to consider ten categories, to account for the spatial heterogeneity in local abundance. We then assess how the trajectory to commonness is affected by (1) various demographic characteristics and dispersal rates, and (2) the interception efficacy and the synchronisation of cross-boundary management across patches. This is particularly relevant in the context of legislation that is implemented by groups of countries, such as the European Union IAS regulation 1143/2014 (EU 2014).

We predict that stronger synchronisation in the implementation of cross-boundary management in different patches and higher interception efficacy should limit the ability of a metapopulation to increase its area of occupancy across the network of patches. This will prevent it from reaching categories of commonness characterised by large areas of occupancy. We expect that synchronisation is important for preventing alien species with good long-distance dispersal abilities from establishing in new patches before cross-boundary management is implemented. By contrast, we expect that interception efficacy plays an important role in spread to new patches for all alien species. Finally, we anticipate that time lags will make the efficiency of cross-boundary management less dependent on the synchronisation of cross-boundary managements.

Methods

Categories of commonness and mechanisms of transition between categories

Species range sizes are typically assessed using either the extent of occurrence (the total continuous area over which the species occurs) or the area of occupancy (AoO, the area within the extent of occurrence over which a species occurs, for a given spatial grain) (IUCN 2001). Here, we use the AoO for a network of discrete patches of equal size, randomly distributed in space, as it is independent of the spatial distribution of patches, contrary to the extent of occurrence.

Across a network of discrete patches, the abundance of populations occupying different patches will be heterogeneous. To obtain a single summary measure of abundance over a set of independent patches that is independent from AoO, the local mean abundance (LMA), computed as the mean abundance of occupied patches (i.e. discarding empty patches in the computation, otherwise LMA becomes simply proportional to the overall abundance) is used (Gaston et al. 2000; McGeoch and Latombe 2016). However, LMA decreases when new populations with low local abundance establish, which can result in the metapopulation being considered as less common than before. This is logically incorrect, since the species has spread without becoming less abundant overall. In such a situation, abundance has only become spatially heterogeneous. To prevent this logical fallacy and account for the spatial heterogeneity in abundance, two additional categories of commonness are needed: 'Dispersed + abundant somewhere' and 'Sparse + abundant somewhere' (Fig. 1). Here the maximum local abundance (MxLA) of the metapopulation is quantified, as it will not change simply from averaging multiple population abundances. If a metapopulation includes abundant populations in a small number of patches, both the LMA and the MxLA will be large. If a small number of propagules spreads to other patches, the LMA will decrease and can become small, whereas the MxLA will remain high, capturing the constant abundance in the source patches. Species can have different growth rates and dispersal characteristics across a region, and AoO, LMA and MxLA will therefore change over time across the multiple discrete patches (see Suppl. material 1: Appendix A for different archetypes of trajectories to commonness).

The metapopulation model

We apply the analyses in a model system consisting of 20 dimensionless patches with the same carrying capacity, randomly distributed in space in a square region of 100 × 100 distance units. Such patches can intuitively represent entities such as islands, water bodies, or national parks, for which a number of cross-border management measures exist (Kaplan and White 2002; Kark et al. 2015; IUCN 2018). The metapopulation concept can also be extended to represent countries exchanging propagules, whose spatial scale is the one on which biosecurity legislation and measures are more commonly designed and implemented. The distance between patches can then be considered as a proxy to represent differences in the movements of propagules between patches resulting from various pathways between countries, such as the amount of trade and people movements. Patches were at least five distance units from each other. While the size of the chosen model system is arbitrary, it is within the range of realistic cases. For example, the number of countries per continent ranges from 14 to 58, and there are 27 member states in the European Union. Each patch had a carrying capacity of $K = 10,000$ individuals. The population dynamics follows logistic growth:

$$N_{t+1} = round\left(N_t + r \times N_t \times \left(1 - \frac{N_t}{K}\right)\right) \qquad \text{Eq. 1}$$

Table 1. Model parameters and their values. All parameters are combined in models, the only exception being the two dispersal kernels that are used separately from each other.

Parameter name		Parameter symbol	Definition	Parameter values
Population model core parameter		*r*	Per capita growth rate	0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9, 1
Allee effect		*A*	Value of the Allee effect (used to model time lag). A low value indicates a high time lag.	Ø , 0.3 (weak Allee effect), -0.001 (strong Allee effect)
Dispersal parameter	*– Gaussian*	σ	Standard deviation of the Gaussian distribution. Represents dispersal rate.	5, 6, 7, 8, 9, 10
	– Cauchy	γ	Scale parameter of the Cauchy distribution. Represents dispersal rate.	0.5, 1.1, 1.7, 2.3, 2.9, 3.5
Synchronisation of cross-border management		*s*	Number of time-steps (i.e. time) before a new patch starts implementing cross-boundary management. At the most extreme values of s relatively few patches will begin border measures within the time horizon of the simulations. Represents synchronisation.	0, 1, 5, 10, 15, 20
Intensity of cross-border management		*i*	Proportion of immigrating individuals that are eliminated at each time-step. Represents the interception efficacy of the cross-boundary management.	0, 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9
Simulation ID		Ø	ID of the simulation run, characterised by a random spatial distribution of patches. For a given ID, the spatial distribution of patches remains the same when varying the other parameter values.	1, … , 20
Other parameters with fixed values across simulations		*K*	Carrying capacity of each patch	10000
		Ø	Number of patches	20
		Ø	Size of the square area	100 × 100 (dimensionless)
		Ø	Minimum distance between two patches	5 (dimensionless)
		Ø	Number of time steps per simulation	200

where *r* is the per capita growth rate, which varies between 0.1 and 1 (Table 1). Here we use the model in a theoretical context to explore how relative changes in demographic and dispersal characteristics would qualitatively impact the trajectory to commonness of a metapopulation that is, by default, constantly increasing and spreading. Therefore, the values of the carrying capacity and of the number of patches is arbitrary, although the orders of magnitude reflect real systems. We nonetheless ran preliminary analyses to assess the effects of varying these parameters. Simulations with $K = 100$ showed qualitatively similar results, although a larger carrying capacity provided advantages to populations that were able to disperse over long distances because of the increase in number of propagules. Similarly, using more than 20 patches would provide more dispersal opportunities between patches, and as a result the speed at which an alien species would become common is likely to increase.

Patches were initialised with zero individuals of the focal alien species, except for one randomly selected patch, which is initialised with 500 individuals (Suppl. material 1: Fig. B1 in Appendix B). At each time-step, two events occurred: (i) the population of each patch grew following Eq. 1, and (ii) a proportion of the population migrated to other patches with a probability determined by a distance-based gravity model using dispersal kernels. For every focal patch, all patches (including itself) received a score based on the distance between their centres and the focal patch's centre, computed from the chosen dispersal kernel (described below). The scores were then divided by the sum of scores to determine the proportion of propagules from the focal patch either remaining in the focal patch or migrating to another one. That is, each propagule leaving a focal patch necessarily reached another patch. That implies that at each time-step, patches lose individuals due to emigration, and gain others from immigration. If emigration was higher than immigration (which would happen for patches with disproportionately high abundance compared to other patches), the population of the patch decreased, in a classic source-sink dynamic (but this decrease was compensated by local population growth).

The effect of different types of dispersal was compared by running the gravity model with either a Gaussian kernel (Eq. 2) or a Cauchy kernel (Eq. 3) (Suppl. material 1: Fig. B2 in Appendix B). Different dispersal kernels (and combinations of kernels) can be used to model the spread of a population, but the Gaussian and Cauchy distributions represent two extremes (McGeoch and Latombe 2016) (although another trivial extreme case would be a uniform distribution, in which case the metapopulation would simply be equivalent to a single population). Gaussian kernels are typically used to model simple diffusion for which long-distance dispersal is extremely rare. Here we use it to represent a situation in which a population will spread in a network by primarily invading neighbouring patches. The Cauchy kernel is commonly used to model frequent long-distance dispersal events due to having a very fat tail (Nathan et al. 2012; Lewis et al. 2016). Here we use it to represent frequent dispersal between patches distant from each other. The Cauchy dispersal has a narrower peak than the Gaussian kernel, implying that more propagules will remain in a given patch, although the fat tail means that the propagules emigrating from a patch can do so over longer distances. These two kernels also offer the advantage of being characterised by a single parameter (contrary to stratified dispersal and many other fat-tail kernels), simplifying simulation analyses.

$$G(d) = \frac{1}{\sqrt{2\pi\sigma^2}} e^{\frac{-d^2}{2\sigma^2}} \qquad \text{Eq. 2}$$

$$C(d) = \frac{1}{\pi\gamma\left[1+\left(\frac{d}{\gamma}\right)^2\right]} \qquad \text{Eq. 3}$$

where *d* is the distance between the centres of two patches, and σ and γ represent the dispersal rate of the individuals (Table 1; Suppl. material 1: Fig. B2 in Appendix B).

The model was run for 200 time-steps for each replicate. That enabled the averaged abundance across the 20 patches to reach at least 9500 individuals, except for at the lowest growth and dispersal rates. 20 replicates were run for each set of parameter values (Table 1). For each replicate, a new random spatial configuration of the patches was used (Suppl. material 1: Fig. B1 in Appendix B).

In addition, we implemented time lags using weak and strong Allee effects to explore the consequences of time lags in population growth on the efficacy of cross-boundary management (Taylor and Hastings 2005; Berec et al. 2007; Hui and Richardson 2017). Species with a weak Allee effect can be especially problematic in practice, as they may remain undetected locally for a long time while spreading in other patches before increasing in abundance, but this time lag in return can enhance the efficiency of proactive management measures. The Allee effects were modelled using the following equation:

$$N_{t+1} = round\left(N_t + r \times N_t \times \left(1 - \frac{N_t}{K} \right) \times \left(\frac{N_t + A * K}{K} \right) \right) \qquad \text{Eq. 4}$$

A was set to 0.3, a value similar to those used in other studies (García-Díaz et al. 2019), for the weak Allee effect. *A* was set to -0.001 for the strong Allee effect, because preliminary simulations showed that higher values would prevent the metapopulation from spreading (see Suppl. material 1: Fig. B3 in Appendix B for the effect of changing the value of parameter *A* on the growth rate of a population).

Cross-boundary management

To model cross-boundary management between patches, we restricted immigrating propagules to successfully reach a patch with a probability *i* (varying from 0.1 to 1; Table 1). Migrating propagules had a probability 1 – *i* of being eliminated. This probability, which represents the efficacy of cross-boundary management, was identical for all patches in a simulation. The number of individuals reaching a patch at distance *d* from a source patch is therefore on average $N(t) \times i \times G(d)$ or $N(t) \times i \times C(d)$. By setting $i > 0$, we consider that management will only ever be partial, as results would be trivial otherwise. Although full containment is approachable in some cases (e.g. Bailey et al. 2011), achievable efficacy depends on the species and life forms considered (Panett and Cacho 2012). Note that we did not include any management affecting the local abundance within patches, to isolate the effect of cross-boundary management.

To represent challenges linked to relative differences in the effective implementation of legislation in different countries and levels of cooperation between them, we introduced the synchronisation term *s* between patches in the model. *s* represents the time delay after which cross-boundary management starts being implemented in a new patch (i.e. the opposite of synchronisation). Once a given patch starts applying cross-boundary management, it applies for the rest of the simulation. Setting the time delay *s* to 0 represents perfect synchronisation. We then ran simulations so that during every *s* time-step, a new random patch starts implementing cross-boundary management, until all patches apply cross-boundary management (with *s* ranging from 1 to 20; Table 1). The values for *i* and *s* were chosen to cover a range that was large enough to observe some effects on the modelled populations' path to commonness using this theoretical model. In practice synchronisation therefore represents differences in the existence of suitable legislation, or in the effectiveness of implementation of cross-border biosecurity legislation across countries for a given species, as different countries or regions can have different priority species. By varying *i* and *s*, we therefore explore the efficiency of different types of cross-border management in reducing the time and trajectory by which a species becomes abundant in all patches for different local population growth rates and rates of spread between patches.

Computation of the categories of commonness

For assessing the path to commonness of a metapopulation in a given simulation using the categories of the framework, the outputs of all time-steps of the 20 replicates were used without implementing any cross-boundary management or time lag (i.e. 200 × 20 = 4000 sets of values) for each dispersal kernel; we applied the following thresholds: a metapopulation changed category if the population of an occupied patch reached three quarters of the carrying capacity on average (i.e. LMA or MxLA > 7500), if more than three quarters of the patches were occupied (i.e. AoO > 15), or if residence time reaches half the number of time-steps. Since in our model a metapopulation necessarily becomes more common as time passes, increasing the number of time-steps during a simulation results in more time-steps for which maximum AoO, LMA and MxLA are attained, which artificially increases the number of time-steps for which the metapopulation is classified as 'Highly successful' or 'Successful'. Therefore, only the first 100 time-steps for each simulation were used to better show the effect of varying the parameter values on the path to commonness, setting the residence time threshold to 50 time-steps. This combination of thresholds enabled all categories of commonness to be represented in the simulations, and enabled us to better discriminate the effect of the different model parameters on the simulation outputs. For each simulation, the proportion of the number of time-steps spent in each category of the 100 time-steps was computed. This proportion was then averaged over the 20 replicates of each parameter combination and used to assess the path to commonness for each combination of parameter values.

Relative effect of cross-boundary management with and without time lag

We assessed if the effect of cross-boundary management was higher in the presence of an Allee effect compared to logistic growth, i.e. if cross-boundary management changes the time spent in a category more when a time lag is present. First, we compared the time (number of time-steps) spent in a category of commonness with and without cross-boundary management, using the following formula (the 'sparse' category is used here as an example):

$$prop\_rel(Sparse, i \neq 0, s \neq 0) = prop(Sparse, i \neq 0, s \neq 0) \times \frac{1 + prop\ (\ Sparse\ , i \neq 0, s \neq 0)}{1 + prop\ (\ Sparse\ , i = 0, s = 0)} \qquad \text{Eq. 5}$$

This formula prevents divisions by 0 when a metapopulation did not reach the category without cross-boundary management ($i = 0$, $s = 0$). It also gives the same result (0) when a metapopulation did not reach the category with cross-boundary management for different ($i \neq 0$, $s \neq 0$) combinations, regardless of the outcome without cross-boundary management. A low value indicates that the metapopulation spends less time in the category when cross-boundary management is applied (the values are bounded between 0 and 0.75).

Eq. 5 was applied to the logistic growth and the Allee effects separately, and the difference *prop_rel_Allee*() – *prop_rel*() was then computed. A positive difference indicates that the proportion of time spent in a category of commonness increased following application of cross-boundary management when a time lag was applied relative to the logistic growth, whereas a negative difference indicates that this proportion decreased. In other words, non-zero values indicate that, for the same intrinsic growth and dispersal rates, time lag enhanced the effect of cross-boundary management.

Results

Trajectories to commonness under different demographic and dispersal characteristics in the absence of cross-boundary management

During a simulation run, metapopulations transited through different categories of commonness, with the specific sequence depending on the spatial distribution of patches. Fig. 2 shows how, for a given combination of parameter values, a metapopulation changed from one category to another as time passed, with differences between spatial distributions indicated by differences in the time step at which transitions occurred. To summarise these results, the area covered by each category in a barplot (visualised by a specific colour in Fig. 2) was divided by the total area, therefore representing the proportion of time spent in a category over a simulation run with a specific combination of parameter values (Figs 3–6).

In the absence of cross-boundary management, no metapopulation was classified as ‘Not common’ at the end of the simulations. Except for the minimum values of growth and dispersal rate, the majority of the simulations reached high abundance and occupancy, often quickly (i.e. the ‘Successful’ category, often transiting through the ‘Highly Successful’ category; Figs 3A, C, 4A, C). Under a Gaussian kernel and at low dispersal, populations were only present in a few patches, and reached high abundance with a speed depending on the per capita growth rate (i.e populations with low growth rate remained in the ‘Newly established’ category for a long time before transiting to the ‘Constrained’ category, via ‘Incipient’ when growth rate increased). As growth rate increased, simulations reached the ‘Successful’ category, because high local abundance provided propagules to disperse to other patches. For low growth rate and high dispersal, metapopulations dispersed quicker, reaching the ‘Sparse + abundant somewhere’ via the ‘Dispersed’ category. Very few simulations reached the ‘Sparse’ category, because population size in the initial patch increased over time. For high growth and dispersal rates, metapopulations first rapidly increased in occupancy, followed by their local abundance, and therefore reached ‘Highly successful’ via the ‘Dispersed’ and the ‘Dispersed + abundant somewhere’ category (Figs 3A, 4A).

Results were qualitatively similar for the Cauchy dispersal, as shown by the similar colour distributions (compare Fig. 3A, C). There were nonetheless quantitative differences, as the establishment of small populations in several patches within a short time

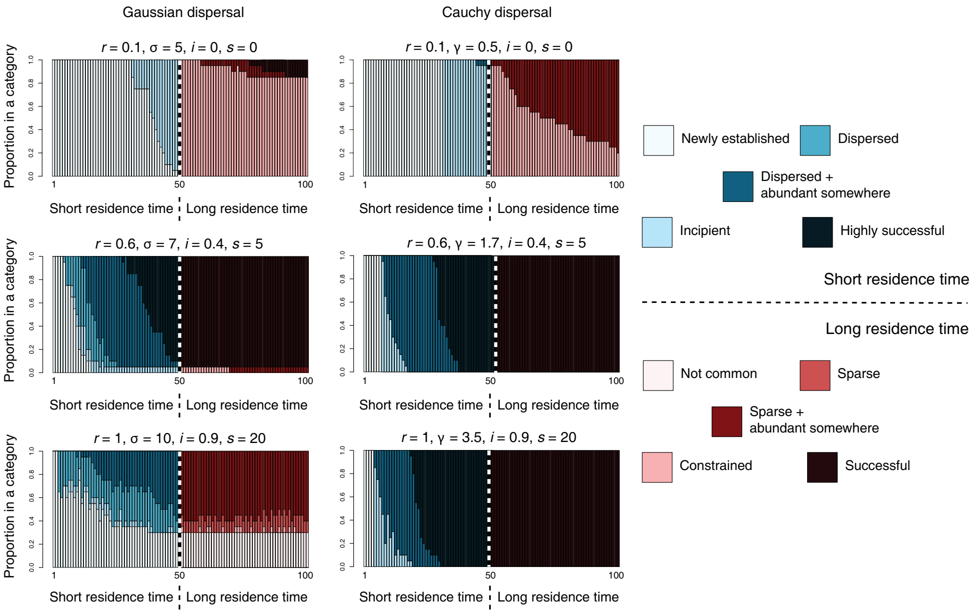

Figure 2. Modelling the fate of alien species populations and their assignment to different categories of commonness through time for the Gaussian and Cauchy dispersal kernels, for specific combinations of per capita growth rate, dispersal capacity, interception efficacy and synchronisation of cross-boundary management (low, intermediate and maximum over the three columns), using the framework presented in Fig. 1. The lengths of the bars represent the proportion of simulations ending in a given category for a given time step, over the 20 replicates (each replicate being characterised by a different spatial distribution of the patches).

through long-distance dispersal events led to (i) more widespread populations with high local abundance (expressed by a higher proportion of time spent in the 'Dispersed + abundant somewhere', 'Highly successful' and 'Successful' categories), and (ii) very few simulations resulting in the 'Constrained' category (Figs 3C, 4C).

The impact of cross-boundary management on the trajectories to commonness

Cross-boundary management preventing the migration of propagules between patches had a much higher effect on populations with a Gaussian compared to those with a Cauchy dispersal kernel (compare the differences between Fig. 3A, B and Fig. 3C, D, between Fig. 4A, B and Fig. 4C, D; compare the changes in colours between Figs 5 and 6). In the case of Gaussian dispersal, interception efficacy was especially important, as shown by the variation in time spent in each category as interception efficacy increased and the fact that almost no population reached the 'Successful' category at high interception efficacy (Figs 3B, 4B; top row of the 'Successful' matrix in Fig. 5). As interception efficacy increased, populations became less widespread, but still had high

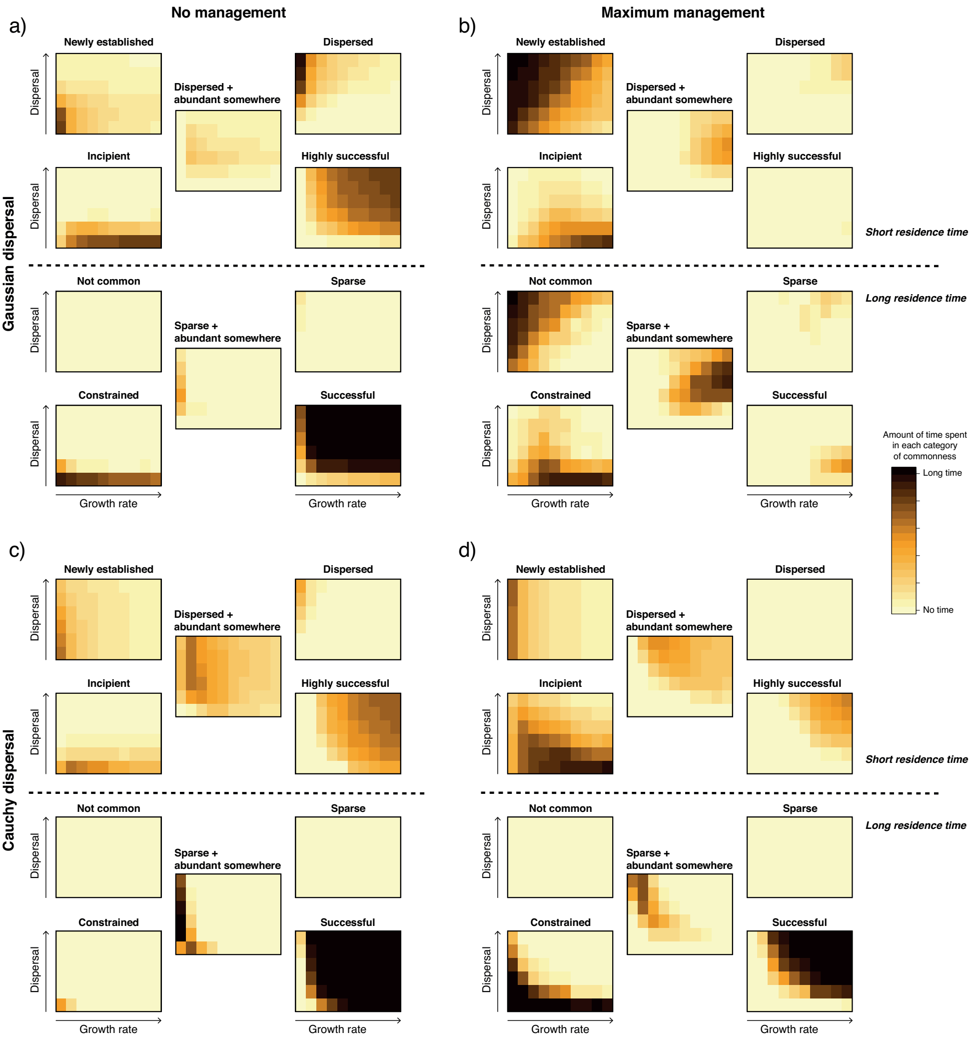

Figure 3. Modelling the fate of alien species populations with different population growth and dispersal rate, and their assignment to different categories of commonness, without (**a, c**) and with (**b, d**) maximum cross-boundary management (lowest and highest interception efficacy and synchronisation), for the logistic growth and the Gaussian (**a, b**) and Cauchy (**c, d**) dispersal kernels, using the framework presented in Fig. 1. Colours of the cells represent the proportion of time spent in each category of commonness for a specific combination of parameter values, with dark brown representing 50% of time and light yellow 0%. Simulations have been done for 20 patches with a carrying capacity $K = 10\ 000$, and the outputs were averaged over 20 replicates. Bottom-left corner is the lowest set of parameter values (see Table 1), representing low population growth and dispersal rate.

local abundance. This is reflected by the decline in the proportion of populations in the ‘Successful’ and ‘Highly successful’ categories, whereas the proportion of ‘Newly established’, ‘Not common’, ‘Constrained’ and ‘Sparse + abundant somewhere’ increased

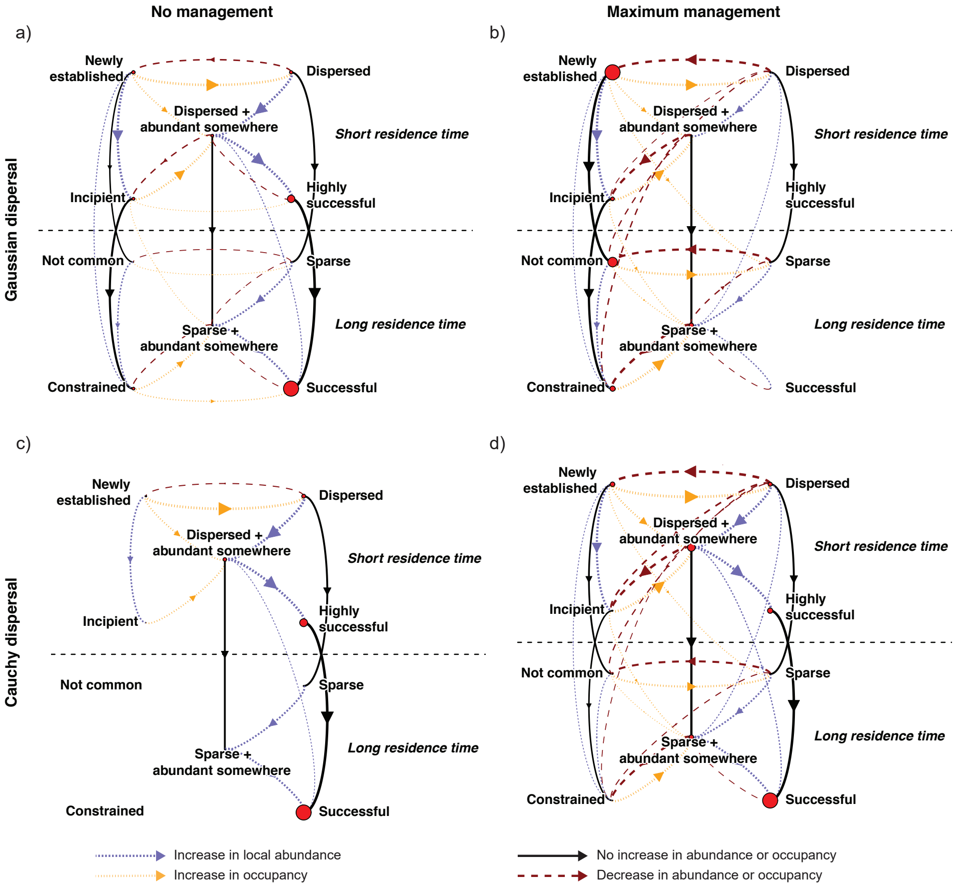

Figure 4. Transitions between different categories of commonness without (**a, c**) and with (**b, d**) maximum cross-boundary management (lowest and highest interception efficacy and synchronisation), for logistic growth, using the framework presented in Fig. 1, for the Gaussian (**a, b**) and Cauchy (**c, d**) dispersal kernel. Arrow width represents the frequency with which a metapopulation transited from one category to another, averaged over all combinations of growth and dispersal rate (i.e. averaging all cells in a matrix of Fig. 3). As in Fig. 1B, blue arrows represent an increase in local abundance, an orange represents an increase in occupancy, and black arrows represent no increase in either. Dark red arrows represent a decrease in either abundance or occupancy (which can happen as when abundance and occupancy values are close to the thresholds, and migrating propagules are intercepted). Simulations have been done for 20 patches with a carrying capacity $K = 10\,000$, and the outputs were averaged over 20 replicates.

(moving up in the matrices of Fig. 5). The effect of synchronisation was only apparent at high interception efficacy, and had an important impact on the capacity of the species to become common, as shown by the large increase in time spent in the 'Newly established' and 'Not common' categories and a decline in the 'Dispersed + abundant

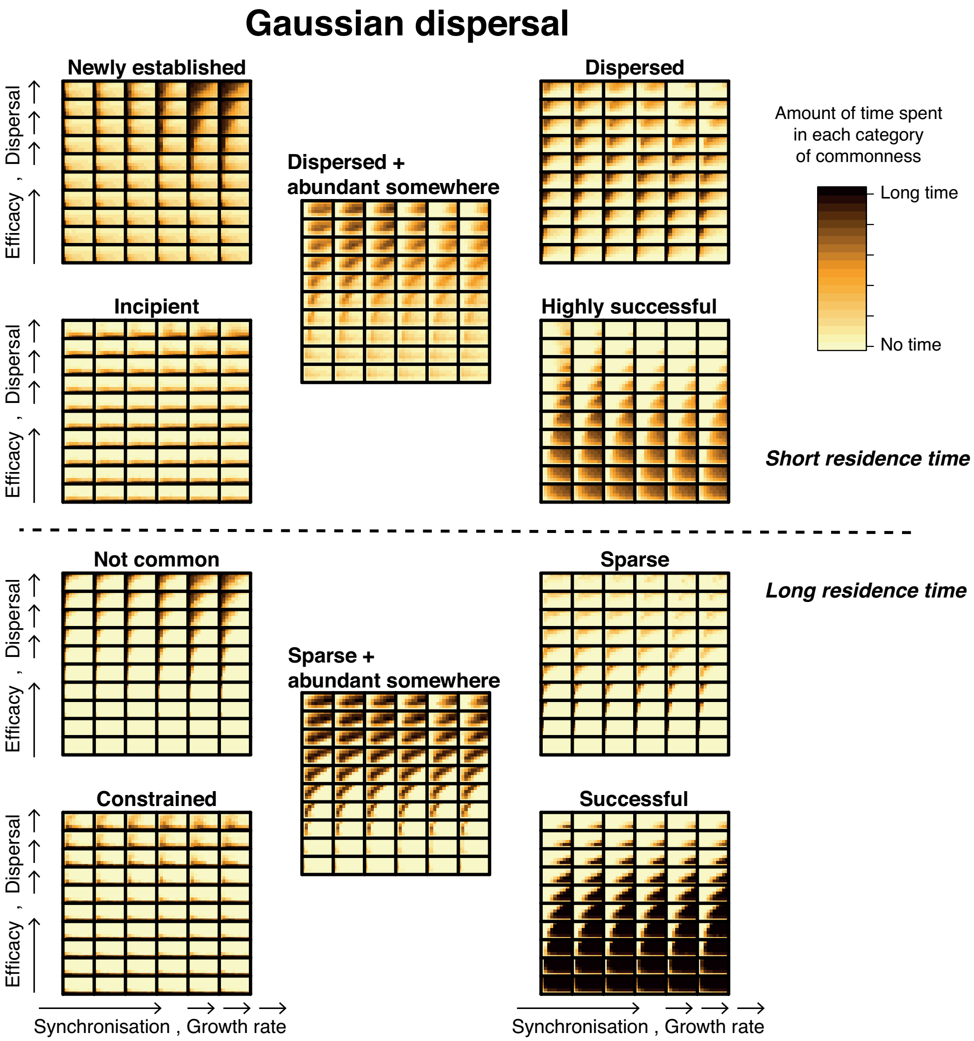

Figure 5. Effect of varying the interception efficacy and synchronisation of cross-boundary management for the Gaussian dispersal kernel on the fate of alien species populations and their assignment to different categories of commonness, using the framework presented in Fig. 1. Colours of the cells represent the proportion of time spent in each category of commonness for a specific combination of parameter values, with dark brown representing 50% of time and light yellow 0%. Results are presented so that variations in per capita growth and dispersal rates are nested within the synchronisation and efficacy of biosecurity measures. That is, within each category of commonness, each small rectangle represents a set of simulations for a given set of interception efficacy and synchronisation values. Within each small rectangle, the values of growth and dispersal rate are varied. Small rectangles in the bottom-left corners of each category of commonness are the lowest set of interception efficacy and synchronisation values, i.e. no cross-boundary management, and are the same as the matrices presented in Fig. 3A. Small rectangles in the top-right corners of each category of commonness are the highest set of interception efficacy and synchronisation values, and are the same as the matrices presented in Fig. 3B. Simulations have been done for 20 patches with a carrying capacity $K = 10\ 000$, and the outputs were averaged over 20 replicates.

somewhere' and 'Sparse + abundant somewhere' categories (moving right in the top rows of the matrices of Fig. 5).

Although no within-patch management was implemented, cross-boundary management eventually caused species commonness to decline (dark red arrows in Fig. 4). This was a result of the effect of numerous migrating propagules being eliminated when dispersal was high, therefore countering demographic effects. This is also why, under high growth and dispersal rates, species reach the 'Sparse + abundant somewhere' rather than the 'Successful' category, the latter being mostly reached at intermediate dispersal rate (top-right of the corresponding matrices in Fig. 3B).

For the Cauchy dispersal kernel, cross-boundary management only had a substantial effect on population spread at high interception efficacy and high synchronisation (top-right of the matrices in Fig. 6). Contrary to the Gaussian dispersal kernel, for which the effect of interception efficacy was progressive, there was a threshold of 0.6 under which interception efficacy had no detectable effect (i.e. more than half of the propagules had to be intercepted; compare bottom and top halves of the matrices in Fig. 6). Once this threshold was attained, the effect of interception efficacy and synchronisation became apparent and was progressive, and mostly limited the spread of the metapopulation. Cross-boundary management then mostly increased the time spent in the 'Incipient' and 'Constrained' categories, and decreased the time spent in the 'Highly successful' and, to a lower extent, in the 'Dispersed + abundant somewhere' and the 'Successful' categories. However, with a Cauchy dispersal kernel even cross-boundary management with high interception efficacy and synchronisation had a limited effect on population spread and growth, and most simulations reached the 'Successful' and some even the 'Highly successful' categories (Figs 3D, 4D).

Variability in the results across the 20 replicates was much higher for the Gaussian than for the Cauchy dispersal kernel (compare Suppl. material 1: Figs C1 and C2 in Appendix C). The paucity of long-distance dispersal events when using the Gaussian kernel resulted in the spatial distribution of the patches being primarily responsible for the spread of an alien species. In contrast, the more likely long-dispersal events of the Cauchy dispersal kernels made the outcome of the simulations largely independent of the spatial distribution of patches.

The impact of time lags on the trajectories to commonness and the efficacy of cross-boundary management

Time lags in the growth rate of local populations led to increasing the time it took for the metapopulation to become common (compare Suppl. material 1: Fig. D5 in Appendix D with Fig. 2, Figs D2 and D4 with Fig. 5, and Figs D3 and D5 with Fig. 6). Using a weak Allee effect was similar to decreasing the growth rate for both dispersal kernels (compare Suppl. material 1: Figs D2 and D3 in Appendix D with Figs 5, 6). When a strong Allee effect was used, almost no simulation reached the 'Highly successful' or the 'Successful' categories, for both the Gaussian and the Cauchy dispersals

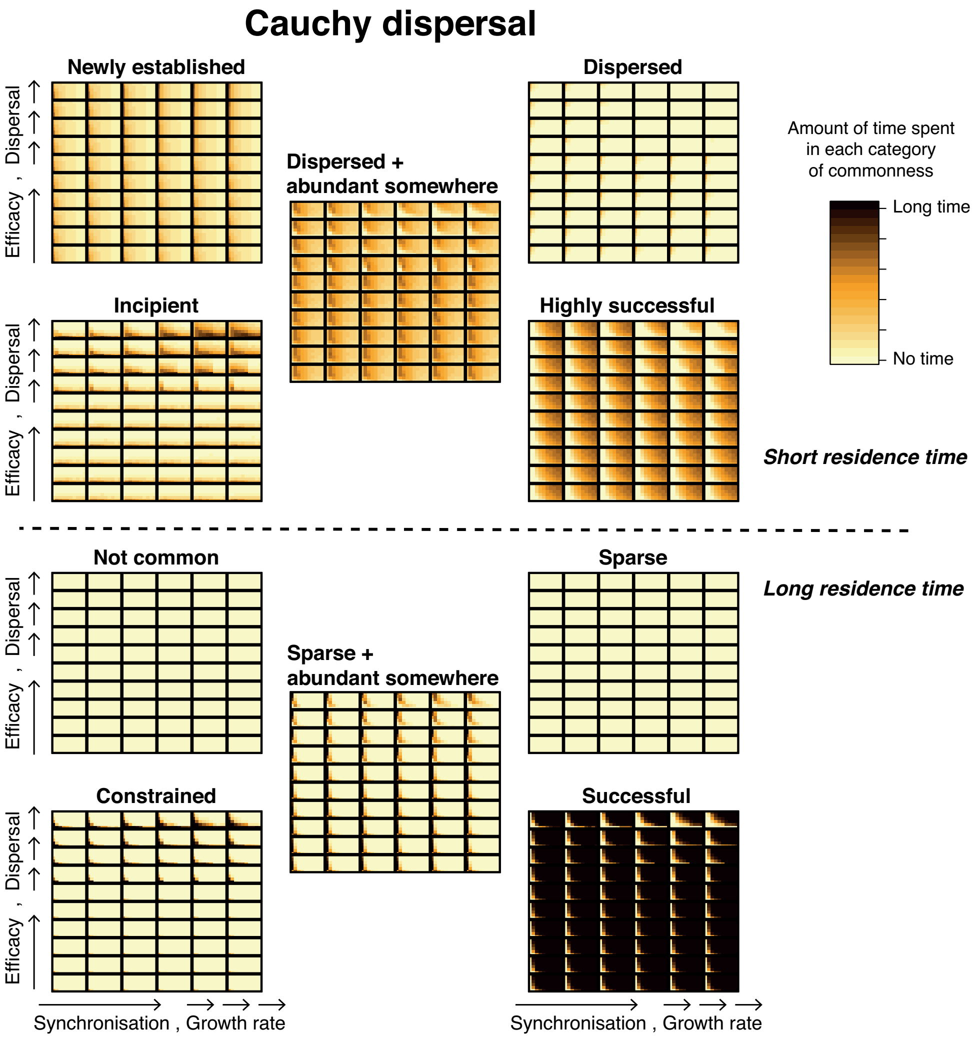

Figure 6. Effect of varying the interception efficacy and synchronisation of cross-boundary management for the Cauchy dispersal kernel on the fate of alien species populations and their assignment to different categories of commonness, using the framework presented in Fig. 1. Colours of the cells represent the proportion of time spent in each category of commonness for a specific combination of parameter values, with dark brown representing 50% of time and light yellow 0%. Results are presented so that variations in per capita growth and dispersal rates are nested within the synchronisation and efficacy of biosecurity measures. That is, within each category of commonness, each small rectangle represents a set of simulations for a given set of interception efficacy and synchronisation values. Within each small rectangle, the values of growth and dispersal rate are varied. Small rectangles in the bottom-left corners of each category of commonness are the lowest set of interception efficacy and synchronisation values, i.e. no cross-boundary management, and are the same as the matrices presented in Fig. 3C. Small rectangles in the top-right corners of each category of commonness are the highest set of interception efficacy and synchronisation values, and are the same as the matrices presented in Fig. 3D. Simulations have been done for 20 patches with a carrying capacity $K = 10\ 000$, and the outputs were averaged over 20 replicates.

(Suppl. material 1: Figs D4 and D5 in Appendix D). For the Cauchy kernel, simulations that reached the ‘Successful’ category for logistic growth instead reached the ‘Sparse + abundant somewhere’ category for the strong Allee effect. For the Gaussian kernel, almost all simulations reached either the ‘Not common’ or the ‘Sparse’ category, depending on a threshold in the dispersal parameter.

When a weak Allee effect was used to model time lags, the general effect of cross-border management measures was similar to their application to metapopulations with logistic growth (compare Suppl. material 1: Figs D2 and D3 in Appendix D with Figs 5, 6). For the strong Allee effect and the Cauchy dispersal, a threshold of 0.5 on the interception efficacy over which an effect could be noted was observed, similar to metapopulations with a logistic growth and a weak Allee effect (compare Suppl. material 1: Fig. D5 in Appendix D with Fig. 6). In contrast, a threshold on the interception efficacy appeared for the Gaussian dispersal (Suppl. material 1: Fig. D4 in Appendix D). Over 20% of intercepted propagules, most simulations only reached the ‘Not common’ category (and to a lower extent the ‘Sparse’ category), which was not observed for the logistic growth and the weak Allee effect.

The effect of cross-boundary management also tended to be disproportionately higher for populations with time lags compared to logistic growth, for both the weak and strong Allee effects. The difference in ratios used to compute the relative effect was negative for the ‘Highly successful’ and ‘Successful’ categories (indicating disproportionally less time spent in these categories), and overall positive for the other categories, for both the Gaussian and the Cauchy dispersal (Suppl. material 1: Figs E1–E4 in Appendix E). The only exception was the ‘Sparse + abundant somewhere’ category for the Gaussian dispersal and weak Allee effect, as the time spent in this category was relatively lower with time lags at low growth rate values, and relatively higher at intermediate growth rate values.

Discussion

Effects of cross-boundary management on the trajectories to commonness

This study offers four key insights relevant to the prevention of the spread of alien species across borders of spatial entities (such as countries). First, the large difference in the impact of cross-boundary management on populations with versus without long-distance dispersal suggests that the implementation of preventive measures at the points of entry of a country (eg. at land borders, ports or airports) is unlikely to be efficient for all species. Global connections are increasing, both through trade of goods and movement of people, and preventing such long-distance distance transport of propagules across countries seems unrealistic under the current status-quo (McNeely 2006). It will therefore be important to evaluate how combinations of cross-border management with a range of local management measures (including biocontrol, culling, etc.) will enhance their respective efficiency. Since in our model, cross-border management had a disproportionate effect when time lags were present, this suggests that this combination of ecological dynamics and management intervention may reinforce each other and could be deployed to improve management effectiveness by control measures that simulate a lag effect, i.e. reducing population reproductive output by, for example, biological or other forms of control.

Second, interception efficacy of cross-boundary management has a larger effect on the capacity of a metapopulation to become more common than synchronization between regions, over the range of parameters for which cross-border management has an effect on the spread of the metapopulation. Increasing interception efficacy decreased the growth of metapopulations, which therefore reached the 'Highly successful' and 'Successful' categories less frequently, regardless of the synchronisation between countries, in the absence of long-distance dispersal (i.e. for the Gaussian dispersal kernel). Synchronisation only had a noticeable effect when more than half of the propagules entering a patch were consistently intercepted. When long-distance dispersal occurred (i.e. for the Cauchy dispersal kernel), a combination of both high interception efficacy and good synchronisation between countries was required to substantially limit the ability of the population to become 'Highly successful' or 'Successful', although that only applied for low growth rate and dispersal capacity.

Importantly, there was a clear threshold indicating that at least half the propagules entering a patch were required to be intercepted consistently to prevent the metapopulation from dispersing rapidly (Figs 5, 6). These results suggest that implementing effective national biosecurity measures have the potential to limit the spread and growth of alien species even if other countries are lagging behind in their implementation, but that their efficacy will likely be enhanced if they are implemented simultaneously by multiple countries. Doing so is necessary to prevent the emergence of small, separate populations of alien species, whose detection and eradication has been shown to be more important than that of large populations (Mack and Lonsdale 2002). This result provides support for the importance of the species-targeted, cross-boundary control efforts for invasive alien species of agricultural and environmental concern that have been advocated elsewhere (Epanchin-Niell and Hastings 2010; Kark et al. 2015; Blackburn et al. 2020).

Third, the spatial distributions of the patches had a stronger effect on the time spent in each category of commonness for the populations without long-distance dispersal, as shown by the higher standard deviation in each category (Suppl. material 1: Figs C1–C6 in Appendix C). For populations whose spread follows a diffusion process and which increase their local abundance before spreading to neighbouring regions, cross-boundary management limiting immigration to a new patch is probably not the most efficient management, especially without clear spatial planning. Such spatial planning can be difficult to achieve across different countries with their own constraints and priorities. Instead, early detection combined with removal actions (see e.g. Travis and Park 2004; Chadès et al. 2011 for guidelines on the spatially-explicit management of alien species) or cross-boundary management limiting the emigration from a location where the species is present, may be more efficient. For example, the International Standards for Phytosanitary Measures No. 15 (ISPM15), developed by the International Plant Protection Convention, provides treatment standards for wood packaging materials, to limit the introduction of alien wood-feeding insects (Haack et al. 2014). The Ballast Water Management Convention ensures that ships from signatory countries perform ballast water replacement at least 200 nautical miles from shore, and use approved ballast water treatment systems, to prevent carrying and spreading aquatic alien species (IMO 2004).

Finally, the disproportionately beneficial effects of cross-border management when time lags were implemented in the model suggests that preventive cross-boundary management may provide a substantial advantage to contain the spread and growth of undetected alien species undergoing time lags. Time lags have been shown to impair the prediction of future invasions, therefore impeding proper application of management actions (Taylor and Hastings 2005). However, the relationship between cross-boundary management and time lags is often neglected (see e.g. table 1 in Tobin et al. 2011).

Application of the categories of commonness

Establishing the link between the categories of commonness, species biology, cross-boundary management and *in situ* management measures could improve our ability to understand and therefore to limit the spread of alien species, and therefore their potential impact. The combination of the typological framework with the modelling approach presented here enables exploration of the effects of different levels of interception efficacy and synchronisation of cross-boundary management across different regions, and for species with different demographic and dispersal characteristics.

Applying the framework to a theoretical model setting has shown unexpected results for the path to commonness of populations with different demographic and dispersal characteristics. In particular, the results demonstrate that dispersal can be so high that, combined with very efficient cross-boundary management, this could result in the metapopulation becoming less common than under lower dispersal rates, for the Gaussian dispersal kernel (as shown by the dark colour in the bottom-left of the small squares in the 'Successful' matrix in Fig. 5). Although these simulations are less realistic than other combinations of parameter values, they can be used to conceptualise specific situations. Very high dispersal despite low abundance in the model can represent the existence of hubs through which propagules transit (Floerl et al. 2009). Very high dispersal rate and very efficient cross-boundary management in the model, leading to a decrease in overall abundance, can represent the combination of additional management actions of species already established (Novoa et al. 2018; Martin et al. 2020). In addition, only two types of dispersal kernels, representing a diffusion process and long distance dispersal, were implemented in the model to simplify the analyses and due to computational limitations. In practice, both types of dispersal would therefore occur simultaneously in a metapopulation, with the exact shape of their kernel and their relative rate depending on the species biology and the characteristics of the environment (Pyšek and Hulme 2005). Our simulations were designed to represent two extreme cases between which real species' spread will lie.

In the theoretical model presented here, the time period spent by a population in each category of commonness will be influenced by the parameter values, the number of patches available, the carrying capacity of the patches, and their spatial distribution (Alharbi and Petrovskii 2019). In particular, using parameter values for the two dispersal kernels that allow for a comparison of the results is not straightforward, and we used a visual inspection of the kernels to do so. The thresholds to differentiate the 10 types of commonness were then determined so that each category of commonness would be represented in the simulations. This enabled us to better detect the effect of different cross-boundary management measures on the path to commonness for the two extreme types of dispersal models and the set of parameters used in the simulations.

In practice, thresholds should be based on the biology and the ecology of species (for example on the species ability to maintain stable populations). Using such criteria would allow for global assessments of the state of biological invasions, as is done, for example for species becoming rare with the IUCN Red List of Threatened Species (IUCN 2019). From an applied management perspective, defining the thresholds based on the management capacity of countries may also be appropriate, and could vary in space and time based on the management capacities of a country, the development of novel management methods, and an understanding of how the 'coupled human and natural system' affects invasions (Sinclair et al. 2020).

The model we used therefore represents a canvas on which more realistic and specific models can be based. Such models can be based on the parameterisation of the growth and dispersal rate of specific species (including a more progressive exploration of changes in the frequency of long-distance dispersal events). They can also explore how the spatial distribution, size distribution and environmental heterogeneity of multiple countries can be analysed using this framework of categories of commonness.

Conclusions

Understanding the trajectories of alien species introduced into separate spatial units (e.g. countries, islands, water bodies) that ultimately may lead to commonness is crucial for designing effective management measures. Appreciating that IAS become abundant and expand their ranges in a number of distinct ways provides potential to explore options for designing the most effective, category-specific management strategies (Novoa et al. 2020). The typological framework presented here enables us to analyse the role of cooperation among spatial units for altering how a newly introduced species may become common across them. The theoretical model was designed to be adapted to real systems in the future, including cross-border surveillance, biosecurity or legislation such as the EU regulation on invasive alien species (EU 2014). We consider the following insights particularly relevant for applied purposes: First, spread will be reduced more if some countries implement effective biosecurity, albeit interceptions are not rapidly implemented everywhere (i.e. low management synchronisation but high efficacy) rather than all countries implementing biosecurity at the outset but the rate of interceptions is low (i.e. high management synchronisation but low efficacy). Second, the presence of long-distance dispersal requires a minimum level of interception efficacy to prevent an alien species from becoming common across a set of spatial units, although that only applied for low growth rate and dispersal capacity. Once such a threshold is crossed, synchronisation across spatial units will improve the efficacy of management. Third, time lags in population growth that may result in delayed spread are an important aspect to be considered explicitly for management, as they can amplify the efficacy of such measures. It will be important to assess the generality of these findings for a range of different real cases.

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Supplementary material 1

Appendix A–E

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Data type: Supplementary documentation

Explanation note: **Appendix A.** Archetypes of trajectories to commonness; **Appendix B.** Model characteristics; **Appendix C.** Standard deviation results without time lags; **Appendix D.** Results with time lags; **Appendix E.** Relative effect of pre-border cross-boundary management for the Gaussian dispersal kernel with and without time lags.

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Scale invariance in the spatial-dynamics of biological invasions

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Abstract

Despite the enormous negative consequences of biological invasions, we have a limited understanding of how spatial demography during invasions creates population patterns observed at different spatial scales. Early stages of invasions, arrival and establishment, are considered distinct from the later stage of spread, but the processes of population growth and dispersal underlie all invasion phases. Here, we argue that the spread of invading species, to a first approximation, exhibits scale invariant spatial-dynamic patterns that transcend multiple spatial scales. Dispersal from a source population creates smaller satellite colonies, which in turn act as sources for secondary invasions; the scale invariant pattern of coalescing colonies can be seen at multiple scales. This self-similar pattern is referred to as "stratified diffusion" at landscape scales and the "bridgehead effect" at the global scale. The extent to which invasions exhibit such scale-invariant spatial dynamics may be limited by the form of the organisms' dispersal kernel and by the connectivity of the habitat. Recognition of this self-similar pattern suggests that certain concepts for understanding and managing invasions might be widely transferable across spatial scales.

Keywords

bridgehead effect, coalescing colonies, invasion framework, self-similarity, spread, stratified dispersal

Introduction

The phenomenon of biological invasions occurs among a wide variety of organisms representing virtually all major animal, plant and microbial taxa (Lockwood et al. 2013). Though the details of invasions vary considerably among different species, the existence of common biological processes during all invasions is widely recognized. One of the earliest, simplest and widely applied frameworks for stages through which all invasions pass was proposed by Dobson and May (1986) who recognized three discrete stages: arrival of the species beyond its native range, followed by establishment of the population to a level beyond which extinction is unlikely, and spread into surrounding unoccupied patches. Several variants on this framework have been proposed, but the most widely applied of these break up the arrival stage into two successive stages: transport (movement of propagules from the native to non-native habitat) and introduction (escape or release of individuals following transport) (Duncan et al. 2003; Richardson et al. 2000; Blackburn et al. 2011). In these frameworks, species pass through various population processes and barriers as they move between successive invasion stages.

Here we argue that while these widely applied invasion frameworks have been tremendously useful, they emphasize distinct invasion stages even though all stages biologically ensue from just two demographic processes-dispersal and population growth. This, in turn, may produce scale-invariant properties that characterize invasions across all spatial scales. Given these common underlying mechanisms, different invasion stages can be considered manifestations of similar processes operating at different spatial scales. And as such, the spatial-dynamics of many invasions exhibit common structures that are evident at multiple spatial scales, leading to a self-similar or fractal spatial structure. Below we present the theoretical basis for the emergence of these scale invariance patterns and discuss the resulting practical implications.

Scale invariance

Population growth and dispersal are the two basic population processes that underlie invasions across all stages. These two processes form the basis for both the "early" phase of invasions (arrival / establishment) and the "later" phase (spread) and there is a fundamental similarity in the way these processes are expressed at multiple spatial scales. Inter-continental movement of propagules that found new reproducing colonies is inherently similar to the movement and growth of populations along an expanding population front within a continent. This coupling of dispersal with population growth is a fundamental dynamic occurring at multiple spatial scales to produce both the arrival / establishment and spread invasion phases. Recognizing this underlying similarity suggests that there is a continuum of spatial scales over which these recurring processes operate.

The concept of scale invariance has been widely applied in physics and statistics and refers to characteristics or processes that are constant across multiple scales or energy levels (Stanley et al. 2000). Scale invariance is also referred to as 'self-similarity' which represents the concept that when viewing an object, as one zooms in or out, the spatial structure of objects appears the same. An example of self-similarity are fractals which are geometrical figures in which each part has the same properties as the whole.

Fractals have been applied in many different scientific disciplines and among these, fractals have proven useful for describing spatial patterns in ecology (Keitt and Stanley 1998; Keitt et al. 2002; Marquet et al. 2005). Compared to rigorous theoretical definitions, ecological systems generally do not exhibit true fractals or scale invariance but these concepts do provide insight for describing ecological patterns at multiple scales (Halley et al. 2004). Survey data characterizing the spatial-dynamics of invasions at various spatial scales suggest that biological invasion may be characterized by scale invariant patterns (Fig. 1B–E). Although relatively few studies have compared invasion spread patterns across spatial scales and though radial rates of spread may vary depending upon the scale at which it is measured, there is evidence of similarity in the geometry of spread across scales ranging from intercontinental to local (Mack et al. 2007; Pyšek et al. 2008). Furthermore, recent theoretical work on the mechanisms driving the spatial-dynamics of invasions provides insight into processes responsible for scale invariance (Hallatschek and Fisher 2014). Cannas et al. (2006) used a theoretical model to demonstrate that long-distance dispersal can create a fractal invasion front; they related the fractal dimension of this pattern to the characteristics of the dispersal function. Below, we describe two processes, stratified dispersal and the bridgehead effect; while these processes function at very different spatial scales, their underlying topologies and resultant patterns share a remarkable similarity. As part of both processes, isolated colonies are founded via jump dispersal; these colonies grow and spawn more colonies which ultimately coalesce (Fig. 1A).

Stratified dispersal

As pointed out by Cannas et al. (2006) dispersal plays a key role in creating self-similarity in invasion fronts across multiple spatial scales. The existence of long-distance dispersal coupled with localized dispersal was described as “stratified dispersal” by Hengeveld (1989) who noted that such a phenomenon is common in invading populations. Often, localized dispersal is caused by natural movement of organisms while long-distance dispersal is typically the result of anthropogenic movement of organisms, though human-mediated dispersal can contribute to both long- and short distance dispersal (Wilson et al. 2009; Gippet et al. 2019). Such coupling of long- and short-distance dispersal driving invasion spread has been observed in a variety of organisms ranging from plants to insects (Suarez et al. 2001; Trakhtenbrot et al. 2005; Pyšek et al. 2008; Lockwood et al. 2013). The gypsy moth, *Lymantria dispar*, provides a classic example; over short distances (0–100 m) movement occurs via windborne dispersal of young caterpillars, while long-distance dispersal (5–5000 km) occurs by accidental transport of life stages by humans (Sharov and Liebhold 1998). Theoretical ecologists often describe such movement patterns using leptokurtic “fat-tailed” dispersal kernels (Kot et al. 1996; Hallatschek and Fisher 2014). This same spatial-dynamic pattern of

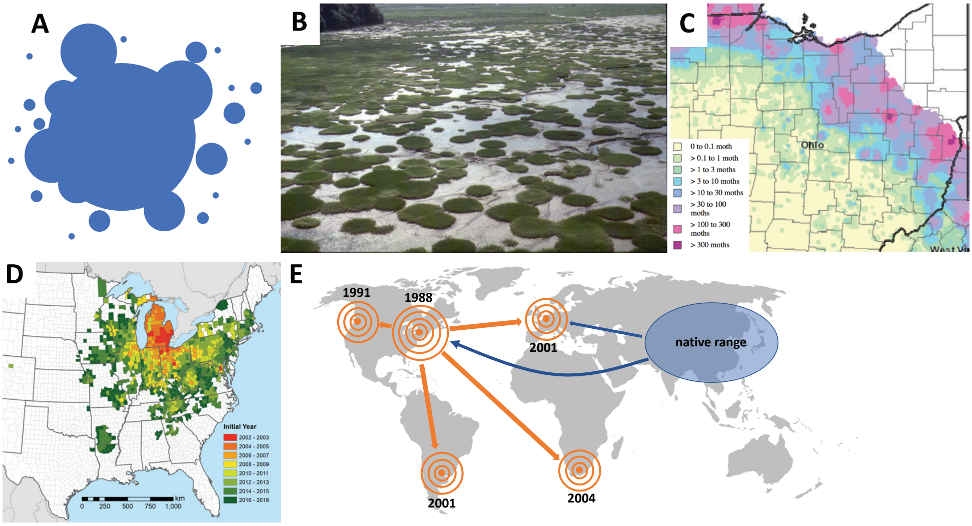

Figure 1. Examples of coalescing colonies seen in the invasions of different species viewed at varying scales **A** conceptual representation of invasion via coalescing colonies **B** aerial photo showing *Spartina alterniflora* invasion into Willapa Bay, WA, (photo by Fritzi Grevstad) **C** spread of the gypsy moth, *Lymantria dispar*, in Ohio, USA. Interpolated pheromone trap captures from 2019 (data at http://yt.ento.vt.edu/da/) **D** spread of the emerald ash borer, *Agrilus planipennis*, in the eastern USA showing year of first discovery by county (data from USDA APHIS) **E** historical global spread of the Harlequin ladybird *Harmonia axyridis* (modified from Lombaert et al. 2010). Eastern North America has functioned as a bridgehead region from which colonization of other continents has originated.

invasion via long-distance dispersal founding coalescing colonies is sometimes referred to as "nucleation" or "nascent foci" in the plant invasion literature (Moody and Mack 1988; Pausas et al. 2006; Milton et al. 2007)

Regardless of the term, stratified dispersal is well known to play a key role in invasion spread. Simple models show that stratified dispersal creates a pattern in which isolated populations form ahead of the invasion front (via long-distance dispersal); these colonies then expand as isolated colonies that ultimately coalesce with each other and the main invasion front (Kot et al. 1996; Shigesada et al. 1995; Hallatschek and Fisher 2014) (Figure 1A). These studies demonstrate that the existence of long-range dispersal plays a key role in elevating rates of range expansion above levels that would occur through simple diffusive dispersal (Higgins and Richardson 1999). This phenomenon of coalescing colonies is a space-time pattern commonly observed in the spread of many types of organisms. Figure 1B–D shows examples in several organisms.

Bridgehead effect

The bridgehead effect is a term used to describe large-scale (global) patterns of invasion in which organisms initially invade one region but this invaded region then becomes a source of propagules for invading more regions (Figure 1E). This phenomenon has been documented in historical global patterns of invasions for several individual plant and animal species using genetic markers (e.g. Lombaert et al. 2010). Bertelsmeier et al. (2018) characterized the bridgehead effect for an entire taxonomic group consisting of ants (Hymenoptera: Formicidae) invading the USA; most ant species arriving at US ports are native to Africa, but they predominantly arrive on shipments originating from previously invaded portions of Central America which function as bridgehead regions. While theories have been proposed to explain the bridgehead effect based upon evolution of greater invasiveness in bridgehead populations, Bertelsmeier and Keller (2018) found little evidence supporting these theories and showed that the phenomenon more likely results from purely demographic reasons in which initial invasion of bridgehead regions results in dense populations which then serve as sources of propagules that invade other regions. Bridgehead dynamics are also driven by global transportation networks that channel invasions into hubs from which populations subsequently spread into surrounding regions (Tatam 2009). Bertelsmeier et al. (2017) describe a global pattern recurrently seen among various ant species; alien populations establish in multiple continents followed by expansion of these populations into adjacent regions.

Though operating at a much larger scale, the bridgehead effect shows a remarkable resemblance to stratified dispersal. Both processes are characterized by initial founding of isolated colonies which grow, spawn more colonies and ultimately coalesce. The net result of the bridgehead effect is the creation of invasion patterns at large spatial scales that are similar to that of coalescing colonies resulting from stratified dispersal seen at smaller spatial scales.

Not all invasions exhibit either stratified dispersal or the bridgehead effect and the reasons for this may be varied. For one, dispersal of some species is not characterized by long-distance dispersal. For example, the historical spread of muskrats, *Ondatra zibethica*, in Europe (Ulbrich 1930) was continuous, without jumps, apparently due to the lack of long-distance dispersal (dispersal is relatively short ranged with little anthropogenic movement in this species). Another factor that profoundly affects spatial-dynamics during the spread of invading species, is habitat connectivity (With 2002). Connectivity of habitats may vary with spatial scale and the constraints that connectivity places on spread may limit the spatial dynamics of invading populations from exhibiting scale invariance.

Implications

Introduction of alien species through human agency is a major component of global change, affecting biodiversity patterns and composition at multiple scales of organization. Here we describe a phenomenon frequently seen in the spatial-dynamics of biological invasions that reflects a scale invariant pattern operating across scales ranging from continents to landscapes. The existence of these consistent patterns of spatial-dynamics suggests that the stages of arrival, establishment and spread can be considered descriptions of a fundamentally similar scale invariant process at different spatial scales. While several invasion frameworks provide extensive detail of the various phases through which invasions progress, our description here of scale invariant patterns suggest an underlying similarity among invasion phases and future frameworks may be able to incorporate these similarities in a simpler structure.

There are implications that emerge from this scale-invariant perspective on invasions. First is the suggestion that approaches currently applied to model invasion spread at relatively small spatial scales could be applied to characterize the spatial dynamics of global (intercontinental) invasions. Several types of models have been developed to describe the role of stratified dispersal in the spatial dynamics of invading populations during the spread stage (e.g., Shigesada et al. 1995; Kot et al. 1996; Lewis and Pacala 2000). Similarly, gravity models are often applied to model localized invasion spread (Potapov et al. 2011). New insight may be gained by applying these approaches to model bridgehead dynamics in invasions at global scales.

Another implication of scale invariance is that some of the strategies applied to manage invasions at large global spatial scales could potentially also be applied to manage spread at more local scales. For example, surveillance and eradication are widely applied by national governments to detect and eliminate nascent invading populations in their countries. Though there are relatively few examples of successful barrier-zone programs within countries or regions (Liebhold and Kean 2019), this strategy could be applied at smaller spatial scales to contain local invasion spread. One of the few examples of such application of surveillance and eradication at a local level to contain spread is the current program to contain gypsy moth spread in North America by deploying thousands of traps along the expanding population front to detect isolated populations that are eradicated in order to contain populations (Tobin and Blackburn 2007). These types of strategies have sometimes been applied to contain the spread of plants (Moody and Mack 1988) but rarely considered for animal invasions.

Identification of the roles of bridgehead effects and stratified dispersal have both been consequential developments that have improved our understanding of biological invasions. Recognition that these are self-similar phenomena, reflecting the scale invariance of invasions, may lead to further insights into the study of invasions. Ultimately, such developments in our understanding of invasions can lead to more effective biosecurity measures and ultimate mitigation of the impacts of biological invasions in the future.

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RESEARCH ARTICLE

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The cost and complexity of assessing impact

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Abstract

The environmental and socio-economic impacts of invasive species have long been recognised to be unequal, with some species being benign while others are disastrous. Until recently there was no recognised standard impact scoring framework with which to compare impacts of species from very different taxa. The advent of the Environmental Impact Classification for Alien Taxa (EICAT) and Socio-Economic Impact Classification of Alien Taxa (SEICAT) schemes allows for the possibility of assessing impact through a standard approach. However, both these schemes are still in their infancy and the associated costs of the research that informs them is unknown. We aimed to determine the study costs and complexity associated with assessing invasive species' socio-economic and environmental impacts. We used amphibians as a model group to investigate papers from which EICAT and SEICAT scores could be drawn up to 2019. Our analysis shows that studies that resulted in higher impact scores were more costly. Furthermore, the costs of studies were best predicted by their complexity and the time taken to complete them. If impact scores from EICAT and SEICAT are allowed to inform policy, then we need to carefully consider whether species with low scores represent true impact, or require more research investment and time. Policy makers needing accurate assessments will need to finance larger, more complex, and rigorous studies. Assessing impacts in low and middle income countries may need investment using international research collaborations and capacity building with scientists from high income areas.

Keywords

amphibians, EICAT, environmental impact, invasive species, socio-economic impact; SEICAT, study complexity

Introduction

Invasive species have long been recognised to produce a wide range of environmental and socio-economic impacts (Elton 1958). Early attempts to provide lists of '100 worst invasives' (Lowe et al. 2000) were extremely popular, but subjective in terms of which species were included – and why. Instead, comparing impacts between invasive species requires a framework that provides equivalence at the environmental or socio-economic level for impacts of organisms across Kingdoms: from *Caulerpa racemosa* var. *cylindracea* (Kingdom: Bacteria) to *Felis catus* (Kingdom: Animalia). Evidence of impacts can range from anecdotal observations, to laboratory and field experiments, which quantify environmental degradation or socioeconomic impacts (Hawkins et al. 2015; Bacher et al. 2018). This wide range of study types show extreme variation in research costs and are not equivalent in terms of the rigour of their findings (Probert al et. 2020). Assessments made without robustly designed ecological and socio-economic inquiries should be treated with caution (see Christie et al. 2019).

More complex ecological and socio-economic research designs, including those of alien species impacts, are likely to require considerable investment. Full scale field trials with complex designs (e.g., Before-After Control-Impact or Randomised Control Trials) are desirable, as these more robust designs lead to greater power to detect true effects' direction and magnitude (Christie et al. 2019). However, studies on invasions are more likely to be 'natural experiments' with simple designs, such as pre- and post-invasion (e.g., Before-After, Control-Impact or After). Even these simple field experiments are considerably more costly to implement than laboratory experiments or simulations of field conditions, such as mesocosms (Christie et al. 2019). Similarly, designing and implementing social science surveys to elicit the types and severity of socio-economic impacts associated with invasive species requires considerable time and expertise. The costs of designing and administering surveys depend on the study design (e.g., the number and size of human populations to be surveyed, efforts required to obtain a representative sample from the population, means by which the surveys are implemented). Therefore, estimating the impacts of invasions at the landscape scale is likely to cost far more than a simulation or experiment that has lower power to detect impacts of larger magnitude. It seems likely then, that more complex experiments at greater scales will follow smaller investigations that show indications of impacts, but that these initial cheaper inquiries will lack the power or confidence of the more expensive endeavours.

New attempts to produce indices of invasion impacts have consolidated around separate environmental and socio-economic impact classifications of alien taxa (Blackburn et al. 2014; Hawkins et al. 2015; Bacher et al. 2018), and one (i.e., Environmental Impact Classification for Alien Taxa; EICAT) has subsequently been adopted by the International Union for Conservation of Nature (IUCN). Unlike the IUCN Red List, both EICAT and SEICAT (Socio-Economic Impact Classification of Alien Taxa) predominantly use peer reviewed literature to make their assessments. Studies need to be carried out at scales that are appropriate to the invasive population, and the invaded environment, and those studies that cannot meet these requirements are scored with a lower confidence level (Hawkins et al. 2015). When the cost of conducting a study on invasive population impacts is variable, it seems likely that cheaper research will result in impacts of lower magnitude, and/or confidence: i.e. scores using these studies will not reflect true impact. Such a result would likely produce unequal diagnosis of the relative impacts of invasive species in a world that already radically differs in investment in conservation (McCarthy et al. 2012). This is particularly worrisome considering the role that EICAT in particular can play in terms of informing policy and legislation and conservation planning (Kumschick et al. 2020)

There is already evidence of global inequality in assessments of alien impacts. Early attempts to classify impacts of taxonomic groups at a global level have emphasised the paucity of coverage for birds (30%; Evans et al. 2016) and amphibians (38%; Kumschick et al. 2017). Regional assessments indicate high levels of coverage in economically wealthy areas (e.g. environmental impacts 79% and socio-economic impacts 75% for European invasive plants; Rumlerová et al. 2016). Evans and Blackburn (2020) highlighted this geographic disparity in the availability of data on alien birds, demonstrating that data availability was related to alien bird residence time, richness, and economic status of the country. Notably, all but two alien birds have been found to have minor impacts on human well-being (Evan et al. 2020). These studies imply that there is likely disparity between the true impact of any alien species, and the impact realised by implementing scoring frameworks, such as the ICAT schemes, because they rely on the true impact to be captured by published research. This difference may relate to the country where impacts are realised, if insufficient research funding is available, or the complexity of the study (if studies are poorly designed or insufficiently long). Therefore, the research and policy community implementing or using these frameworks face a problem moving forward: how can we achieve a representative impact level for all alien species, without sufficient or adequate peer reviewed literature? Or on an economic level: will the impact score of species be independent of research costs?

In this paper, we attempt to respond to these questions by examining the EICAT and SEICAT status of alien amphibians globally, and the costs associated with contributing underlying studies. Previous scoring of amphibians used literature up until May 2015 (see Measey et al. 2016), but literature on alien amphibians as a group have a near exponential growth (van Wilgen et al. 2018), and are therefore useful as a model for trends in invasion literature more widely. Here we aim to determine: (1) whether studies that result in higher impact scores cost more to conduct, (2) whether impact is related to study complexity or time taken to conduct the study, (3) whether EICAT and SEICAT scores demonstrate changes through time (up to 2019), and (4) whether different EICAT and SEICAT scores occur with equivalent confidence. Lastly, we use four case studies to illustrate how EICAT and SEICAT scores have been assessed for particular species based on research publications.

Materials and methods

Compilation of Literature

We followed the methods of Measey et al. (2016) to build an updated species list for established alien amphibians (105 spp), including consulting new compendia on the topic (+ 19 spp; Capinha et al. 2017), giving us a total of 124 species. We searched Web of Science in September 2019 for publications since 2015 (inclusive) using the most recent taxonomic name (or combinations of older names if any taxonomic movement had occurred since 2015; cf Frost 2019) and a composite term for invasive species [e.g. TS = ("*Ambystoma tigrinum*") AND TS = (alien OR invasive OR non-native OR exotic OR non-indigenous OR feral)]. We read titles and abstracts of resulting literature from the searches and obtained electronic copies of any studies that appeared to indicate a study on invasive amphibians (see van Wilgen et al. 2018 for details).

Scoring EICAT and SEICAT

After compiling all literature, we followed Hawkins et al. (2015) to assign an EICAT level in the corresponding impact category to fit any content relating to impact: Minimal Concern, Minor, Moderate, Major and Massive (hereafter MC, MN, MO, MR and MV, respectively). If no EICAT impact level could be ascribed, the paper was retained with a score of Data Deficient (DD). In the case that a score was assigned, we also scored a confidence level (low, medium or high), based on the criteria provided by Hawkins et al. (2015). In brief, the confidence score considers the type of data, the spatial scale of the study, and unanimity of evidence. This process was carried out for every paper published since May 2015 on any alien amphibian, and added to existing data on impact scored for studies prior to this (Kumschick et al. 2017; Bacher et al. 2018). Note that one paper could be scored for more than one alien amphibian species, or more than one category, as appropriate to the data it contained. Therefore, the total number of papers is less than total impact scores.

The same procedure was conducted for SEICAT, but following the guidelines set down by Bacher et al. (2018). We remained cognisant that papers which had been scored for EICAT could also carry SEICAT scores, and vice versa.

EICAT and SEICAT scoring analysis

We reasoned that over any given period of time, if there was no change in EICAT or SEICAT scoring, studies conducted in any period were likely to have equal chances of receiving the same proportions of EICAT or SEICAT scores as those received overall. Alternatively, an effect could be supported if the proportion of higher impacts (MR and MV) increased relative to the proportion of lower impacts (MC, MN and MO). Because the number of studies (see van Wilgen et al. 2018), and those to which EICAT or SEICAT scores could be attributed, have been increasing over time, we found it necessary to use only studies after 2000 when there were consistently more than three scores per year. Thereafter, we conducted a linear regression on the proportion of high to low impacts ((lower-higher)/total) per year in R (v 3.6.3; R Core Team 2020). Similarly, we tested whether the proportion of higher confidence scores (medium and high) have changed through time compared to lower confidence scores.

Costs of Conducting Studies

In each case where EICAT and SEICAT scores were determined for studies published in the last four years, we contacted the corresponding author of the study, to obtain research costs. We did not consider asking authors of earlier studies as we were concerned that accurate records of funding would not be available. We asked for the costs of the entire project in the form of a questionnaire (see Suppl. material 1), approved by Stellenbosch University's Social, Behavioural and Education Research (SBER) committee (project: 2019-13163). Specifically, we requested information on the amount of time spent by different members of the research team in conducting the study and producing peer-reviewed papers and the costs of their time (i.e., wage rates). We further requested information on costs of travel, accommodation, equipment used in the field or the lab, publication, and any other relevant costs associated with the study. If the equipment used in the study could be used for other research (e.g. computers, cameras, centrifuges) we asked the authors to estimate the percentage of total use of the equipment that was attributable to the study. Finally, we asked the monetary units used to pay these costs and the years in which the costs were incurred.

All study costs were converted to United States Dollars (USD) using the purchasing power parity (PPP) rates of currency conversion for the year(s) in which study costs were incurred, and the consumer price index (CPI) was used to convert these costs to 2018 USD by accounting for inflation since the time of the study. We obtained CPI measures from the United States Bureau of Labor Statistics. PPP measures were obtained from Organisation for Economic Co-operation and Development (OECD) data. The OECD calculates PPP measures based on the relative prices of consumer goods and services, equipment goods, occupations, and construction projects in different countries. PPP measures deviate from standard currency exchange rates because PPP takes relative price levels and costs of living in different countries into account. That is, by converting wages using the PPP we determined what equivalent USD income would have allowed the individual to maintain the same standard of living in terms of goods and services they could purchase if they were living in the USA rather than the country where the study was conducted (i.e. Australia, India, South Africa, etc.). Similarly, by converting non-wage research expenses to USD using the PPP we accounted for different price levels in different countries. This allowed us to compare study costs without the confounding effect of different salaries and price levels for goods and services across different countries of the world, and means that the costs we present can be directly compared.

For studies for which we obtained costs, we scored the complexity of the study design using the categories provided by Christie et al. (2019). The categories included (from simple to complex) were: After, Before-After, Control-Impact, Before-After-Control-Impact, and Randomised Control Trial. Along with study design complexity, time taken to conduct the study was also scored. We did not include time taken to publish the study or any delays between the finalisation of data collection and writing up of the study.

Costs and Impact analysis

In order to determine whether costs (USD PPP) are aligned with EICAT impact score or confidence, we conducted generalized linear mixed effects models (GLMM) using the *lme4* package (Bates et al. 2015) in R (v 3.6.3; R Core Team 2020). Prior to analyses, model assumptions (e.g. normality, homogeneity and independence) were assessed for all variables. The independence of impact score and confidence was assessed with a Spearman's Rank Correlation test. The response variable, Cost (USD PPP), was transformed using natural logs to meet the underlying statistical assumptions of normality. Restricted Maximum Likelihood (REML) methods were used to compare models with different fixed effect structures. A full model included two fixed factors, EICAT impact score and confidence as explanatory variables. We did not anticipate the need to assess models with interaction effects between our predictor variables. We used the continent on which the studies had been conducted as a random effect to account for potential autocorrelation within continents (following Evans and Blackburn 2020). Variance of random effects were minimal (s. d. < 2.00). Relative importance of competing models was evaluated using Akaike information criterion (AIC) and log likelihoods. To evaluate the variance of data explained by each model, R^2m (marginal: variance explained by the fixed effects) and R^2c (conditional: variance explained by the fixed and random effects) was calculated using the package *MuMin* (Barton and Barton 2019).

The effect of both study design complexity and the time taken to conduct the study (as predictor variables) on EICAT impact scores (response variable) were analysed using GLMMs, as above. Model assumptions (normality, homogeneity and variable independence) were assessed. The residuals from this analysis were not normally distributed and we were unable to normalize them by transformation. A full model included fixed effects, design complexity and time. All models included the random effect continent. Variance of the random effect, continent, was minimal (s. d. < 2.00).

Results

Scoring

We found 334 publications published since May 2015 that were on alien amphibians included in our updated list. This included two species (*Desmognathus monticola*; *Bufo japonicus*) that had not been previously on the list of Measey et al. (2016) or Capinha et al. (2017). Of the publications found, 109 papers could be scored (with 112 scores on 49 species) for impacts using the EICAT framework (see Suppl. material 2). Of all publications found, only eight new papers contained information that could be used to score socio-economic impacts according to SEICAT.

Cost of studies

We found that cheaper studies equated with lower EICAT impact scores ($p = 0.0060$; model 1 Table 1; Figure 1). The model that included confidence (model 3) was not appreciably worse (within 2 delta AICs) but the R^2 estimates indicate that confidence did not explain more of the data (Table 1). Confidence and impact score were not correlated ($S = 8789.3$, $p = 0.4457$). No relationship between the confidence score and the study cost was found (see Table 1).

Our data showed that study design (complexity) and time taken to conduct the study were significantly related to EICAT score ($p = 0.0007$). The highest EICAT scores (MR and MV) were obtained from Before-After studies which took longer to conduct, and lower scores typically came from shorter studies 'After' invasions had taken place (Table 2). Although the model with study design alone (model 1) was within 2 delta AICs, it was not favoured as it explained less observed variance in the data (Table 2).

Impact score changes across time

We noticed three general trends in EICAT scores over time. Firstly, that the amount of literature in the last four years that generated impact scores (not including DD) was equivalent to nearly a third of total scores (112 out of 362). Second, we found a sig-

Table 1. Results of general linear mixed models for costs (USD PPP) of studies contributing to EICAT impacts of amphibians. Impact and Confidence are both calculated when scoring papers using EICAT criteria (see Hawkins et al. 2015). Delta AIC is the difference in Akaike information criterion values (AIC) between models, and Wi (Akaike weight) is the relative support a model has from the data compared to the other models in the table. Marginal (R2m) and conditional (R2c) variance of the fixed effects are reported for each model.

Model number	Variables (fixed effects)	Log likelihoods	Number of parameters	Delta AIC	Wi	R^2m	R^2c
1	Impact	-55.5126	4	0.0000	0.6392	0.1536	0.2687
3	Impact + Confidence	-55.5028	5	1.9631	0.2395	0.1534	0.2701
4	Null	-58.4994	3	3.9564	0.0884	0.0000	0.1925
2	Confidence	-58.4872	4	5.9319	0.0329	0.0006	0.1948

Table 2. Results of general linear mixed models for impact score of studies contributing to EICAT impacts of amphibians. Design levels are taken from Christie et al. (2019) and Time is the period under which the study took place according to the authors in the published paper.

Model #	Variables (fixed effects)	Log likelihoods	Number of parameters	Delta AIC	Wi	R^2m	R^2c
3	Design + Time	-45.9335	5	0.0000	0.5004	0.3222	0.3447
1	Design	-46.9898	4	0.1126	0.4730	0.2806	0.2806
2	Time	-50.0588	4	6.2506	0.0220	0.1337	0.1759
4	Null	-52.6122	3	9.3574	0.0046	0.0000	0.0474

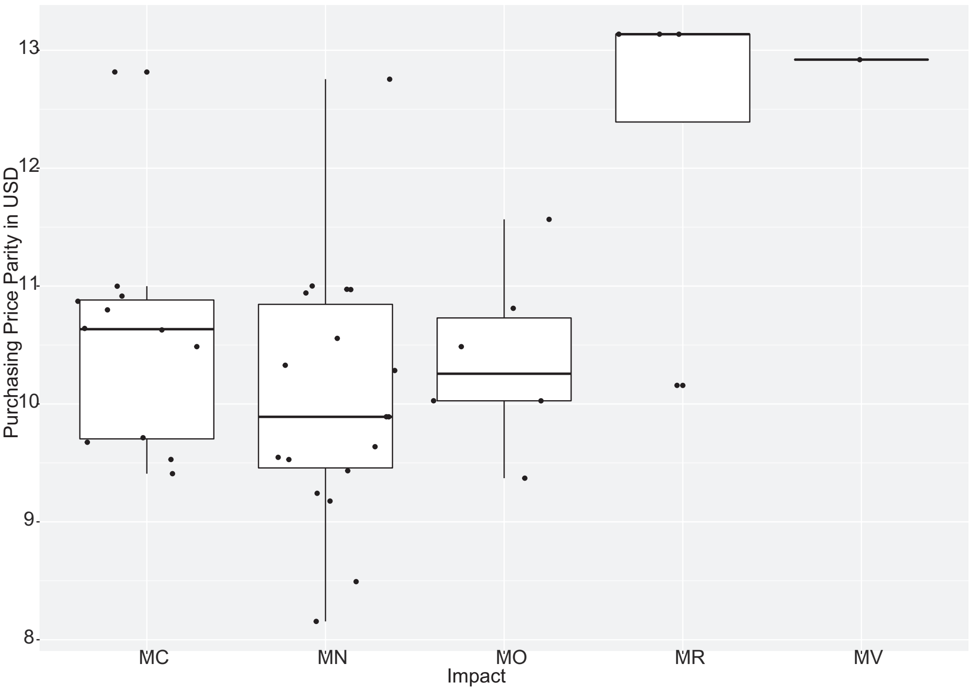

Figure 1. Distribution of costs spent per publication and their EICAT impact level scored. Studies providing higher impacts (MR and MV) cost more money, but studies scoring the lowest impact (MC) cost more on average than those that have medium impact (MN and MO). Cost of the study is ln(USD) purchasing price parity (PPP). Impact scores follow Hawkins et al. 2015: Minimal Concern (MC), Minor (MN), Moderate (MO), Major (MR) and Massive (MV).

nificant negative trend ($F_{1,17}$ = 7.451, p = 0.014) with increasing proportions of lower impact studies over time: i.e. studies that scored MR or MV are reduced compared to the total number of scores since 2000. Lastly, we found that the proportion of studies scored with low confidence has a significant negative trend since 2000 ($F_{1,17}$ = 11.48, p = 0.003). Our overview of all data (Figure 2) shows that impact scores are higher since the 1990s than in the decades preceding this.

When compared with previous scores (Kumschick et al. 2017), we found that 25% (11 of 45 species) of all amphibians had increased their EICAT impact or confidence in the four years since the original score was determined (Table 3a). This included a growth in the assessed list by 12% (five species), which were previously not assessed (NA) due to a lack of literature. Notably, scores changed for the cane toad, *Rhinella marina*, from Major (MR) with high confidence to Massive (MV) with medium confidence (see below). Additionally, the confidence score on Major impacts of the African clawed frog, *Xenopus laevis*, changed from medium to high (see below).

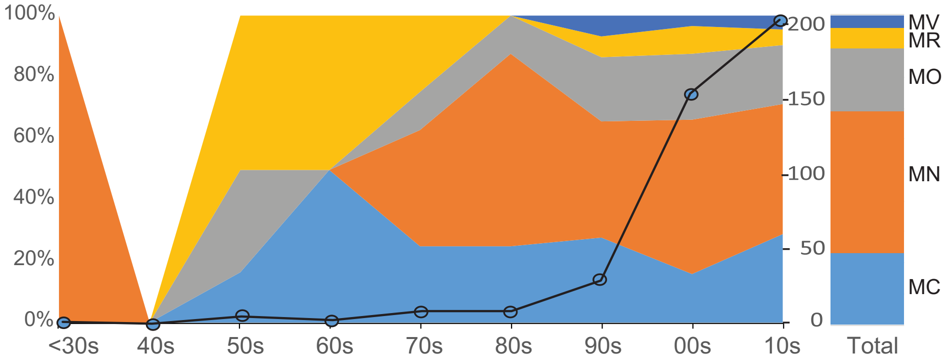

Figure 2. The change in the proportion of amphibian EICAT impact scores over time (decadal scores starting from the 1930s). Solid shapes represent the percentage of scores (left scale) with totals for the entire period and score codes on the right (total = 424). Black line shows number of papers scored in the same decadal time slots, with scale to the right.

Table 3. Amphibian species that have changed their Environmental Impact Classification for Alien Taxa (EICAT) or Socio-Economic Impact Classification for Alien Taxa (SEICAT) assessment since 2015 (Measey et al. 2016; Kumschick et al. 2017; Bacher et al. 2018), and their associated costs. NA not applicable. Impact scores follow Hawkins et al. 2015: Minimal Concern (MC), Minor (MN), Moderate (MO), Major (MR) and Massive (MV).

Species name	Impact	Confidence	Mechanism	Year	Change from	Reference
(a) EICAT						
Bufo japonicus formosus	MO	medium	(6) Poisoning/ toxicity	2019	NA	Kazila and Kishida (2019)
Desmognathus monticola	MC	medium	(1) Competition	2017	NA	Bush et al. (2017)
Eleutherodactylus planirostris	MN	low	(4) transmission of diseases	2019	MC (1) med	Rivera et al. (2019)
Fejervarya kawamurai	MN	medium	(2) Predation	2019	NA	Takeuchi et al. (2019)
Glandirana rugosa	MN	medium	(2) Predation	2018	NA	Van Kleeck and Holland (2018)
Hoplobatrachus tigerinus	MO	medium	(2) Predation	2019	MN (1) low	Mohanty and Measey (2019b)
Ichthyosaura alpestris	MN	low	(2) Predation	2017	MC (4) low	Palomar et al. (2017)
Lissotriton vulgaris	MN	low	(3) Hybridisation	2019	NA	Dubey et al. (2019)
Polypedates leucomystax	MN	medium	(5) Parasitism	2018	MN (5) low	Hasegawa et al. (2018)
Rhinella marina	MV	medium	(6) Poisoning/ toxicity	2017	MR (6) high	Doody et al. (2017)
Xenopus laevis	MR	high	(2) Predation	2018	MR (2) med	Courant et al. (2018)
(b) SEICAT						
Eleutherodactylus coqui	MO	high	(S2) Material and immaterial assets	2019	MN S2 high	Kalnicky et al. (2019)
Hoplobatrachus tigerinus	MO	medium	(S2) Material and immaterial assets	2019	NA	Mohanty and Measey (2019a)
Sclerophrys gutturalis	MN	low	(S3) Health	2017	NA	Measey et al. (2017)

SEICAT Scoring

Of the eight new papers for SEICAT scoring, one species (out of the previously scored 6 species) increased its SEICAT impact score, and two studies provided data on species for which there was no previous score (Table 3b). In the four years since the original study, there has been a 25% (three species) increase in species scored for SEICAT since the search made by Measey et al. (2016), and subsequently scored for SEICAT by Bacher et al. (2018).

Confidence scores

For EICAT, we found that the number of papers decreased for each increasing impact score, except for the category MC, which is similar in size to MO (Figure 3). However, as the impact score increased, the proportion of studies with low confidence decreased and the proportion of high confidence studies increased.

Both the data collected from costs of studies (n = 35), and the number of changes in scores (Table 2) were of limited inferential value on their own. We therefore provide four case studies that illustrate the diversity of studies that we found.

Case Studies

Indian bullfrogs – The Indian bullfrog, *Hoplobatrachus tigerinus*, native to the Indian subcontinent, has invasive populations on the Andaman archipelago and Madagascar (Mohanty et al. in press). The use of this large-bodied species for human consumption has been the primary pathway for its introduction and secondary transfers. Despite its high invasion potential, *H. tigerinus* invasion dynamics have only been studied in detail on the Andaman archipelago (Mohanty et al. in press). Kumschick et al. (2017)

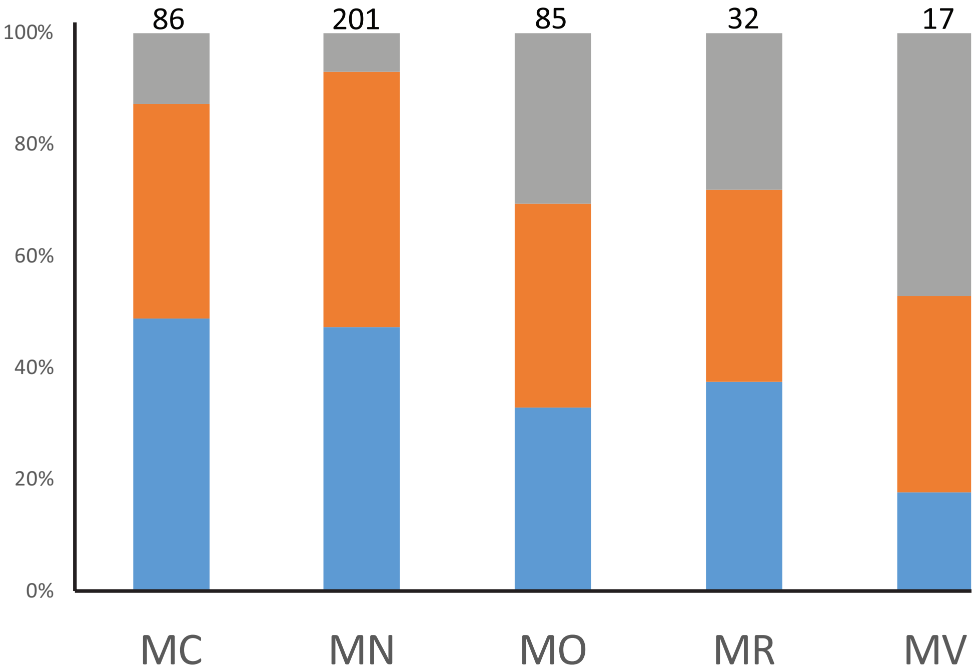

Figure 3. Changes in the frequency (number at bottom of column), and proportion of confidence (high – grey, medium – orange, and low – blue) in each of the five impact Environmental Impact Classification for Alien Taxa (EICAT) categories scored for amphibians. Impact scores follow Hawkins et al. 2015: Minimal Concern (MC), Minor (MN), Moderate (MO), Major (MR) and Massive (MV).

assigned *H. tigerinus* an EICAT score of Minor with low confidence; the species was considered 'Data Deficient' under SEICAT (Bacher et al. 2018). The EICAT score was based on observations of extremely high densities of *H. tigerinus* at a few sites in Madagascar (Griffin 2010), leading to inference of competition. Mohanty et al. (in press) revised both EICAT and SEICAT assessments of the species on the basis of three recent publications, (Mohanty and Measey 2018, 2019a, b). The revised 'maximum recorded impact' was Moderate with medium confidence for EICAT (drastic reduction in survival of endemic frogs *Microhyla chakrapanii* and *Kaloula ghoshi*), costing 2018 USD 11 736. This revised assessment resulted from a mesocosm experiment, carried out over three months, that aimed to assess impact (Mohanty and Measey 2019b), equivalent to a Control Impact study (moderate complexity). A new SEICAT score of Moderate with medium confidence (ceasing of poultry-keeping) was assigned at a cost of 2018 USD 22 626, based on a year-long questionnaire-based survey of 91 villages on the Andaman archipelago. However, this study's bigger aim was to reconstruct the invasion history of the species (Mohanty and Measey 2019a). The invasive population (on the Andaman archipelago) is unlikely to attain a higher EICAT or SEICAT score at this time, given its relatively recent invasion (Mohanty and Measey 2019a). However, the associated confidence scores could be improved by conducting large-scale, before-after-control-impact experiments and focussed socio-economic surveys, for EICAT and SEICAT scores respectively.

African clawed frogs – The African clawed frog, *Xenopus laevis*, is native to southern Africa, but was exported globally from South Africa from the 1930s (van Sittert and Measey 2016) first for pregnancy testing, then as a model amphibian in research laboratories (Gurdon and Hopwood 2000), and lastly in the pet trade (Measey 2017). The first studies on invasive populations were conducted in California and published in the 1980s (McCoid and Fritts 1980), but the discovery of increasing invasive populations around the world (van Sittert and Measey 2016) led to this becoming one of the most well studied alien anurans (van Wilgen et al. 2018). The European Union invested ~$1.1 million USD in a 5 year project (INVAXEN) to understand European invasions of *X. laevis*. As part of this larger effort, researchers designed a study to measure the impacts of the French population of *X. laevis* on native amphibians at 76 sites in a transect from the introduction site (~1980) and through the invaded area and into uninvaded areas of the same region (Courant et al. 2018), equivalent to a Control-Impact study (moderate complexity). Researchers found a significant negative relationship between amphibian diversity and increasing *X. laevis* density, and that amphibian diversity increased as distance from the introduction site increased. Two amphibians (*Bufo spinosus* and *Triturus cristatus*) were not detected when *X. laevis* was present. The extirpation of these native species from within the invaded range in France increased the EICAT impact score to Major, with medium confidence. The study was conducted within a single year and is estimated to have cost 2018 USD 25 777. No literature allows for SEICAT impact scores to be assessed for invasive *X. laevis*, although fishermen in the region have complained that since the invasion, the quality of leisure fishing has reduced due to fewer fish being caught and interference by unintended capture of *X. laevis* (J. Courant pers. com.). Given the current scale and locations of invasions, the EICAT score is not expected to increase with further study, but more studies from other invasions may increase the confidence. A targeted study is still required to produce a SEICAT score.

Cane toads – Cane toads, *Rhinella marina*, are native to the Americas, ranging from the southern United States to central Brazil (Shine 2010). During the early 20th century, these toads were extensively moved around the world as a biocontrol agent for invertebrate pests. In 1935, 101 *R. marina* were imported into Australia from Hawaii (Easteal 1981; Shanmuganathan et al. 2010) and by 1947 over 60 000 Australian-born juvenile *R. marina* had been produced and were released (Easteal 1981; Shanmuganathan et al. 2010). The potential threat these toads posed to Australian ecosystems was identified from the outset of their arrival, with Froggatt (1936) stating that "*this great toad, immune from enemies, omnivorous in its habits, and breeding all the year round, may become as great a pest as the rabbit or cactus*"; however it took several decades before notable impacts on wildlife became apparent (Breeden 1963; Pockely 1965; Rayward 1975). Owing to these early concerns, the toad's 80 year long range expansion across northern Australia has been both well-documented and modelled (e.g. Sabath et al. 1981; Freeland and Martin 1985; Urban et al. 2008; Doody et al. 2019), with substantial resources being invested into toad research. For example, between 1986 and 2009 the Australian Government invested over ~$13.8 million USD into *R. marina* research, management, community groups, and education (R. Shine pers. comm.). The ecological impacts have been far-reaching (Shine 2010), including competition with native species (Greenlees et al. 2006; Bleach et al. 2014; Taylor et al. 2017), multiple native species population declines (Phillips et al. 2009; Fukuda et al. 2016; Taylor et al. 2017), localised extinctions (Oakwood and Foster 2008; Doody et al. 2017), trophic disruption (Greenless et al. 2006; Doody et al. 2015), and community-level reorganisation (Brown et al. 2013; Feit et al. 2018; Brown and Shine 2019).

The previous EICAT assessment identified *R. marina* as one of the top 10 amphibian species with the highest Maximum Recorded Impacts, receiving the listing of Major impacts in both the Predation and Poisoning/toxicity categories (Kumschick et al. 2017). Our current reassessment has up-listed the *R. marina* Maximum Recorded Impacts from Major with high confidence to Massive with medium confidence within the category of Poisoning/toxicity. This shift was a result of a study based in the Northern Territory and aimed at quantifying community-level impacts and examining ecological responses post-invasion (Doody et al. 2017); equivalent to a long-term Before-After study (moderate complexity). The impacts of toads in the region resulted in extirpations (e.g., complete removal of two species of predator and the dramatic reduction of a third), community-level changes (e.g., the mesopredator-release of one species), and no indication of ecological recovery 12 years post-invasion (Doody et al. 2017). The study also notes that *R. marina* are too prolific and widespread to eradicate (Shine and Doody 2011; Doody et al. 2017), resulting in their impacts being functionally irreversible by the Hawkins et al. (2015) definition. The study was conducted intermittently over 12 years and is estimated to have cost 2018 USD 408 737. We note that this cost estimate is conservative because we only included costs that could definitely be attributed to the published research findings. Further research looking for similar findings across a wider geographic area or an example of a complete species extinction would likely serve to increase the EICAT confidence rating for the Massive impact score (currently rated at medium confidence). Additionally, the previous SEICAT assessments of *R. marina* had listed the maximum impact score as Major with medium confidence (Bacher et al. 2018) and it is likely that further research into the socio-economic impacts of *R. marina* are required and may yield higher SEICAT impact and confidence scores if the appropriate attention is given to this topic.

Guttural toads – The guttural toad, *Sclerophrys gutturalis*, is a common African bufonid naturally distributed across central and southern Africa (Telford et al. 2019). Guttural toads were first introduced to Mauritius and Reunion in 1922 and 1927, respectively, as an attempt at biocontrol for invertebrate pests (Cheke and Hume 2008; Kraus 2009; Dervin et al. 2014; Telford et al. 2019). These toads are now widespread across both islands and a recently introduced population in Cape Town, South Africa, became established in 2000 (de Villiers 2006; Vimercati et al. 2018; Telford et al. 2019). Due to their extensive predation on Mauritian land-snails (Griffiths 1996), Kumschick et al. (2017) assigned *S. gutturalis* an EICAT score of Moderate with low confidence, based on a study that equates to After design (low complexity). Although there are growing concerns regarding the potential impact of *S. gutturalis* on native species in the Mascarene Islands and Cape Town, South Africa (Griffith 1996; de Villiers 2006), hardly any research has been conducted regarding its impact. A recent publication noted that property owners are more willing to support the removal of toads in Constantia due to their loud reproductive call that can be heard over hundreds of metres (Measey et al. 2017). The objectives of this study were to provide a historical overview of invasive amphibian dispersal pathways in southern Africa, give an overview of legislation in South Africa regarding amphibian invasions and assess the status of three invasive amphibian populations in South Africa, namely *Hyperolius marmoratus, Xenopus laevis* and *Sclerophrys gutturalis*. Although Measey et al. (2017) did not aim to describe the socio-economic impact of *S. gutturalis*, the anecdotal evidence presented in this study allowed us to assign a SEICAT score for *S. gutturalis*. The change from Data Deficient to Minor for Health/Social, spiritual and cultural relations with a low confidence level came at an estimated cost of 2018 USD 58 110. Given sufficient directed work, particularly on Reunion and Mauritius where local endemism is high, we consider that the EICAT and SEICAT scores and confidence in them will increase.

Discussion

We found that for EICAT impact scores, but not confidence in those scores, the costs of studies that produce higher impacts are more expensive. Moreover, higher EICAT impact scores were obtained from studies with more complex designs that took longer to conduct. For our amphibian dataset, we found that highest impact scores have only been elucidated in the last 20 years of research, and that studies with higher confidence are also more recent. The implications of our findings are that it will not be possible for the IUCN to categorise the true impact of alien species using EICAT (and, should they choose to adopt it, SEICAT) without increased investment in research. This is especially true in areas of the world that do not currently have the resources to invest in more costly research – a pattern already seen for data availability in birds (Evans and Blackburn 2020). Moreover, for many invasive species we cannot expect that studies conducted rapidly will convey the true EICAT score at that point in time. Our data indicates that preliminary studies should act to recommend whether or not more, longer term studies are warranted. For example, in the past four years, new literature has changed the status of even the most well studied invasive amphibian, *R. marina* (see van Wilgen et al. 2018) from MR to MV (i.e. from a reversible impact to an irreversible impact), in a study that took more than 12 years to conduct (Doody et al. 2017) at a cost of USD 408 737. If the same pattern continued across all taxa as we have shown for amphibians, the consequence will be that species with potentially high EICAT or SEICAT impact scores will go unrecognised because of insufficient research investment. It seems likely that this will impact the assessment using the ICAT schemes of all invasions in regions from lower middle-income economies, unless research funding is specifically targeted towards invasion science in these regions, or funds obtained in wealthier regions are leveraged to develop international research collaborations.

There may be reasons why amphibians are not representative of all invasive groups. Although the rise in data available is currently exponential (van Wilgen et al. 2018), sparse older data (pre 2000) does not allow for a quantitative assessment of impact during this time. For example, all but one amphibian scored as MV (except *R. marina*) include the impact mechanism of hybridisation (see Kumschick et al. 2017). As this requires a genetic diagnostic not widely available before the late 1990s, studies had not previously proved this mechanism, and so MV was nearly absent. Other taxa that have more impact mechanisms contributing to higher impact scores could be investigated to determine changes in impact over time. While we show that higher impacts were associated with more expensive studies, there are other possible explanations that may explain this pattern. For example, the perception of high impacts (independent of scoring schemes) may stimulate greater investment in research. The information provided here about *R. marina* and *X. laevis* supports this supposition, but other species (e.g. Asian spiny toad, *Duttaphrynus melanostictus*) achieve high impacts with few studies (see Measey et al. 2016). It is important to note that both *R. marina* and *X. laevis* have received this investment where they have invaded high income countries, while the impact from their introduction to less wealthy regions remains comparatively understudied.

In this study, we show that a relatively short period of time (less than four years) is enough to make considerable changes to the global list of EICAT and SEICAT amphibian scores. Papers from which EICAT and/or SEICAT can be scored have grown by around 25%, with increases in the number of species assessed as well as increasing impact scores for species already assessed. Unsurprisingly, a small number of species were assessed for the first time, including two species that were not featured in previous lists of established alien amphibians (Kraus 2009; Measey et al. 2016; Capinha et al. 2017). Currently, the IUCN aims to update Red List entries every five years. Our study suggests that this periodicity is appropriate to the ICAT schemes, but that ad hoc updates may be appropriate when project findings suggest that this may result in a status change. It can be hoped that when EICAT is more widely acknowledged in the scientific community (through use by the IUCN), that more studies will be designed to incorporate the specific impact mechanisms and suggest appropriate scoring, much as they are currently for the IUCN Red List.

Overall, we found that higher EICAT scores displayed a higher proportion of studies with high confidence. This is evidence of our supposition that only studies with greater investment and more complex designs (cf Christie et al. 2019) are able to demonstrate Major or Massive impacts. We acknowledge that it is possible for studies demonstrating Massive impacts to be very cheap, such as the extinction of a well-known endemic on an island as the result of an invasion, and that these are not infrequent (cf Pyšek et al. 2017). However, although such impacts are possible for amphibians, none has been recorded as their largely invertebrate prey items are not comparatively well studied, thereby introducing another source of impact bias. It is noteworthy that the lowest EICAT score, Minimal Concern (MC), has fewer contributing papers than Minor (MN), with the majority of them having low or medium confidence. In our dataset, most studies resulting in low impact scores (MC and MN) were not aiming to determine impacts of invasive species. It is possible that because our dataset involved only established species, it is more difficult to demonstrate the absence of impact (MC) than Minor impact (MN), explaining the skew in the numbers of papers in these categories. This is in contrast to studies resulting in MO, MR or MV that are primarily focussed on impact. The mechanisms of most research funding mean that simple preliminary studies from small funds showing some impact (perhaps with low confidence) are required before researchers will motivate for funds to conduct more complex experimental research. Policy frameworks are extremely important to motivate for such funding (e.g. CBD, IPBES 2013).

We continued to find very few studies that provided impact scores for SEICAT (Bacher et al. 2018), and this is similar to other studies for different taxa that have attempted to implement this framework (see Evans et al. 2020). This is perhaps unsurprising as our methods have an inherent bias to sampling from the scientific over the socio-economic literature. But there is a growing interest in socio-economic studies in invasion science, and we expect to see these assessments growing in confidence over time. Currently, it is not possible to say whether SEICAT will suffer from the same issues (e.g., costs linked to impact score, and impact score linked to study complexity) that we observed in EICAT, but it is important that this be assessed in the future.

Summary

Here, we provide the first set of estimates of the cost of published studies used when implementing the ICAT schemes. We found evidence that more expensive and complex studies are needed to score the highest levels of impacts for amphibians. This is something that should concern those who wish to implement the use of these scores as we show that the highest scores may require high levels of funding, investment of time and expertise to achieve. If scores inform policy, then this may result in a circularity where poor investment in impact forming research results in true impacts not being revealed.

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Supplementary material 1

Questionnaire

Authors: John Measey, Carla Wagener, Nitya Prakash Mohanty, James Baxter-Gilbert, Elizabeth F. Pienaar

Data type: Questionnaire

Explanation note: Questionnaire sent to authors of papers in review.

Link: https://doi.org/10.3897/neobiota.62.52261.suppl1

Supplementary material 2

Amphibian EICAT & SEICAT scores

Authors: John Measey, Carla Wagener, Nitya Prakash Mohanty, James Baxter-Gilbert, Elizabeth F. Pienaar

Data type: Scores from literature review

Explanation note: EICAT and SEICAT scores and confidence for globally established amphibian species.

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REVIEW ARTICLE

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Advancing research on alien species and biological invasions

Harmonising the fields of invasion science and forest pathology

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Abstract

Invasive alien species are widely recognised as significant drivers of global environmental change, with far reaching ecological and socio-economic impacts. The trend of continuous increases in first records, with no apparent sign of saturation, is consistent across all taxonomic groups. However, taxonomic biases exist in the extent to which invasion processes have been studied. Invasive forest pathogens have caused, and they continue to result in dramatic damage to natural forests and woody ecosystems, yet their impacts are substantially underrepresented in the invasion science literature. Conversely, most studies of forest pathogens have been undertaken in the absence of a connection to the frameworks developed and used to study biological invasions. We believe this is, in part, a consequence of the mechanistic approach of the discipline of forest pathology; one that has been inherited from the broader discipline of plant pathology. Rather than investigating the origins of, and the processes driving the arrival of invasive microorganisms, the focus of pathologists is generally to investigate specific interactions between hosts and pathogens, with an emphasis on controlling the resulting disease problems. In contrast, central to the field of invasion science, which finds its roots in ecology, is the development and testing of general concepts and frameworks. The lack of knowledge of microbial biodiversity and ecology, speciation and geographic origin present challenges in understanding invasive forest pathogens under existing frameworks, and there is a need to address this shortfall. Advances in molecular technologies such as gene and genome sequencing and metagenomics studies have increased the "visibility" of microorganisms. We consider whether these technologies are being adequately applied to address the gaps between forest pathology and invasion science. We also interrogate the extent to which the two fields stand to gain by becoming more closely linked.

Keywords
coevolution, emerging, forest pathogens, invasion framework, invasive forest pathogens, microbial invasions, tree disease

Introduction

Invasive alien species (IAS) present a major threat to global biodiversity, ecosystem services, economies and human health. In the present era of globalisation, and with no end in sight to the accumulation of alien species worldwide (Seebens et al. 2017), this threat continues to grow (Pyšek et al. 2020). The field of invasion science has been established to address the issues arising from the introduction of alien species and resulting biological invasions. It is grounded in invasion ecology, but has expanded to include non-biological lines of enquiry, including economics, ethics, sociology, and inter- and transdisciplinary studies (Hui and Richardson 2017). While IAS are represented by organisms across all taxonomic groups, much of the body of work in the field of invasion science has been focussed on plants and animals (Pyšek et al 2008; Wilson et al. 2020a). Many key texts fail to consider microorganisms, or if they are mentioned, they do so only briefly (e.g. Mooney et al. 2005; Lockwood et al. 2013). In contrast, there have been a number of recent reviews on microbial invasions, including invasive forest pathogens (IFPs), however, these have generally been written by microbiologists, or where dealing specifically with forest pathogens, forest pathologists (Desprez-Loustau et al. 2007; Fisher et al. 2012; Santini et al. 2013; Gladieux et al. 2015; Ghelardini et al. 2017). Nonetheless, IFPs remain generally poorly connected with invasion frameworks, limiting the application and usefulness of these concepts.

The low level of recognition regarding the importance of forest pathogens in invasion science is concerning, when considering the substantial effects of IFPs and their ability to completely alter landscapes. IFPs have been responsible for many disastrous outbreaks of diseases in commercial, natural and urban forests. Well known historical examples include chestnut blight (caused by *Cryphonectria parasitica*), Dutch elm disease (*Ophiostoma ulmi sensu lato*), *Phytophthora cinnamomi* in southwest Australia, and in more recent history, sudden oak death (*Phytophthora ramorum*) and ash dieback (*Hymenoschyphus fraxineus*) (e.g. Brasier and Buck 2001; Rizzo and Garbelotto 2003;

Shearer et al. 2007; Pautasso et al. 2013; Rigling and Prospero 2018). These and other diseases have fundamentally altered ecosystems, with entire tree species practically eliminated from the landscape. For example, the second pandemic of Dutch elm disease is estimated to have killed between 30 and 50 million elms in the United Kingdom alone (Brasier 2008). Likewise, chestnut blight functionally removed mature American chestnut (*Castanea dentata*) trees from natural landscapes within 30 years of its arrival (Brasier, 2008; Loo, 2008), and sudden oak death is having a similar impact on tanoak (*Notholithocarpus densiflorus*) in Oregon and California (Cobb et al. 2012). Common ash (*Fraxinus excelsior*) is now threatened in much of its natural distribution across Europe, with mortality rates as high as 85% recorded from sites infected with *H. fraxineus* (Pautasso et al. 2013; Coker et al. 2019). In addition to dramatic changes in forest canopy composition, direct and indirect effects on communities, including losses of important ecosystem services, are increasingly reported following these invasions. Mitchell et al. (2014) highlighted the wide-ranging ecological implications of ash dieback resulting from *H. fraxineus* infection. Likewise, the invasive fungal pathogen *Austropuccinia psidii* (cause of myrtle rust), has significantly altered species richness and abundance in Australian rainforest communities, within a short period of time (Fernandez-Winzer et al. 2020).

Coevolution between forest pathogens and their hosts, together with pressures from competition, predation and parasitism, has contributed to the complexity and stability of natural ecosystems. Severe disease outbreaks by native pathogens under natural environmental conditions, are therefore rare (Burdon and Thrall 2009). Importantly, this coevolution between hosts and pathogens has occurred under a particular set of environmental conditions (Stenlid and Oliva 2016). Pathogens are therefore contained by geographical, environmental and evolutionary barriers, with these barriers impeding spread to novel hosts and limiting their potential to cause severe disease outbreaks. However, release from any one of these barriers may result in pathogenic behaviour, and the emergence of a new disease.

The term emerging infectious disease (EID) has its history in the medical and veterinary fields, but has also been applied to diseases of plants (Anderson et al. 2004). Of the three means by which an EID can arise, generally only one, the crossing of geographical barriers due to human mediated dispersal, is recognised as a process leading to biological invasions (Ogden et al. 2019). Within the context of forest pathology, a challenge when faced with the emergence of a new disease is determining whether this is due to the introduction of an alien species, or the consequence of a native pathogen being favoured by changing environmental conditions. The latter scenario has become increasingly common under conditions of habitat disturbance and climate change (Desprez-Loustau et al. 2006; Paap et al. 2018). The lack in knowledge of microbial biodiversity and ecology, speciation and geographic origin confound the problem of defining emerging diseases from an invasion perspective. While recent advances in molecular technologies have increased the "visibility" of microorganisms, the paucity of information remains a challenge. It is, therefore, understandable, but remains concerning, that pathogens are strikingly underrepresented in invasion science.

The clearest evidence for this underrepresentation is that among the IUCN list of 100 of the World's Worst Invasive Alien Species (Lowe et al. 2000), only six are microorganisms. And of these, only three (*Cryphonectria parasitica*, *Ophiostoma ulmi sensu lato* and *Phytophthora cinnamomi*) are forest pathogens. A more recent example is that of the European Union list of alien species of Union Concern. Despite two updates, forest pathogens (and microorganisms in general) remain absent from this list (European Union 2019). Another example is South Africa's http://invasives.org.za, which includes information about invasive plants, animals and insects, but not microorganisms, despite the presence of globally regulated species such as *Austropuccinia psidii* and *Fusarium circinatum* (Wingfield et al. 2008; Roux et al. 2013).

There have been previous calls for increased cooperation between microbiologists and invasion scientists. For example, Desprez-Loustau et al. (2007) highlighted the underrepresentation of fungi in the field of biological invasions, most likely due to a lack of scientific knowledge of fungal biodiversity and ecology. They hoped to raise awareness among mycologists and ecologists of the fungal dimension of invasions, and they identified the need to intensify research in fungal ecology to address the issue of future introductions. More recently, Wingfield et al. (2017) observed that forest pathologists have frequently undertaken epidemiological studies in the absence of any reference to, or reflection on, invasion science principles or frameworks, and called for closer collaboration between the disciplines.

This review interrogates the history of the disciplines of forest pathology and invasion science, seeking insights as to why the two fields have remained relatively unconnected. We consider several explanations for this disconnect and highlight the need to resolve these issues. By adopting the frameworks of invasion science, forest pathologists may be able to better understand how and why invasions occur. Importantly, also where, when and how invasions can be stopped or mitigated. The issue of microbial invasions has been described as one of the most pressing topics facing invasion science (Ricciardi et al. 2017; Thakur et al. 2019). Therefore, a greater inclusion of IFPs and microorganisms in general, is essential for the continued advancement of the field of invasion science. For the purpose of this review we consider IFPs in the strict sense, as a subgroup of IAS i.e. of alien origin and a consequence of human mediated dispersal.

A brief history of forest pathology and invasion science

Forest pathology

The Greek philosopher Theophrastus (c. 371 – c. 287 BC) was the first to study and write about disease of trees, cereals and legumes. However, it was not until the mid-1800s that the role of pathogenic microorganisms in causing plant disease was understood. Anton de Barry, a German surgeon, botanist and microbiologist, is recognised as the founding father of modern plant pathology and modern mycology. In 1861, de

Barry documented in detail the life cycle of *Phytophthora infestans* and provided experimental evidence to demonstrate its role of as the causal agent of potato late blight. In doing so, he refuted the long-standing doctrine of "spontaneous generation", and the discipline of physiological plant pathology was born (Kutschera and Hossfeld 2012).

Forest pathology emerged soon afterwards, as a branch of plant pathology dealing with diseases of woody plants growing in natural ecosystems, plantations and urban environments. The German forester Robert Hartig is widely regarded as the "father" of forest pathology. His work characterised and linked *Heterobasidion annosum* to conifer root and butt rot (published in 1874), refuting the notion of decay being responsible for the spontaneous generation of fungi by showing that fungi were the cause of decay (Shigo 1967).

The first half of the 1900s saw only a small number of forest pathologists working worldwide. Interestingly much of today's understanding of forest pathology is still underpinned by the work of these few early pioneers (Boyce 1938; Peace 1962). Historically, the focus of forest pathology was centred on determining the cause and control of specific disease problems; essentially, a mechanistic approach adopted from the broader field of plant pathology. Rather than investigating the origins of the microorganism, the processes driving its arrival, or determining the basic underlying biology of the disease system, the emphasis was primarily on controlling the resulting disease problem.

Forest pathology has been strongly shaped by the influences of microbiology and health sciences, quintessential to its plant pathology roots. However, forest pathology is also a sub-field of forestry and as such, has dealt with long time scales and diverse environments, much more so than classic agronomic crop-based plant pathology (Desprez-Loustau et al. 2016). In addition to severe disease outbreaks caused by IFPs, forest health is also marked by important tree declines. Manion (1981) formalised the tree decline concept, incorporating abiotic and biotic predisposing, inciting and contributing factors. In contrast to crop pathology, where systems are simplified and intensely managed, forest pathology deals with complex and long-lived ecosystems. The environmental differences play a significant role in determining host-pathogen interactions and their subsequent outcomes.

Within the context of forest pathology, two diverging branches of the discipline have arisen. This has come about as a result of two broad settings in which forestry is undertaken; plantation forestry versus natural and semi-natural forests. Planted forests are generally very simplified ecosystems, more similar to a crop than to a natural forest. This type of silviculture, combined with a wide use of non-native tree species is the dominant, if not exclusive, form of forestry in the Southern Hemisphere (South America, South Africa, New Zealand and to an extent, Australia), and also East and South East Asia. They are typically monospecific, and characterised by both native and non-native trees mostly of the genera *Pinus*, *Eucalyptus* and *Acacia* (Wingfield et al. 2015; Burgess and Wingfield 2017). Consequently, the focus of forest pathology today has arguably remained more closely linked to the mechanistic approach of plant pathology. While there is some plantation forestry in the Northern Hemisphere including genera of *Pinus*, *Picea*, *Pseudotsuga*, *Populus* and *Eucalyptus*, the experiences of forest pathologists in the Northern Hemisphere have tended to come mostly from a silviculture based on native species cultivated in natural or semi-natural environments, or from plantations of native species. Here, silvicultural practices have long been implemented to manage native forest tree species with the objective of optimising timber production and maintaining tree cover. A less mechanistic and more ecological approach to forest pathology has evolved from this setting. Broadly speaking, management of native forest tree species, including dealing with disease problems, has long been practiced in Europe, North America and Russia (Manion et al. 1981; Tainter and Baker 1996). However, until recently, response to the emergence of a new forest disease has focused on how to manage the outbreak, and not on why, how and from where the causal agent has arrived. This approach is typically mechanistic and is likely derived not only from plant pathology, but also from the past approach to human diseases, where treatments have historically focused on limiting symptoms, as opposed to eliminating the causal agent.

Invasion science

The discipline of invasion science is a relatively young field. In 1958, the British biologist Charles Elton (1958) published *The Ecology of Invasions by Plants and Animals*, describing for the first time the biology of invasive organisms, and noting their importance as drivers of ecosystem change. By the 1980s, there was a growing body of accounts in the literature of non-native species invading novel environments. There was also the realisation that increased world trade and travel were leading to an increased frequency of biological invasions. Furthermore, that the negative effects associated with the invasion of non-native species presented one of the greatest threats to native ecosystems and biodiversity (Macdonald et al. 1986; Mooney and Drake 1986).

A meeting of the Scientific Committee on Problems of the Environment (SCOPE) held in 1982, identified that the invasive spread of organisms introduced by humans outside of their native ranges was a problem of global concern (Reichard and White 2003). In the period following this meeting, an important series of books and journal articles were produced on the topic. And it was largely from this foundation that the field of invasion science emerged as a discipline in its own right (Hui and Richardson 2017).

An important issue encountered in the field of invasion science is that researchers concerned with different taxa and different environments developed their science and the associated terminology, along parallel but independent lines. This has led to the use of synonymous terms for the same processes, and multiple definitions for the same term. There are also differences in how the process of invasion is described with regard to the taxon being studied. Consequently, different frameworks have been adopted across the different taxa and environments (Blackburn et al. 2011). This is probably most obvious in the approaches used in the study of plant and animal invasions. Plant biologists have commonly adopted the terminologies and frameworks of Richardson et al. (2000), while researchers undertaking studies of animal invasions have generally adopted the frameworks (or modifications thereof) first proposed by Williamson (1996).

The lack of agreement on usage of terminology has been acknowledged as bringing an added complication to an already challenging field (Blackburn et al. 2011; Lockwood et al. 2013; Pereyra 2016; Courchamp et al. 2017). In the last decade, there has been a strong push to align the terminologies and concepts used across different taxa and environments such as the terminology proposed by the IUCN Environmental Impact Classification for Alien Taxa (EICAT) (Hawkins et al. 2015). Perhaps a redeeming factor here has been that these scientists, whether dealing with plant invasions or animal invasions, come from fields that are strongly based in ecology and conservation biology. This has resulted in a strong common approach with regards to addressing the problem. It has clearly also assisted greatly in moving towards a common framework for studying plant and animal invasions, which has been achieved through the development of a "unified framework for biological invasions", developed by Blackburn et al. (2011). A similar effort to better align terminologies between the fields of invasion science and forest pathology has yet to be undertaken. Box 1 includes a number of terms for which varying definitions are applied by the two fields.

Recognition of invasion science by forest pathologists

The term "invasion" was first linked with a forest pathogen by Weste and Taylor (1971), to describe the development of disease following the establishment and spread of *Phytophthora cinnamomi* in the Brisbane Ranges of Australia. It was not until the early 2000s, however, that "invasive" and variations thereof, were more widely applied to forest pathogens, e.g. *Phytophthora lateralis* Port Orford Cedar root rot (Jules et al. 2002), *Phytophthora kernoviae* (Brasier et al. 2005). The continued introduction of economically and environmentally damaging forest pathogens and their establishment in novel areas has highlighted the need for forest pathologists to look to invasion science for insights on how to better understand the processes leading to invasion and spread of IFPs (Brasier 2008; Loo 2008; Santini et al. 2013; Scott et al. 2019).

A rising interest and acknowledgment of the importance of invasion science as a concept relevant to forest pathology is reflected in the uptake of the use of the term "invasive", or variations thereof, in contemporary publications by forest pathologists. To provide a view of how this has changed in recent years, we conducted a search using the Web of Science BIOSIS Citation Index^{SM} record data, for articles published between 1965 and 2019 that included the terms "forest", "pathogen" and "invas*". For comparison, we conducted searches for the same period using the terms "emerg*", "alien", "exotic" and "non-native", together with "forest" and "pathogen". The results are shown in Figure 1. Throughout the 1990s and early 2000s, there are few records for any combination of the terms. From this point, however, there is a marked increase in the use of the terms "invas*" and "emerg*", with steady increases also for "alien", "exotic" and "non-native". There is a continued increase in records including the terms

Box 1. Terminology used in this review.

Alien/non-native/non-indigenous/exotic/foreign – An organism (species, subspecies or lower taxon) transported outside of its native range, either intentionally or unintentionally by human agency.

Native/indigenous – An organism that has evolved in a given area or that arrived there by natural means, without human intervention.

Endemic – An organism occurring naturally only in a particular geographic region. In a pathology context, endemic may also refer to a pathogen (or resulting disease) that is characteristic of a particular population, environment or region (i.e. it is permanently established).

Cryptogenic – Taxa deemed to be alien, but without definitive supporting evidence.

Invasibility – The properties of a community, habitat or ecosystem determining its inherent vulnerability to invasion by alien organisms.

Invasiveness – The traits of an organism e.g. life-history traits and modes of reproduction, that determine its ability to invade, i.e. to overcome the barriers to invasion.

Invasion process – A series of stages (transport, introduction, establishment, and spread) through which an organism must pass before it is considered invasive.

Invasive alien species (IAS) – A self-sustaining (naturalised/established) population of a species accidentally or intentionally introduced by human actions, to an area outside of their native geographic range, into an area where they are not naturally present. While not all definitions include impact, others specify IAS cause, or are likely to cause, socio-cultural, economic, or environmental harm or harm to human health.

Emerging alien species – An organism whose incidence or geographical distribution is increasing notably, or a newly introduced or newly described species. The causes of emergence may be multiple and complex, but it is generally accepted that human activities (e.g. accidental introduction, modifications of land use) play an important role (Seebens et al. 2018).

Emerging Infectious Disease – An infectious disease appearing in a population for the first time, or that may have existed previously but is rapidly increasing in incidence or geographic range (WHO: https://apps.who.int/iris/handle/10665/204722; Ogden et al 2019).

Invasive forest pathogen (IFP) – A pathogenic microorganism (a species, subspecies, race, or forma specialis) introduced by human actions to an area outside its natural distribution, where it behaves as an agent of disease on native or alien trees or shrubs.

Epidemiology – The study of the spatial and temporal changes occurring during epidemics caused by populations of pathogens in populations of hosts, under influences of the environment – in short, how disease develops in populations.

Naturalised – A self-sustaining population of an intentionally or unintentionally introduced alien species that has adapted to, and reproduces successfully, in its new environment. The term established has been used synonymously.

Spill-over – A concept first proposed for animal pathogens, to describe the process of pathogen transmission from a reservoir population with a high pathogen prevalence, to a novel host population with which it has come into contact (Daszak et al. 2000). The concept has also been defined as “cross-species transmission of disease without the establishment of a self-sustainable population onto the new host” (Giraud et al. 2010).

Spill-back – If an alien species is a competent host for a native pathogen/parasite, the population of the pathogen/parasite builds up on this host and “spills-back” onto native hosts (Daszak et al. 2000).

Host-jump – From an evolutionary perspective, it is defined as “a colonisation of a new host species that leads to increasing genetic separation from the parent population until speciation is complete” (Thines 2019). In an ecological sense, refers to a pathogen moving from its coevolved host to a novel host, a situation facilitated by contact between previously geographically separated host species (e.g. host-jump from introduced host to native host in novel environment, or native microorganism jumping to introduced host). Also referred to as “host-shift”.

Hitchhikers – Within a forest pathology context, the term refers to microorganisms transported with asymptomatic plants, including pathogens. While “hitchhiker” has not been formally defined in the invasion literature, it has been used to describe species that are carried by chance or unknowingly, in relation to the “stowaway” pathway (Harrower et al. 2018). This pathway, however, precludes biological connection to the organism with which they are transported. The definition by forest pathologists would place it within the “contaminant” pathway of the Convention on Biological Diversity classification, however, there is no instance in the invasion terminology linking it to this pathway.

“invas*” and “emerg*”, and while “exotic” tracks these for a number of years, use of the latter three terms stabilises in contrast to the continued rise of “invas*” and “emerg*”. The results reflect the uptake of “invasive”, or variations thereof, by forest pathologists,

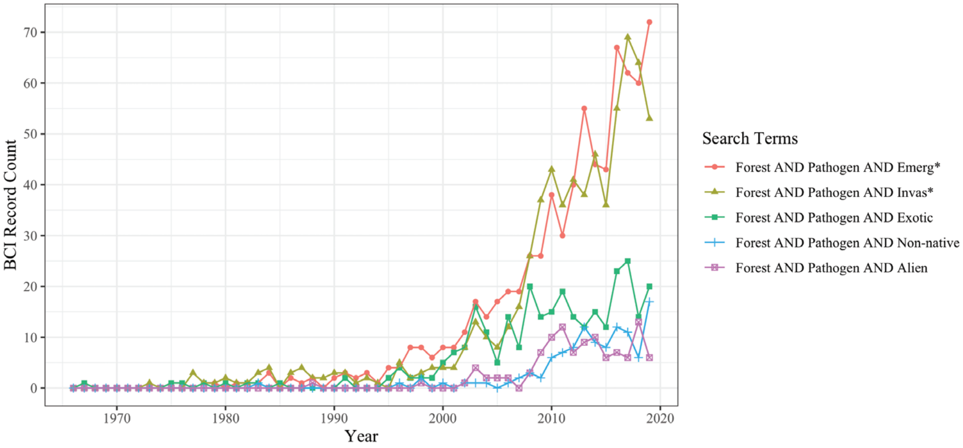

Figure 1. Number of record counts returned from a Web of Science search including the terms "forest" and "pathogen" together with the terms "invas*", "emerg*", "alien", "exotic" and "non-native", for the years 1965–2019.

but also demonstrate that "emerging" remains a relevant concept. It is appropriate for describing diseases caused by cryptogenic species, and is also the most appropriate term to apply to the growing number of instances where native microorganisms become disease-causing agents under global change. Also, of note is that invasion scientists have recently started using the term "emerging" to acknowledge the challenge of invasions by organisms not previously encountered as aliens (Seebens et al. 2018). The term "emerging alien species" is used to describe those that are detected as aliens for the first time, i.e. with no previous invasion history (Seebens et al. 2018), consequently, it is challenging to predict their impact and spread (Pyšek et al. 2020).

Policy and regulation

Although pathologists have only recently adopted the invasion vocabulary, regulations regarding introduced plant pests and pathogens predate those on invasive species, with the first international convention to inhibit the spread of plant pests signed in 1878 (MacLeod et al. 2010). This highlights the early recognition of the threat posed by alien pests and pathogens, to the extent that it justified the establishment of international regulations. However, policy and regulation remain an area where plant and animal invaders are treated in different conventions to plant pests.

Phytosanitary regulations in most countries are based on the International Plant Protection Convention (IPPC; https://www.ippc.int/about/convention-text) and the World Trade Organisation (WTO) Agreement of the Application of Sanitary and Phytosanitary Measures (SPS, http://www.wto.org/english/res_e/booksp_e/agrmntseries4_sps_e.pdf) (Eschen et al. 2015). The IPPC makes provision for international trade within a plant protection agreement, and aims to prevent and control the introduction and spread of pest organisms including weeds and invasive species, of plants, plant products, and wild plants, while the SPS provides for plant protection within a trade agreement (MacLeod et al. 2010). The current provisions have received criticism with regards to their ability to protect wildlife (including undomesticated plants), as the focus of the SPS and IPCC is largely on plants of economic importance (Dunn and Hatcher 2015; Roy et al. 2017). Further, a conflict of interest arises in that the primary aim of the WTO is to promote international trade rather than protect the environment, and the SPS aims to prevent countries from implementing protectionist trade barriers, to minimise the disruption plant health regulation might impose on trade (Brasier 2008; Dunn and Hatcher 2015).

The Convention on Biological Diversity (CBD) was established with the objectives of safeguarding biodiversity, ensuring its sustainable use, and equitable sharing of benefits from genetic resources. IAS are specifically addressed in the CBD Aichi Biodiversity Target 9: "By 2020, invasive alien species and pathways are identified and prioritised, priority species are controlled or eradicated, and measures are in place to manage pathways to prevent their introduction and establishment" (http://www.cbd.int/sp/targets/). While the IPPC and the CBD share some common ground and seek to find ways to cooperate (MacLeod et al. 2010), Roy et al. (2017) highlight the underrepresentation of pathogens in alien species regulation, and suggest the threats posed by alien pathogens (including IFPs) should receive greater attention by CBD Parties, to fully address the requirements of Aichi Target 9.

Outdated paradigms

There is a perception amongst some invasion scientists that forest pathology does not fit in studies of invasion biology because it is not related to the ecology of natural ecosystems. While this view may be somewhat appropriate for pathology conducted in agriculture or commercial forestry, not all forest pathology is conducted in this setting. There are also many situations where plantations are established adjacent to native forests accommodating related hosts, as is commonly found for *Eucalyptus* plantation forestry (Burgess and Wingfield 2017). Invasion scientists work within a paradigm focussed on native ecosystems, and while a large body of research on invasions applies to natural areas, not all IAS affect natural ecosystems, and urban areas are particularly vulnerable to the establishment of IASs (Cadotte et al. 2017; Paap et al. 2017a; Potgieter et al. 2020). In addition to aiding the introduction and establishment of IASs, urban areas may also act as bridge-heads from which invasive species may spread out of cities (Paap et al. 2017a; Reed et al. 2020; Potgieter and Cadotte 2020). It can be argued that until the 1980s, biological invasions by plants and animals were considered as confined to anthropogenically disturbed areas. One of the working groups of the SCOPE programme on ecology of biological invasions was specifically tasked to address invasions in nature reserves, asking 'Can an undisturbed community be invaded by introduced species?' (Usher 1988). It is only in more recent years that a shift has occurred towards studying invasions in natural environments (Foxcroft et al. 2017).

Many forest pathologists, even contemporary ones, have come from a classical plant pathology background, as opposed to one focussed on forestry or ecology. Consequently, their studies have had a stronger focus on local and micro-processes, on individual organisms and their interactions, and on finding immediate solutions to the problem, rather than embracing a more ecological approach (Wingfield et al. 2017). While many studies conducted into tree declines and tree diseases are based on the disease triangle or tree decline spiral, and are therefore less micro-process focused (Dukes et al. 2009; Ramsfield et al. 2016; Stenlid and Oliva 2016; Ghelardini et al. 2017), greater collaboration between invasion scientists and forest pathologists should be encouraged, especially in the Southern Hemisphere. Where such collaborations have been undertaken, greater insights into the dynamics of pathogen invasion have been identified (e.g. Soubeyrand et al. 2018).

Emerging forest diseases vs invasive forest pathogens

As previously noted, when investigating a new forest disease, it is not always immediately obvious whether the outbreak results from the arrival of an alien pathogen, or is driven by environmental change. The term “emerging” does not require knowledge of the alien status of the causal agent, and encompasses the range of scenarios under which diseases of trees can develop. This includes damaging host-jumps that may occur following the establishment of an alien host. A notable example is that of *Austropuccinia psidii*. This rust fungus jumped from native Myrtaceae in its natural range in South America to introduced *Eucalyptus* (Coutinho et al. 1998; Glen et al. 2007). Disease may also emerge where an environmental barrier is lifted e.g. habitat disturbance or climate change leading to a native microorganism causing disease on a coevolved native host (Paap et al. 2017b, 2018).

Where disease establishes as a result of the introduction of an alien pathogen, this may be on either a native or alien host, or both. In some instances, this constitutes “pathogen reunion”, i.e. an alien pathogen arrives and establishes on a coevolved alien host, e.g. *Teratosphaeria nubilosa*, translocated with *Eucalyptus* trees, causing leaf blotch in plantation forests of South Africa (Hunter et al. 2008). Here, the novel environment together with monoculture plantings are conducive to disease development. An IFP may also establish on a naïve host which is alien to the invaded region e.g. *Fusarium circinatum*, causal agent of pine pitch canker, a devasting disease of plantation *Pinus* in South Africa (Wingfield et al. 2008). This fungus causes disease on *Pinus* spp. and with no congeners present in South Africa, has never jumped to native hosts. Lastly, there is the scenario of IFPs causing disease on native hosts, represented by some of the best-known forest diseases such as Dutch elm disease and chestnut blight. The challenge presented with regards to determining origins of disease-causing agents, as outlined in the above scenarios, has likely been a contributing factor to the historical underrepresentation of IFPs in invasion science.

Recognition of alien status

Thousands of years of movement of plants, and with them the movement of microorganisms, has led to a situation where many pathogens are viewed as having cosmopolitan distributions i.e. naturalised (Santini et al. 2018). This is especially the case for agricultural crops. Historically, there has been less movement of forest trees than crop plants. But, with increasing international trade, especially the movement of plants for planting, and the growing use of planted forests, this situation is changing and resulting in increasing threats and challenges. However, the biogeography of most fungi (and microorganisms in general) remains largely unknown. The absence of such baseline data means that when a new disease emerges, it must be determined whether this is due to the arrival of an alien species, a host-jump by a native species to an alien planted host, or the result of a native pathogen that has evolved increased virulence or been favoured by changing environmental conditions. As such, assigning alien status is often challenging (Desprez-Loustau et al. 2010). For example, *Diplodia sapinea*, is an important pathogen of pines, causing various symptoms including shoot blight, canker, tip dieback, cone infections and blue stain (Swart and Wingfield 1991). It was first described in Scandinavia in 1822, but has a worldwide distribution and has caused disease losses in all pine plantation areas of the Southern Hemisphere, as well as in the USA, China and Europe (Desprez-Loustau et al. 2006). Some species of pine may suffer severe damage in non-native plantations, with the same species only being marginally affected in their natural range. *Diplodia sapinea* is present as a latent pathogen in healthy tissues (Bihon et al. 2011), with the incidence and severity of disease strongly correlated with stress factors (Swart and Wingfield 1991). It is probable that it was introduced to many regions with the movement of host material (Burgess and Wingfield 2002). Despite its global distribution and increasing importance under changing climatic conditions, and numerous population genetic studies using microsatellite markers (Brodde et al. 2019; Müller et al. 2019), the origin of *D. sapinea* remains unknown.

The problem of assigning alien status is exacerbated by the vast diversity of microbial taxa, their cryptic and inconspicuous nature, and our resultant poor knowledge of microbial communities. For example, the number of fungal species on earth is unknown, but estimates range from 1.5 to several million, the majority of which have not yet been described (Crous et al. 2015; Hawksworth and Lüking 2017). The lack of 'visibility' of microorganisms has been repeatedly provided as the reason for their absence from invasion science (Desprez-Loustau et al. 2007; Sakalidis et al. 2013; Wingfield et al. 2017; Thakur et al. 2019). Most IFPs remain undetected until visible negative impacts are observed within the recipient environment. In addition to the long lag times between arrival and detection, a diagnostics stage is required. The organism must be isolated, identified and Koch's postulates (proof of causality) fulfilled, to definitively determine the causal agent. By the time the disease problem is noticeable, and the causal agent diagnosed, the pathogen is often well established. This complicates management, and makes IFPs very difficult to contain, let alone eradicate, particularly once they have established in natural environments. For example, the present outbreaks of *Xylella fastidiosa* ssp. *multiplex* in Europe have been much more challenging to manage in the natural Maquis environment where it has a wide host range, than *X. fastidiosa* ssp. *pauca* in commercial olive groves (CoDiRO, Olive Quick Decline Syndrome) (Landa et al. 2020). Another classic example is the impact of the 'biological bulldozer' *P. cinnamomi* in Australia. Management of this pathogen presents greater challenges in natural ecosystems (Dunstan et al. 2010) than in avocado and other crop plants (Drenth and Guest 2004; Ramírez-Gil et al. 2017).

Microorganisms, including IFPs, have in part been overlooked in invasion science because of the vast diversity of taxa and problems relating to naming of organisms (e.g. Cowan et al. 2013; Hawksworth and Lücking 2017). For perspective, the phylogenetic "distance" amongst species of a single yeast genus, *Saccharomyces*, is equivalent to that between all of the known mammals and birds (Dujon 2006). This is before even considering other fungi, let alone the diversity amongst bacteria, viruses and oomycetes. It would be naïve to not acknowledge that within this vast diversity of organisms, very different biological strategies must exist for microbial invaders. This is in contrast to the move to unify into a single treatment the frameworks for studying all invasions, and it potentially dilutes our ability to address these invasions effectively (Wingfield et al. 2017). For example, Burgess and Wingfield (2017) identified seven different scenarios to account for how diseases of one genus, *Eucalyptus*, have moved and established within Australia and globally. Consequently, a framework for IFPs requires a nuanced approach to accommodate the overarching role of the environment in the outcome of novel interactions between hosts and pathogens.

A further confounding factor faced by forest pathologists is the challenge of accurate identification of microorganisms. Only in the last 30 years has there been a shift from the use of morphology-based to evolutionary biology-based species concepts (Harrington and Rizzo 1999; Taylor et al. 2000). Recent developments in molecular technologies and phylogenetic analysis have facilitated species identification at a much higher resolution than that based on morphology. There are now many examples of morphologically identical cryptic species that, without the application of DNA sequencing techniques, would never have been delineated as different species. For example, it was originally thought the pathogen causing cankers of *Eucalyptus* in South Africa belonged to the same genus as the fungus devastating chestnuts, *Cryphonectria parasitica*. It has since been determined, through the use of DNA-based technologies, that the disease on *Eucalyptus* can be caused by four different species, all belonging to the distantly related genus *Chrysoporthe* (Gryzenhout et al. 2004).

Name-based biosecurity will remain challenging for microorganisms. Disagreements regarding definitions of species present a confounding factor, and genetic diversity in microbe populations (with various genetic strains or mating types showing variation in virulence or host range) cannot be accounted for under a name-based approach (McTaggart et al. 2016). Rapid molecular diagnostics (Luchi et al. 2020), advances in high throughput sequencing (Hamelin and Roe 2019) and studies of microbial diversity in poorly explored ecosystems (Tedersoo et al. 2014; Desprez-Loustau et al.

2016) are areas of research with the potential to enhance our ability to better predict and prevent future invasions, and should continue to be pursued.

While there is an obvious lack of knowledge regarding the biodiversity, ecology, speciation and geographic origin of many IFPs, of all the categories of microorganisms, pathogens (including IFPs) are amongst those most widely studied. Information concerning the status (native or alien) is even less known for many other groups of microbes. The impacts of non-pathogenic microorganisms, including endophytes, saprophytes and mycorrhizal fungi, are less apparent than those of pathogens. Despite this, these microorganisms may still affect important ecosystems functions, and likely play an important role in facilitating invasions by other taxa. There has been a growing acknowledgement of the importance of studying and understanding these invasions (see Desprez-Loustau et al. 2007; Litchman 2010; Gladieux et al. 2015; Crous et al. 2016; Dickie et al. 2017; Thakur et al. 2019).

Towards a framework for forest pathogens

Within the discipline of invasion science, researchers studying different taxonomic groups and different environments have developed separate ways of investigating IASs. There have been efforts to reconcile these differences (see Blackburn et al. 2011; Gurevitch et al. 2011; Thomsen et al. 2011), however, forest pathologists (even more broadly microbiologists) are generally absent as authors from the literature in which the frameworks most widely used for studying invasions have been proposed. For example, the Blackburn et al. (2011) unified framework is predominantly focussed on animal and plant invasions. Wingfield et al. (2017) presented a response to this framework from a forest fungal pathogen perspective, highlighting the important issues relevant to understanding invasions by IFPs. Furthermore, how these are poorly understood and typically poorly considered in general invasion science literature. IFPs are essentially a subset of IASs (microorganisms causing disease on woody plants), and a subset of EIDs (those that establish by human mediated introduction). The terminology and frameworks of EIDs (e.g. Hatcher et al. 2012; Dunn and Hatcher 2015) and IASs (e.g. Blackburn et al. 2011) should thus both be explored to inform our understanding of the invasion process of forest pathogens. While microorganisms present a unique set of challenges with regard to being understood as IAS, acknowledging these challenges will assist in modifying frameworks to accommodate IFPs.

Microorganisms as invaders

Where microorganisms have been considered by invasion scientists, e.g. Blackburn and Ewen (2017), the focus has often been on microorganisms as "drivers" or "passengers" of invasions, rather than as invaders in their own right. Many types of microorganisms play crucial roles in alien plant invasions (Traveset and Richardson in press). For example, the novel weapon hypothesis (NWH), proposed by Price et al. (1986), suggests that when an alien host arrives with a coevolved benign organism (e.g. endophyte or latent pathogen), such an alien organism may infect native host species in the recipient environment. If the organism negatively impacts the native host to a point where it is considered to have increased the likelihood of its alien host's establishment, then it can be considered a novel weapon.

Within the field of infectious diseases, the process by which a coevolved organism infects a novel host may be viewed as a type of "spill-over". The concept was developed within the context of animal and human pathology (Daszek et al. 2000), however, has subsequently also been applied to plant pathogens (Power and Mitchell 2004; Blitzer et al. 2012). Spill-over may, however, occur independently of conferring advantage to the alien host, and is thus not strictly linked to the NWH. For example, the invasion by the chestnut blight pathogen, *C. parasitica*, devastated American chestnut populations, but did not favour the invasiveness or facilitate the establishment of Asian chestnut species with which it arrived. In forest pathology the mechanism by which microorganisms arrive as "hitchhikers" on asymptomatic germplasm, and move to novel hosts (as a result of human-mediated introductions) has rather been considered under the term "host-jump" (Slippers et al. 2005; Burgess et al. 2016).

Pathways of introduction

The introduction of microorganisms (including IFPs) to novel regions generally occurs via the two categories of unintentional transport: "contaminant" and "stowaway", as classified in the Convention on Biological Diversity categorisation of pathways of introduction (CBD 2014). Within this categorisation, it is specified that organisms transported as contaminants interact directly with the commodity, while stowaways use a vector to move between locations, without interacting with this vector (Harrower et al. 2018). Putative pathogens such as those belonging to the genus *Phytophthora* may be transported with potted plants (Migliorini et al. 2015), either as stowaways (present in the soil but without interacting with the plant), or as contaminants (should they be biologically linked to the plant). They may also be transported via more obscure means, such as stowaways in soil transported with traded used cars (Ridley et al. 2000). The term "hitchhiker" is used by forest pathologists to refer to microorganisms transported with asymptomatic plants, which would align it with the "contaminant" pathway – specifically the sub-category "parasites on plants" (Burgess et al. 2016). However, the term "hitchhiker" in invasion science, precludes biological connection to the organism with which they are transported, and only occurs in the "stowaway" category. Further, the use of the term "contaminant", is arguably inappropriate for microorganisms present as endophytes or in other symbiotic relationships with their hosts. Despite the efforts to accommodate IFPs in the CBD pathway categorisation, there is a need to better harmonise the terminologies used in the two fields (cf. Faulkner et al. 2020 for a broader critique of the CBD pathway categorisation).

Impacts

Studies of impacts of IFPs have often focussed on effects on other trophic levels (e.g. the impacts of *Phytophthora cinnamomi* on vegetation structure), as this is where negative impacts are most readily observed (Desprez-Loustau et al. 2007). The impacts of IFPs on microbial communities is a deeply understudied area. One example illustrating the potential for impacts at the same trophic level comes from studies of the invasion by the aggressive IFP *Hymenoschyphus fraxineus* (causal agent of ash dieback). Following invasion, *H. fraxineus* replaces the native decomposer *H. albidus* (McKinney et al. 2012). Another interesting example is the new invader *Ophiostoma novo-ulmi* completely replacing the less aggressive and old invader *Ophiostoma ulmi* in Europe (Brasier 1998). Thakur et al. (2019) proposed a "network" approach to provide a better understanding of interactions among species at different trophic levels, following establishment of alien microorganisms. Monitoring such interactions over long time scales will enhance our ability to understand the dynamics and impacts of IFPs on hosts, communities and ecosystems (Thakur et al. 2019).

Examining the long-term impacts of invasions e.g. level of impact, extent and rate of spread, may provide insights into pathogen or environment traits linked to the outcome of the invasion. A well-documented example is that of oak powdery mildew in Europe. Desprez-Loustau et al. (2019) describe the ecological and evolutionary trajectory of this pathogen complex over the course of a century. This, from its initial impact characterised by severe damage typical of pathogen invasion dynamics (with disease epidemics resulting in tree mortality), to the current equilibrium between host and pathogen, which has resulted in decreased disease severity. Desprez-Loustau et al. (2019) utilise a modelling approach to investigate the eco-evolutionary dynamics of the oak powdery mildew pathosystem, and highlight the value of such systems to explore the evolution of virulence and resistance following invasions, in the context of changing environments.

A consolidated effort is required to move from studies of interactions between individual species to those at the community level. Perhaps this can be achieved by the network approach proposed by Thakur et al. (2019), or through landscape epidemiology, a recently developed field that merges concepts of disease epidemiology with landscape ecology (Holdenrieder 2004; Lundquist and Hamelin 2005; Meentemeyer et al. 2012). This discipline links molecular and microbial observations of disease distribution with measurements of biotic and abiotic conditions, incorporating spatiotemporal complexity in epidemiological systems at the landscape level. Further, Oliva et al. (2020) proposed the development of a functional ecology approach to forest pathology, focussing on building functional trait databases to assist forest pathologists in dealing with the increasingly complex problems posed by forest pathogens under global change.

Eradication feasibility

There are numerous examples of successful eradication of plant pathogens from man-made settings, particularly in controlled environments such as greenhouses (Pluess et al. 2012). However, eradication of established IFPs in natural ecosystems is incredibly challenging, and the few successful cases of IFP eradication known globally were achieved prior to spread into natural ecosystems. For example, fire blight is a destructive and highly infectious disease of apples, pears and other members of the family Rosaceae, caused by the bacterium *Erwinia amylovora*. In 1997, fire blight was detected in Australia, at the Royal Botanic Gardens, Melbourne (Jock et al. 2000). Following this detection, an intensive eradication and surveillance programme was undertaken, leading to successful eradication (Rodoni et al. 2006). *Fusarium circinatum*, a fungal pathogen that causes pitch canker disease of pine (Gordon 2006; Wingfield et al. 2008), is considered to be one of the most important pathogens affecting *Pinus* seedlings and mature trees in many countries. *Fusarium circinatum* outbreaks have been officially eradicated in France and Italy, with the success of the eradication efforts attributed to early detection, constant surveillance and control measures (Vainio et al. 2019). In each of these examples, eradication was likely only possible due to detection in the very early stages of establishment, with outbreaks confined to urban environments such as gardens, parks and nurseries. The earlier diseases are detected, and management interventions initiated, the greater the likelihood that eradication or containment measures will be successful, and at lower economic and environmental cost (Luchi et al. 2020).

The examples of the fire blight and pitch canker diseases were of pathogens well-known elsewhere in the world. Consequently, they were relatively easily recognised when they first appeared and techniques and tools for identification were well-established, facilitating rapid diagnostics. This is very different in the case of tree diseases of unknown cause such as pine wilt caused by the pine wood nematode (*Bursaphelenchus xylophilus*), or sudden oak death caused by *P. ramorum*; both took many years, in the former case decades, before the causal agents became known (Mamiya 1983; Fielding and Evans 1996; Werres et al. 2001). A recent example demonstrating the issues arising from knowledge gaps in fungal diversity, exacerbated by limited surveillance, is that of ash dieback in Europe. The first reports of dieback were from Poland in the early 1990s; however, it was not until 2006 that the cause of mortality was found to be a biotic agent, *Chalara fraxinea* (Pautasso et al. 2013). Initially, this anamorphic fungus was linked morphologically to a saprotrophic leaf colonising ascomycete, *Hymenoschyphus albidus*. This species was long known in Europe, but not as a fungus causing disease. Only five years later did molecular investigations show the teleomorph of *C. fraxinea* was actually a previously undescribed cryptic species (Queloz et al. 2011), the IFP *H. fraxineus*. This long delay in recognising the alien origin of the fungus precluded its inclusion in quarantine lists. By the time its alien status was recognised, the pathogen and resulting ash mortality had already reached many other European countries.

Horizon scanning

There are many examples of IFPs that were not known to cause disease, and others even unknown to science, prior to their establishment in a novel environment (Brasier

2008; Wingfield et al. 2015). This lack of baseline information presents major challenges with regards to predicting the next microbial invader, and constrains our ability to undertake pest risk analysis (Roy et al. 2017). Horizon scanning (systematic examination of potential threats and opportunities) presents an opportunity to prioritise actions and identify knowledge gaps (Roy et al. 2017). The IUCN Environmental Impact Classification for Alien Taxa (EICAT) is a horizon scanning tool developed as an objective framework for the assessment of all taxa (Hawkins et al. 2015; Kumschick et al. 2020). Mechanism 5 of the framework provides for classification of impact by parasites and pathogens, however, the framework has, to the best of our knowledge, not yet been applied to any IFPs, either by forest pathologists or invasion scientists.

Eschen et al. (2019) proposed the concept of *ex-patria* sentinel plantings (sentinel plantations), i.e. species native to a plant importing continent growing in an exporting one, monitoring these plants can lead to the identification of novel pathogen-host associations; and of *in-patria* sentinel plantings (sentinel nurseries), i.e. species native to the exporting continent, growing in their own continent. Identification of native pest-host associations provide information for the risk of introducing harmful organisms through the trade of plant commodities. Such efforts contribute relevant information to gap fill pest risk analysis, and can aid the development of measures to mitigate introduction risks (Britton et al. 2010; Eschen et al. 2019).

Conclusion

The paucity of knowledge for many aspects of microorganisms has presented challenges to understanding them as IASs, and has likely led to their underrepresentation in the invasion science literature. Advances in molecular techniques have provided powerful tools with which to study IFPs. This arises as techniques make it possible to identify pathogens more easily and accurately, greatly enhancing our knowledge of these organisms and their biogeography and ecology. Hamelin and Roe (2019) and Luchi et al. (2020) provide comprehensive reviews of advances in molecular methods and genomic tools, and their potential applications for bio-surveillance. However, forest pathologists need to be sure to ask the appropriate questions, if they are to adequately apply these tools, and this relies on an understanding of ecology (Zinger et al. 2019).

Technologies are advancing rapidly, and are commonly ahead of available knowledge of the pathogen systems being studied. Consequently, there is a risk for incorrect assumptions to be made due to poor sampling strategies (Zinger et al. 2019). Thus, forest pathologists should more actively apply ecological concepts to the pathosystems they study. High-throughput molecular techniques may contain sequencing errors, lack of replication, experimental contamination and PCR (primer) induced biases are all potential pitfalls requiring consideration (Dickie 2010; Zinger et al. 2019). There are, however, now a number of examples where newly developed molecular tools have been successfully utilised to investigate pathways of introduction and spread of IFPs (e.g. Dutech et al. 2012; Garbelotto et al. 2013; Gross et al. 2014; Landa et al. 2020).

Trees live for very long periods and can be exposed to pathogens over their lifespan. They establish complex interactions among both beneficial and detrimental microorganisms including those that make up their microbiomes (Kemler et al. 2013; Thompson et al. 2017). Therefore, a more ecological, rather than a purely mechanistic approach, needs to be applied to the study of tree pathosystems. Equally, the role of microorganisms as invasives, as well as in influencing the invasibility of environments, must become an area of research focus within invasion science. In addition to the arrival of IFPs, the health and resilience of forest ecosystems worldwide is being impacted by global change factors including climate and land use change and increased pollution. The effects of forest disturbances (wildfires, droughts, storms, pest and pathogen outbreaks) will be altered under these conditions, with the potential for increased vulnerability to IFPs. A rise in complex diseases and tree declines under global change is a major challenge facing forest pathologists (Anderson et al. 2004; Desprez-Loustau et al. 2006; Pautasso et al. 2015; Trumbore et al. 2015; Ghelardini et al. 2016).

Invasions by pathogens into forest ecosystems lead to the decline and loss of keystone species, resulting in irreversible impacts. By not using the terminology of invasion science, and by remaining disconnected from the frameworks developed and used to study biological invasions, much of the work of forest pathologists has been ignored by the wider invasion science community. Aligning terminologies and experimental designs with those utilised by invasion scientists will allow forest pathologists to reach a larger audience, in turn generating opportunities for collaboration.

For well-studied pathosystems, forest pathologists have a deep understanding of the biology of the organisms they work with. This adds layers of complexity, but also allows for more nuanced explanations. The disease triangle is a central component of plant pathology, illustrating the interactions between a host, a pathogen, and an environment – the three key aspects determining the extent to which disease will develop. This approach may also bring benefits to invasion ecology. For example, Perkins et al. (2011) proposed an adaptation in the form of the invasion triangle, incorporating the three components – the invader, site biotic characteristics, and environmental conditions of the site, as a tool for understanding and predicting why species are invasive in specific environments.

Microorganisms are gaining greater attention in the field of invasion science. As noted by Ricciardi et al. (2017), microbial ecology is becoming increasingly relevant to understanding and managing invasions. These organisms cannot be ignored. They constitute important components of all ecosystems, and are a vital part of community ecology and ecosystem functioning, as well as representing an important component of IASs. In the same way that disturbance may facilitate invasions (Wilson et al. 2020), IFPs play a considerable role in modifying ecosystems. And where a native forest species is functionally eliminated from an ecosystem following the establishment of a high impact IFP, an empty niche remains, with the potential for this to be filled by an alien plant species.

There has been a recent call for pathologists and entomologists to work together in response to the rising threat to forests posed by invasive pests and pathogens (Jactel et al.

2020). The authors argue that while traditionally considered separate disciplines, many tools and conceptual frameworks underpinning pathology and entomology can and should be shared, to meet the common goal of improved forest protection. Similarly, Nunez et al. (2020) proposed the strengthening of collaborations between ecologists, epidemiologists, sociologists, and biomedical researchers, to develop an expanded invasion science discipline (see also Hulme et al. 2020). Such an approach, embedded in the philosophy of the "One Health" concept recognising the interrelatedness of human, animal and ecosystem health (Xie et al. 2017), has the potential to make meaningful contributions to global biosecurity.

Against this background, a unified framework inclusive of IFPs should be designed. This should incorporate the basis of existing frameworks but also acknowledge and accommodate their shortfalls. This approach will facilitate the establishment of a more inclusive and a truly unified framework in the future (Wilson et al. 2020b). Clearly, the continued promotion and application of multiple disciplinary approaches to forest pathology and invasion science research is critical, if we are to adequately understand and address the complex challenges of identifying and managing forest pathogen invasions.

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Applying the Convention on Biological Diversity Pathway Classification to alien species in Europe

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Abstract

The number of alien species arriving within new regions has increased at unprecedented rates. Managing the pathways through which alien species arrive and spread is important to reduce the threat of biological invasions. Harmonising information on pathways across individual sectors and user groups is therefore critical to underpin policy and action. The European Alien Species Information Network (EASIN) has been developed to easily facilitate open access to data of alien species in Europe. The Convention on Biological Diversity (CBD) Pathway Classification framework has become a global standard for the classification of pathways. We followed a structured approach to assign pathway information within EASIN for a subset of alien species in Europe, which covered 4169 species, spanning taxonomic groups and environments. We document constraints and challenges associated with implementing the CBD Pathway Classification framework and propose potential amendments to increase clarity. This study is unique in the scope of taxonomic coverage and also in the inclusion of primary (independent introductions to Europe) and secondary (means of dispersal for species expansion within Europe, after their initial introduction) modes of introduction. In addition, we summarise the patterns of introduction pathways within this subset of alien species within the context of Europe.

Based on the analyses, we confirm that the CBD Pathway Classification framework offers a robust, hierarchical system suitable for the classification of alien species introduction and spread across a wide range of taxonomic groups and environments. However, simple modifications could improve interpretation of the pathway categories ensuring consistent application across databases and information systems at local, national, regional, continental and global scales. Improving consistency would also help in the development of pathway action plans, as required by EU legislation.

Keywords

accidental introduction, alien species, deliberate introduction, pathways, secondary spread

Introduction

Over the last decade, there has been considerable improvement in understanding macro-ecological determinants of biological invasions (Pyšek et al. 2020b), their impacts (Vilà et al. 2011; Hulme et al. 2013; Katsanevakis et al. 2014; Kumschick et al. 2015; Galanidi et al. 2018; Bradley et al. 2019; Magliozzi et al. 2020) and their management (e.g. Robertson et al. 2020; Csiszár and Korda 2017; Dufour-Dror 2013). Increasing availability of regional inventories of alien species has been instrumental for testing invasion theories and hypotheses at local, national, regional, continental and global scales, all with the shared ambition to provide macroecological generalisations, for instance across taxonomic groups, environments and habitats (e.g. Pyšek and Richardson 2010, Pyšek et al. this volume). For Europe, the compilation of information on more than 12 000 alien species from a wide range of taxonomic groups, through the EU-funded project Delivering Alien Species Inventories for Europe (DAISIE 2009; hereafter called the DAISIE project; data now available on GBIF, www.gbif.org), has been the basis of many broad scale analyses. This also includes the accumulation rates of alien species over time (Hulme et al. 2009) and the role of past and present environmental and economic factors in determining regional alien species richness (Pyšek et al. 2010; Essl et al. 2010) or interplay of invasions and extinctions leading to the homogenisation of regional floras (Winter et al. 2009). The DAISIE project and its database, have subsequently contributed to assessments at the global scale, including analyses of trends of increase of naturalised species (Seebens et al. 2017) and distribution patterns of alien species across the globe (van Kleunen et al. 2015; Dawson et al. 2017; Pyšek et al. 2017).

It has been repeatedly suggested that one of the most effective strategies to prevent new introductions of invasive alien species (IAS) and, hence, to limit future costs to society and protect biodiversity and ecosystems, is through the management of major (or "priority") pathways and corresponding vectors (Carlton and Ruiz 2005; Hulme 2009; Pyšek and Richardson 2010; Ojaveer et al. 2018; Tsiamis et al. 2020). Information on the native range of the species and pathways of introduction often accompany checklists of alien species (e.g. Garcia-Berthou et al. 2005; Nentwig 2007; Minchin et al. 2013; Katsanevakis et al. 2015). Therefore, this represents an opportunity to assess and compare the relative importance of pathways across environments and taxa (Wilson et al. 2009; Liebhold et al. 2012; Essl et al. 2015). The probability of an alien species having impact increases with the number of pathways and some pathways are associated with introduction of more impactful alien species than others. As an example, plants introduced as contaminants are disproportionately less likely to have ecological impacts than those introduced through other pathways (Pergl et al. 2017). Pathway management is aimed at diminishing the propagule pressure of alien species (Lockwood et al. 2005, 2009; Simberloff 2009) and reflects the common wisdom that prevention and early action are more cost-effective than dealing with the consequences of introduction/invasion (Kaiser and Burnett 2010; Pluess et al. 2012).

Acknowledging the importance of assessing patterns in pathways where alien species arrive within new regions (primary introductions) or their spread following introduction (secondary spread), a standardised pathway terminology and hierarchical classification was proposed (Hulme et al. 2008). This framework has been extensively used in various studies assessing variation in pathways of introduction across different environments, taxonomic groups and ecological impacts (Katsanevakis et al. 2013; Essl et al. 2015; Roques et al. 2016; Pergl et al. 2017). Notably, the Hulme et al. (2008) classification formed the basis for the Convention on Biological Diversity (CBD) Pathway Classification framework (2014; https://www.cbd.int).

The DAISIE database, including the records of impact, pathways and associated references, was added to the European Alien Species Information Network (EASIN; Gatto et al. 2013). EASIN (https://easin.jrc.ec.europa.eu/easin) has been developed by the European Commission's Joint Research Centre (JRC; Katsanevakis et al. 2012) and supports the implementation of Regulation (EU) no. 1143/2014 on Invasive Alien Species (European Union 2014; Genovesi et al. 2015, hereafter referred to as the EU IAS regulation). EASIN initially adopted the pathway classification framework proposed by Hulme et al. (2008) and classified the pathways of the alien species included in the EASIN catalogue through members of its Editorial Board (Katsanevakis et al. 2015; Nunes et al. 2015; Tsiamis et al. 2016).

Successively, a new unified system to categorise introduction pathways of alien species was proposed by the CBD (2014) through the document UNEP/CBD/SBSTTA/18/9/Add.1 to improve the understanding of the most relevant vectors (agents that transport the alien species such as trains, containers, ships etc.) and activities of introduction of alien species. The CBD Pathway Classification framework has since become a standard for pathway terminology, which is a key requirement for interoperability and harmonisation of databases (Groom et al. 2017, 2019), risk analysis and large-scale studies (Pergl et al. 2017; Saul et al. 2017; Deriu et al 2017; Tsiamis et al. 2018; Korpinen et al. 2019), but unfortunately, there is a paucity of available information on pathways of introduction from continents other than Europe. The CBD Pathway Classification framework distinguishes pathways as either intentional or unintentional introductions or, alternatively, unaided spread of alien species. Correspondingly, these broad pathways are divided into six categories: Release; Escape; Transport – contaminants; Transport – stowaway; Corridors; and Unaided. As the level of detail required in pathway classification depends on the management goal (see Essl et al. 2015), a number of subcategories are used. The subcategories follow some of the associated economic uses, but some important areas are merged together (e.g. 'contaminant on animals' includes both contaminated animal products in the trade of fur, leather and wool and also the trade of living animals). A user-friendly technical guide to apply the CBD Pathway Classification framework, including detailed definitions with illustrative examples for assigning the different pathway subcategories, was developed (Harrower et al. 2017).

A number of pathways associated with the introduction of alien species have been well-documented. These include the ornamental horticultural trade (Dehnen-Schmutz et al. 2007a, b; Lambdon et al. 2008; EPPO 2012; van Kleunen et al. 2018), forestry (Křivánek et al. 2006; Brundu and Richardson 2016) for terrestrial plants, ballast water transport, aquaculture, ornamental trade, stocking for freshwater invaders (Gherardi et al. 2007, 2009; Nunes et al. 2015), shipping, aquaculture for marine alien species and other corridors (Galil et al. 2009; Katsanevakis et al. 2013). However, the pathways and vectors of introduction of many alien species are unknown, particularly for those that have been introduced accidentally (e.g. many arthropods; Rabitsch 2010).

The EU IAS regulation requires EU Member States to carry out a comprehensive analysis and prioritisation of the pathways of unintentional introduction and spread of invasive alien species of Union concern. This is based on the number or volume of species or the potential adverse impact caused. A description of the active pathways of introduction and spread, including where relevant vectors and commodities with which the species is generally associated, is also required for risk assessments according to the EU IAS regulation (Roy et al. 2018) and for prioritisation and pest risk analysis according to IPPC/EPPO standards (Brunel et al. 2010; Tanner et al. 2017). Pathway prioritisation analyses according to the EU IAS Regulation, using the CBD Pathway Classification framework, are already published for a number of EU countries (e.g. Belgium: Adriaens et al. 2018; Germany: Rabitsch et al. 2018; Greece: Zenetos et al. 2018; Italy: Servello et al. 2019;). However, these studies differ in their approach of using the CBD Pathway Classification framework and the ways in which the classification has been modified, including addition of pathway categories or subcategories. In addition, many EU countries ask for detailed analysis beyond the requirement of the Regulation, including specifically the intentional pathways or species that can be regulated by policy (Pergl et al. 2016a).

In this paper, we discuss issues arising from the implementation of the CBD Pathway Classification framework, based on an expert assessment within the EASIN database, to assigning pathway information for a large subset of alien species in Europe. We summarise the patterns and trends amongst the taxon groups in this dataset, which is based on the experience gained through the process. We also discuss the potential amendments which may be required to the CBD Pathway Classification framework to improve consistency in its application. We are aware that the set of taxa is not exhaustive and does not randomly cover the full alien species pool in Europe; however, no comparable dataset is currently available that uses the primary and secondary pathways in the detailed CBD Pathway Classification framework. Therefore, this study can be considered as the first and only experience available globally and carried out on a large scale to align the pathway information of a regional database with the proposed CBD Pathway Classification framework.

Methods

Study area and assessed alien species

The study was based on review and classification of pathways for alien species in Europe as part of a study funded by the European Commission to populate the EASIN catalogue. The EASIN catalogue was established by the EU, but it covers the whole area of Europe (https://easin.jrc.ec.europa.eu/easin/Catalogue). Pathways, based on Hulme et al. (2008), were initially assigned by the Joint Research Centre (JRC) of the European Commission for selected species covering a range of taxonomic groups and environments. A proportion of the above pathways (catalogue version from 2017) did not directly map on to a single pathway within the CBD Pathway Classification framework (see comparison of CBD and EASIN subcategory comparison in Tsiamis et al. 2017). Therefore, the set of species provided by the JRC for this study was focused on species for which there was not a direct match to a single CBD pathway and where additional information is required to determine the correct CBD pathway assignment. The list of species included aliens *to* and aliens *in* Europe (*sensu* Lambdon et al. 2008) and comprised 4169 alien species, representing a 30% of the entire EASIN species catalogue (Katsanevakis et al. 2015). The alien species were classified in seven broad taxonomic groups and environment (further referred as *taxonomic/environmental groups*) and assigned to experts for evaluation (Table 1). Recognising taxonomic constraints, the large group of parasites (IPPC terminology; excluding insects) was divided into microorganism (Fungi & Pathogens) and larger organism such as nematodes. The list of assessed species included alien and cryptogenic ones (mainly marine species) whose native/alien status in the study area is not clear.

Table 1. Number of alien species included in the study (see Suppl. material 1 for the full list of species) classified by taxonomic/environmental group. EASIN species number of species within the EASIN catalogue for each taxonomic/environmental group (http://alien.jrc.ec.europa.eu/SpeciesMapper; accessed April 2020).

Taxonomic/environmental groups	No. of assessed taxa	EASIN species
Algae	129	150
Microorganisms	567	900
Marine and Freshwater invertebrates	718	2300
Nematodes	39	170
Plants	434	6600
Terrestrial invertebrates	2102	3400
Vertebrates	180	700

Pathway assignment

For each species, 3–4 experts with knowledge of the specific taxonomic/environmental groups were selected. Each expert was assigned a subset of alien species and performed searches of the scientific literature (WoS), online repositories of information on alien species (e.g. CABI Invasive Species Compendium, CABI abstracts, DAISIE database, EPPO Global Database) and grey-literature to find information on primary introduction and secondary spread pathways. For each assessed alien species, these pathways were then assigned to one or more of the CBD pathways categories and subcategories and at least one supporting reference was given for each recorded pathway. This was based on the CBD Pathway Classification guidance document that was developed during the same period (Harrower et al. 2017). Although the focus was on Europe (excluding the outermost regions of the EU Member States), introduction pathway information from other regions in the world or, in some cases, pathway information not linked to any specific region, was used to infer potential pathways of entry to, and/or spread within Europe. Similarly, where information was lacking for the assessed species, pathway information for closely-related species was used to infer pathways.

Primary and secondary (spread) pathways

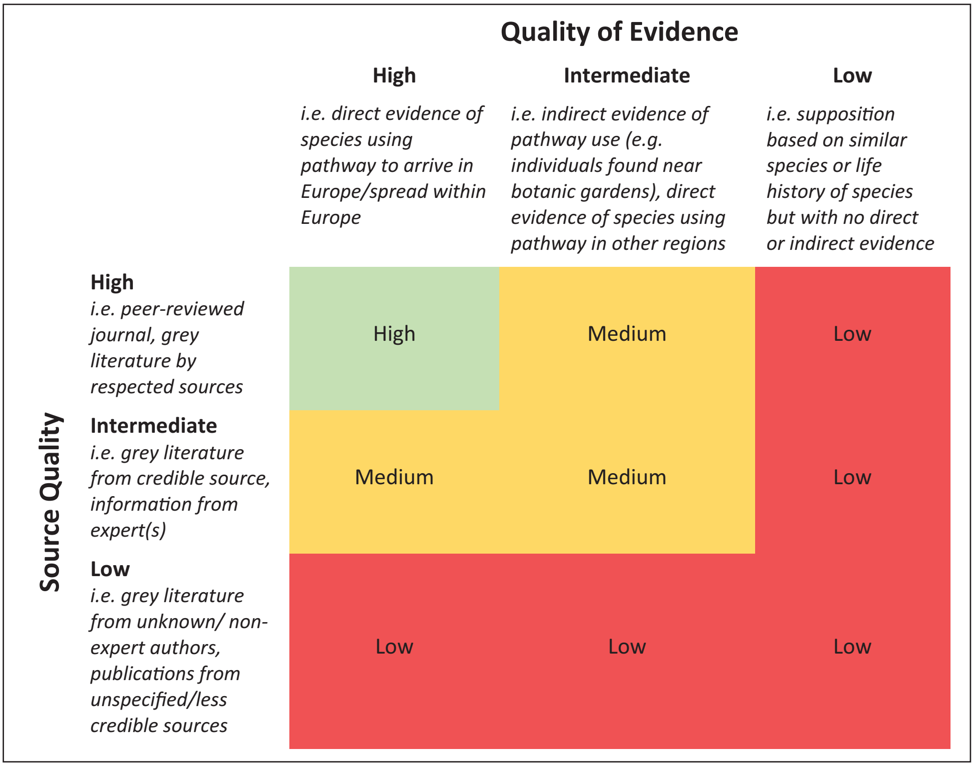
As many alien species spread within or between neighbouring regions through secondary pathways, which often differ from the primary ones, each assessor had to distinguish between the primary and secondary pathway(s). Primary pathways in this study covered all independent introductions to Europe from regions of their native range and also from regions outside Europe where they are alien. Secondary pathways cover means of dispersal or transfer of species between country/regions where the species is non-native after introduction through the primary pathway(s) (i.e. from a European country/region where the species is alien to another European country/region where it is also alien, but was not previously present). The primary pathways were not applied to species with both a native and alien range within Europe (alien *in*) because the assignment of pathways was at the European scale.

Levels of confidence

In addition to the pathway assignments, experts were asked to provide a measure of their confidence (i.e. low, intermediate or high) for each pathway assigned to an alien species. To determine the confidence related to a given pathway assignment, several aspects were considered. Two of the most important aspects were the quality of the source in which the pathway information was found and the quality and appropriateness of the evidence itself (see Fig. 1). For instance, a pathway assignment based upon information in a peer-reviewed scientific paper which report direct evidence of transport of the species by a particular vector in the target region would have a high confidence. On the other hand, an assignment, based on an expert's statement with no additional direct evidence or link to a peer-reviewed source, would be considered as low confidence.

Peer-review process

The pathways and associated confidence level assigned by an expert were subsequently reviewed by another expert from the same taxonomic/environmental group within the



	Quality of Evidence		
Source Quality	**High** *i.e. direct evidence of species using pathway to arrive in Europe/spread within Europe*	**Intermediate** *i.e. indirect evidence of pathway use (e.g. individuals found near botanic gardens), direct evidence of species using pathway in other regions*	**Low** *i.e. supposition based on similar species or life history of species but with no direct or indirect evidence*
High *i.e. peer-reviewed journal, grey literature by respected sources*	High	Medium	Low
Intermediate *i.e. grey literature from credible source, information from expert(s)*	Medium	Medium	Low
Low *i.e. grey literature from unknown/ non-expert authors, publications from unspecified/less credible sources*	Low	Low	Low

Figure 1. Confidence matrix illustrating the criteria for assigning levels of confidence for species pathways records. Redrawn from Harrower et al. (2017).

project team. For each pathway assignment, the reviewer could either agree with the initial expert or disagree with the assigned pathway and/or its confidence level. Reviewers were also asked to provide any comments and/or justification related to their decision. In addition to agreeing or disagreeing with the assignments made by the initial expert, the reviewers were also invited to assign new additional primary or secondary pathways for the species, if any. The final assignment to pathways and confidence levels were then reviewed by additional experts from the same taxonomic/environmental group.

Results

We were not able to provide any pathway information for 327 fungi and pathogens, 51 terrestrial arthropods, eight aquatic invertebrates (marine and freshwater) and one plant (*Carduus nutans*), because of a lack of available evidence. Therefore, the final list of species with at least one pathway was 3782. In total, the assignment of pathway information resulted in 7658 taxon/pathway combinations, supported by 2288 references (i.e. unique articles, web pages, reports). With the exception of plants and terrestrial arthropods, the number of identified secondary pathways was lower than that of primary introductions, with the greatest relative difference observed for vertebrates (Table 2).

Table 3 shows a detailed matrix for the taxonomic/environmental groups and the CBD Pathway Classification framework subcategories, divided by the primary introduction and secondary spread pathways. Amongst the release category, the subcategories, hunting and fishery in the wild (including game fishing), were only assigned to primary introductions. For the escape category, fur farms were only found in primary pathways. Contaminated bait within Transport-contaminant was not present neither in primary nor in secondary pathways. Introductions along terrestrial human-made infrastructures (tunnels and land bridges) were recorded only in secondary spread.

There was variation in the frequency of CBD Pathway Classification (sub)categories relevant to primary and secondary introduction/spread across taxonomic groups and environments (Table 3). Aquatic organisms are most commonly introduced by unintentional pathways such as stowaways, contaminants and corridors. Microorganisms and nematodes are most commonly introduced as contaminants which are also an important pathway for their secondary spread. On the other hand, plants and verte-

Table 2. Number of alien species within each broad taxonomic/environmental group assigned to introduction (primary pathway) and spread (secondary pathway).

Taxonomic/environmental groups	Primary introduction	Secondary spread
Algae	126	36
Microorganisms	221	100
Marine and Freshwater invertebrates	620	207
Nematodes	29	19
Plants	298	303
Terrestrial invertebrates	1345	1499
Vertebrates	177	15

brates are often introduced intentionally through direct release to nature and plants are additionally escaping from confinement. For most taxonomic/environmental groups, secondary spread is most commonly through Unaided /natural spread across borders and not so much intentional spread by humans (Tables 3, 4).

The confidence levels of pathway assignments varied amongst the taxonomic groups. Pathways assigned to fungi and pathogens had the highest percentage of low confidence amongst groups, whereas vertebrates, plants and parasites were typically assigned with intermediate or high confidence (Fig. 2).

Discussion

Our study highlights that the importance of different pathways differs amongst taxonomic/environmental groups and for both primary introductions and secondary spread in Europe. However, it is apparent that some of the CBD Pathway Classification framework subcategories were not used at all or were relevant for only a few species (see Table 4; e.g. contaminated bait, tunnels and land bridges). This is, in part, because the names of these pathways have been kept unchanged amongst databases. Consequently there was a high probability of a direct match from the original EASIN pathway classification scheme to the CBD Pathway Classification framework (and, thus, these species did not appear in our assessment).

The ease of assigning pathway information using the CBD Pathway Classification framework depends on the availability of information. For many species, there was limited evidence available and many records were based on grey literature sources and consequently were assigned low confidence. This is highlighted also by Faulkner et al. (2020) who identified that the complexity of the CBD Pathway Classification framework when compared with the classification of Hulme et al. (2008) may cause some problems. The potential bias due to limited knowledge of species-pathway association was transparently documented by assigning confidence levels and a three-step process of peer-review. The confidence was generally higher for the taxa having a higher number of well-documented intentional introductions, such as vertebrates and plants, than for those species introduced unintentionally.

We are aware that the pre-selection of the species in this study may introduce biases. The dataset described in this study has a limited coverage of some large taxonomic groups (e.g. only about 400 species of plants were included from the 6600 species within the EASIN catalogue). Nevertheless, this pathway dataset covers about one third of the alien flora and fauna of Europe and so, we believe, the observed patterns of pathways have wide relevance. Furthermore, the analysis presented is limited by the fact that the pathways were not prioritised according to their relative importance, for example, in terms of rates of introduction or propagule number, because of lack of robust data. In addition, the importance of specific pathways can vary regionally and temporally (Pyšek et al. 2011, Roques et al. 2016). The discrepancy between the number of assessed species (Table 1) and presented primary and secondary pathways (Table 2) is caused by the evidence-based approach of this study. It can be expected that "Unaided /natural spread across borders" will be common across most of the alien species included here; however, as there were no direct references, the pathway was recorded only for a few of the species.

Table 3. (part 1) Percentages within the broad taxonomic/environmental groups and numbers (in brackets) of records per taxon/pathway combinations and CBD Pathway Classification subcategories. Data are shown separately for introduction (primary pathway) and spread (secondary pathway).

	Pathway type (Hulme et al. 2008)	**Release in nature**							
	CBD Pathway Classification category	**Biological control**	**Erosion control/ dune stabilization (windbreaks, hedges, …)**	**Landscape/flora/fauna "improvement" in the wild**	**Fishery in the wild (including game fishing)**	**Hunting**	**Introduction for conservation purposes or wildlife management**	**Release in nature for use (other than above, e.g., fur, transport, medical use)**	**Other intentional release**
Primary introduction	Algae								
	Microorganisms								
	Marine and Freshwater invertebrates				0.7 (5)				
	Nematodes								
	Plants		6.5 (28)	2.8 (12)				1.2 (5)	2.3 (10)
	Terrestrial invertebrates	0.2 (4)							0.1 (2)
	Vertebrates	2.8 (5)		2.2 (4)	23.3 (42)	22.2 (40)	3.3 (6)	1.1 (2)	28.3 (51)
Secondary spread	Algae								
	Microorganisms								
	Marine and Freshwater invertebrates								0.1 (1)
	Nematodes								
	Plants		7.6 (33)	2.5 (11)				1.8 (8)	1.8 (8)
	Terrestrial invertebrates	0.2 (4)							
	Vertebrates						0.6 (1)		

Table 3. Part 1 continued.

	Pathway type (Hulme et al. 2008)	**Escape from confinement**											
	CBD Pathway Classification category	**Agriculture (including Biofuel feedstocks)**	**Farmed animals (including animals left under limited control)**	**Forestry (including afforestation or reforestation)**	**Fur farms**	**Aquaculture / mariculture**	**Botanical garden/zoo/aquaria (excluding domestic aquaria)**	**Pet/aquarium/terrarium species (including live food for such species)**	**Horticulture**	**Ornamental purpose other than horticulture**	**Research and ex-situ breeding (in facilities)**	**Live food and live bait**	**Other escape from confinement**
Primary introduction	Algae						0.8 (1)	2.3 (3)					
	Microorganisms												
	Marine and Freshwater invertebrates		0.1 (1)			1.1 (8)		1.1 (8)				0.3 (2)	
	Nematodes												
	Plants	8.1 (35)		4.6 (20)		0.7 (3)	6.2 (27)	6 (26)	10.9 (47)	46.4 (201)			0.5 (2)
	Terrestrial invertebrates		0.2 (4)					0.5 (11)			0.2 (5)		0 (1)
	Vertebrates		0.6 (1)		2.2 (4)	10 (18)	2.8 (5)	11.1 (20)				0.6 (1)	7.2 (13)
Secondary spread	Algae					0.8 (1)							
	Microorganisms	0.4 (1)											
	Marine and Freshwater invertebrates		0.3 (2)					0.7 (5)				0.6 (4)	0.1 (1)
	Nematodes												
	Plants	7.2 (31)		3 (13)		0.7 (3)	5.3 (23)	3.5 (15)	9.7 (42)	13.6 (59)	0.5 (2)		1.6 (7)
	Terrestrial invertebrates										0.2 (5)		
	Vertebrates												

Table 3. Part 2.

	Pathway type (Hulme et al. 2008)	**Transport- contaminant**									
	CBD Pathway Classification category	**Contaminant nursery material**	**Contaminated bait**	**Food contaminant (including of live food)**	**Contaminant on animals (except parasites, species transported by host/vector)**	**Parasites on animals (including species transported by host and vector)**	**Contaminant on plants (except parasites, species transported by host/vector)**	**Parasites on plants (including species transported by host and vector)**	**Seed contaminant**	**Timber trade**	**Transportation of habitat material (soil, vegetation,…)**
Primary introduction	Algae				51.2 (66)	1.6 (2)	0.8 (1)				
	Microorganisms	72.5 (174)		3.8 (9)	7.1 (17)		18.3 (44)	24.6 (59)	25.8 (62)	5.4 (13)	20.8 (50)
	Marine and Freshwater invertebrates				12.7 (90)	5.6 (40)	1.3 (9)		2.5 (18)		
	Nematodes	30.8 (12)		2.6 (1)		30.8 (12)	10.3 (4)	46.2 (18)	10.3 (4)	5.1 (2)	30.8 (12)
	Plants	0.9 (4)		0.9 (4)	2.3 (10)	0.2 (1)	0.5 (2)	0.5 (2)	14.5 (63)	0.9 (4)	3.5 (15)
	Terrestrial invertebrates	11.3 (232)		11.8 (241)	0.1 (2)	3.5 (72)	32.2 (660)	0.9 (18)	2 (42)	2.8 (57)	8.5 (175)
	Vertebrates	3.3 (6)			0.6 (1)		1.1 (2)	1.1 (2)	0.6 (1)	0.6 (1)	0.6 (1)
Secondary spread	Algae				4.7 (6)						
	Microorganisms	10 (24)			3.8 (9)	0.4 (1)	5 (12)	2.9 (7)	0.4 (1)	0.4 (1)	9.2 (22)
	Marine and Freshwater invertebrates	0.1 (1)			6.1 (43)	4.8 (34)	1.1 (8)		0.3 (2)		2 (14)
	Nematodes	15.4 (6)			7.7 (3)	30.8 (12)	7.7 (3)	7.7 (3)			25.6 (10)
	Plants	2.3 (10)		0.5 (2)	6.2 (27)	0.5 (2)	2.1 (9)	0.9 (4)	21.5 (93)	0.5 (2)	13.4 (58)
	Terrestrial invertebrates	10.3 (211)		13 (267)	0.1 (3)	3.3 (68)	35.7 (733)	0.5 (11)	2.9 (59)	5.2 (107)	10.4 (213)
	Vertebrates										0.6 (1)

Table 3. Part 2 continued.

	Pathway type (Hulme et al. 2008)	**Transport- stowaway**											**Corridor**		**Unaided**
	CBD Pathway Classification category	**Angling/fishing equipment**	**Container/bulk**	**Hitchhikers in or on airplane**	**Hitchhikers on ship/boat (excluding ballast water and hull fouling)**	**Ship/boat ballast water**	**Ship/boat hull fouling**	**Machinery/equipment**	**People and their luggage/equipment (in particular tourism)**	**Organic packing material, in particular wood packaging**	**Vehicles (car, train, …)**	**Other means of transport**	**Interconnected waterways/basins/seas**	**Tunnels and land bridges**	**Natural dispersal across borders of invasive alien species that have been introduced through pathways 1 to 5**
Primary introduction	Algae					32.6 (42)	53.5 (69)					0.8 (1)	17.8 (23)		
	Microorganisms							2.1 (5)	2.5 (6)	2.5 (6)	0.8 (2)		1.7 (4)		1.3 (3)
	Marine and Freshwater invertebrates	0.3 (2)			0.1 (1)	53.7 (381)	48 (341)		0.1 (1)			2.4 (17)	15.9 (113)		0.1 (1)
	Nematodes		5.1 (2)					10.3 (4)	17.9 (7)	7.7 (3)	10.3 (4)				
	Plants		0.2 (1)		0.7 (3)	1.8 (8)	0.2 (1)	0.9 (4)	0.2 (1)	0.9 (4)	0.9 (4)	0.9 (4)	0.2 (1)		
	Terrestrial invertebrates		2.9 (60)	0.4 (8)	4.4 (90)		0 (1)		0.3 (7)	1.7 (34)	0.9 (18)	0.2 (4)			0.1 (2)
	Vertebrates				17.8 (32)	13.3 (24)	1.1 (2)	0.6 (1)	0.6 (1)			0.6 (1)	5.6 (10)		
Secondary spread	Algae	7 (9)				5.4 (7)	15.5 (20)								15.5 (20)
	Microorganisms							1.7 (4)	1.7 (4)		1.3 (3)		2.5 (6)		20.8 (50)
	Marine and Freshwater invertebrates	1.4 (10)			0.3 (2)	12.4 (88)	7.2 (51)	2 (14)		0.1 (1)		0.4 (3)	2.3 (16)		5.9 (42)
	Nematodes		5.1 (2)					5.1 (2)	5.1 (2)	2.6 (1)	5.1 (2)				5.1 (2)
	Plants	0.2 (1)			2.8 (12)	0.7 (3)		20.1 (87)	4.2 (18)	0.9 (4)	6 (26)	3.2 (14)	2.1 (9)	0.2 (1)	19.4 (84)
	Terrestrial invertebrates		0.3 (7)	0 (1)	2 (41)		0 (1)		0.8 (17)	2 (40)	4.6 (95)	0.1 (2)	0 (1)		2.6 (54)
	Vertebrates												1.1 (2)		6.1 (11)

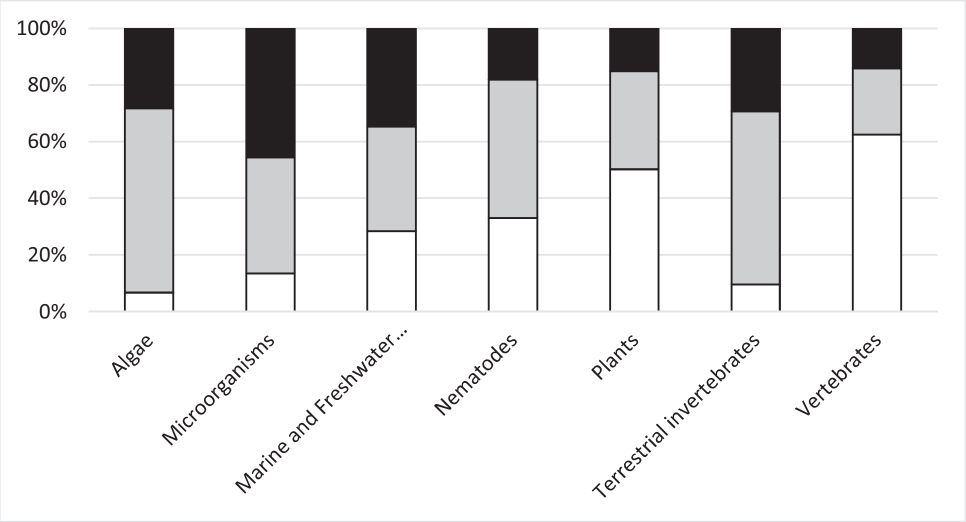


Figure 2. Percentages of species – pathway combinations assigned high (black), intermediate (grey) or low (white) confidence by the experts assigning the categories across different taxonomic/environmental groups.

Use of the CBD (sub)categories for national policies

The CBD Pathway Classification framework has value for underpinning prioritisation of pathways – to assist in development of policies and in their implementation, i.e. executing pathway management activities. It can be combined with assessments of impacts (Pergl et al. 2017; Saul et al. 2017) to prevent their introduction and manage the spread of the most invasive and harmful alien species (Meyerson and Reaser 2003; Hulme 2011). Some pathways and taxonomic groups contribute disproportionally to the overall risk from IAS (Essl et al. 2015; Pergl et al. 2017) and these should be the subject of increased attention. However, to fully assess the potential risk of each pathway, not only is the proportion of species with negative impact relevant, but also the propagule pressure (Blackburn et al. 2020), climatic match to the source region (Faulkner et al. 2017) and other factors like presence/absence of sanitary and phytosanitary measures need to be used.

The terminology in the CBD Pathway Classification framework and in other broadly-used schemes is somewhat different. Although the CBD Pathway Classification framework provides a detailed level of pathway categories and subcategories, in a number of cases, the framework lacks a clear connection to trade and policy regulation terminology. Indeed, in other systems, a well-defined terminology for trade exists (e.g. International Plant Protection Convention/International Standards for Phytosanitary Measures, the EU Combined Nomenclature for custom and trade, https://comtrade.un.org). In addition, there is a plethora of possible combinations of pathways and vectors, some of which have been described in literature with specific terms (e.g. acclimatisation societies and gardens; van Kleunen et al. 2018). Therefore, based on our experience in assigning pathway classifications and corresponding

Table 4. The three most frequently assigned CBD Pathway Classification framework subcategories associated with each broad taxonomic/environmental group for both introduction (primary pathway) and spread (secondary pathway). Rel – Release, Esc – Escape, Cont – Contaminant, Stow – Stowaway, Cor – Corridor, Un – Unaided (Hulme et al. 2008).

Taxonomic/ environmental group	Primary introduction	Secondary spread
Algae	**Stow:** Ship/boat hull fouling; **Cont:** Contaminant on animals (except parasites, species transported by host/vector); **Stow:** Ship/boat ballast water	**Stow:** Ship/boat hull fouling; **Un:** Natural; **Stow:** Angling/fishing equipment
Microorganisms	**Cont:** Contaminant nursery material; **Cont:** Seed contaminant; **Cont:** Contaminant on plants (except parasites, species transported by host/vector)	**Un:** Natural; **Cont:** Contaminant nursery material; **Cont:** Transportation of habitat material (soil, vegetation,…)
Marine and Freshwater invertebrates	**Stow:** Ship/boat ballast water; **Stow:** Ship/boat hull fouling; **Cor:** Interconnected waterways/basins/seas	**Stow:** Ship/boat ballast water; **Stow:** Ship/boat hull fouling; Contaminant on animals (except parasites, species transported by host/vector) **Un:** Natural
Nematodes	**Cont:** Parasites on plants (including species transported by host and vector); **Cont:** Contaminant nursery material; **Cont:** Parasites on animals (including species transported by host and vector); **Cont:** Transportation of habitat material (soil, vegetation, …)	**Cont:** Parasites on animals (including species transported by host and vector); **Cont:** Transportation of habitat material (soil, vegetation, …); **Cont:** Contaminant nursery material
Plants	**Esc:** Ornamental purpose other than horticulture; **Cont:** Seed contaminant; **Esc:** Horticulture	**Cont:** Seed contaminant; **Stow:** Machinery/equipment; **Un:** Natural
Terrestrial invertebrates	**Cont:** Contaminant on plants (except parasites, species transported by host/vector); **Cont:** Food contaminant (including of live food); **Cont:** Contaminant nursery material	**Cont:** Contaminant on plants (except parasites, species transported by host/vector); **Cont:** Transportation of habitat material (soil, vegetation,…); **Cont:** Contaminant nursery material
Vertebrates	**Rel:** Other intentional release; **Rel:** Fishery in the wild (including game fishing); **Rel:** Hunting	**Un:** Natural; **Cor:** Interconnected waterways/basins/seas

confidence levels, to alien species within the EASIN catalogue, in the following sections, we discuss the problems encountered and propose modifications to the CBD Pathway Classification framework.

The way forward: suggestions to amend the CBD Pathway Classification framework. Modification of the CBD Pathway Classification framework subcategories and revised descriptions (Table 5)

We argue that some of the CBD Pathway Classification framework subcategories or, rather, their descriptions, are not sufficiently distinct so their delimitation and interpretation, in some cases, overlap (see also Faulkner et al. 2020). Detailed descriptions are published in the guidance document (Harrower et al. 2017). Therefore, the CBD

Pathway Classification framework has to be used jointly with this document, but to date, there appears to be a lack of evidence that this is the case from citations in scientific literature. The lack of clarity is caused by using the short subcategory names that do not describe all the facets of the pathway. For instance, the short name "Contaminant on plants" could be perceived to include "Contaminant nursery material" and, to some degree, "Contaminant – Transportation of habitat material", which are separate pathways. One possible improvement, as discussed by the expert team, might be to cross-reference the subcategories, i.e. the description for Contaminant on plants could be "Contaminant on plants that are not part of the nursery trade" (or plants for planting). Other examples might include the contamination of seeds (Seed contaminant subcategory), where the seeds are also food items. This issue is covered, for example, by IPPC, that, according to ISPM 5 (FAO 2015), uses the term "grain" as a commodity class for seeds transported for processing or consumption and not for planting and blurred delimitation of the category "Food contaminant (including of live food)". However, cross-referencing might be a suboptimal approach for dissemination of findings of pathway analyses to public and policy; the pathway subcategories titles need to be sufficiently short to be used widely in figure legends and communication documents. For this reason, each subcategory should also have a concise short description, as well as the detailed description. The concise descriptions should give the most pertinent information while the longer description should have all information required to limit the risk for confusion regarding what is included and what is not.

Some pathways are relatively specific ("Biological control", "People and their luggage/equipment – in particular tourism"), while others are broader and less specific. Examples are the CBD pathway subcategories like "Seed contaminant", "Contaminant on animals (except parasites and species transported by host/vector)" or "Timber trade". These groups include a variety of different sources and vectors that can be controlled at borders and regulated. Specifically, the pathway "Contaminant on animals" is based on a number of activities, mainly related to the breeding of animals and trade with products derived from them. This subcategory applies, for example, to seeds/propagules on the fur or in the digestive tract of live animals, as well as to animal products (or by-products) – for example, on the skin and in the wool. It also includes, for example, transport in bedding. The pathway "Timber trade" includes logs, sawn timber and processed wood products (e.g. furniture) or sawdust and firewood. Similarly, the pathway "Seed contaminant" would be better split into at least two pathways as the risk of introduction differs greatly between contaminants of seeds for planting, compared with contaminants of seed that will be processed for food production (see our comment above and definition of "Food contaminant (including of live food) " or as animal feed.

We are not recommending an increase of the hierarchical levels of the CBD Pathway Classification framework, but to adjust the width of the subcategories and their direct link to vectors and possible legislation management. In many cases there is a residual subcategory "other" (e.g. "Other intentional release", "Other escape from confinement"), so that one possible approach would be to specify and split this residual

Table 5. Summary of some issues (including illustrative examples) and recommendations for changes to the CBD Pathway Classification framework or accompanying guidance document.

Topic	Issues	Example	Recommendation
Modification of subcategories	Pathway subcategory too broad and thus ambiguous	Seed contaminant	Divide into two subcategories: 1. contaminants of seeds for planting, 2. contaminants of seed that will be processed for food production or as animal feed
	Overlap amongst pathway subcategories	Agriculture, Horticulture, Ornamental purpose other than horticulture (horticulture is an industry process compared to ornamental purposes)	Ensure clear definitions, consistent with standard use in other sectors. Classify pathways to horticulture as a branch of agriculture separated clearly from ornamental use.
Revision of descriptions	Short pathway names attributed within the framework are unclear or ambiguous	Contamination on plants	Contamination on plants that are not part of the nursery trade
Allow revisions based on new and emerging pathways	Vector does not correspond to the pathway category	Intentional release in the wild of aquarium kept species is different from unintentional Escape from Confinement.	Assign to the "Release" – Other intentional release or add a new vector category "Release"-aquarium/ terrarium-zoo species
	Biological invasions are dynamic processes and there is a need to update the classification accordingly including emerging pathways	Floating marine litter	Assign floating marine litter to the pathway "Transport – stowaway"
		Bilge waters as a secondary means of transport	Assign to the pathway "Transport – stowaway" other means of transport
		The release of by-catch fish in commercial fishing	Assign to "Transport-stowaway" Angling/fishing equipment" category.

subcategory, limiting the number of unclassified pathways. Adopting a nested structure in the pathway descriptions would need to be reflected in the database structures and most of the data would be available at a less detailed scale.

Furthermore, we found that it is difficult to separate the pathways for "Horticulture" and "Ornamental purposes other than horticulture". The distinction is based on the risk or event of escape from a private garden compared to an escape from horticultural (commercial, industrial) facilities. Indeed, although the risk is vastly different, based on information available, there is often the possibility to use only a single pathway, that corresponds to Escape from culture/captivity: gardening. In the guidance document (Harrower et al. 2017), there is some overlap in defining "Agriculture", "Horticulture" and "Ornamental purpose other than horticulture". A possible solution could be to apply the definition from the ISHS (International Society for Horticultural Science; https://www.ishs.org/) for horticulture as a branch of agriculture and to consider AIPH (International Association of Horticultural Producers; http://aiph.org/)

for ornamental horticulture, traditionally considered as a branch of horticulture. This is supported by the traditional view that vegetables are included in horticulture and not in agriculture. In addition, it is certainly useful to consider at least two different scales of these subcategories, to differentiate between the industrial and home use of agricultural and horticultural crops and ornamental plants. Many typical horticultural crops in Europe have a very low risk of escape, regardless of whether they are cultivated in home gardens or intensively over large areas (Pergl et al. 2016b). In contrast, a large number of ornamental species might easily escape from gardens, while they might be more safely kept in dedicated commercial horticultural facilities by responsible growers (Anderson et al. 2006; Bayón and Vilà 2019).

There was also some confusion in the use of the high level categories Stowaway and Contaminant. This appeared to be remedied following detailed consideration of the definitions within the Guidelines. On the one hand, experts agreed that, where the alien species has a trophic or abiotic relationship to a specific substrate, meaning it cannot survive without it, it is clearly a Contaminant. The uncertainty arises where an alien species is typically associated with a substrate, but is able to survive away from it. These two subcategories are distinguished by the nature of the contaminated substratum; if the contaminated substratum is itself a commodity and a vector, then the assigned pathway should fall in the Contaminant category. However, if the contaminated substratum is only a vector (physical or biological), then the assigned pathway should fall in the Stowaway category.

Parasitic alien species, whether in or on plants or animals, were mostly easy to categorise. The categories of pathways related to parasites, however, appear to be less useful in terms of managing the IAS, without the information on pathways applying to the host species (see, for instance, Navajas et al. 2012). Harrower et al. (2017) suggested that subcategories, such as "Contaminant on animals", "Parasites on animals", "Contaminant on plants" and "Parasites on plants", should all be renamed by replacing the "on" in the title with "of", for example, "Contaminant of animals". This would improve clarity by ensuring these subcategories refer to species transport on or in the species. As it currently stands, the title implies that the subcategories should only be used for species that are transported externally on the plant or animal.

In aquatic environments, plastics or other human-made floating materials can travel considerable distances on ocean currents and are capable of transporting and spreading reproductively viable biota (see review in Rech et al. 2016). For example, following the Japanese tsunami in 2011, colonies of living bryozoan *Schizoporella japonica* (alive with embryos) were found on the Hawaiian Islands and in North America after traversing the Pacific Ocean (McCuller & Carlton, 2018). It is, therefore, possible that such colonies may develop on natural and artificial objects which may become flotsam, providing a pathway of introduction and spread. With an increase in drifting marine litter, this potential vector is becoming increasingly prevalent (Barnes 2002; Ivkic et al. 2019). Whilst drifting litter is transported by natural forces (pathway Unaided), it is considered that the presence of anthropogenic marine litter is a human influence, without which fouling species would not be able to make use of prevailing currents to spread rapidly. Therefore, we think that the pattern fits better to the "Transport-stowaway" – other means of transport as a primary pathway.

Bilge waters are another issue for the aquatic environment and identified as an important vector. The metabarcoding analysis of 23 bilge samples collected from yachts and motorboats operating commercially and recreationally in two boating hubs in New Zealand's South Island, led to the identification of five alien species, including the polychaete, *Boccardia proboscidea* (Fletcher et al. 2017). Even though they are in the current CBD Pathway Classification framework categorised to ballast water, due to their different character and aspect of regulation, they better fit to "Transport-stowaway: other means of transport".

The release of by-catch fish in commercial fishing can be a relevant pathway of secondary spread. This will depend on fishing and discard practices, with the highest risk from bottom trawlers. Survival rates of discarded fish (e.g. *Plotosus lineatus* in the Mediterranean Sea) are unknown, but can be high for some species. Such secondary spread was classified by Galanidi et al. (2019) as "Release in nature: other intentional release – fisheries discards", but fits also to the "Transport-stowaway: Angling/fishing equipment" category.

Lack of data leading to low confidence

Assessments of presence and impact of IAS is always affected by the uncertainty in available data (Probert et al. 2020). The lack of available information on introduction and secondary spread pathways for a high number of species is problematic. For example, a number of alien species have been recorded only a few times. It is often challenging to establish whether this pattern is the result of independent primary introduction events or of secondary spread after a single introduction. However, in some cases genetic analyses have provided evidence of independent introductions, for example, in insects or plants (Bras et al. 2019; Neophytou et al. 2019). It is likely that the importance of the pathways within stowaways has been underestimated in terrestrial arthropods because a large number of the categorisations within our exercise were based on the biology of the transported species and their host organism, especially for those associated with plants, but only a few of these arthropods were actually intercepted along the putative pathways (Eschen et al. 2015). By contrast, transport as hitchhikers in vehicles or containers is increasingly observed (Rabitsch 2010). A number of experts flagged that species that contaminate consignments, such as wood furniture or woollen products, are not easily assigned to the pathway descriptions and thus not easily categorised.

The biogeographic status of many species remains uncertain. These species are flagged as 'cryptogenic' when there is medium uncertainty about their origin, that is, whether they are native or alien or 'data deficient' when there is high uncertainty on their biogeographic status (Essl et al. 2018). For such cryptogenic or data deficient species, it is counter-intuitive to assess primary pathways (if we knew that they were introduced with a specific pathway, we would be certain of their alien status). For these species, it makes sense to assess only the secondary spread pathways.

Additional comments for policy and pathway management

One of the greatest challenges experienced by the project team in assigning pathways based on the CBD Pathway Classification framework was ensuring the accurate classification of intentional releases from pathways classified only amongst those listed as "Escape from confinement". A notable example is the "Pet/aquarium/terrarium species (including live food for such species)". Indeed, this subcategory has been systematically used also to cover species which were introduced in a country intentionally for such purpose, but that either escaped in the environment accidentally or were released intentionally (for example, in the case of animals abandoned). Similarly, this may be the case also with other subcategories, such as "Live food/bait", "Horticulture", "Ornamental purpose other than horticulture" etc. (for example, in the case of live baits or cut plants dumped in the environment).

As stated in the guidelines on the CBD Classification Pathway framework (Harrower et al. 2017), the rationale behind the choice of a subcategory should be the primary intention of introduction, because this is of value in informing relevant stakeholders (and consequently has clear implications for the management of pathways). However, this approach was not always considered appropriate. This situation can be exemplified through one of the pathways considered of increasing concern: the intentional release of aquarium species into the wild (Zenetos et al. 2016), in contrast to cases of actual escapees from aquaria, for example, the escape of *Caulerpa taxifolia* from the Monaco aquarium and its introduction to the Mediterranean Sea (Jousson et al. 1998). Although intentional releases of aquarium species should be assigned in the "Release in nature" category under the CBD Pathway Classification framework, they are currently assigned as "Escape from confinement: Pet/aquarium/terrarium species (including live food for such species)". The rationale was that these species were initially imported for a confined environment (aquarium) and then introduced into the wild 'escaping from the confinement'. However, aquarium species are most often intentionally dumped into the waters and should, therefore, be assigned to the "Release" pathway category. Recognition of the importance of this pathway of introduction would facilitate appropriate measures including communication campaigns, for example, targeting citizens and so preventing such releases. Typical measures relevant for the "Escape" category (unintentional) mainly focus on involving the relevant stakeholders, inviting them to adopt voluntary codes of conduct or adopting rules for limiting importation/trade. On the other hand, measures relevant for the "Release" category (intentional) mainly focus on public awareness or the registration of animals kept in captivity. Raising public awareness is critical for the management of marine IAS (Giakoumi et al. 2019) and could be undermined if IAS released by aquarium hobbyists are classified as escapees. The same considerations are relevant to the release of aquatic or terrestrial species for religious ceremonies. The release of captive animals to gain spiritual favour is a widespread religious practice, especially amongst Buddhists and Taoists (Wasserman et al. 2019; Magellan 2019). For all these cases of pet/aquarium/terrarium species intentionally released in the wild, we suggest a new subcategory "Release in nature: Pet/aquarium/terrarium species" to be added under the "Release" pathway category. In this way, it will be possible to differentiate classification and proposed management measures between intentional releases and unintentional escapes of such species. Nevertheless, we recognise that implementing such change may alter the overall rationale behind the CBD Pathway Classification framework and relevant guidance document by Harrower et al. (2017). Therefore, it would require a systematic, measured and analytical revision of the classification system, otherwise there is a risk that there could be greater confusion than the change would aim to solve.

Conclusions

A pathway framework needs to be based on sound science while flexibly accommodating the dynamic nature of biological invasions to satisfy policy and practitioner needs underpinning research and management of IAS. It is important that the compilation of information, such as pathways of introduction for alien species, follows global standards (see, as example, the Darwin Core Initiative; Groom et al. 2019) to ensure wide use and applicability. However, in developing a standard, it is also important to consider the social, spatial and temporal variation inherent to the process of biological invasions (see example for WRA; Gordon et al. 2010). The CBD Pathway Classification framework provides a robust and adaptable approach for assigning pathway information across taxonomic/environmental groups and has been a first ambitious attempt to unify approaches at the global level. It is critical that the published guidance (Harrower et al. 2017), which provides supporting information, is globally used and tested to ensure consistency of application across information systems.

It is essential that the experts, who assign pathways, openly share information and provide updates to the CBD Pathway Classification framework guidance to reduce ambiguity. To date, the broad hierarchical CBD Pathway Classification framework provides a tool which can be applied in diverse contexts, enabling rapid analysis of changing patterns and trends in biological invasions to be communicated rapidly and transparently, so that periodical updates will increase its value and effectiveness over time. However, it is essential that modifications are agreed collaboratively and communicated to everyone using the framework to reduce subsequent inconsistencies in use. We describe potential discrepancies and potential solutions to provide an updated CBD Pathway Classification framework (Table 5). The major issue simply relates to better description of individual pathway subcategories with global relevance. Our analysis, covering a large geographic area and different taxonomic groups and environments, highlights the value and applicability of our suggested modifications.

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Supplementary material 1

Table S1

Authors: Jan Pergl, Giuseppe Brundu, Colin A. Harrower, Ana C. Cardoso, Piero Genovesi, Stelios Katsanevakis, Vanessa Lozano, Irena Perglová, Wolfgang Rabitsch, Gareth Richards, Alain Roques, Stephanie L. Rorke, Riccardo Scalera, Karsten Schönrogge, Alan Stewart, Elena Tricarico, Konstantinos Tsiamis, Andrea Vannini, Montserrat Vilà, Argyro Zenetos, Helen E. Roy

Data type: pathway data

Explanation note: Assessed species with assignment to CBD Pathway Classification subcategories and the relevant references. P indicates primary introduction and S secondary spread. Subcategories: **Release** 1 Biological control, 2 Erosion control/ dune stabilisation (windbreaks, hedges, …), 3 Landscape/flora/fauna "improvement" in the wild, 4 Fishery in the wild (including game fishing), 5 Hunting, 6 Introduction for conservation purposes or wildlife management, 7 Release in nature for use (other than above, e.g. fur, transport, medical use), 8 Other intentional release; **Escape** 9 Agriculture (including Biofuel feedstocks), 10 Farmed animals (including animals left under limited control), 11 Forestry (including afforestation or reforestation), 12 Fur farms, 13 Aquaculture / mariculture, 14 Botanical garden/zoo/aquaria (excluding domestic aquaria), 15 Pet/aquarium/terrarium species (including live food for such species), 16 Horticulture, 17 Ornamental purpose other than horticulture, 18 Research and ex-situ breeding (in facilities), 19 Live food and live bait, 20 Other escape from confinement; **Transport – Contaminant** 21 Contaminant nursery material, 22 Contaminated bait, 23 Food contaminant (including of live food), 24 Contaminant on animals (except parasites, species transported by host/vector), 25 Parasites on animals (including species transported by host and vector), 26 Contaminant on plants (except parasites, species transported by host/vector), 27 Parasites on plants (including species transported by host and vector), 28 Seed contaminant, 29 Timber trade, 30 Transportation of habitat material (soil, vegetation,…); **Transport – Stowaway** 31 Angling/fishing equipment, 32 Container/bulk, 33 Hitchhikers in or on aeroplane, 34 Hitchhikers on ship/boat (excluding ballast water and hull fouling), 35 Ship/boat ballast water, 36 Ship/boat hull fouling, 37 Machinery/ equipment, 38 People and their luggage/equipment (in particular tourism), 39 Organic packing material, in particular wood packaging, 40 Vehicles (car, train, …), 41 Other means of transport; **Corridor** 42 Interconnected waterways/basins/seas, 43 Tunnels and land bridges; **Unaided** 44 Natural dispersal across borders of invasive alien species that have been introduced through pathways 1 to 5.

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DISCUSSION PAPER

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Advancing research on alien species and biological invasions

The application of selected invasion frameworks to urban ecosystems

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Abstract

Urbanization is a major driver of global change. Profound human-mediated changes to urban environments have provided increased opportunities for species to invade. The desire to understand and manage biological invasions has led to an upsurge in frameworks describing the mechanisms underpinning the invasion process and the ecological and socio-economic impacts of invading taxa. This paper assesses the applicability of three commonly used invasion frameworks to urban ecosystems. The first framework describes the mechanisms leading to invasion; the second and third frameworks assess individual species, and their associated environmental and socio-economic impacts, respectively.

In urban areas, the relative effectiveness of the barriers to invasion is diminished (to varying degrees) allowing a greater proportion of species to move through each subsequent invasion stage, i.e. “the urban effect” on invasion. Impact classification schemes inadequately circumscribe the full suite of impacts (negative and positive) associated with invasions in urban areas. We suggest ways of modifying these frameworks to improve their applicability to understanding and managing urban invasions.

Keywords

Biological invasions, framework, impacts, invasive alien plants, urban ecosystems

Introduction

Urbanization is now a major agent of change for social, economic, and ecological systems (Mumford 1961). In urban areas land transformation, climate alteration, and the addition and elimination of species from regional species’ pools have created unprecedented ecosystems that challenge traditional approaches to management and conservation (Hobbs et al. 2009; Kowarik 2011). There are an abundance of invasion frameworks that variously describe the transport, success, impact, and management of alien species[*] (e.g. Davis et al. 2000; Shea and Chesson 2002; Ruiz and Carlton 2003; Catford et al. 2009; Blackburn et al. 2011; Colautti et al. 2013; Blackburn et al. 2014; Bacher et al. 2018; Cadotte et al. 2018), and which were developed to guide research into the ecology and management of invasions in non-urbanized areas. However, it is increasingly recognized that urban areas not only play a significant role in species' invasion (Rebele 1994; Shochat et al. 2010), but also that managers generally lack both a robust understanding of how urban areas influence invasions across taxa, and a conceptual and theoretical understanding of how the urban environment and species interact to shape invasions (Cadotte et al. 2017). This paper assesses how well frequently used and highly cited invasion frameworks fit urban ecosystems. We focus on plant introductions as they are ubiquitous in the urban landscape and are often actively managed. The key to assessing frameworks is to understand how urban-specific drivers like reduced competition, nutrient enrichment, pathogen/pest control, gardening/planting, importation based on human use/values, and human perception of management priorities, all shape species' persistence and spread. We assess the ability of frameworks to accommodate these urban-specific drivers and further suggest ways to alter frameworks to make them pertinent for understanding and managing invasions in urban areas.

Invasion frameworks

Basic understanding of invasion and management frameworks needs to be evaluated in urban ecosystems for several reasons. Firstly, urban areas are directly shaped by human activities that can transport and foster alien species. Secondly, the beliefs, priorities, and concerns of human populations in urban areas directly impact the creation and implementation of management policies for invasive alien species. Many frameworks exist to classify biological invasions, for example, by pathways of dispersal (Hulme et al. 2008; Wilson et al. 2009), general invasion processes (Williamson et al. 1996; Richardson et al. 2000), and impact assessment schemes (Kumschick et al. 2012; Nentwig et al. 2016). We do not aim to examine how all these frameworks apply to urban areas (though any generalized framework's applicability to urban areas should be assessed) but rather we assess three commonly used frameworks that evaluate and explain the invasion process and associated impacts.

We selected three invasion frameworks: the Unified Framework for Biological Invasions (Blackburn et al. 2011), the Environmental Impact Classification of Alien

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[*] A note about terminology. There are a variety of terms used to identify and describe imported species, some of which are less emotive than others (Colautti and MacIsaac 2004), but to better align with frameworks, we will use 'alien' to describe species introduced into new regions due to human activities. We recognize that native species can become invasive, but for this paper, 'invasive' refers only to alien species. Invasive alien plants refer to alien plant taxa which are invasive.

Taxa scheme (EICAT, Blackburn et al. 2014; modified by Hawkins et al. 2015); and the closely-related Socio-Economic Impact Classification of Alien Taxa (SEICAT, Bacher et al. 2018). The first framework provides a terminology and categorization for alien species' populations at different points in the invasion process. The second and third frameworks assess individual species and their associated environmental and socio-economic impacts, respectively. We selected these frameworks as they are among the most widely adopted (Wilson et al. 2020). For example, the Unified Framework by Blackburn and colleagues (2011) has been proposed for use in international biodiversity standards (i.e. Darwin Core, Groom et al. 2019). EICAT is receiving increasing international support and has recently been adopted by the International Union for the Conservation of Nature (IUCN) (IUCN 2020). Here, we assess how these apply to urban areas and whether additional considerations are required.

The frequently employed and commonly cited Unified Framework for Biological Invasions proposed by Blackburn et al. (2011) combines previous stage-based and barrier models into a single conceptual framework, employing an effective terminology to describe the underlying elements and processes involved in invasions (see Fig. 1). They divide the invasion process into a series of stages, and for a species or population to move onto the next stage, it must overcome a series of barriers, e.g. geographical (transport), survival (establishment), and dispersal (spread). This framework not only focusses attention on these discrete stages, but also on the bottlenecks where policy and management actions can reduce invasions.

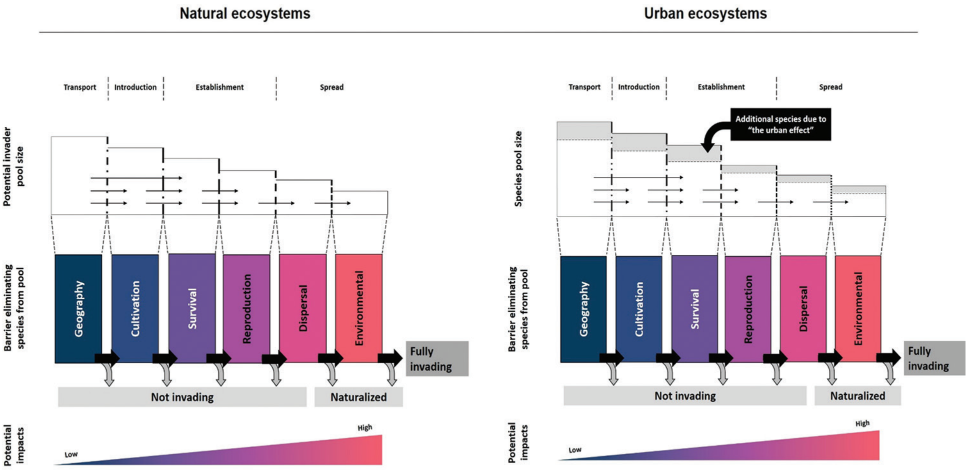

Figure 1. The unified framework for biological invasions by Blackburn et al. (2011) on the left showing how alien species must pass through a series of barriers to establish and invade a new area. At each stage, the pool of species passing through decreases. However, in urban ecosystems, the invasion barriers are changed, resulting in different species crossing each barrier and, in general, more species moving through each of the invasion stages, i.e. the "urban effect" on invasion. The magnitude of an alien species' impact is likely to increase along the invasion framework (introduction – naturalization – invasion continuum) in both natural and urban ecosystems. However, in urban areas, this impact will manifest in different ways (e.g. greater socio-economic impact).

The EICAT scheme classifies alien taxa in terms of the magnitude of their impacts on the environment. It relies on published evidence of impacts via an exhaustive literature search to identify all published literature on the impacts of each alien taxon under assessment. Each impact record for an alien taxon is classified into one of five sequential categories in ascending order of impact, from "Minimal Concern" to "Massive" depending on the level of biological organization (individual, population, community or ecosystem) impacted. This includes the mechanisms (and magnitude) of impact for each taxon, a confidence score for each record, and additional information including the spatial location at which the impact is realized, and which native species are impacted.

Based on the capability approach from welfare economics, the SEICAT scheme presents a system for ranking and comparing the negative impacts of alien taxa on human well-being. The process also relies on published evidence to classify alien taxa based on changes in human activities that result from their impacts. By focusing on changes in people's activities, SEICAT captures impacts of introduced species on human well-being that systems based on monetary values cannot. The scheme defines eight categories into which alien taxa can be classified according to the magnitude of changes in people's realized activities. This classification is analogous to the EICAT and IUCN Red List schemes (Mace et al. 2008).

Invasibility of urban ecosystems

Urban environments result in novel ecological patterns and processes, and dynamics (Faeth et al. 2005; Wilby and Perry 2006; Pickett et al. 2008; Ricotta et al. 2009; Williams et al. 2009; Kowarik 2011; Alberti 2015), which can benefit taxa that are generalist, fast-growing, rapid at reproducing, and resilient to stress and disturbance (Cadotte et al. 2017). The pool of species in any city will be a filtered subset of the regional pool of native species along with other species from the global species' pool, introduced directly through human activities (Aronson et al. 2016). These introductions can be intentional or accidental. Alien species are more likely to benefit from, or at least be less impacted by, urbanization compared to native species simply because they represent a non-random subset of species with appropriate behavioural or life-history traits and strategies (Ariori 2014). Human activities associated with urbanization present improved invasion opportunities for alien plant species by, for example, removing the negative effects of competition or control from enemies (Faeth et al. 2005; Alberti 2015). This, coupled with the novel environmental conditions in cities (e.g. novel habitats, high spatial heterogeneity, increased resource availability, high disturbance levels, and altered climatic conditions), provides opportunities for alien species with appropriate life-history attributes to flourish. Additionally, cities are highly interconnected through transport routes and trade activities. Culture, language, shared history, industrial products and transcontinental trade agreements could be as important for directed movement between cities as geographical distance (di Castri 1990; Maluck and Donner 2015; Khanna 2016), thus explaining the movement of alien plants (Chapman et al. 2017). As a result, cities are often the first entry point for new alien species (Pyšek et al. 2010). High levels of propagule pressure (e.g. through repeated introductions of alien plant species for the horticultural trade) also increases the likelihood of successful establishment.

Through sustained human facilitation in cities, intensive cultivation and repeated introductions of many alien species, biotic and abiotic manipulation, humanity's preference for traits associated with high reproductivity (e.g. large showy flowers, colourful fruits), greater number and diversity of pathways and vectors that can facilitate the movement of alien plants, and increased levels of human-mediated habitat disturbance, collectively increase the likelihood of establishment and spread of alien plant species in urban areas.

Applying invasion frameworks to urban systems

Introduced alien species must pass through a series of barriers before naturalizing in their new environment (Blackburn et al. 2011; Fig. 1). Specifically, urban areas reduce the effectiveness of barriers thereby increasing the number of species that could potentially establish and increase the range of dispersal compared to neighbouring natural areas (Table 1). The Unified Framework will only classify an alien species' population as invasive in an urban setting if the invasion is one among several other invasion foci. The previous invasion stage categories explicitly require alien populations to be self-sustaining outside of captivity or cultivation, termed "in the wild". This is not always applicable in urban contexts and highlights an important shortcoming of the framework. During the invasion process, species will cause a range of ecological and socio-economic impacts (either negative and/or positive), and in urban areas these impacts can be more complex and felt more acutely. Box 1 provides a case study of a successful urban invader and describes the mechanisms facilitating the invasion process. Below we discuss how the barriers to invasion defined by Blackburn et al. (2011), as well as two impact classification schemes (EICAT and SEICAT), differ in urban systems.

Unified Framework for Biological Invasions

Urban areas as hotspots of globalization provide significant opportunities for alien species' introduction

Human activities are progressively weakening biogeographical barriers to dispersal (di Castri 1990; Helmus et al. 2014), resulting in the establishment and spread

Box 1. The vine that strangled a city.

The perennial herbaceous vine *Vincetoxicum rossicum* (Kleopow) Barbar. (Asclepiadaceae; syn. *Cynanchum rossicum*), also known as dog-strangling vine, is a prolific invader in the city of Toronto, Canada. Below we describe how *V. rossicum* overcame the barriers to invasion defined by Blackburn et al. (2011) to become one of the most impactful invaders in the city.

Geographic barrier

Vincetoxicum rossicum was directly imported into the city of Toronto in the late 1800s from the Ukraine and planted as an ornamental and for erosion stabilization in several locations in the city (Kricsfalusy and Miller 2008).

Captivity barrier

There was a significant lag period before *V. rossicum* became a species of concern, but by the 1980s, it had become widespread and abundant in Toronto, especially in urban woodlots and meadows. Its ornamental use, likely facilitated by the nursery trade, provided opportunities for its escape from captivity (Kricsfalusy and Miller 2008).

Survival barrier

Gardeners allowed *V. rossicum* to escape its natural enemies, resulting in much improved fitness. It demonstrates wide environmental tolerance to variations in light intensity and soil moisture (DiTommaso et al. 2005; Douglass et al. 2009).

Reproduction barrier

Seeds of *V. rossicum* are often polyembryonic, giving rise to two, three and (rarely) four seedlings (Ladd and Cappuccino 2005). Unpalatable to herbivores and occupying ample, low-competition habitat resulting from urban disturbances, *V. rossicum* has extremely high fecundity in Toronto.

Dispersal barrier

Vincetoxicum rossicum possesses feathery pappus-covered seeds that are easily carried by wind, and with cars and trains creating air currents, seeds can travel long distances along linear corridors (Ladd and Cappuccino 2005).

Environmental barrier

Vincetoxicum rossicum successfully establishes and survives across a range of disturbance regimes, and improved growth has been shown in more disturbed habitats (Averill et al. 2010). In its native range, this vine largely grows in forest understories, but in Toronto it grows across several habitat types including gardens, lawns, hedgerows, forest understories, and fully open meadows.

Box 1. Continued.

Impacts

Having successfully overcome these barriers, *V. rossicum* negatively impacts native biodiversity – it reduces the diversity of plant and other trophic levels by excluding species with certain traits (DiTommaso et al. 2005; Ernst and Cappuccino 2005; Sodhi et al. 2019; Livingstone et al. 2020). It produces chemicals (Douglass et al. 2009) which can inhibit growth of other plants (allelopathy), alter soil biota, and make foliage unpalatable to native herbivores. It is considered the most impactful and difficult-to-manage plant invader in the city.

Figure B1. An urban site in Toronto, Canada, where the invasive *Vincetoxicum rossicum* forms a monoculture in open and understory habitats (photo credit: LJ Potgieter).

of an increasing number of alien plant species (Ricotta et al. 2014), especially as increasing globalization of trade connects more places with greater movement frequency (Hulme 2009). New international air, land, and sea trade links open novel pathways for the spread of alien species. As hubs of human activity, urban areas are often the first entry point for newly introduced alien species (Pyšek et al. 2010), and so result in a greater proportion of alien species (relative to native species) in urban than in rural or natural areas (Rebele 1994).

Table 1. The barriers to invasion proposed by Blackburn and colleagues (2011) in the context of urban areas, and the underlying mechanisms driving invasion in urban areas. *Indicates potential mechanisms strengthening the barriers to successful establishment of alien plants in urban areas.

Barriers to invasion	Urban effect on barriers	Facilitating mechanisms	References
Geographic	Significant opportunities for alien species introduction	• Urban areas are often the first entry point for newly introduced alien species. • Cities serve as transportation and trade hubs, and are highly interconnected, thus increasing the movement of species globally.	Pyšek et al. (2010)
Captivity or cultivation	Significant opportunities to escape captivity / not relevant	• Horticultural activities result in a major pathway for the repeated importation of many alien plants into urban areas (e.g. gardens which serve as regular sources of alien plant propagules). • Small urban settlements act as launching sites for plant invasions into natural areas. • Alien species introduced unintentionally by humans directly into the new environment.	Dehnen-Schmutz et al. (2007); Bigirimana et al. (2012); McLean et al. (2017); Padayachee et al. (2019)
Survival	Significant potential for survival opportunities, unlike neighbouring, less disturbed areas	• Humans manipulate abiotic and biotic conditions to improve the survivorship of alien plant species. For example, reducing competition, increasing nutrient and water input, and altering soil pH. • Urban heat island effect can provide suitable conditions for more heat-tolerant alien plants. • Selective breeding and dissemination of 'urban suitable' genotypes. • Intra- and inter-specific hybridization can create novel, potentially invasive genotypes. • *Repeated introductions of the same species at a location (propagule pressure) can increase the likelihood of successful establishment.	Gilbert (1989); Ellstrand and Schierenbeck (2000); Kowarik (2005), Kowarik (2011)
Reproduction	Potential opportunities for reproductive success for *some* alien plants	• Habitat fragmentation selects for species with high seed production. • Selective breeding or intraspecific hybridization of cultivars can increase reproductive success. • Longer growing season and earlier flowering and seeding for alien plants in response to urban climates. • Cultivar selection for desirable traits can inadvertently result in greater fecundity. • *Habitat fragmentation reduces the size and increases the isolation of urban plant populations, increasing extinction risk and reducing pollination.	Cunningham (2000); Kitajima et al. (2006); Culley and Hardimann (2008); Huebner et al. (2012); Dubois and Cheptou (2017)
Dispersal	Potential for dispersal opportunities unlike neighbouring less disturbed areas	• Alien plants which possess traits conducive to effective dispersal through prominent urban dispersal pathways are more likely to proliferate, such as wind dispersal by vehicle traffic. • *Many alien plants do not possess the appropriate suite of traits required for efficient dispersal in urban areas. • *Increased propagule pressure can enable alien species to overcome urban dispersal barriers despite poor dispersal abilities.	Aronson et al. (2007); von der Lippe and Kowarik (2007)
Environmental	Environmental conditions provide potential opportunities for alien plant spread	• High level of heterogeneity and disturbance results in frequent colonization opportunities for alien plants. • *Habitat fragmentation can limit the spread from established alien plant populations. • *High levels of disturbance can also act as a barrier to the establishment of some plant species.	Kowarik (1995); Donaldson et al. (2014)

Urban areas have more alien taxa in captivity and cultivation, and so greater propagule pressure.

Invasibility is strongly influenced by propagule pressure (Colautti et al. 2006). In addition to neighbourhood propagule pressure that originates with propagules dispersing from naturalized populations within invaded habitats (spread stage) (Davis et al. 2016), urban areas are exposed to large numbers of alien plant propagules through repeated local introductions and high numbers of propagules in each introduction (e.g. gardens serve as regular sources of plant propagules). This increases the likelihood of their establishment and persistence even in suboptimal microsites (overcoming abiotic barriers and biotic resistance) (Rejmánek et al. 2005; Kowarik et al. 2013). The horticultural industry has been a particularly important pathway around the world (Dehnen-Schmutz et al. 2007), and the escape of ornamental plants from cultivation in gardens has resulted in some of the most extensive biological invasions (Bigirimana et al. 2018; Holmes et al. 2018).

The effect of propagule pressure on invasibility is also apparent in smaller urban settlements which can act as launching sites for plant invasions into rural (Cilliers et al. 2008) and natural areas (McLean et al. 2017) as they can be more numerous in the landscape and share proportionally greater boundaries with their surroundings compared to large cities. Life-history traits such as flower size, fruit size, and growth rates have driven the importation of many alien plants into urban areas (Aronson et al. 2007). These traits are usually associated with reproductive success and allow species to establish and spread into new environments (Moodley et al. 2013).

The captivity and cultivation barrier might also be skipped entirely by alien species which are introduced unintentionally by humans (e.g. as a contaminant (stowaway) of a commodity) (Blackburn et al. 2011). Owing to an increased number and variety of entry methods, urban areas experience multiple accidental introductions (Padayachee et al. 2019).

Human intervention improves the survivorship of alien species

Inherent features of the urban landscape could serve to select for species that are able to persist under more stressful conditions or rapidly take advantage of the resource-rich conditions. For example, higher temperatures associated with urban areas (i.e. urban heat island effect) might select for the establishment of alien plants preadapted to warmer conditions than the natural environment provides (Sukopp 2004). An introduced population can fail to establish because individuals in the population either fail to survive or survive but fail to reproduce (Blackburn et al. 2011). However, human intervention can improve the survivorship of alien species by, for example, reducing competition by purposefully removing undesirable individuals (lowering biotic resistance), increasing nutrient and water input, or altering soil pH (Gilbert 1989). The net result is that a wide range of species experience positive fitness in urban areas that would otherwise be unable to complete their life cycles and successfully reproduce.

Below the species' level, genotypes proving successful in urban areas are selectively bred (e.g. for flowering, architecture, foliage and for disease-resistance traits) and are widely disseminated through plant exchanges and the horticultural trade (regulated and unregulated) (Kowarik 2005; Sæbø et al. 2005; Dehnen-Schmutz et al. 2007), the fertile taxa of which have the opportunity to naturalize. Intraspecific hybridization and selection can also act to create novel, potentially successful genotypes (Ellstrand and Schierenbeck 2000) adapted to the selection pressures of the urban environment.

While the survival barrier in urban areas might be high for some species, the failure of individuals or populations to survive is not just a consequence of the environment, for subsequent human-mediated introductions of the same species at that location could succeed (Blackburn et al. 2011). Thus, propagule pressure can reduce the effectiveness of the survival barrier.

Urbanization can enhance reproductive success of *some* alien plants

Urban habitats are highly fragmented, thus reducing the size and increasing the isolation of urban plant populations, resulting in a decline in pollinator services and ultimately lowering reproductive success of plants (Dubois and Cheptou 2017). However, the process of habitat fragmentation generally selects for species with high seed production (Cunningham 2000), seed banking capabilities, high dispersal capacity, and independence from mutualisms, such as specific pollinators and specialized mycorrhizae (Huebner et al. 2012). A small proportion of the urban flora will possess traits which satisfy these requirements (Aronson et al. 2007; Knapp et al. 2008). Together with high levels of propagule pressure and human intervention aimed at increasing alien plant survivorship, these species can proliferate within and around urban areas (e.g. Alston and Richardson 2006). For example, survivorship can be increased by reducing competition and increasing nutrient and water input, enabling alien plants to direct more energy to reproduction, greatly increasing the probability of forming self-sustaining populations.

While selective breeding or intraspecific hybridization of cultivars can reduce invasive potential (Anderson et al. 2006), such domestication efforts can also increase reproductive success (Culley and Hardimann 2008). Selection for desirable traits (such as showy appearance) can also inadvertently result in greater fecundity (Kitajima et al. 2006). Phenological changes associated with warmer urban conditions can result in earlier flowering and seeding and an expansion of the growing season, potentially placing alien plants at a reproductive advantage (Huebner et al. 2012).

The complex network of dispersal pathways and vectors in urban areas facilitates the movement of *some* alien plants.

Urban areas comprise a complex network of pathways and vectors that can facilitate plant movement within the urban matrix and into surrounding natural areas (Padayachee et al. 2017). Alien plants which possess traits suited to effective dispersal either along dispersal pathways such as roads and railways (e.g. wind-dispersed *Pennisetum setaceum*, Rahlao et al. (2010), and *Vincetoxicum rossicum*, DiTommaso et al. (2018)), or via movement of topsoil or garden waste (Hodkinson and Thompson 1997) are more likely to proliferate in urban areas. For example, long-distance dispersal by vehicles occurred more frequently for seeds of invasive alien plants than for native species (von der Lippe and Kowarik 2007). Moreover, rivers passing through urban areas can also promote alien species' spread (Planty-Tabacchi et al. 2001; Burton et al. 2005).

Alien plant species with fleshy fruits are more likely to expand their range in urban environments because of their ability to utilize bird dispersal (Aronson et al. 2007). Many alien plants do not possess the appropriate suite of traits required for efficient dispersal in urban areas. However, increased propagule pressure in urban areas can enable alien species with poor dispersal abilities to overcome urban dispersal barriers (e.g. by increasing the likelihood of seed dispersal).

Urban areas provide environmental conditions favourable for the spread of *some* alien plants

In urban areas, abiotic conditions such as climate, land use, pollution, and nutrient loads are dramatically altered through human intervention (Kowarik 2011). Cities provide a much greater array of diverse habitats and environmental conditions compared to natural areas of the same size (Sukopp and Starfinger 1999; Schmidt et al. 2014). This high level of heterogeneity means that there are many habitat patches (at different levels of disturbance) which can be exploited by alien plant species with different ecological demands. For example, roadsides serve as disturbance corridors that provide environmental conditions favourable for the establishment of alien plants (von der Lippe and Kowarik 2008; El-Barougy et al. 2018).

Habitat fragmentation greatly increases the amount of edge habitat, which can increase the susceptibility of vegetation patches to disturbances (Bar-Massada et al. 2014). Increased levels of human-mediated disturbance can increase the number of alien plant species in urban areas through the colonization of disturbed or newly created habitats (Kowarik 1995). However, high levels of disturbance can also act as a barrier to the establishment of some plant species not well adapted to the altered environmental conditions. Consequently, some alien taxa might be widespread along roadsides and other disturbed areas but struggle to invade natural ecosystems (e.g. *Centranthus ruber*, Holmes et al. 2018), and vice versa.

The influence of management

While the relative importance of the barriers to reproduction, dispersal, and environment for determining invasion success can be greater in urban areas compared to natural areas (Table 1), management interventions aimed at strengthening the geographic, cultivation and survival barriers can reduce the pool of potentially invasive plant species. As an example, the geographic barrier can be strengthened by policies that limit the importation of species and increase biosecurity measures. The cultivation barrier can be increased by policies that prohibit sale of some species. Finally, the survival barrier can be increased by municipal programs that promote the use of native over alien species to reduce the active support of less desirable species through gardening.

Impact classification schemes (EICAT and SEICAT)

A taxon with a high ecological impact in a rural or natural environment will not necessarily have the same impact in an urban environment, or impact at the same spatial and temporal scales. Generally, the magnitude of an alien species' impact (which can be highly variable and context-dependent, Ricciardi et al. 2013) is likely to increase from population and species to community and ecosystem effects along the invasion framework (Pyšek and Richardson 2010). This can occur in both natural and urban ecosystems (Fig. 1), however in urban areas, these impacts can be more complex and manifest in different ways (e.g. greater socio-economic impacts). Aside from general shortcomings (for example, EICAT does not directly assess how many native species are affected; see Kumschick et al. 2020 for further details), the application of the ICAT Schemes in urban areas presents additional challenges.

Combining the ICAT Schemes might achieve a more comprehensive assessment of the negative ecological and socio-economic impacts from an invasion. Both schemes explicitly focus on deleterious impacts and do not set out to weigh deleterious against beneficial impacts to determine the net value of an introduction of an alien taxon (cf. Vimercati et al. 2020). However, an assessment of the positive impacts (benefits) provided by alien taxa is particularly important in urban areas where many species have been deliberately introduced to provide ecosystem services (e.g. for ornamental, horticultural, or land reclamation purposes with corresponding social, economic and environmental benefits) (Boland and Hanhammer 1999; Salisbury et al. 2015; Potgieter et al. 2017; Vaz et al. 2017), and where people have formed close connections with these species over time. For example, the invasive Norway maple, *Acer platanoides*, was commonly planted in large Canadian cities, such as Toronto, and is often seen as an iconic Canadian species by urban dwellers. So much so that the image of its leaf was mistakenly used on Canada's $20 bill, instead of the native sugar maple, *Acer saccharum*, that adorns the Canadian flag.

Robust and comparable data on the impacts of most alien species are still lacking, and in many cases, uncertainties in impact assessments remain significant (Simberloff et al. 2013; Probert et al. 2020). The higher number and diversity of stakeholders in urban areas means there is a greater chance of strongly divergent perceptions and opinions regarding the impacts of alien species (Potgieter et al. 2019) – the perception of the impact of our example invader in Toronto (Box 1) depends on the degree of ecological engagement of the respondent (Livingstone et al. 2018). Complex socio-cultural and economic connections to human residents confound impact assessments and subsequent management thresholds (Gaertner et al. 2016). As the ICAT Schemes' classifications are governed by the best available data, achieving accurate impact classifications for specific alien taxa in urban areas can be difficult and expensive (Measey et al. 2020). It is also challenging to relate a change in human activity to a specific species because of the diversity of alien taxa and high levels of habitat heterogeneity in urban areas.

With ongoing dissemination of alien plant propagules, there are likely to be significant time-lags before any impact is realized (Mack et al. 2000). This has knock-on effects for impact classification as only published evidence is considered by the ICAT Schemes' assessors, resulting in a potentially lower impact and therefore a lower management priority being assigned to a species. Additionally, an in-depth review of the literature is not likely to comprehensively address all possible impacts (especially social impacts), which can be highly context-specific and dependent on the stakeholder group assessed, for example, wealthy landowners versus marginalized inner-city communities. Effective engagement with all relevant stakeholders is required to ensure a comprehensive assessment of all impact scenarios (Novoa et al. 2018).

Urban areas present increased economic and social opportunities for people compared to rural or natural areas (Elmqvist et al. 2013). As a result, people's capabilities and the activities in which they can engage, are enhanced. There is therefore a greater likelihood for invasive alien plants to influence people's capabilities and realized activities, which ultimately affects their well-being. A clear understanding of the ways in which alien (and invasive) species affect biodiversity and ecosystem functioning, and the subsequent changes to the provision of ecosystem services (and disservices) is needed if the effects on human well-being are to be comprehensively assessed (de Groot et al. 2002; Kremen 2005; Haines-Young and Potschin 2010; Vaz et al. 2017; Vimercati et al. 2020). For example, in Cape Town, South Africa, invasion by Australian acacias, *Eucalyptus* and *Pinus* species displaces native vegetation, increasing the frequency and severity of wildfires, and reducing surface water flows (van Wilgen et al. 2012). The resulting loss in biodiversity, risk of damage to infrastructure, and decreasing water sources, all significantly impact the safety and well-being of the city's residents. Invasive alien plants can also sustain or enhance ecosystem functioning in their adventive range, for example, by increasing net primary production, pollinator support, decomposition rates, and nitrogen cycling (Ehrenfeld 2003; Corbin and D'Antonio 2004; Liao et al. 2008; Salisbury et al. 2015). This can lead to the maintenance or augmentation of ecosystem services or disservices with implications for human well-being (Charles and Dukes 2007; Eviner et al. 2012; Vaz et al. 2017). Empirical evidence evaluating this nexus is emerging but remains scarce in urban areas.

The way forward

With an abundance of invasion frameworks and a growing body of literature exploring the many facets of invasions in urban areas, it is important to consider whether current invasion frameworks apply to urban systems.

Biological invasions represent a complex societal issue. Consequently, impact assessments and subsequent management decisions should include input from a wide range of stakeholders to elucidate the positive and negative effects of invasive alien plants in urban areas (e.g. Potgieter et al. 2019; Vimercati et al. 2020). Transparent and replicable approaches are needed to document the different consequences of invasive alien plants for different groups of stakeholders. For example, Kumschick et al. (2012) provide a framework for the prioritization of invasive alien plants for management according to their impact. It includes both a scientific impact assessment and the evaluation of impact importance by affected stakeholders, and accounts for both positive and negative impacts of invasive alien plants (thereby accommodating potential conflicts of interest). Potgieter et al. (2018) use multi-criteria decision tools to develop a prioritization approach for managing invaded areas across an urban landscape. However, more work is needed to test the applicability of such frameworks to urban systems around the world and how suitable frameworks will need to be modified accordingly. For example, Kumschick et al.'s (2012) proposed 'impact categories' will need to be modified to address the full spectrum of potential impacts of invasive alien plants in urban areas.

Urban areas have a complex network of dispersal pathways and vectors that can facilitate the movement of alien plants. Existing pathway frameworks (e.g. Hulme et al. 2008; Wilson et al. 2009) are likely to effectively accommodate urban dispersal pathways, though a shift in emphasis on certain dispersal categories will be required. For example, horticulture (categorized as 'cultivation' *sensu* Wilson et al. 2009) is a prominent urban dispersal mechanism. Yet, more quantitative evidence is needed to elucidate the full suite of urban dispersal pathways and vectors.

Urbanization provides insights into how species will respond and interact under future global change scenarios (Lahr et al. 2018). So, future frameworks circumscribing the invasion process would benefit by including the urban dimension. Viewing invasive species' success and impact as complex and variable in human-dominated landscapes will provide managers and policy makers with the necessarily complex frameworks to address alien species' prioritization and control in an increasingly altered world.

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Understanding uncertainty in the Impact Classification for Alien Taxa (ICAT) assessments

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Abstract

The Environmental Impact Classification for Alien Taxa (EICAT) and the Socio-Economic Impact Classification of Alien Taxa (SEICAT) have been proposed to provide unified methods for classifying alien species according to their magnitude of impacts. EICAT and SEICAT (herein "ICAT" when refered together) were designed to facilitate the comparison between taxa and invasion contexts by using a standardised, semi-quantitative scoring scheme. The ICAT scores are assigned after conducting a literature review to evaluate all impact observations against the protocols' criteria. EICAT classifies impacts on the native biota of the recipient environments, whereas SEICAT classifies impacts on human activities. A key component of the process is to assign a level of confidence (high, medium or low) to account for uncertainty. Assessors assign confidence scores to each impact record depending on how confident they are that the assigned impact magnitude reflects the true situation. All possible sources of epistemic uncertainty are expected to be captured by one overall confidence score, neglecting linguistic uncertainties that assessors should be aware of. The current way of handling uncertainty is prone to subjectivity and therefore might lead to inconsistencies amongst assessors. This paper identifies the major sources of uncertainty for impacts classified under the ICAT frameworks, where they emerge in the assessment process and how they are likely to be contributing to biases and inconsistency in assessments. In addition, as the current procedures only capture uncertainty at the individual impact report, interspecific comparisons may be limited by various factors, including data availability. Therefore, ranking species, based on impact magnitude under the present systems, does not account for such uncertainty. We identify three types of biases occurring beyond the individual impact report level (and not captured by the confidence score): biases in the existing data,

data collection and data assessment. These biases should be recognised when comparing alien species based on their impacts. Clarifying uncertainty concepts relevant to the ICAT frameworks will lead to more consistent impact assessments and more robust intra- and inter-specific comparisons of impact magnitudes.

Keywords
Alien species, confidence score, EICAT, invasive species, risk, SEICAT

Introduction

Understanding the impacts of alien species in their recipient environments is a key research theme in invasion science (Strayer et al. 2006; Pejchar and Mooney 2009; Vilà et al. 2011; Kumschick et al. 2015). However, making comparisons between taxa is difficult as invasions are context-dependent and measurements of impact are not collected using a consistent method (Courchamp et al. 2017). As such, different frameworks have been developed to guide invasion biologists towards more standardised approaches which facilitate comparisons amongst invasion scenarios (Nentwig et al. 2010, 2016; Blackburn et al. 2014). In 2014, Blackburn and colleagues proposed a systematic method for classifying impacts across alien taxa, based on the effects of alien species on native biota. The resulting Environmental Impact Classification System for Alien Taxa (EICAT) (Blackburn et al. 2014; Hawkins et al. 2015) is conceptually based on the International Union for the Conservation of Nature's (IUCN) Red List of Threatened Species, which uses a ranked classification scheme to determine the global conservation status for individual species (IUCN 2012). Since its publication, the EICAT protocol has been formalised (IUCN 2020a, b; Hawkins et al. 2015) and applied to various groups including birds (Evans et al. 2016, 2018a), amphibians (Kumschick et al. 2017), gastropods (Kesner and Kumschick 2018), some mammals (Hagen and Kumschick 2018), marine fishes (Galanidi et al. 2018) and bamboos (Canavan et al. 2019). More recently, Bacher et al. (2018) proposed an adapted version of the EICAT framework to address socio-economic impacts (SEICAT) caused by alien species. The currency used to measure impact for this scheme is observed changes to human activities and/or well-being and, to date, SEICAT has been applied to amphibians, birds, marine fishes, some mammals and gastropods, in conjunction with the EICAT assessments (Bacher et al. 2018; Evans et al. 2020; Galanidi et al. 2018; Hagen and Kumschick 2018; Kesner and Kumschick 2018).

In the ICAT classification schemes, assessors first conduct a comprehensive literature search to collate all impact records for a given alien species. They then classify each of these impact records into one of the five ICAT semi-quantitative scenarios, according to the magnitude of the impact. For instance, under EICAT, impact magnitudes are hierarchically structured, based on the level of organisation of the native population(s) (i.e. individuals or populations) in which they cause an effect: MC (Minimal Concern; negligible level of impact, but no impact on the performance of native individuals is detected), MN (Minor; the performance (e.g. growth, reproduction) of native individuals is decreased by the alien, but no impact at the native population level is detected), MO (Moderate; the alien causes a decline in at least one native population), MR (Major; the alien causes a local extinction of at least one native population, but this local extinction is reversible, which means that the native species could recolonise the area if the alien population were removed), MV (Massive; the alien causes an irreversible local extinction of at least one native population). If there is no relevant information to derive an impact score, then a species is classified as Data Deficient.

A key aspect of each assessment involves assigning a confidence score for each recorded impact to provide an estimate of uncertainty. Both frameworks adopt a similar approach as the Intergovernmental Panel on Climate Change (IPCC) and the European and Mediterranean Plant Protection Organization (EPPO) to deal with uncertainty (Mastrandrea et al. 2010; Holt et al. 2012; Kenis et al. 2012). The assessor must assign a confidence score of either high, medium or low, based on guiding probabilities (Table 1), to each impact report, depending on how confident they are that the assigned impact magnitude is true i.e. could the actual impact be lower or higher than what is classified. Although several key sources of uncertainty are identified in the guidelines (IUCN 2020a; Hawkins et al. 2015; Bacher et al. 2018), whether the current consideration of uncertainty is sufficient has not been critically evaluated.

Inadequately accounting for uncertainty when assigning impact magnitudes could lead to incorrect judgement calls and potentially to non-relevant prioritisation and mismanagement of species. Todd and Burgman (1998) demonstrated how incorporating uncertainty into the conservation status of species can cause differences in the assessment outcome, potentially altering conservation priorities. McGeoch et al. (2012) described the uncertainties associated with alien species listing and demonstrated how they produce inconsistencies at the taxonomic and geographic scale. Insufficient handling of uncertainty may not only be detrimental for the native taxa (EICAT) and human societies (SEICAT) that are affected by alien species; it can lead to public distrust in invasion science and reduce the success of future management and restoration programmes (Liu et al. 2011). Failure to effectively capture and communicate uncertainty may lead to ill-informed decisions, causing people to potentially undermine management objectives (Ascher 2004), which is of particular concern to invasive species management where public support is critical for achieving management outcomes (Bremner and Park 2007; Kraus and Duffy 2010; Novoa et al. 2017; Russell and Stanley 2018).

To address potential sources of uncertainty relevant to the ICAT assessments, we evaluate the current consideration when assigning confidence scores, identifying where uncertainties may arise during the assessment process. In the first part of this manuscript, we explain the key concepts and definitions of uncertainty relevant to the ICAT frameworks and map these along the assessment process. We then proceed to identify new sources of uncertainty currently not considered under the framework guidelines and discuss how these may play a role in both the evaluation of information and the final ICAT scores. In doing so,

Table 1. The three current confidence levels (high, medium, low) assigned to individual impact reports using the ICAT frameworks. Guiding probabilities are given in the guidelines to aid the assessor in interpreting their level of confidence into one of the three qualitative categories.

Confidence level	Approximate probability of the impact being correct
High	~90%
Medium	~65–75%
Low	~35%

we develop a more comprehensive understanding of uncertainty relevant to ICAT assessments, which may be of conceptual relevance to other aspects of risk assessment, particularly when extracting and evaluating impact information from various sources.

General types of uncertainty and how they can be expressed

Uncertainties arise because our knowledge of systems is incomplete and we often deal with imperfect information; thus, uncertainty is inherent to all scientific research (van der Bles et al. 2019). In some cases, uncertainty can be minimised through the collection of additional information, yet it is impossible to eliminate uncertainty altogether (Regan et al. 2002). In cases where uncertainty cannot be reduced, best practice involves quantification of–and when this is not possible, sufficient acknowledgement of–where uncertainties remain and how they may alter the interpretation of evidence (Fischhoff and Davis 2014). Common expressions of uncertainty in science are usually communicated through quantitative terms such as confidence intervals, standard deviations and probability distributions, but generally, they capture only parts of the overall uncertainty (e.g. measurement error).

A taxonomy of uncertainty applicable to ecological research was described by Regan et al. (2002), who distinguish between two key types of uncertainty: epistemic and linguistic (Table 2). Given their broad applicability to ecological concepts, these expressions of uncertainty are relevant to ICAT assessments and have recently been considered in developing a framework for uncertainty in invasion science (Latombe et al. 2019). Epistemic uncertainties arise because of our limited knowledge of the system of interest. They can generally be reduced with increasing information; however, obtaining a complete understanding of such systems is almost always impractical, hence the necessity to use simplified models to characterise the true state (Regan et al. 2002). Different types of epistemic uncertainty are relevant to the understanding of alien species impacts in general. These include natural variation, measurement error, systematic error, model uncertainty and subjective judgement (Table 2; Regan et al. 2002). Linguistic uncertainties arise because language is imprecise and changes over time cause terminology to be both used inconsistently and open to interpretation (Regan et al. 2002). The different types of linguistic uncertainty include vagueness, context-dependency, ambiguity, indeterminacy of theoretical terms and underspecificity (Table 2). It is clear that linguistic uncertainty has pervaded invasion science, given the numerous attempts to standardise concepts and definitions to improve consistency across the discipline (Wilson et al. 2020; Colautti and MacIsaac 2004; Richardson et al. 2010; Blackburn et al. 2011).

Considering uncertainty for ICAT assessments

Uncertainty directly relevant to the ICAT assessments can be considered at two levels: 1) the impact report level and, 2) the species level. The impact report level is the individual record of impact (of an alien species at a specific location and point in time) that is documented in some form–such as a journal article of grey literature—and assigned

Table 2. Different types of epistemic and linguistic uncertainties and their definitions which are relevant to the ICAT assessment process (Regan et al. 2002).

Epistemic	Linguistic
Natural variation Variations in the variables measured in the study system (e.g. temporally, spatially).	*Vagueness* Arises since language allows borderline cases. Particularly relevant to ordinal categories (e.g. high, medium, low) where arbitrary and/or poorly defined cut-offs exist.
Measurement error Imperfections in the measurement equipment or observational techniques which generates random deviation in the measurement data from the true value. Includes operator error and instrument error.	*Ambiguity* When words have more than one meaning and it is unclear which meaning is intended.
Systematic error Bias in the measuring equipment or sampling procedure that generates non-random deviations from the true value (e.g. via poorly-calibrated equipment). This also includes error resulting from the deliberate judgement of a person to exclude (or include) data.	*Context dependence* Lack of specificity related to the context in which something is to be understood. For example, understanding the meaning of something being "small" requires knowledge as to whether the description refers to an insect or a plant.
Model uncertainty Arises due to the necessary simplifications (models) used to represent physical and biological systems.	*Underspecificity* Occurs when there is unwanted generality i.e. there is a lack of specificity to ensure complete understanding.
Subjective judgement Occurs as a result of the interpretation of data, often when data are scarce and/or error prone. Particularly relevant to expert judgement.	*Indeterminacy of theoretical terms* Arises as the meaning of terms can change over time. For instance, this source of uncertainty is particularly relevant to taxonomic terms, which may be subject to revision, leading to changes in the names of species or higher-level groups.

an impact score. In contrast, the species level summarises all the individual records of impact for a particular alien taxon (IUCN 2020a).

Uncertainties relevant at the impact report level

The different types of epistemic and linguistic uncertainty emerge across various stages relevant to an ICAT assessment; first, uncertainties will arise when the impact observation is initially observed and/or measured; second, when the impact is communicated in some form of report and third, when the ICAT assessment is conducted (Figure 1). Any uncertainty that arises at any one stage will continue to be present at all subsequent stages, with uncertainty propagating throughout the process, from the initial impact observation to the final ICAT assessment. Thus, all uncertainties that arise prior to the impact assessment are encapsulated in the subsequent stages (Figure 1). All uncertainties relevant here are included in the *impact report* box of Figure 1.

Uncertainty initially emerges in the form of natural variation, which corresponds to spatial and temporal changes occurring within the study system. An appropriate study design will identify a suitable temporal and spatial scale under which impacts of the alien species can be characterised (Christie et al. 2019).

The next step at which uncertainties emerge is when the impact is observed and measured. Here, four new sources of epistemic uncertainties are identified: measurement error, systematic error, model uncertainty and subjective judgement (Figure 1). Each of these uncertainties may not necessarily be relevant for every impact report as the

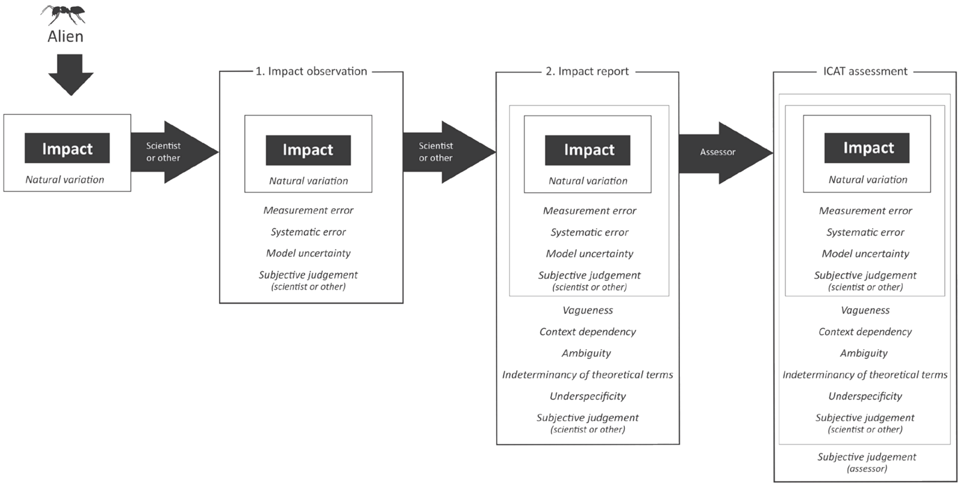

Figure 1. Uncertainties propagate across the process of an impact assessment. The first source of uncertainty emerges due to natural variation associated with the occurrence of an alien species' impact on native biota. Uncertainties arise at three key stages when information on the impact of an alien species is captured 1) the impact observation stage; i.e. when the impact is measured 2) the impact report stage; i.e. when the impact is communicated in some form of report and finally, 3) at the ICAT assessment stage; i.e. when the assessment is conducted. Any uncertainty that arises will be carried through to the subsequent stages, as illustrated through the encapsulation of uncertainties across the process.

ICAT assessments allow the use of different information sources (see Table 3 for the key differences in impact records between EICAT and SEICAT that should be considered). For instance, media reports of a change in local human activities-in response to an alien species-deriving from interviews with residents will not be subject to model uncertainty.

Although currently not directly addressed in the framework guidelines (IUCN 2020a; Hawkins et al. 2015; Bacher et al. 2018), linguistic uncertainties are important for assessors to consider when informing the confidence score. Linguistic uncertainties are of direct relevance for ICAT assessments: they occur when the impact observations, or measurements, are described in a report with imprecise and inconsistent language. Often linguistic uncertainty will be difficult to reduce retrospectively. In some cases, linguistic uncertainty (such as a vaguely described methodology of the impact study) may mask the ability to identify epistemic uncertainties.

The assessment process

Under the published guidelines, assessors are instructed to capture the key sources of epistemic uncertainty for each impact report and ascribe these to one overall level of confidence (IUCN 2020a; Hawkins et al. 2015; Bacher et al. 2018). Following the succession of guidelines, the consideration of uncertainty has been somewhat revised. The most recently-revised EICAT guidelines (IUCN 2020a) identify five major sources of uncertainty that the assessor must consider when assigning a confidence score: i) data quality and type ii) spatial and temporal scale and iii) confounding effects iv) study design and v) overall coherence of evidence. These sources of uncertainty are also relevant for SEICAT; however, given that the currency used to measure impact differs between the two frameworks (native species' populations vs. human activities), interpretation and importance of different uncertainties may vary to fit the criteria and concepts for each framework (Table 3).

When evaluating the magnitude of an impact, the assessor interprets the information contained in the impact report and, when possible, translates this information into one of the five ICAT magnitudes. As impact reports were not aimed at testing the assessment criteria (e.g. which level of organisation of the native population is affected by the alien), the assessor has to interpret the information at hand, a process which inevitably introduces a new source of uncertainty. It may be difficult for ICAT assessors to identify limitations generated by the way the impact was measured and reported. Ideally, authors of an impact study will address limitations with their research; however, ICAT assessors must critically assess all available information (e.g. study design, statistical analyses) to identify potential weakness in the inference of the data. It is at this stage–where the impact measurement is reported—that linguistic uncertainties become relevant and should ideally be recognised by assessors, who should be aware of how language may influence their interpretation of the information.

Assessments will be further compounded by systematic error (i.e. when the assessor systematically decides to include or exclude information that they should otherwise exclude or include) and subjective judgement (Regan et al. 2002). These sources of uncertainty initially become relevant when the assessor conducts a literature review to extract the records of impact for an alien taxon, then decides which fit the framework criteria. For instance, there may be some confusion as to what sources of impact should be included in assessments. Under the EICAT guidelines, impacts are defined as changes to the environment that reduce native biodiversity or alter ecosystem functioning to the detriment of a native species (Hawkins et al. 2015). Therefore, the inclusion of laboratory and mesocosm experiments presents a grey area when considering impact reports. In many cases, such experiments can be informative towards identifying the mechanism(s) through which an alien species impacts on native biodiversity and if native individuals are (potentially) suffering in their performance. However, laboratory and mesocosm studies will always be limited to revealing impacts of MC or MN, given that EICAT measures impacts based on native communities. Therefore, a decline of a natural population or its local extinction cannot be inferred from artificial settings, but such experiments may be useful to provide information about the mechanisms of impact. If assessors include laboratory- or mesocosm-derived sources of information in EICAT assessments, they should be clearly specified as such. Subjective judgement arises due to the interpretation of information; it emerges at the initial impact observation and continues to appear throughout the assessment procedure as each person involved in the process introduces their own form of subjective judgement (Figure 1). An ICAT assessor's subjective judgement is the primary form of uncertainty that we can minimise by clarifying concepts appropriate to assigning confidence scores and improving the consistency amongst assessors when using the two assessment schemes. Subjective judgement is also

Table 3. Major sources of uncertainty are identified in the IUCN (2020a) EICAT guidelines. Each source of uncertainty is relevant to both the EICAT and the SEICAT schemes; assessors must consider each source when assigning confidence scores. The two frameworks differ in their currencies used to measure impact (native populations [EICAT] versus human activities [SEICAT]). Therefore, contextual understanding of how these uncertainties may influence confidence scores is required. We highlight some aspects of how considering uncertainty may differ between EICAT and SEICAT below.

Source of uncertainty	For EICAT	For SEICAT
Presence of confounding effects		
Assessors must consider whether invasive species are drivers or passengers of the recorded impact (MacDougall and Turkington 2005; Bellard et al. 2016; Doherty et al. 2016; Blackburn et al. 2019). Further, they must consider whether there is any evidence for additional driver(s) of change causing the observed effects.	A major challenge in understanding the impacts of alien species is to disentangle the driving causes of biodiversity declines. Studies/reports range from being simple negative correlations between alien and native populations to before-after-control-impact studies, which may influence the data quality and interpretation (Kumschick et al. 2015; Christie et al. 2019). Often, observed correlations between alien species and native biodiversity loss are reported, but the cause of change is not the alien. For instance, the driving cause of change may be habitat modification that facilitates the alien, which works simultaneously to cause a negative impact on native species. An example would be an alien species that establishes and thrives in an urban area may not be the driver of native bird declines; rather, it could be that loss of resources due to urbanisation are causing the native birds to decline.	Alien species altering human activities should be considered in the same way as for EICAT, i.e. the assessor must ask the question "is the alien driving the recorded changes?" However, with SEICAT, given that people can directly communicate the reason for reducing or discontinuing an activity, it may be possible to get a better understanding of the causality behind the recorded impact magnitude with much higher confidence.
Study design		
The ICAT frameworks evaluate the different levels of impact, whereby each step change in a category reflects an increase in the order of magnitude of the particular impact so that a new level of organisation is involved (individuals, population, community). A study/report may describe an impact affecting one organisation level (e.g. performance of the individual), but gives no information of relevance to a higher level (e.g. if the impact reduces the population size). This aspect of uncertainty can be captured by considering the directionality of uncertainty for each impact report.	A study that is designed to assess the impacts of an alien on the individual performance, but does not capture any information about impacts to the population cannot be assigned higher than an MN. This does not mean that the true impact is not higher and thus, the impact report cannot be assigned a high confidence. High confidence scores can be assigned when the criterion of the magnitude higher than the one assigned has been investigated and found to be not true.	Reports relevant for SEICAT may not capture the true level at which the alien is causing an impact. Often, individual people are interviewed to obtain information on the alien's impacts and their experience may not represent the true state of the entire community.

Source of uncertainty	For EICAT	For SEICAT
Data quality and type		
Based on the ICAT guidelines (IUCN 2020a; Hawkins et al. 2015; Bacher et al. 2018), impacts can be classified as either *inferred* or *observed*. Assessors might misinterpret the purpose of this distinction, by considering observational studies as the only studies reporting *observed* impacts (i.e. this presents a form of linguistic uncertainty present in the guidelines). Rather, we assert that assessors should focus only on the quality of the report, given the invasion scenario.	Data used to derive EICAT scores are most frequently sourced from primary (i.e. not secondary referencing) and grey literature.	A decrease in the size of human activity may not be quantified but *inferred* from the evidence. For example, studies of diseases and parasites transmitted by aliens affecting humans will rarely report quantitatively on how they affect activities, although the authors may infer such effects. Data used to derive SEICAT scores are more likely to be anecdotal forms of evidence; personal communications and media reports often contain information of relevance to SEICAT. Although anecdotal evidence may be thought of as lower quality information (Bacher et al. 2018), given people can directly communicate behavioural changes in response to alien species, evidence deriving from such information may reveal the true state of impact. However, as SEICAT uses the change in activity size as the measure of impact, information on how many people participate in the activity and on the local population size, is required for high confidence reports.
Spatial scale		
Understanding if the impact has been recorded at a relevant spatial scale to capture the assigned impact magnitude accurately.	Assessors should ask if the study was conducted on a scale over which native species in the region of interest can be characterised. This requires a basic understanding of what constitutes a local population for a given species. A population can be difficult to delimit given suitable habitat for a species is usually fragmented across a landscape and further, populations are often managed within geopolitical jurisdictions. It may be particularly difficult to discern if an alien taxon causes a decline in population from available data with high confidence. Surveys may make it appear as if the population has declined, when in reality, species that are mobile may avoid areas when an alien species occurs.	The 'focal region' for SEICAT can be highly variable given densities of human communities. Impacts may be assessed on scales ranging from small villages to large metropolitan areas. Therefore, data about the number of people affected (i.e. those that reduce their activity) and the population size across the geographic scale should be included in the assessment when the information is available.

Source of uncertainty	For EICAT	For SEICAT
Temporal scale		
In earlier guidelines, the temporal scale at which the impact was previously recorded was not considered important since the ICAT frameworks assign magnitude, based on the highest impact (Hawkins et al. 2015; Bacher et al. 2018). However, it is important to assess how the "true" impact varies with the temporal scale. Uncertainty at the temporal scale is important in two aspects, whereby the study may not capture a relevant time period to detect maximum impact or the study provides an inaccurate snapshot that is not reflective of impact; for instance, the study focused on one season or was just too short to be able to capture any change.	Changes in native population size may be limited to only a short period (e.g. seasonally), which generally has little effect on reducing the overall population size. Assessors should consider that the impact report may provide only a snapshot in time and determine how relevant the impact is at a suitable temporal scale.	The same issues relating to temporal scale for EICAT are relevant for SEICAT.
Coherence of evidence		
At the individual impact report level, assessors must determine whether all the evidence points towards the same direction or whether evidence may be contradictory or ambiguous.	A study relevant for EICAT may present conflicting evidence based on different variables measured to determine impact. For instance, a study measuring more than one physiological variable of a native species in response to an alien may indicate both negative and positive effects (e.g. a reduction in height of plant growth but increase in leaf area size).	There may be conflicting reports from individuals as to whether an alien species is causing reductions in activity size.

relevant to uncertainties when summarising impacts at the species level (see below). Additionally, it must be considered how the written synthesis of ICAT assessments and the justifications of classifications may propagate linguistic uncertainty further.

Directionality of uncertainty

Uncertainty in impact assessments means that the true impact can be higher or lower than the one assigned. However, assessors may be confident that an impact magnitude is not lower than the one assigned, but could be higher (or vice versa). Thus, uncertainty can be asymmetrically distributed around the assessment value; it may be larger in one direction than in the other. This directionality aspect of uncertainty is currently not captured using the confidence scores, yet may provide important insight to impacts. Using EICAT as an example, it may be that the assessor assigns a minor impact score (MN) to an impact record that robustly demonstrates that an alien taxon affects the performance of individuals of a native species and, thus, is not negligible (i.e. not MC). However, given the study did not address (i.e. measure) whether the impact is causing a decline in the local population, it is not possible to know whether the 'true' impact caused by the alien taxon is higher (MO, MR or MV). For instance, studies that assess physiological responses of native species to invasive species do not necessarily relate such effects beyond the individual (i.e. effects on fitness resulting in declining populations) (Graham et al. 2012). Such cases are quite distinct to impact records that sought to quantify population responses to an alien species, yet found no evidence in support of population decline. Since documenting directionality in uncertainty related to each impact record may improve our overall understanding of potential impacts, this information may be particularly useful once several records of impact are obtained for a single species. Directionality in uncertainty, therefore, presents an important facet of uncertainty to recognise when using the ICAT schemes.

Uncertainties relevant at the species level

Presently, there is no consideration of uncertainty beyond the confidence score assigned to each impact report (IUCN 2020a; Hawkins et al. 2015; Bacher et al. 2018). The ICAT assessment schemes adopt the precautionary principle, whereby the overall classification of an alien taxon is based on the highest magnitude the taxon has reached. Therefore, there is no distinction between species with the same highest impact magnitude, regardless of whether there are few or many accounts of impact. It is also important to acknowledge additional sources of uncertainty which influence the ability to conduct assessments for alien taxa. As these uncertainties occur beyond the individual impact report level, they are not captured by the confidence score as currently described. Uncertainties due to the biases in the collected and the existing (or produced) impact reports contribute to the quality of final assessments, making them of direct relevance when comparing taxa based on ICAT scores. If alien taxa are compared, based on the highest magnitude they have been observed to cause (Hawkins et al. 2015; Bacher et al. 2018), it is pertinent that their highest impact magnitude caused in nature is documented and that these data have been adequately collected and assessed using the ICAT frameworks. It is likely that the more impact reports for an alien species that are produced, collected and assessed, the higher the chance that the maximum impact of the alien taxon will be detected and correctly classified. We recognise three important aspects to evaluate when looking at species-level comparisons: biases in existing data, data collection and data assessment.

Biases in the existing data

The availability of impact records will vary widely within (Evans et al. 2018b) and between taxa (Vilà et al. 2010) and will not necessarily be reflective of impact severity (Evans and Blackburn 2019). Indeed, of the larger taxonomic groups that have been assessed (amphibians, bamboos, birds), the majority of species are classified as data deficient (Evans et al. 2016; Kumschick et al. 2017; Canavan et al. 2019). As biases in biological records (Isaac and Pocock 2015) and within invasion biology are evident (Pyšek et al. 2008), some taxa will be disproportionately represented when conducting literature searches necessary for ICAT assessments. Gaps may be driven by funding availability with regions associated with higher economic status investing more in invasive species research (Pyšek et al. 2008; Bellard and Jeschke 2016). Further, it is usual for a lag time between an alien species becoming established and research effort on the species in the new environment to be observed (Essl et al. 2015; Lyons et al. 2019). Due to this and other reasons, such as the nature and duration of the peer-review process, the dissemination of impacts reports is often delayed (Vilà et al. 2019). Even well-studied species may not have impacts measured that can be easily transferred to ICAT scores, potentially rendering it data deficient or with few reports from which to derive an impact magnitude. For instance, alien species may be well documented to impact via various mechanisms (e.g. predation, competition) under laboratory settings, but poorly represented under natural conditions. Often, biological aspects, related to mechanisms of impact, are well-researched (e.g. dietary overlap, aggressive behaviour) for alien species, but the effects on native biodiversity are not measured, rendering such studies irrelevant to EICAT assessments. Our main suggestion regarding the bias in–or lack of–existing and relevant impact data, is to adapt future impact reports to EICAT criteria: studies should focus more on the changes in the impacted native populations (in natural conditions) and less on the alien populations.

Biases in the data collection

Inconsistencies amongst assessors may be driven from the initial stage of data collection (the literature review), with variation attributed to different search strategies employed by individual assessors (Kumschick et al. 2017). Reproducibility in science is a major topic of discussion (Baker 2016; Fanelli 2018) and how systematic literature searches are conducted is often poorly detailed leading to non-reproducible results (Cooper et al. 2018; Faggion and Diaz 2019). Assessors should be specific on how they conduct their literature searches to promote transparency, which in turn, will facilitate more robust inter-specific comparisons if data requires additional reviewing. Furthermore, documentation of the sources used to score species and the final data for assessments should be published with studies using the assessment schemes (see also Kumschick et al. 2020). Another major difficulty in data accessibility may arise from language barriers that affect the assessor's ability to collate impact reports. This is likely to be particularly applicable for SEICAT assessments, where it is expected that relevant reports of impacts on human well-being will, more often, be published in local languages. Discussions with people in local languages to identify socio-economic issues arising from the presence of alien species may facilitate assessments of species that are otherwise data deficient and help better understand additional human dimensions of biological invasions. Much regional evidence on the impacts of alien species will be confined to sources of information, such as local government reports and student theses.

Biases in the data assessment

Additional inconsistencies amongst assessors may occur because the criteria of the ICAT frameworks are interpreted and applied differently; individual assessors will inevitably introduce their own level of bias to the process of both assigning impact categories and confidence scores. A recent study by González-Moreno et al. (2019) found variation in scoring species' impacts amongst assessors for different assessment schemes, including EICAT. Although a level of subjectivity is inevitable, some of this uncertainty may be reduced through improvement in the protocol, such as the refinement of guidelines, which is already reflected in the succession of EICAT guidelines (Blackburn et al. 2014; Hawkins et al. 2015; IUCN 2020a). However, clarification about the changes and ensuring these are effectively communicated will be important to maximise consistency (see Volery et al. 2020, as the application of different versions of the guidelines may further lead to inconsistencies across different assessments. Conducting workshops, training sessions and developing online tools that help guide assessors through the process–giving examples where uncertainty is most likely to arise–might help reduce these uncertainties. Refinements can be made as feedback from assessors identifies more issues that require additional explanation or adaptation.

It is worth noting that, given the variation observed amongst assessors when applying scoring schemes (Matthews et al. 2017; González-Moreno et al. 2019), confidence scores are likely to be subject to a similar level of inconsistency. The accompanying probabilities (Table 1) to each of the three qualitative confidence scores are intended to reduce variation in the interpretation of terms. Indeed, differences in the interpretation of the descriptions of uncertainty are known to occur amongst individuals (Budescu and Wallsten 1985). Presenting linguistic descriptions and corresponding likelihoods can, therefore, reduce the misinterpretation of confidence scoring (Budescu et al. 2014). The degree of consistency amongst assessors when assigning confidence scores should be examined to determine whether refining the expressions of confidence is necessary to reduce potential misinterpretation.

Conclusions

To produce robust impact assessments and facilitate the comparison of impacts between taxa, procedures must adequately account for uncertainties (McGeoch et al. 2012). We have highlighted key sources of uncertainty to consider when conducting the ICAT assessments and emphasised the importance of acknowledging all forms of uncertainty even when not directly relevant to informing confidence scores. As uncertainties propagate throughout the various stages of any ICAT assessment (deriving from both the impact measurer/reporter and the ICAT assessor), it is important that they are clearly defined and acknowledged to improve the overall impact assessment procedure. However, it should be noted that it will be impossible to address all types of uncertainty in any framework due to unforeseeable changes in the system under investigation or other unknown unknowns.

As the ICAT frameworks become more readily applied across different taxonomic groups, uncertainties must be appropriately considered to improve the overall ability to correctly classify impacts. By improving the consideration of uncertainty under the ICAT guidelines, we may increase the functionality of the tool for researchers and practitioners. All other things being equal (i.e. control effort, cultural values, positive impacts etc.), species that will be the best candidates for prioritisation will be those that have the highest impact with high corresponding confidence.

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MAcroecological Framework for Invasive Aliens (MAFIA): disentangling large-scale context dependence in biological invasions

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Abstract

Macroecology is the study of patterns, and the processes that determine those patterns, in the distribution and abundance of organisms at large scales, whether they be spatial (from hundreds of kilometres to global), temporal (from decades to centuries), and organismal (numbers of species or higher taxa). In the context of invasion ecology, macroecological studies include, for example, analyses of the richness, diversity, distribution, and abundance of alien species in regional floras and faunas, spatio-temporal dynamics of alien species across regions, and cross-taxonomic analyses of species traits among comparable native and alien species pools. However, macroecological studies aiming to explain and predict plant and animal naturalisations and invasions, and the resulting impacts, have, to date, rarely considered the joint effects of species traits, environment, and socioeconomic characteristics. To address this, we present the MAcroecological Framework for Invasive Aliens (MAFIA). The MAFIA explains the invasion phenomenon using three interacting classes of factors – alien species traits, location characteristics, and factors related to introduction events – and explicitly maps these interactions onto the invasion sequence from transport to naturalisation to invasion. The framework therefore helps both to identify how anthropogenic effects interact with species traits and environmental characteristics to determine observed patterns in alien distribution, abundance, and richness; and to clarify why neglecting anthropogenic effects can generate spurious conclusions. Event-related factors include propagule pressure, colonisation pressure, and residence time that are important for mediating the outcome of invasion processes. However, because of context dependence, they can bias analyses, for example those that seek to elucidate the role of alien species traits. In the same vein, failure to recognise and explicitly incorporate interactions among the main factors impedes our understanding of which macroecological invasion patterns are shaped by the environment, and of the importance of interactions between the species and their environment. The MAFIA is based largely on insights from studies of plants and birds, but we believe it can be applied to all taxa, and hope that it will stimulate comparative research on other groups and environments. By making the biases in macroecological analyses of biological invasions explicit, the MAFIA offers an opportunity to guide assessments of the context dependence of invasions at broad geographical scales.

Keywords
climate, colonisation pressure, geographic range, habitats, invasion stages, non-native, propagule pressure, residence time, species traits, vertebrates

Introduction

Macroecology as a tool to study biological invasions

Invasive alien species introduced by humans to areas beyond their native distributions (Richardson et al. 2000; Blackburn et al. 2011) are a major threat to the world's biodiversity and economy (McGeoch et al. 2010; Blackburn et al. 2014; Brondizio et al. 2019; Pyšek et al. 2020). The numbers of alien species (and the subset of them that are invasive) are increasing rapidly world-wide and there is no sign of deceleration (Hulme et al. 2009; Seebens et al. 2017, 2018). Ongoing globalisation (Perrings et al. 2010), increasing levels of ecosystem modification, and climate warming (Walther et al. 2009) are expected further to accelerate alien species introductions, naturalisations and impacts (Essl et al. 2011a; Hulme 2017; Haeuser et al. 2018).

Research in invasion science over the last 30 years has focussed on questions aimed at improving predictions about which species will form invasive populations, and where these will occur (Drake et al. 1989; Rejmánek 2000; Kolar and Lodge 2002; Pyšek and Richardson 2007). These questions were motivated by the desire to prevent and mitigate the multiple environmental and socioeconomic impacts of alien species. This body of research has given us a better understanding of the importance of context dependence in biological invasions (Sapsford et al. 2020) and of the interactions among the multiple key drivers that influence the outcome of invasion (e.g. Higgins and Richardson 1998; Simberloff and von Holle 1999; Blumenthal 2006; Sol et al. 2008b; Pyšek et al. 2009a, 2015). This complexity is now fully appreciated and has been addressed by the development of numerous hypotheses and concepts (Catford et al. 2009; Enders et al. 2018, 2020; Jeschke and Heger 2018), theoretical frameworks (e.g. van Kleunen et al. 2010a; Gurevitch et al. 2011; Strayer 2012; Hulme et al. 2020; Wilson et al. 2020) and statistical models of macroecological patterns (e.g. Rouget and Richardson 2003; Thuiller et al. 2006; Wilson et al. 2007; Küster et al. 2008, 2010; Pyšek et al. 2009a, b, 2015; Castro-Díez et al. 2011; Schmidt and Drake 2011; Dawson et al. 2017; Essl et al. 2019). Since multiple factors determine invasion success and impacts, invasions can only be understood in the specific context in which they occur (Novoa et al. 2020; Sapsford et al. 2020). For this reason, studies need to be designed to consider the roles of these multiple factors to ensure that meaningful interpretations of outcomes can be made.

Given that thousands of alien species have established populations and spread across previously unoccupied environments, we are now in a position to (and indeed urgently need to) develop an understanding of the macroecological processes that underpin biological invasions. Macroecology is the study of large-scale (i.e. from hundreds of square kilometres to global in terms of space; from decades to centuries in time; and for large numbers of species or a broad range of taxonomic groups) patterns in the distribution and abundance of species, and the processes that determine those patterns (Gaston and Blackburn 2000; McGill 2019). To qualify as macroecological, a study needs to meet the scale requirement in at least one dimension; in invasion science, it is rare that studies conform to this definition in all three dimensions (but see Seebens et al. 2017, 2018) as can be inferred from the overview of studies presented in Appendix I.

Macroecology seeks to identify generality in complex ecological systems through comparative study of their properties, such as species assemblages or geographic ranges; it therefore addresses issues such as spatial and temporal variation in species richness, interspecific variation in abundance and range size, and how biological and environmental properties influence these aggregate entities (McGill 2019). For biological invasions, exploring macroecological patterns in the invaded range is a natural extension of research aiming to understand why some aliens become abundant and widespread while others do not, and why some sites accrue more alien species than others.

Attempts to associate biological traits and environmental characteristics with broad-scale patterns in the distribution, abundance, and richness of alien species have built on decades of macroecological research on native species. The assumption underlying this approach is that the ecologies of alien and native populations will be determined by the same drivers, albeit not necessarily in exactly the same way. For example, physiological tolerances of individuals to temperature or precipitation in the native range can be retained for many species in the alien range and climatic niche shifts are quite rare among terrestrial plant invaders (Petitpierre et al. 2012, but see Hulme and Barrett 2013; Early and Sax 2014; Atwater et al. 2018; Datta et al. 2019). Similarly, unless species' life histories change when they move to a new range, effects of these

Table 1. Summary of 102 studies addressing macroecological patterns in biological invasions, with respect to the factors that are studied. Only studies meeting at least one of the following criteria were selected: address a large scale in terms of space (from hundreds of square kilometres to global), time (from decades to centuries) or taxonomy (for large numbers of species or a broad range of taxonomic groups). See Appendix I for the list of studies on which these statistics are based. Only six studies (5.9% of the total examined) considered all but one of the seven factors distinguished, 10 studies (9.9%) explored the effect of five factors, and 13 (12.9%) addressed four factors. The vast majority of studies (72, i.e. 71.3%) considered three factors or fewer.

		Factors investigated						
Number of papers	**Number of factors studied in combination**	**Alien species traits**	**Habitats and climate in native range**	**Habitats and climate in alien range**	**Socioeconomic factors**	**Colonisation and propagule pressure**	**Residence time**	**Invasion stages**
0	**7**							
2	**6**	×	×	×	×	×		×
2	**6**	×	×	×	×	×	×	
1	**6**	×	×	×	×		×	×
1	**6**	×	×		×	×	×	×
4	**5**	×	×	×	×		×	
2	**5**	×	×	×		×		×
1	**5**	×	×	×		×	×	
1	**5**	×		×	×		×	×
1	**5**	×	×			×	×	×
1	**5**		×	×	×	×		×
2	**4**	×	×			×		×
2	**4**	×	×		×	×		
2	**4**	×	×			×	×	
2	**4**	×	×				×	×
1	**4**	×	×	×	×			
1	**4**	×		×		×		×
1	**4**	×		×	×			×
1	**4**	×				×	×	×
1	**4**	×			×	×	×	
6	**3**	×				×		×
4	**3**	×		×		×		
3	**3**	×	×	×				
3	**3**	×	×					×
2	**3**	×	×		×			
2	**3**	×		×	×			
2	**3**		×	×		×		
1	**3**	×		×				×
1	**3**	×		×			×	
1	**3**	×	×			×		
1	**3**	×			×			×
8	**2**	×		×				
6	**2**	×						×
3	**2**	×	×					
2	**2**	×				×		
2	**2**	×			×			
1	**2**	×					×	
1	**2**		×	×				
1	**2**				×	×		
1	**2**				×			×
19	**1**	×						
1	**1**			×				
1	**1**					×		
102		**93**	**40**	**41**	**27**	**37**	**19**	**34**

traits on macroecological patterns in the native range should be maintained in the alien range. Plant species that are good competitors should retain this ability in the invaded range; some will become even better competitors due to enemy release (e.g. Keane and Crawley 2002), and some will become invaders by behaving in the same way as in their native range (Firn et al. 2011; Parker et al. 2013; Colautti et al. 2014).

The assumption that the ecologies of alien and native populations will be determined by the same drivers might not hold if the traits of conspecific individuals in the alien and native populations differ, e.g. due to founder effects, or evolution, or if resource limitation differs, e.g. when species move from an N-limited to a light-limited system. However, and more fundamentally, the identity and location of alien populations are determined by human activities, in a manner that is of a different order and type to that for native populations (Wilson et al. 2009). Thus, while human activities undoubtedly profoundly affect macroecological patterns in native populations (e.g., Gaston and Blackburn 2003; Faurby and Araújo 2017), the macroecological patterns and processes of alien populations are more strongly mediated by anthropogenic influences (Richardson et al. 2000; Blackburn et al. 2011). For example, similar factors seem to influence the native and alien range sizes of pine species (Richardson and Bond 1991), but alien range sizes are additionally profoundly influenced by anthropogenic factors (McGregor et al. 2012; Procheş et al. 2012).

Context dependence in biological invasions: evidence from literature

With respect to alien abundance and distribution, a growing literature shows that some species traits are generally associated with the capacity to form self-sustaining populations that spread from points of introduction (i.e. invasive *sensu* Pyšek and Richardson 2007; van Kleunen et al. 2010b). For example, Pyšek et al. (2009a, 2015) used a source-area approach (as defined by Pyšek et al. 2004b) to show that the success of Central-European plant species introduced to other areas of the world results from the interaction of their distribution in the native range, habitats they occupy there, their biological traits, propagule pressure as a consequence of human use, and residence time. Jeschke and Strayer (2006) showed that invasiveness was related to native range size for mammals, birds and freshwater fish alien to Europe and North America. Recent studies revealed that fast life-history strategies, that allow for rapid increase in population size, characterise successful alien mammals (Capellini et al. 2015), reptiles (Allen et al. 2017) and plants (Richardson and Rejmánek 2004; van Kleunen et al. 2010b), while alien birds rather adopt slow strategies (Sol et al. 2012). In birds and mammals, a generalist life-style characterised by behavioural flexibility and larger trait variation is associated with successful establishment (Sol et al. 2008a, 2012; González-Suárez et al. 2015), while in insects specialised species seem to be more successful (Rossinelli and Bacher 2015). At the global scale, Dyer et al. (2016) showed that variation in the alien geographic range size of birds was positively associated with native geographic range size, while there was no effect of either body mass or ecological specialisation controlling for other variables. Environmental factors, including climate and habitat match between source and target regions (Thuiller et al. 2005; Hejda et al. 2009; Kalusová et al. 2013) are also likely to be important for invasiveness. For example, Duncan et al. (2001) showed that alien bird species with larger geographic ranges in Australia had a larger area of climatically suitable habitat on the continent.

For plants, several studies have addressed the role of traits in invasions in concert with other factors codetermining invasiveness (e.g. Herron et al. 2007; van Kleunen and Johnson 2007; Gravuer et al. 2008; Küster et al. 2008), but none of them simultaneously: (i) used a global dataset, (ii) analysed different stages of invasion process, (iii) took characteristics of the native and introduced ranges, such as its size, climate or habitat affiliation, into account together with species traits, and (iv) included the effect of residence time and propagule pressure (Table 1, Appendix I). Thuiller et al. (2006) studied how species traits, characteristics of the native and introduced ranges, residence time, and human usage shape the distribution of invasive alien plant species, but they based their analysis on the invading species pool in the target region of South Africa. Hamilton et al. (2005) analysed the role of several species traits in invasions at different spatial scales but, while they accounted for phylogenetic effects, they did not address different stages of the invasion process, and nor did they consider distributional characteristics in native ranges. Van Kleunen et al. (2007) studied different invasion stages by analysing introduction through horticultural trade and subsequent naturalisation separately, and employed distributional characteristics together with species traits, but only for species within the family Iridaceae. Gravuer et al. (2008) considered human and biogeographic factors as well as traits and three invasion stages, but only for a single genus (i.e. *Trifolium*). Küster et al. (2008) considered distributional characteristics and focused on important interactions among ecological characteristics for one invasion step. Dawson et al. (2009) addressed multiple stages of alien plant invasions for multiple genera in concert with a number of traits, but only for invasions in the tropics. Essl et al. (2011b) explored interactions among native range size, climate match, habitat affiliations, colonisation pressure and propagule pressure, but only for conifer naturalisations. McGregor et al. (2012) examined the role of species traits, biogeographic attributes (including native range size) and human factors on the likelihood of introduction and naturalisation of pine species in separate regions in the Northern and Southern hemispheres.

The need for a formal framework addressing large-scale context dependence in biological invasions

Despite advances in our understanding of invasion dynamics as discussed above, models in the literature that seek to elucidate the determinants of naturalisation and invasion success of alien species from a macroecological perspective (regional to global) rarely include a complete suite of factors that have been acknowledged as key elements in the process (Table 1, Appendix I). Yet, the application of models that analyse multiple factors in concert to determine their relative importance is crucial to address properly the role of biological traits promoting species invasiveness. Importantly, because of the context dependence of invasions, the real effect of a particular trait can be confounded, for example, if a species possessing a trait is introduced more frequently, or has had a longer time to adapt to, or take advantage of, conditions in the invaded area. Similarly, studies that ignore effects of, for example, habitats in which the species occurs either in the native and/or invaded range may overestimate the role of biological traits, which in turn may result in spurious predictions (Pyšek et al. 2015; Duncan et al. 2019). At the same time, factors interacting with the species traits themselves, such as propagule pressure and residence time, play important roles in determining the outcome of particular invasions.

Here, we develop a formal framework to explore the context dependence of invasions at broad geographical scales, and to increase awareness that macroecological analyses can yield biased results if these issues are ignored. We discuss different aspects of the framework by using examples of previous macroecological studies mostly based on plants and birds, as these two groups have been studied in most detail from this perspective. However, we believe that the framework is applicable to a broad range of taxa, and we hope that it will stimulate comparative research in other groups and environments.

MAcroecological Framework for Invasive Aliens (MAFIA): the rationale

At the core of the MAFIA is the notion that three classes of factors and their interactions explain invasions: (i) alien species traits, (ii) location characteristics, and (iii) factors related to introduction events (Fig. 1). This rationale has been mostly used in the animal invasion literature (e.g. Duncan et al. 2003) but is generally applicable across taxa. Event-related factors include propagule pressure and other human factors (e.g. pathways, and date of introduction that determines the residence time), but also, for example, the season during which the species is introduced (summer, winter). These interactions, with the exception of climate matching (which is often treated as a main factor instead of an interaction), have rarely been considered to date. However, an introduction of an alien species with traits suited to establishment in the local abiotic environment and biotic community, with a sufficiently large founding population size, will still fail if, e.g. the resource availability at the time of introduction is insufficient (i.e. a mismatch of location and event characteristics; Fig. 1). For example, it has been shown that propagule pressure only emerges as a strong predictor of invasion success of pest insects alien to Europe if the interaction with host availability and the degree of climate matching is taken into account (Bacon et al. 2014, see also Duncan 2016). Failure to recognise and explicitly incorporate interactions among the main factors clearly impedes our understanding of which macroecological invasion patterns are shaped by the environment, and of the importance of interactions between the species and their environment.

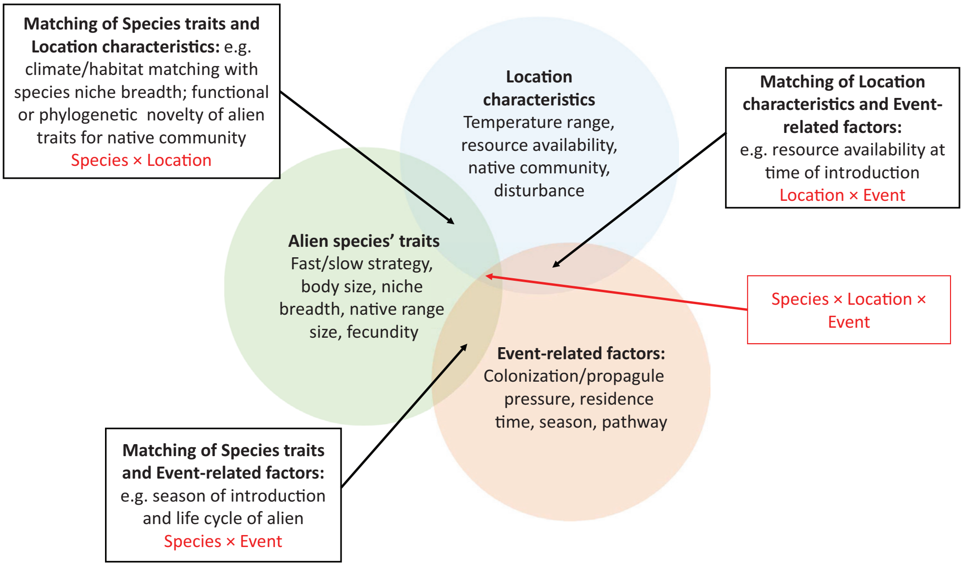

Figure 1. A proposed comprehensive typology of factors and their interactions (represented by intersections in the Venn diagram) that explain invasions: Alien species traits, Location characteristics, and Event-related factors. Intersections between two (or all) these main classes of factors denote situations where their combinations determine invasions, e.g. the climate at a location needs to match the niche requirements of the alien to result in a successful invasion. For a successful invasion, all factor classes and their interactions need to be favourable (Species × Location × Event), i.e. a species with suitable traits is introduced to a suitable habitat in a region with matching climate and the propagule numbers arriving during that introduction event are enough to allow for successful establishment, possibly resulting in invasion.

Another key notion is that the macroecological processes of biological invasions are underpinned both by biological and environmental characteristics (that are used to explain the distribution, abundance, and richness of alien species in their native ranges), and by human factors that influence the probability and magnitude of transport and introduction of alien species, and whether, where, and when a species is given the opportunity to succeed. Such human factors include the origin, destination, and means by which species are transported (Sinclair et al. 2020), the locations, identities, numbers of introduction events, numbers of species (colonisation pressure; Lockwood et al. 2009), individuals or propagules (propagule pressure; Lockwood et al. 2005) being introduced, and residence time (Forcella and Wood 1984; Rejmánek 2000; Pyšek and Jarošík 2005; Wilson et al. 2007; Williamson et al. 2009; Gassó et al. 2010), as well as spatial (by widespread dissemination or abundant plantings; Hanspach et al. 2008) and temporal (by long history of cultivation; Rouget and Richardson 2003) variation in these factors.

The awareness of these considerations is at the heart of the MAFIA, depicted in Fig. 2. In macroecological analyses, invasion science aims to explain the occurrence and success of alien species in regional floras and faunas (i.e. their richness, diversity, distribution, abundance, as well as spatial and trait relationships) by using a number of factors related to species traits, and both environmental- and socioeconomic,

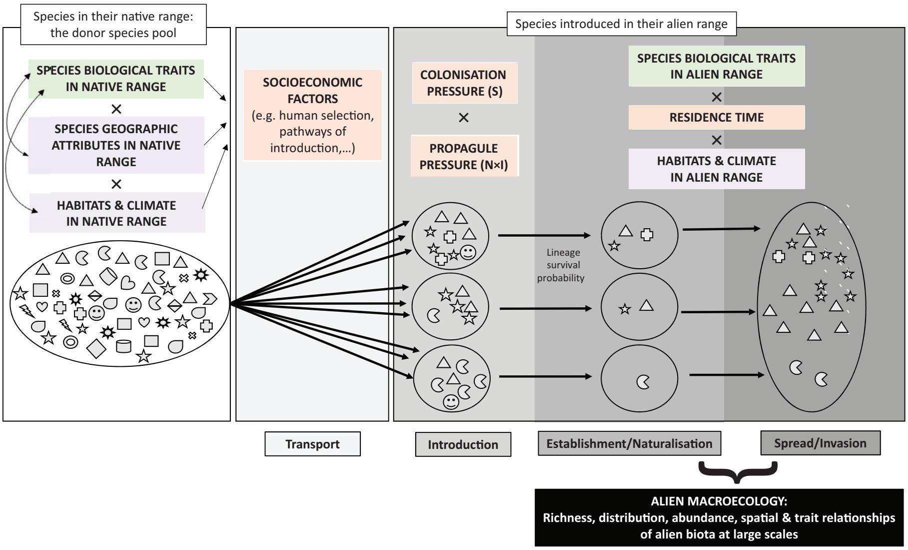

Figure 2. The Macroecological Framework for Invasive Aliens (MAFIA). The classes of factors introduced in Fig. 1 are distinguished by using the same colour codes, i.e. Alien species traits (including their values in the native range) in green, Location characteristics in blue and Event-related factors in orange, and individual factors are shown as operating along the introduction-naturalisation-invasion continuum (INIC). Species geographic attributes and Habitat & Climate in native range are in a different colour (purple) because they influence both Alien species traits and Event-related socioeconomic factors (by influencing the probability that a species will be transported by humans from its native range) but are not directly related to the Location characteristics in introduced range (i.e. to where the species will be introduced). Lineage survival probability is the probability that any one of the introduced individuals leaves a surviving lineage (i.e. founds a population). S, number of species introduced; N, number of individuals introduced per introduction event; I, number of introduction events. See text for explanation.

i.e. human-related, characteristics (Fig. 2). The interaction 'Species biological traits × Geographic attributes × Habitats × Climate × Socioeconomic factors (Introduction pathways and Site/Propagule & Colonisation pressure/Residence time)' needs to be considered in combination to make progress in explaining and predicting plant and animal naturalisation and invasion success, as well as impacts.

Underpinning the MAFIA is the well-established unified framework for biological invasions (Blackburn et al. 2011) and its predecessors for plant (Richardson et al. 2000) and animal invasions (Williamson and Fitter 1996). These frameworks recognise that the invasion process can be conceptualised as a sequence of stages that a species has to pass through to become introduced from its native range and to become alien in the new range, and that each stage acts as a filter that potentially restricts the species that are exposed to each following stage in the sequence (Blackburn et al. 2011; Richardson and Pyšek 2012). The MAFIA thus builds on the introduction-naturalisation-invasion continuum (INIC – Richardson et al. 2011) concept, and some others such as the TEASI framework that formalised the different steps of invasion process based on the notion that factors important at previous steps percolate through to later steps (Leung et al. 2012).

The MAFIA, by explicitly mapping the factors that influence macroecological patterns in alien species onto the invasion pathway, not only helps to identify how anthropogenic effects interact with species traits and environmental characteristics to determine observed patterns in alien distribution, abundance, and richness (amongst other features), but also clarifies why overlooking anthropogenic effects can lead to spurious conclusions. It has been repeatedly shown that different factors influence different stages of the invasion process (Kolar and Lodge 2001; Moodley et al. 2013); socioeconomic factors are suggested to be generally important early in the invasion process, whereas biogeography, ecology, and evolution play more important roles at later stages (Williamson 2006; McGeoch et al. 2016). Thus, if we cannot determine exactly at which stage of the invasion process each analysed taxon is, or if we merge the alien species for analyses regardless of their status (casual, naturalised or invasive; *sensu* Blackburn et al. 2011 and Richardson et al. 2011), it becomes impossible to identify the importance of invasion drivers. Another general problem associated with macroecological analyses is that the quality of data available for large numbers of species comprising whole floras and faunas is often low, and some of the factors thus remain unconsidered (Pyšek et al. 2009a; Gioria et al. 2012, 2019; Kueffer et al. 2013) (Appendix I). The MAFIA recognises that understanding this context is vital to understanding invasion outcomes.

Because of context dependence, the factors mediating the outcome of invasion processes can act to bias some analyses. For example, factors concerning introduction events, e.g. propagule and colonisation pressure (Lockwood et al. 2005; Simberloff 2009) and residence time (Rejmánek 2000; Castro et al. 2005; Pyšek and Jarošík 2005; Williamson et al. 2009; Pyšek et al. 2011), can confound analyses of the effect of alien species traits. Both propagule and colonisation pressure and residence time have fundamental effects on the outcome of invasion (see below) and set the stage upon which the differences in biological traits act in influencing the invasion success of a species (Lonsdale 1999; Colautti et al. 2006; Catford et al. 2009; Fig. 2). However, if the goal is to explore the alien species traits by location interaction (e.g. to assess which types of species tend to become invasive where), it would be inappropriate to compare species with different event characteristics, such as species that were provided with a different periods of time to adapt to the novel environment (residence times) and/or were introduced in different quantities (propagule pressure) (Wilson et al. 2007; Pyšek et al. 2009b, 2015). This is particularly the case if there is covariance between alien species traits and introduction events (e.g. reptiles that are easier to breed are more common in the pet trade; van Wilgen et al. 2010), or covariance between locations and introduction events (e.g. plants tend to be more frequently introduced to lowlands areas than mountains; Alexander et al. 2011).

Elements of the framework

In this section we explore in detail how individual factors captured by the MAFIA, and their interactions, affect the outcome of invasions at the macroecological scale, and what is the evidence in literature for the role they play. We address these issues along the stages of the invasion process, from transport and introduction to naturalisation and invasion, with discussion on effects of propagule pressure and climate integrated within these sections. The importance of the context brought about by residence time, alien species traits and habitats is discussed in separate sections. For each element of the framework, we indicate to which of the three classes of factors (Figs 1, 2) it is related (Traits – Aliens species traits; Location – Location characteristics; Event – Event-related factors).

Species in their native range: the donor species pool [Traits]

Not all species have alien populations but, in principle, the size of the alien species pool (i.e. alien species richness) can to a large degree be attributed to the size of the donor species pool, dispersal success (incl. human transport, human commensalism and perceived utility) and the fit to the new environment in terms of environmental matching between donor and recipient regions (Karger et al. 2016). It therefore follows that, at the global level, observed aliens are a subsample of the world's native species pool (though exceptions could occur where alien species hybridise and speciate in their new ranges; Ellstrand and Schierenbeck 2000; Levin 2003; Flores-Moreno et al. 2015; Brandenburger et al. 2019). Which species from this pool get entrained on the invasion pathway depends on the interaction of the socioeconomic motivations or determinants for translocation, and the distribution and characteristics of the species (Hulme et al. 2008; Essl et al. 2015; Sinclair et al. 2020). These latter features affect the probability that a species is selected (deliberately or otherwise) for transport. For example, a large native geographic range has been suggested to be among the best determinants of invasion success in seed plants (Rejmánek 1996; Goodwin et al. 1999; Hui et al. 2011), but this factor may affect invasiveness in several ways. First, having a large native range increases the probability of a species being selected for transport (Blackburn and Duncan 2001a) and therefore experiencing high propagule pressure (Cassey et al. 2004c). Second, the traits that allowed the species to achieve a large native range might also allow it to have a large alien range (Booth et al. 2003; Pyšek et al. 2009a; Dyer et al. 2016). Further, a large native range has been proposed to increase the probability that a species will sample a broader range of habitats and becomes better equipped for competition and novel interactions with species in the introduced ranges (Sax and Brown 2000). Nevertheless, this is not true for all taxa. For example, for parrots it has been shown that large geographic range size is a strong predictor of which species are transported outside their native ranges, and which transported species are subsequently introduced, but not which introduced species succeed in establishing (Cassey et al. 2004b); the net result of this, however, is that alien parrots tend to be those with large native ranges.

The biogeographic location of the native range also matters, as not all species pools are equally likely to be sampled for potential aliens. For example, bird species introduced in the 19th and early 20th centuries came primarily from Europe, were more likely to be introduced to regions of the British Empire, and were more likely to concern species in families of game birds (e.g. pheasants, ducks, and pigeons). These patterns arise because introductions in this period were largely driven by the deliberate activities of Acclimatisation Societies – organisations specifically aimed at promoting introductions of beneficial species, such as game animals, and which were especially active in British colonies (di Castri 1989; Pipek et al. 2015; Dyer et al. 2017).

The relative size and age of species pools in species' native versus alien range also helps to indicate potential evolutionary imbalances (Fridley and Sax 2014). Alien species that have evolved over a longer period of time and in a more competitive and stable environment (e.g. mainland vs islands) tend to have higher competitive ability than co-occurring native species. As plant invasions in the Czech Republic, New Zealand, and eastern North America demonstrate (Fridley and Sax 2014), species from regions with highly diverse evolutionary lineages are more likely to become successful invaders in less diverse regions.

Disentangling the relative roles of species traits and properties of native geographic ranges in the context of anthropogenic effects is thus a fundamental task for invasion science. Knowing the extent to which the characteristics of the native range of a species can explain and predict its invasion, and under what contexts, would improve the precision of prediction systems used in weed-risk assessment (e.g. Pheloung et al. 1999; Weber et al. 2009).

Transport and introduction: socioeconomic factors, propagule pressure, and colonisation pressure [Event]

There are at least three important consequences of the intersection of the socioeconomic motivations for introduction of aliens from the native species pool. First, the identities of introduced species are a non-random subset of all species that could have been introduced (see also Karger et al. 2016; Maurel et al. 2016). This can have significant consequences for our perceptions of the kinds of species that become invasive, and for our interpretation of the resulting macroecological patterns. For example, introduced wildfowl species are larger-bodied, on average, than those wildfowl that have not been introduced (Blackburn and Duncan 2001a). It follows that established wildfowl species are likely also to be large-bodied, and that the macroecological patterns expressed by alien wildfowl will be a consequence of how body size might influence the distribution and abundance of these species. It is important to factor such non-randomness into any analysis of later stages of the invasion process, including macroecological analyses, or incorrect conclusions about processes are likely to be reached (Cassey et al. 2004a; Pyšek et al. 2009a; Hui et al. 2014).

Second, sites to which species are introduced also depend on interactions between introduction pathways and the donor species pool. Again, incorrect conclusions about processes are likely to be reached without factoring in this context, especially as native species are not distributed randomly with respect to evolutionary history or associated traits, and hence pathway locations and species-pool composition interact. For example, socioeconomic changes in societies around the world have driven changes in the reasons for, and the geographical dimensions of, human-induced movement of bird species (Blackburn et al. 2009; Dyer et al. 2017); the source regions, destinations and identities of introduced species have shifted significantly in recent decades. Bird introductions are now driven largely by the pet trade, especially in rapidly developing economies in the Middle and Far East. This may explain why alien bird species follow Bergmann's rule (Fig. 3), such that the average body mass exhibited by alien bird assemblages decreases toward the equator (Blackburn et al. 2019). Alien bird species appear to follow closely the relationship exhibited by native birds (Olson et al. 2009), but this is to a large extent a consequence of the fact that large-bodied species have been introduced at higher latitudes, on average, than small-bodied species, followed by latitudinal variation in establishment success that is independent of body mass (Blackburn et al. 2019). Historical introductions driven by Acclimatisation Societies tended to prefer large-bodied species and higher latitudes than recent introductions, which tend to be cage bird species such as parrots and estrildid finches, and to occur at lower latitudes (Dyer et al. 2017).

Third, patterns of selection from native species pools along different introduction pathways will affect the numbers of species (colonisation pressure; Lockwood et al. 2009) and individuals (propagule pressure; Lockwood et al. 2005; Simberloff 2009) that are introduced to different locations around the world. Models have shown repeatedly that the random selection of individuals from a species pool with realistic population structure will result in more species, and more individuals per species, in larger samples, as may occur for example in species transported in ballast water (Lockwood et al. 2009). More abundant species are more likely to be transported in this way. The same patterns hold for planned introductions (Cassey et al. 2004c). Variations in the levels of invasion among recipient communities, habitats or regions could be, in some cases, simply due to differences in the numbers of arriving aliens (Williamson 1996).

Lonsdale (1999) and Duncan et al. (2019) showed for plants and birds, respectively, that alien species richness at a location is a function of the number of species introduced to the location and the probability that any given introduced species establishes a viable population. Duncan et al. (2019) further showed that, for a closed system such as an island, establishment in turn is a function of the number of individuals introduced, and the probability that any one of those individuals leaves a surviving lineage (lineage survival probability; Fig. 2). Thus, alien species richness is primarily a consequence of the introduction process, and specifically colonisation and propagule pressures. These anthropogenic effects are fundamental to understanding the invasion process, and must be explicitly considered if the alien macroecological patterns that result are to be interpreted correctly (this is particularly notable early on in the invasion process, e.g. when looking at factors that determine the site of first detections; Huang et al. 2012). As an analogy, attempting to understand the drivers of alien species richness by performing a manipulative experiment in which the number of species added to each treatment was unknown would be unwise. It is similarly difficult to unravel the

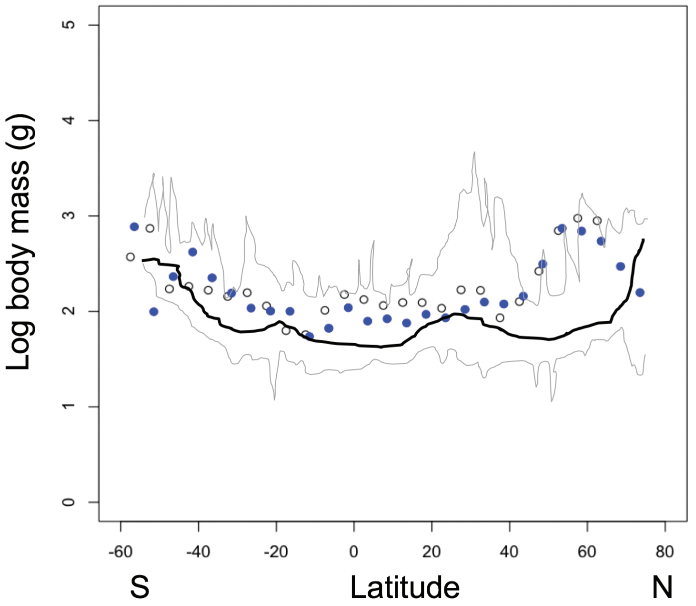

Figure 3. Latitudinal variation in body mass for introduced (black, unfilled circles) and established (blue, filled circles) alien bird species worldwide, together with the mean (thick line) and range (thin line) of the relationship for native bird species. See text for details. Data from Blackburn et al. (2019) and Olson et al. (2009).

drivers of alien species richness in natural experiments where colonisation pressure is unknown. Duncan et al. (2019) carried out simple sensitivity analyses to show that by far the strongest determinant of alien species richness in their model was colonisation pressure; they show that increasing propagule pressure or lineage survival probability will increase alien species richness, but only up to an asymptote imposed by colonisation pressure. All else being equal, increasing colonisation pressure allows alien species richness to continue to grow as a linear function. While this model technically applies to closed systems, and it is not clear whether it applies to all taxa, most alien bird species at least do not spread far from points of introduction (Dyer et al. 2016). The implication is that for birds in most broad locations, colonisation pressure is a much more influential driver of incursion than spread. For many plant invasions, however, new population foci create potent propagule pressure sources that drive invasions much more quickly than the size and other dimensions of the source population, as demonstrated, for example, by the invasion of *Opuntia stricta* in Kruger National Park, South Africa (Foxcroft et al. 2004).

Data on colonisation pressure are rarely available for taxa other than vertebrates (i.e. alien species that were intentionally released outside of captivity, but see also insects released for biocontrol; Rossinelli and Bacher 2015). Quantification of colonisation pressure requires data on the number of species introduced in total, but data on failed invasions are generally scarce (but see Diez et al. 2009). Propagule pressure is also extremely difficult to measure at a large scale for plants (Fig. 4). Therefore, vari-

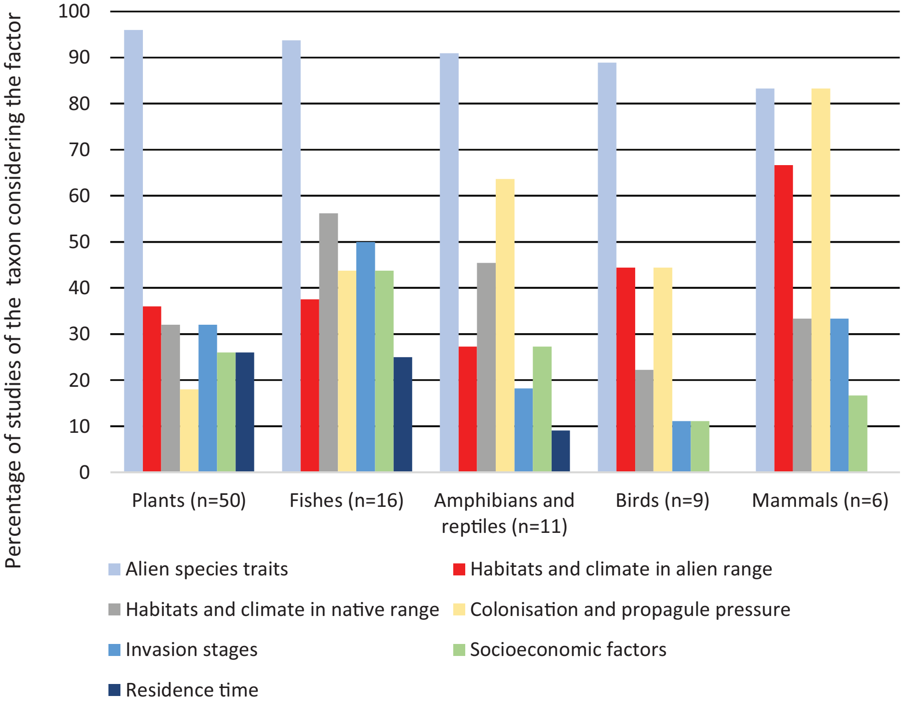

Figure 4. Overview of the frequency of factors included in 92 macroecological studies of plants and vertebrates. The figure shows that the majority of studies in all taxonomic groups focus on traits, but that there is a difference among plants and animals in the frequency of studies addressing propagule and colonisation pressure, that is greater in the latter. On the contrary, plant studies more commonly address the role of residence time. Based on studies listed in Appendix I ; note that studies on invertebrates, fungi, and cross-taxonomic studies are not shown here (n = 10).

ous quantitative surrogates have been used to attempt to capture variation in these key parameters. For example, the number of visitors to nature reserves (Lonsdale 1999; McKinney 2002), human population size or density (McKinney 2001, 2002; Pyšek et al. 2002; Taylor and Irwin 2004), the amount of trade and economic activity (Taylor and Irwin 2004; Pyšek et al. 2010; Essl et al. 2011a), species availability on the market (Dehnen-Schmutz et al. 2007a, b), the number of cultivars developed (Canavan et al. 2017), the type of land use such as the proportion of agricultural land and pastures (Chytrý et al. 2008b), or the number and distribution of botanic gardens (Hanspach et al. 2008; Hulme 2011) have all been used as proxies for propagule pressure in plants.

Despite the difficulty in accounting accurately for propagule pressure, it has been convincingly demonstrated that this factor, both over space (by widespread dissemination, abundant plantings, extensive release) and time (by long history of cultivation or captivity) fundamentally influences the probability of invasions by alien plant species (Rouget and Richardson 2003; Chytrý et al. 2008b). Models incorporating propagule pressure typically prove superior to those invoking only environmental parameters for explaining distribution patterns and abundance of invaders at a regional scale (Rouget and Richardson 2003) and only once propagule pressure of invaders is factored out, can the real effects of diverse physical and biotic factors on the outcome of plant invasions be identified (Chaneton et al. 2002).

Naturalisation and invasion stage: establishment and spread [Traits & Location]

Anthropogenic factors in the transport and introduction stages of the invasion influence the identities and numbers of species available for establishment at different locations, and the composition of the founding populations of those species (event-related effects). In general, propagule pressure needs to be sufficiently high to allow the founding population to escape the stochastic effects of demography, environment, genetics, and Allee effects, although the inherently random nature of these effects means that some very small founding populations avoid them. Following introduction, features of the new environment (including resource availability, disturbance regimes, environmental conditions, and native biota), and the ways that these features interact with the biological traits of the alien species, come into play in determining which species establish viable and persistent populations. Effectively, these features and traits determine lineage survival probability (Fig. 2). Populations that establish can then go on to spread across the new environment, by an ongoing sequence of establishment events realised through (and depending on) both their life history traits and further human-mediated dispersal. The spatial and temporal patterns in the distribution, abundance, richness and traits of the alien species that result, and the relationships between these population- and community ecology processes, are the fodder of the macroecological patterns and large-scale biological invasions (Fig. 2).

Even at this 'terminal' point in the macroecological study of biological invasions, however, it is important to remember that observed relationships bear the imprint of previous stages in the invasion process (Leung et al. 2012; Donaldson et al. 2014). For example, the right-hand ('Invasion') part in Fig. 2 presents a cartoon of the distributional extent and abundance of four hypothetical established alien species, plus the relative spatial positions of those populations in an oval region. A naïve assessment of these patterns might conclude that species represented by the triangle and star are naturally more invasive, being more abundant and having wider distributional (and latitudinal, if we assume the figure maps to the cardinal points) extents than the species represented by the cross and crescent. Species richness appears to decrease from the top (north) to the bottom (south) of the region. Species in the north tend to have pointed edges, with that in the south having more curves (although sample size is low to make inferences about traits). However, all these conclusions need to be tempered by information on which species were introduced, where and when, and in what numbers. In Fig. 2, we see that more species were introduced to the north than the south; we see that introduced species in the south were more likely to have had curved edges, while those in the north were more likely to have had points. Those species that established were generally those introduced in larger numbers. The star and triangle species were introduced more widely than the cross and crescent. The crescent species was only introduced in the south. All of this context modifies our conclusions, and demonstrates that we cannot reliably make the conclusions if we analysed only the current distribution pattern.

Field data for assemblages of alien species show that the effects depicted in Fig. 2 are real and complex. For example, the extent of the distribution ranges of established alien bird species increases with latitude poleward of the tropics, consistent with the well-known ecological pattern known as Rapoport's rule, but ranges are smaller in the tropics (Stevens 1989). However, this pattern is largely a consequence of the latitudinal distributions of where bird species have been introduced, which is only modified slightly by latitudinal variation in establishment (Dyer et al. 2020). Hence, while alien and native bird species both follow Rapoport's rule, the mechanisms underlying the similar patterns are unlikely to be the same (Dyer et al. 2020). The same is true for Bergmann's rule in alien and native bird species (Blackburn et al. 2019), as noted earlier.

Various elements of introduction context may also interact. For example, individual pathways can deliver species with different levels of invasiveness (Thellung 1912; Pyšek et al. 2011), and species arriving via different pathways may differ in the impacts they cause (Pergl et al. 2017). The way in which species are introduced and spread around by humans within the new range can also have long-lasting impacts on invasion patterns. For example, trees used for forestry tend to be introduced to a few rural sites in large numbers, whereas ornamental trees tend to be introduced to many urban sites in low numbers, leading to profound differences in the pattern of the occurrence of invasions across spatial scales (Donaldson et al. 2014).

Residence time [Event]

An important human-related effect on macroecological patterns of alien species that manifests most strongly in the naturalisation and invasion stages is residence time (Rejmánek 2000; Castro et al. 2005, Pyšek and Jarošík 2005, Williamson et al. 2009, Pyšek et al. 2011). For plants, residence time relates to species' geographic alien range sizes but also their invasion status – in the Czech Republic casual species have significantly shorter mean residence times than naturalised and invasive aliens (Pyšek and Jarošík 2005), and in south-east Australia, alien graminoids with longer minimum residence times are more likely to be classified as invasive than non-invasive (Catford et al. 2016). Many regions contain species that have not been present long enough for them to naturalise and become invasive – yet, the importance of any particular plant trait in determining the success or failure of invasion is discernible only after the species has either established or failed in a new region. The longer a species is present, the more it is provided with opportunities for adaptation and spread, i.e. the more windows of opportunity it will encounter (Johnstone 1986). Another example of interaction with residence time is the lack of natural enemies in the new region following introduction, such as pathogens, herbivores or parasites. This process can operate on the scale of centuries, as shown for the accumulation of pathogens by alien plant species in North America (Mitchell et al. 2010).

Residence time interacts also with propagule pressure: the longer the species is present in a region, the greater the size of the propagule bank, and the greater the probability of dispersal, establishment, and founding of new populations (Rejmánek et al. 2005; Richardson and Pyšek 2006). In Europe, the effect of residence time is very long-term, and is still obvious after several millennia of plant invasions, as demonstrated for archaeophytes in the Czech Republic and UK (species introduced since the beginning of Neolithic agriculture until the end of Medieval; Pyšek et al. 2004a). Those archaeophytes that invaded soon after the beginning of Neolithic agriculture are still more common and have wider distribution ranges than those that arrived later (Pyšek and Jarošík 2005). Likewise, alien birds with longer residence times have larger alien range sizes worldwide (Dyer et al. 2016). However, the effect in birds is largely a consequence of species with longer residence times having been introduced to more locations, and only the effect of number of locations is significant in multivariate analysis (Dyer et al. 2016). Positive relationships between residence time and distributional extent have also been documented for many regional alien floras (Forcella and Harvey 1983; Crawley et al. 1996; Wilson et al. 2007; La Sorte and Pyšek 2009; see Rejmánek et al. 2005 and Pyšek and Jarošík 2005 for a review), although the influence of colonisation and propagule pressures here remain unexplored. Thus, failure to incorporate information on residence time may lead to spurious conclusions as, for example, we would expect species with different residence times to have different alien range sizes by chance alone (Wilson et al. 2007; Pyšek et al. 2009b, 2015).

Alien species traits [Traits]

To date, most invasion studies have attempted to explain the macroecological determinants of invasion by alien species and their assemblages by focusing on factors related to species traits and environmental characteristics, thus the interaction 'Species biological traits × Geographic attributes × Habitats × Climate'. Few studies have explicitly considered event-related factors and their interactions with other factors. Searching for traits associated with invasiveness is partly practically motivated, and there is growing evidence that some species are inherently better equipped, i.e. have a more suitable suite of traits, to become invasive after translocation to new areas by humans (Pyšek and Richardson 2007; van Kleunen et al. 2010b). Identifying species with the potential to become weedy or pests based on their traits should provide information on the likely mechanisms by which a species becomes invasive, and the likely impacts it will have. It therefore provides a template for assessing the likely success of management options (Novoa et al. 2020). To achieve this, however, we need to identify the "real" and direct effects of the respective traits that can be then included into risk-assessment schemes, because often traits are associated with biases (e.g. resulting from variation in propagule pressure, residence time, pathways, habitats or other factors that are not explicitly addressed in analyses). Indeed, the few available studies that do account for this complexity suggest that the role of species traits is strongly context dependent, and that traits interact with other factors – there is a complex interplay of species' traits, habitats occupied in both the native and invaded range (Hejda et al. 2009, 2015), characteristics of recipient ecosystems and native communities (Catford et al. 2019), and human activities (which influence propagule pressure and residence time in the new region) in determining invasion in novel environments (Bacon et al. 2014). Using multivariate approaches to examine suites of species traits linked with invasiveness may help to account for some of this context dependence (Kimmel et al. 2019).

Recent research on alien plants has shown that some of the species traits that were not commonly considered in the past due to the lack of information for large numbers of species forming floras play important roles in invasions. Such traits include seed bank persistence (Gioria et al. 2019), germination characteristics (Brändle et al. 2003; Gioria and Pyšek 2017), reproductive traits such as fecundity (Moravcová et al. 2010, 2015), and karyological characteristics such as genome size and ploidy levels (Kubešová et al. 2010; Pandit et al. 2014). The results of our models are only as good as the information available, and not considering a key trait can result in the influence of another trait being spuriously over-emphasised. Similarly, it has been shown in birds that missing important factors in the analyses might identify spurious effects determining invasion success. For example, propagule pressure is a major driver of establishment success and has been shown to be correlated to many species' traits in alien birds, like native range or body size (Cassey et al. 2004c). Analyses ignoring propagule pressure misidentified such species' traits as drivers of invasion success (Blackburn and Duncan 2001b).

In a study of European plants naturalised in North America, the effects of species traits on invasion were indirect, via their effect on the number of native-range habitats occupied and frequency of cultivation in the native range, and the importance of the biological traits was nearly an order of magnitude less than that of the breadth of the habitat niche, propagule pressure, and residence time (Fig. 5; Pyšek et al. 2015). This agrees with a previous study that reported direct effects of biological traits on the global invasion of Central-European species only during the most advanced stage of invasive spread, while the effects of traits on the probability of a species becoming naturalised were indirect (Pyšek et al. 2009a). Both these plant studies used the source-area approach (Pyšek et al. 2004b), looking at the pool of native European species invading elsewhere, therefore ignoring potential selection effects and post-invasive evolution in traits (Guo et al. 2018), but this approach is justified by the fact that a large fraction of species do not need to undergo evolutionary change for invasion (Parker et al. 2013; Colautti et al. 2014) and behave the same way abroad as at home (Firn et al. 2011; Petitpierre et al. 2012).

Moreover, the traits that confer an advantage at one stage of the process and in a particular habitat may be neutral or even detrimental at another phase and/or in a different habitat. For example, while small genome size played a role in the naturalisation of alien species in the Czech Republic, it did not separate invasive species from those that are not invasive (Kubešová et al. 2010; see also Küster et al. 2008).

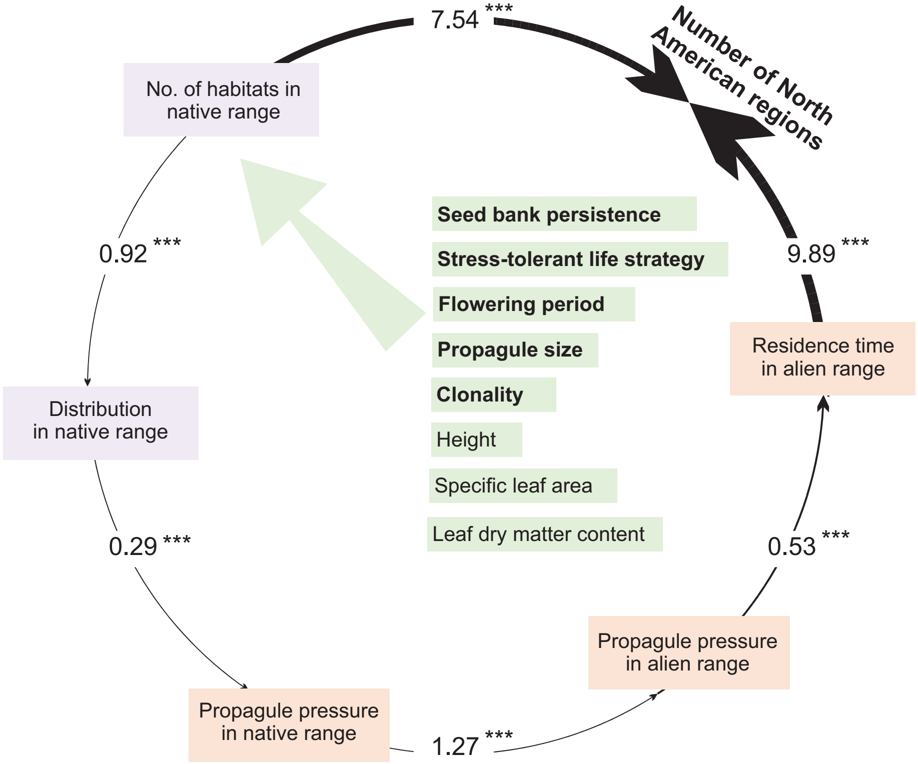

Figure 5. The number of North American regions in which Central-European species have become naturalised is driven by the combination of factors related to geographic attributes (the species' performance in its native range, i.e. habitat niche and distribution); propagule pressure (measured by using proxies related to human use of the species both in its native and invaded range) and residence time (the time since introduction to North America) that represent the event-related factors; and a suite of alien species traits that affect the species' invasion success indirectly, via their effect on the habitat niche in the native range (see Fig. 1 and 2 for explanation of colour codings); significant traits are shown in bold. The width and magnitude of numbers on arrows showing relationships between drivers is proportional to the value of the coefficient. Significance is indicated as: *** $p < 0.001$. Adapted from Pyšek et al. 2015.

Habitats [Location]

To know whether a region, community or habitat is more invasible we need to ask not only whether it has more alien species, but whether it is intrinsically more susceptible to invasions. Intrinsic invasibility can only be determined if processes of immigration and extinction are taken into account (including colonisation pressure), as pointed out by Lonsdale (1999), and if the relative invasiveness of the pool of invading species is also considered (Catford et al. 2012). Lonsdale's concept of invasibility has proved extremely useful in emphasising the role of colonisation pressure (although he used the term 'propagule pressure') and pointing out the difference between invasibility (or vulnerability to invasion) of a region, community or habitat and a simple number of invasive species it harbours; for the latter the term 'level of invasion' has become broadly used (Chytrý et al. 2005; Hierro et al. 2005; Catford et al. 2012).

There is a consensus in the research community that in biological invasions, the invaded habitats and invading species are 'a key-lock principle', and need to be studied in concert for a complete picture (Shea and Chesson 2002). The majority of hypotheses in invasion ecology have received support in some circumstances (and failed in others), but those hypotheses that merge the habitat- and species-perspective perform best (Richardson and Pyšek 2006; Jeschke et al. 2012). At the regional scale of temperate Europe, the type of habitat that is invaded by alien plants has been shown to play an even greater role than climate and propagule pressure (Chytrý et al. 2008b). Yet, studies exploring factors underlying the outcome of species introductions at the regional and global scale, even those that do include a number of different factors, usually do not consider the identity and characteristics of habitats (e.g. structure, disturbances regimes, nutrient or water supply, etc.), in either native nor alien distribution range (Appendix I). This is of key importance because these habitat characteristics determine the mechanisms of invasion acting in a particular site; yet, papers that to some extent combine the effect of habitats with other factors are exceptions rather than the rule (Pyšek et al. 2015).

Available analyses comparing the range of habitats occupied by species in their native and invaded range suggest that for some species there is a shift in habitat use attributable to the invasion process. While naturalised plant species inhabit a comparable spectrum of habitats in both ranges, invasive species tend to occupy a wider range of habitats in their invaded than in their native range (Hejda et al. 2009). This supports the idea that the invasion phase of the process is associated with extension of the spectrum of occupied habitats, hence broadening species' habitat niches (Pyšek et al. 2009a). Another research direction in habitat-oriented invasion ecology is looking at habitat affinities that alien species exhibit in their native range and analysing how this preadaptation affects their success as invaders (Hejda et al. 2015; Kalusová et al. 2017). In a study of European plants introduced to North America, the direct effect of native-range habitat legacy and residence time were the main factors associated with the likelihood that a species would naturalise – more important than propagule pressure measured by a proxy related to species' human use (Fig. 5; Pyšek et al. 2015). This key role of habitat legacy in shaping invasion dynamics accords with studies showing the strong effect of the breadth of habitat niche on invasion success (Hejda et al. 2009; Kalusová et al. 2013) and supports the notion that abundant, widely distributed species are superior competitors due to their ability, acquired over evolutionary history, to tolerate a wide range of abiotic conditions, use a broad spectrum of resources, and resist a large number of potential enemies (Sax and Brown 2000). Macroecological studies that explore how species with different traits interact with habitat characteristics are rare (but see Divíšek et al. 2018); more work on this topic is needed to improve our understanding of this kind of context dependence in invasion macroecology.

One of the main reasons why, in the majority of models of plant naturalisation and invasion, habitats are not considered is the lack of data on habitat affinities of alien species for most continents other than Europe (see Chytrý et al. 2016), and on the variation in this characteristic by regions. Since habitats have a strong effect on the outcome of invasion (Chytrý et al. 2008a, b) and on the way alien species integrate into local communities (Divíšek et al. 2018), such models may provide biased results or yield a low predictive ability due to exclusion of this important determinant. Similarly, testing of hypotheses in invasion ecology without taking habitats into account may mask the validity of concepts that do not hold across all environments, but may still be true under specific circumstances.

Another aspect of the interaction of habitat with pathway is that alien species intentionally brought into new regions (e.g. pets, aquarium related introductions, and horticulture) often escape or are released in places with suitable local conditions (e.g. similar habitats as in their native range) or close to human settlements and other sites favourable for alien species spread such as harbours, roads, etc. Given that the majority of successful alien plants are introduced through horticulture (Hanspach et al. 2008; Lambdon et al. 2008; Pyšek et al. 2012; van Kleunen et al. 2018), this phenomenon may have important consequences for macroecological patterns.

Recommendations: statistical and modelling considerations, and data gaps

Models aimed at predicting absolute alien species richness have a low to moderate accuracy in the region where they were developed and poor accuracy in new regions (Capinha et al. 2018). Predictions of relative species richness also suffer from limitations. We argue that such problems are largely attributable to the failure of the models to give adequate attention to the multitude of processes affecting invasion outcomes. We have proposed a comprehensive typology of factor classes and their interactions that are needed to explain invasions: alien species traits, location characteristics, and event-level factors (Fig. 1). These three classes of factors can be further subdivided, e.g. location-related factors into geography/topography, habitat, and climate (see above). All these factors, however, might interact differently at specific stages of the invasion process. These interactions must be given explicit consideration in macroecological analyses of invasive aliens to arrive at sensible conclusions. A framework for stage-specific best-practise risk-assessment (TEASI; Leung et al. 2012), which explicitly addresses Transport, Establishment, Abundance, Spread, and Impact, could be combined with approaches that recognise the context dependence at each stage. Related to this, one needs to be explicit about the response variable analysed, be it the likelihood of being introduced, overcoming the naturalisation threshold, or range size, spread rate, or impact. Many studies do not distinguish adequately among response variables and simply name them “invasion success” or similar.

Methodologically, a wide range of approaches is available, though many are not frequently employed. An increasing number of studies employ the source-area approach (Prinzing et al. 2002; Pyšek et al. 2004b; Thuiller et al. 2005; van Kleunen et al. 2007; Blumenthal et al. 2009; Bucharova and van Kleunen 2009; Mitchell et al. 2010; Pyšek et al. 2015), where a source pool of species native to a certain region is followed for their post-introduction performance in another region. Focusing on this specific trajectory allows us to minimise confounding variation that arises when multiple source areas of introduction are considered, both in terms of evolutionary predispositions acquired in disparate regions of origin, as well as various historical contingencies that shape introduction dynamics. Using a source-pool approach, Pyšek et al. (2015) used species traits, habitats, propagule pressure, and residence time to model the number of regions in North America colonised by Central-European plant species. To do so, they employed confirmatory path analysis (structural equation modelling) on a complex invasion model. Few studies have analysed which species in a particular source pool have been translocated, the characteristics of those species or the reason for the introduction, with the exception of bird introductions (see above). However, this is a key omission, as observed differences may be entirely due to which species in the source area were selected for translocation. Once in the new region, target-region specific analyses (see van Kleunen et al. 2010a) are sensible, recognising, though, the properties of the specific species pool that arrived.

Using joint species distribution models, O'Reilly-Nugent et al. (2019) modelled changes in the cover of alien and native plant species, and were able to identify three out of 72 aliens that were having a strong competitive impact on the community. Though at a different scale, the method seems appropriate to be applied in the MAFIA framework. A range of methods for joint species distribution modelling, applicable across various scales, are now available (e.g. Pollock et al. 2014). Golivets et al. (2019) studied complex, non-linear relationships between environment and plant invasions into forests, using boosted regression trees and non-linear Bayesian regression.

With the development of Community Assembly by Trait Selection (CATS; Shipley et al 2006; Warton et al. 2015b) the classical fourth-corner problem (Legendre et al. 1997) and its implementation in joint models for abundance (Warton et al. 2015a), the analysis of trait × environment interactions, have become much more powerful and flexible. Milanović et al. (2020) used this method to relate environmental variables and traits with the area of occupancy in Germany with respect to different stages of the invasion process. In another stage-specific approach, Catford et al. (2019) used hierarchical linear regression models (Pollock et al. 2012; Jamil et al. 2013) to identify variables associated with invasion of non-resident species. Their indicators of invasion success were occupancy and abundance at two stages of invasion (establishment and spread).

We believe that the approaches outlined above will also be applicable to model further interactions, such as traits × temporal dynamics, or traits × propagule pressure. We are, though, unaware of an approach that incorporates interactions among all three classes of factors mentioned above (location, event, species) in a framework that considers the resulting species pool of a previous stage in the invasion process, as to derive unbiased conclusions throughout all stages. Most promising are complex hierarchical Bayesian approaches (see Zurell et al. 2016 for a dynamic species distribution modelling approach) consisting of different submodules separately modelling each stage and providing the results to the next step in the analysis.

All the models above are only applicable if the data are of sufficient quality. Data gaps can constrain our understanding of invasion processes. In particular, we often know little about key anthropogenic factors – notably colonisation pressure and propagule pressure. These factors must be considered to obtain an unbiased view of the processes, but there are few reliable proxies for such factors (Blackburn et al. 2020). Similarly, analyses can be biased if data on key species traits are missing (e.g. because they are logistically difficult to collect, such as reproductive traits of plants; Moravcová et al. 2015). Therefore, data should be collected in a comparative manner, rather than taken from opportunistic observational data. Such ad hoc data will be biased by habitat, native vs invaded region (Parker et al. 2013), and other contexts, and hence frequently show larger within-species variation than among-species variation (see Kattge et al. 2020). For example, fecundity expressed as the amount of seeds produced, based on data collected in a comparative manner, was one of the most important traits discriminating naturalised and invasive species in the Czech flora (Moravcová et al. 2010, 2015). More detailed information on seed bank longevity beyond the simple categorisation based on whether a species builds a persistent seed bank (Kleyer et al. 2008), such as the amount, density, and survival times of seeds in the soil is also still largely not available, yet this trait has been recently shown to be of importance for naturalisation and invasion (Gioria et al. 2012, 2014). Similarly, increasing knowledge on dates of introduction of alien species to particular regions of the world and accumulation of such data in the First Records Database has improved our understanding of temporal dynamics of biological invasions at the global scale (Seebens et al. 2017, 2018). For the detection of alien species, remote sensing techniques represent a promising tool for obtaining information across large scales on some components of MAFIA such as habitat structure, resource availability, land-use, as well as proxies for propagule pressure (e.g. Weiers et al. 2004; Huang and Asner 2009; Skowronek et al. 2017; Vaz et al. 2019). To date, remote sensing has largely been used to detect the spatial distribution of alien species in space and time, and its use to derive explanatory macroecological variables to interpret such patterns has so far been limited.

To some degree, incomplete data on invasions might be comparable to incomplete citizen science species distribution data. These suffer typically from heterogeneous and non-random sampling, false absences, false detections, and spatial autocorrelation in the data. To overcome these problems, occupancy models are increasingly used (Altwegg and Nichols 2019). They consist of two different elements, separating the observation process from biological processes. In invasion ecology, a module accounting for observational bias might be a solution. In the context of the MAFIA, it would be useful to explore whether a similar approach could be used, i.e. incorporating a model component accounting for imperfect detection or knowledge of introduction processes, but the field of model-based data integration is quite new and evolving (Isaac et al. 2020). Simple models, i.e. those just adding additional proxies as covariates, are likely to be inappropriate to account for the biases in knowledge and detection. In non-manipulative observational studies in particular, one needs critically to discuss whether their data are appropriate to derive the conclusions drawn and which biases in input data are likely to cause certain biases in results.

Our understanding of the role of macroecological processes in invasions can only advance if we are able to build a mechanistic framework that incorporates the most relevant factors (event, location, species) and their interactions, as well as biases that arise through human selectivity along the invasion sequence, resulting from the fact that invasions are part of a 'coupled human and natural system' (Sinclair et al. 2020, see also Howard 2019). We believe that the MAFIA is helpful for conceptualising these issues, by explicitly identifying the pathway along which alien macroecological patterns develop, and how biases in observed patterns may be inserted by this pathway. This will hopefully help a mechanistic understanding to emerge. It may also help us to think critically about how we collect and analyse data, striving to measure the relevant factors in a meaningful way instead of indiscriminately adding proxies to oversimplified models. Only if we manage to combine both will invasion ecology become a more predictive discipline.

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Appendix I

Overview of 102 macroecological studies on biological invasions and their classification according to the factors included in the analysis (indicated as ×). The studies were found and selected from 5 literature searches done in Google Scholar using the following terms: (1) predict AND "invasive species", (2) success AND "invasive species" AND "amphibians", (3) success AND "invasive species" AND "birds", (4) success AND "invasive species" AND "mammals", (5) success AND "invasive species" AND "plants", and (6) success AND "invasive species" AND "reptiles". The results of the searches were sorted using the default option "by relevance". From search 1 we reviewed the first 500 results, while we reviewed the first 100 results from searches 2–6. The information on studied organism, scale and main conclusions of each study is provided. The overview does not aim at being exhaustive and includes studies on plants (50), fishes (16), amphibians and reptiles (11), birds (9), mammals (6), vertebrates in general (2), amphipods (1), ants (1), aquatic species (1), arthropods (1), fungi (1), macroinvertebrates (1), wasps (1), and one general study. Note that we do not indicate whether the data on alien species traits come from the native or alien range because in many studies it was difficult to infer where they were measured. The colour coding correspond to that used in Figs 1, 2. IAS = invasive alien species.

Reference	Studied organism	Scale	Alien species traits	Habitats and climate in native range	Habitats and climate in alien range	Socioeconomic factors	Colonisation and propagule pressure	Residence time	Invasion stages	Conclusions of the study
Alcaraz et al. 2005	Fishes	Native and IAS in the Iberian Peninsula	×	×	×	×				IAS generally have larger latitudinal ranges than natives.
Allen et al. 2013	Vertebrates	Alien species in peninsular Florida	×	×	×		×		×	Predictors of establishment and spread differ across vertebrate taxa.
Allen et al. 2017	Amphibians and reptile	Global	×				×		×	Fast life history traits promote invasion success in amphibians and reptiles.
Amiel et al. 2011	Amphibian and reptiles	Global	×				×		×	Introduced alien species with larger brain sizes are more likely to establish and invade.

Reference	Studied organism	Scale	Alien species traits	Habitats and climate in native range	Habitats and climate in alien range	Socioeconomic factors	Colonisation and propagule pressure	Residence time	Invasion stages	Conclusions of the study
Andersen 1995	Plants	Alien species in Denmark	×		×					Alien species, especially in seminatural habitats, are more likely than natives to present fleshy fruits and be dispersed by wind.
Aronson et al. 2007	Woody plants	Alien species in New York	×							Fruit type, life form and origin influence establishment success.
Bacon et al. 2014	Arthropods	Europe		×	×	×	×		×	Quarantine arthropods are more likely to establish if climate matches and hosts are available; propagule pressure only plays a role if these conditions are met.
Ben Rais Lasram et al. 2008	Fishes	Lessepsian fish species invading the Mediterranean Sea	×	×	×	×		×		Residence time and climate match between the native and alien ranges influence invasiveness.
Blackburn et al. 2009	Birds	Global	×						×	Alien species are less likely to be introduced when presenting traits that predispose them to Allee effects. Alien species that can cope with novel environments and have larger body mass have a higher establishment success.
Blackburn and Duncan 2001a	Birds	Global	×	×	×					Avian introduction success depends on the suitability of the abiotic environment at the introduction site.
Blackburn and Duncan 2001b	Birds	Global	×	×	×					The establishment success of exotic birds depends on introduction efforts.
Bomford et al. 2009a	Mammals	Alien species introduced to New Zealand, Australia and Britain		×	×		×			The number of release events and the climate-match between the native and introduced ranges influence establishment success.
Bomford et al. 2009b	Reptiles and amphibians	Global		×	×		×			Introduction effort, climate match and invasiveness elsewhere facilitate the establishment of introduced species.
Bucharova and van Kleunen 2009	Woody plants	North American species introduced into European garden and parks	×			×	×	×		Planting frequency determines naturalisation success.
Cadotte and Lovett-Doust 2001	Plants	Alien species in Canada	×							Alien species are more likely than natives to be annual and biennial, hermaphrodite, have long flowering periods and small fruits, and are less likely to be dispersed by animals. In seminatural habitats, aliens are also more likely to be trees with a high number of seeds per fruit.
Cadotte et al. 2006	Plants	Alien species in Canada	×	×	×					Abundant aliens are more likely to have longer flowering duration, be native to Europe or Eurasia, and grow in variable soil moisture conditions.
Cadotte et al. 2009	Plants	Alien species in Royal National Park (Australia) and the whole Australia	×		×					Relatedness with other IAS can be a useful predictor of invasion success at large spatial scales but not at smaller, landscape scale.

Reference	Studied organism	Scale	Alien species traits	Habitats and climate in native range	Habitats and climate in alien range	Socioeconomic factors	Colonisation and propagule pressure	Residence time	Invasion stages	Conclusions of the study
Capellini et al. 2015	Mammals	Global	×				×		×	Introduced mammals are likely to be highly productive and have a high reproductive output. Greater reproductive output and introduction effort increases success at both the establishment and spread stages.
Cassey et al. 2005	Birds	Global	×		×		×			The characteristics of the introduction events are the most consistent predictors of establishment success.
Colautti 2005	Salmonoid species (fishes)	Alien species in Nevada, USA	×	×	×		×		×	Species presenting large sizes, weight and latitudinal ranges are more likely to be introduced. Propagule pressure affects establishment.
Crawley et al. 1996	Plants	Alien species in the British Isles	×							Aliens are likely to be taller, present larger seeds and no or protracted dormancy, flower earlier or later, and present more pronounced r- or K-strategies than natives.
Dawson et al. 2009	Plants	Alien species introduced to Amani Botanical Garden, Tanzania	×	×			×	×	×	Residence time, growth rate, number of seeds per fruit, seed mass, dispersion by canopy-feeding animals and tolerance to shade facilitates naturalisation.
Dehnen-Schmutz et al. 2007a	Plants	Ornamental plants introduced to Britain				×	×			The period of time a species is available in the market, the number of nurseries selling it and the price of its seeds influence invasion success.
Devin and Beisel 2007	Gammarid amphipods	Alien species native to Western Europe and North America	×	×						Tolerance to salinity increases invasiveness. Invasiveness is affected by a combination of several traits.
Divíšek et al. 2018	Plants	Alien species in temperate Central Europe	×		×				×	Similarity to native species facilitates naturalisation, while dissimilarity facilitates invasions.
Drake 2007	Fishes	Global	×							Parental investment and fecundity influence establishment success.
Duggan et al. 2006	Freshwater fishes	Alien species introduced to Canada and USA	×				×		×	Propagule pressure and body size affect introduction and establishment.
Duncan 1997	Passeriform birds	Alien species introduced to New Zealand					×			Introduction effort (i.e. number of introductions and number of introduced individuals) could predict the invasion success of passeriform birds.
Ellstrand and Schierenbeck 2006	Plants	Global	×							Hybridization stimulates invasiveness.
Ferreira et al. 2012b	Amphibians and reptiles	Global	×							Amphibians and reptiles have similar establishment success.
Ferreira et al. 2012a	Reptiles	Global	×							The presence and richness of native congeners increase establishment success.
Forsyth et al. 2004	Mammals	Alien species introduced to Australia	×		×		×		×	Climate suitability, alien range size, and introduction effort increase establishment and spread.

Reference	Studied organism	Scale	Alien species traits	Habitats and climate in native range	Habitats and climate in alien range	Socioeconomic factors	Colonisation and propagule pressure	Residence time	Invasion stages	Conclusions of the study
Fujisaki et al. 2010	Reptiles	Alien species in Florida	×	×			×			Taxonomic order, maximum temperature match between native range and Florida, sale price, and manageability (difficulty to manage the species as a pet) are significant predictors of establishment success.
Gallagher et al. 2011	*Acacia* sp. (plants)	Alien species native to Australia	×	×						IAS are more likely than non-invasive aliens to be shrubs or trees and have large native ranges.
Gallagher et al. 2015	Plants	IAS in Australia	×	×				×	×	IAS are more likely than naturalised species to be tall and have large specific leaf area, long flowering periods, and high tolerance to environmental conditions in their native range .
García-Díaz and Cassey 2014	Amphibians	Alien species in Australia	×	×		×	×			The availability to be captured, bred and housed in captivity increases the probability of amphibians to be introduced to and transported within Australia.
Gassó et al. 2009	Plants	IAS in Spain	×	×	×	×		×		Wind dispersal, minimum residence time, anthropogenic disturbance, low altitude, short distance to the coastline and dry and hot weather conditions increase invasiveness.
Godoy et al. 2011	Plants	Native and alien species in the Mediterranean region	×							IAS are more likely than native species to present high capacity for carbon gain and high performance over a range of limiting to saturating resource availabilities. Invasive and native species do not differ in their phenotypic plasticity.
González-Suárez	Mammals	Global	×				×			Intraspecific variation in morphological traits increases establishment success.
Goodwin et al. 1999	Plants	European species invading Canada	×							IAS are more likely than non-invasive aliens to be tall and have long flower-periods.
Grabowska and Przybylski 2015	Freshwater fishes	Alien species invading Central Europe	×							Life history traits facilitate the invasion of freshwater fishes in Central Europe.
Gravuer et al. 2008	*Trifolium* sp. (plants)	Species invading New Zealand	×	×		×	×	×	×	Success at all invasion stages is more influenced by biogeographic factors than biological attributes. Biological traits only influence the selection of species for introduction and the relative rates of spread. Different factors determine the probability of plant introduction, naturalisation, and spread.
Grotkopp et al. 2010	Woody horticultural plants	Global	×							IAS have higher relative growth rates than non-invasive aliens.
Hamilton et al. 2005	Plants	Alien species in Eastern Australia	×		×			×		Seed size affects invasion success at both regional and continental scale, while SLA only affects invasion success at continental scale.
Herron et al. 2007	Trees, shrubs and vines (plants)	Species invading New England (USA)	×						×	IAS are likely to have previous invasion history, large native latitudinal ranges, rapid growth rates and non-evergreen leaves. Invasive trees are likely to tolerate shade.

Reference	Studied organism	Scale	Alien species traits	Habitats and climate in native range	Habitats and climate in alien range	Socioeconomic factors	Colonisation and propagule pressure	Residence time	Invasion stages	Conclusions of the study
Higgins and Richardson 2014	*Acacia* sp. and *Eucalyptus* sp. (plants)	Alien species native to Australia	×	×					×	IAS have larger potential range sizes than naturalised aliens. Naturalised aliens have larger potential range sizes than non-naturalised aliens. The effect of traits on invasion success is context dependent.
Jansen et al. 2011	Plants	Alien species in north-eastern Germany			×					Different alien species have different ecological preferences.
Jeschke and Strayer 2006	Vertebrates	Species native to Europe or North America	×				×		×	Propagule pressure and human affiliation affect invasion success across taxa and invasion stages. All other factors affect invasion success differently, specially depending on the invasion stage.
Kolar and Lodge 2002	Fishes	Species alien to the Great Lakes	×			×			×	Aliens are more likely to establish if they present fast growth, tolerate wide temperature and salinity ranges and have a history of invasiveness elsewhere. Aliens with slow growth and tolerating wide temperature ranges spread fast. Nuisance aliens were more likely to have smaller eggs and wider salinity tolerances than non-nuisance aliens.
Küster et al. 2008	Plants	Species invading Germany	×							Among IAS, different ecological strategies (determined by particular combinations of traits) facilitate invasion.
Lake and Leishman 2004	Plants	Alien species in Sydney, Australia	×	×					×	IAS have higher specific leaf area and are more likely to disperse by wind and vertebrates, and less by ants, than non-invasive aliens or natives. In disturbed sites, IAS have smaller seeds and flower longer than natives. Aliens have softer leaves and are more likely to propagate vegetatively than natives.
Lester 2005	Ants	Alien species in New Zealand	×		×		×			Mean temperature at the highest latitude of the introduced range and interception rate determine establishment success.
Lloret et al. 2005	Plants	Alien species in Mediterranean islands	×		×					Aliens are more likely to be more abundant if they reproduce vegetatively, have large leaves, flower in summer for long periods of time and are dispersed by wind and animals. Aliens are more likely to have succulent and fleshy fruits in ruderal and seminatural habitats, respectively.
Lockwood 1999	Birds	Global	×			×				Taxonomy influences the transport and establishment of alien birds.
Maitner et al. 2012	Birds	Introduced species in Florida, New Zealand, and Hawaii	×							Close relatedness to the extant avifauna increases establishment success.
Marchetti et al. 2004a	Fishes	Alien species in watersheds in California, USA	×	×			×		×	Aliens' traits (trophic status, size of native range, parental care, maximum adult size, physiological tolerance, distance from nearest native source) and propagule pressure influence establishment. Physiological tolerance and propagule pressure predict spread. Previous invasion success predicts species integration and impact.

Reference	Studied organism	Scale	Alien species traits	Habitats and climate in native range	Habitats and climate in alien range	Socioeconomic factors	Colonisation and propagule pressure	Residence time	Invasion stages	Conclusions of the study
Marchetti et al. 2004b	Fishes	Aliens in catchments in California, USA	×				×		×	Parental care, physiological tolerance, propagule pressure and previous invasion success predict alien species establishment. Life span, distance from nearest native source, trophic status and prior invasion success predict spread. Maximum size, physiological tolerance and distance from nearest native source predict abundance.
McGregor et al. 2012	*Pinus* sp. (plants)	Alien species introduced to Great Britain and New Zealand	×	×	×		×	×		Human factors are better predictors of introduction and naturalisation than species or biogeographic traits.
Milbau and Stout 2008	Plants	Alien species in seminatural habitats in Ireland	×	×	×	×		×	×	Clonal growth, moisture-indicator value, nitrogen-indicator value, native range, and date of first record affect naturalisation. Ornamental introduction, hermaphrodite flowers, pollination mode, being invasive elsewhere, onset of flowering season, moisture-indicator value, native range, and date of first record affect invasiveness.
Møller et al. 2015	Birds	Alien species introduced in oceanic islands	×		×		×			The ability to thrive in urban areas facilitates the establishment and invasion of birds in oceanic islands.
Moodley et al. 2013	Proteaceae (plants)	Global	×						×	Naturalised aliens are more likely than non-naturalised aliens to have large native ranges, low susceptibility to Phytophthora root-rot fungus, large mammal-dispersed seeds, and the capacity to resprout. IAS are more likely than naturalised species to have large native ranges, be used as barrier plants, be tall and serotinous and have small seeds.
Moravcová et al. 2010	Plants	Alien species in the Czech Republic	×						×	IAS are more likely than naturalised aliens to have a low length/width ratio of propagules, fewer seedlings establish in the autumn, have better capacity for dispersal by wind, and be more fecund.
Moravcová et al. 2015	Herbaceous plants	Alien species in the Czech Republic	×						×	Seed production, propagule properties and height affect invasiveness at the reproduction, dispersal and competition stages respectively.
Moyle and Marchetti 2006	Freshwater fishes	Alien species in California, USA	×	×	×	×	×		×	Different traits affect different stages of the invasion process.
Novoa et al. 2015	Cactaceae (plants)	Global	×			×				Growth form and native range size influence invasiveness.
Olden et al. 2006	Freshwater fishes	Native and alien species in the Colorado River Basin, USA	×	×						Alien opportunists have the highest rates of spread.
Ordonez et al. 2010	Plants	Global	×							Functional trait differences between alien and native species contribute to the success of alien species.
Paavola et al. 2005	Aquatic species	Alien species in European brackish water seas	×		×					Alien species are adapted to the salinity levels of areas with the lowest richness of native species.
Pemberton and Liu 2009	Ornamental plants	Alien species in Florida, USA	×	×			×	×		Propagule pressure and residence time increase the probability of naturalisation. Naturalised aliens are likely to have large native range sizes, be aquatic herbs or vines and belong to the families Araceae, Apocynaceae, Convolvulaceae, Moraceae, Oleaceae or Verbenaceae.

Reference	Studied organism	Scale	Alien species traits	Habitats and climate in native range	Habitats and climate in alien range	Socioeconomic factors	Colonisation and propagule pressure	Residence time	Invasion stages	Conclusions of the study
Philibert et al. 2011	Forest pathogenic fungi	Alien species in Europe	×	×				×	×	Long-distance dispersal, sexual reproduction (in addition to asexual reproduction), spore shape and size, number of cells in spores, optimal temperature for growth and parasitic specialization (host range and infected organs) determine invasiveness.
Prinzing et al. 2002	Plants	European species invading Argentina	×		×	×				IAS are likely to have r-strategy; prefer warm, dry, sunny and nitrogen-rich habitats; and to be used by humans.
Pyšek et al. 1995	Plants	Species introduced to the Czech Republic	×		×	×				Aliens are more likely than natives to be C- and CR- strategists and dispersed by humans. They prefer dry, warm and nutrient-rich habitats. In semi-natural habitats, aliens are mainly tall hemicryptophytes escaped from cultivation. In human-made habitats aliens are mainly therophytes or geophytes, introduced spontaneously.
Pyšek 1997	Plants	Global	×		×	×			×	Clonal alien species are more likely than non-clonal aliens to be introduced deliberately. In wet, old and natural habitats, IAS are more likely than non-invasive aliens to be clonal. However, clonality has a negative effect on invasion success during the dispersal stage.
Pyšek and Jarošík 2005	Plants	Alien species in the Czech Republic	×	×		×	×			American and Asian aliens are likely to disperse by water. Life strategy, origin and dispersal mode are likely to affect invasion success. Residence time determines the influence of height and growth form on invasion success.
Pyšek et al. 2009a	Plants	Aliens native to Central Europe	×	×					×	The characteristics of the native habitats are likely to affect the early stages of invasion, while species traits are more likely to affect later stages.
Pyšek et al. 2009b	Woody plants	Aliens cultivated in the Czech Republic	×				×	×	×	Residence time in Czech Republic and Europe increases the probability of an alien species scaping from cultivation and naturalising respectively. Propagule pressure increases the probability of an alien species escaping cultivation. Species from Asia with small fruits are more likely to naturalise. Residence time and the ability of tolerating low temperatures increase invasiveness.
Pyšek et al. 2010	General	Naturalised species in Europe		×	×	×				National wealth and human population influence invasiveness.
Pyšek et al. 2011	Plants	Species introduced to the Czech Republic	×		×	×		×	×	Human assistance facilitates naturalisation and invasion.
Pyšek et al. 2015	Plants	European aliens naturalising in USA	×	×			×	×		Residence time and number of habitats occupied in the native range are likely to affect the number of occupied regions in the non-native range, while species traits have an indirect effect on naturalisation success.
Ribeiro et al. 2008	Freshwater fishes	Aliens in watersheds in the Iberian Peninsula	×	×			×		×	Prior invasion success affects all the stages of the invasion process. The traits that affect invasiveness are context dependent.

Reference	Studied organism	Scale	Alien species traits	Habitats and climate in native range	Habitats and climate in alien range	Socioeconomic factors	Colonisation and propagule pressure	Residence time	Invasion stages	Conclusions of the study
Rossinelli and Bacher 2015	Parasitic wasps	Global	×	×	×	×	×		×	Parasitic wasps with a narrow host range introduced for biocontrol establish better.
Ruesink 2003	Freshwater fishes	Global	×	×	×	×		×		Aliens that are intentionally introduced several times to a particular area are likely to have impacts.
Ruesink 2005	Freshwater fishes	Global	×	×	×	×	×	×		Aliens are more likely to establish when having small body size, high reproduction rates, are generalists and omnivores, are introduced to isolated areas with high endemism of fish fauna and humans support their establishment.
Sol et al. 2008	Mammals	Global	×	×	×	×	×			Alien mammals with large brains relative to their body mass establish better.
Sol et al. 2012	Birds	Global	×				×			Successful invaders are characterised by life-history strategies in which they give priority to future rather than current reproduction.
Statzner et al. 2008	Macroinvertebrates	Alien species in natural European stream sites	×							IAS are more likely than natives to reproduce frequently; have higher propagule pressure, more ovoviviparity, larger size and longer life; exploit food resources more effectively; and tend to be more dominant in their communities and survive during dispersal.
Sutherland 2004	Plants	Alien species in the USA	×						×	Aliens are less likely than natives to be clonal and adapted to wetlands. IAS are more likely than non-invasive aliens to be monoecious, self-incompatible, perennial and woody.
Thiébaut 2007	Aquatic and semi-aquatic plants	Species native to or invasive in North America and France	×							No differences were found in the distribution and biology of aquatic and semi-aquatic plants between their native and invasive ranges.
Thompson et al. 1995	Plants	Species expanding in England, Scotland, the Republic of Ireland and the Netherlands	×		×					Aliens are more likely than natives to be clonal and present transient seed banks.
Thuiller et al. 2006	Plants	Species invading South Africa	×	×	×	×		×		The distribution of IAS is best explained by the use of species by humans. Different sets of traits affect invasion success in different geographic areas.
Tingley et al. 2010	Amphibians	Global	×	×		×				Introduced species are more likely to be native to the Northern Hemisphere, have large ranges and be sympatric with high densities of humans than non-introduced species. Intentionally introduced species are of larger body size, occupy higher elevations in their native ranges, and are more likely to be native to the Northern Hemisphere than unintentionally introduced species.

Reference	Studied organism	Scale	Alien species traits	Habitats and climate in native range	Habitats and climate in alien range	Socioeconomic factors	Colonisation and propagule pressure	Residence time	Invasion stages	Conclusions of the study
Tingley et al. 2011	Amphibians	Global	×	×	×	×	×	×		The presence and richness of native congeners increase establishment success. Establishment success is higher on islands and in areas with abiotic conditions similar to the native range and with higher presence and richness of native congeners.
van Kleunen et al. 2007	Family Iridaceae (plants)	Species native to Southern Africa	×	×		×				Naturalised aliens are likely to come from low altitudes, have high numbers of subtaxa and be tall.
van Kleunen and Johnson 2007	Plants	European species invading the USA	×							IAS are likely to be self-compatible.
van Kleunen et al. 2010b	Plants	Global	×							IAS are more likely than non-invasive aliens to have high values for performance traits.
van Wilgen and Richardson 2011	Reptiles	Alien species introduced to California and Florida	×							Phylogenetic distance with native species increases establishment success.
van Wilgen and Richardson 2012	Reptiles and amphibians	Alien species introduced to California and Florida, USA	×		×		×			Alien species, especially lizards and frogs, which mature early and come from environments similar to that of the introduction region are likely to establish.
Vila-Gispert et al. 2005	Freshwater fishes	Native and IAS in Catalan streams, Spain	×					×		Aliens are more likely than natives to have large size, long longevity, late maturity, high fecundity, few spawnings per year, and short reproductive span. Species traits do not clearly differentiate native from alien species. Residence time increases invasion success.
Wonham et al. 2000	Fishes	Global				×			×	Different fish families differ in the frequency at which their species are transported and introduced through ballast water, and in their establishment success in the introduced areas.
Williamson and Fitter 1996	Plants	Alien species in Great Britain	×		×					IAS are more likely than natives to be tall, taller than wide, phanerophytes and insect-pollinated and to have large leaves. They also prefer fertile habitats.
Willis et al. 2010	Plants	Concord, Massachusetts, USA	×		×					IAS have a higher ability to adjust their flowering time in response to climate change than native species.
Yessoufou et al. 2014	Mammals	Alien species in South Africa	×		×					Evolutionary history influences invasion success.

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Advancing research on alien species and biological invasions

Double trouble: the implications of climate change for biological invasions

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Abstract

The implications of climate change for biological invasions are multifaceted and vary along the invasion process. Changes in vectors and pathways are likely to manifest in changes in transport routes and destinations, together with altered transit times and traffic volume. Ultimately, changes in the nature of why, how, and where biota are transported and introduced will pose biosecurity challenges. These challenges will require increased human and institutional capacity, as well as proactive responses such as improved early detection, adaptation of present protocols and innovative legal instruments. Invasion success and spread are expected to be moderated by the physiological response of alien and native biota to environmental changes and the ensuing changes in biotic interactions. These in turn will likely affect management actions aimed at eradicating, containing, and mitigating invasions, necessitating an adaptive approach to management that is sensitive to potentially unanticipated outcomes.

Keywords

biosecurity, global change, impacts, management of invasions, research needs

Introduction

Human induced climate change is manifesting in a variety of environmental changes including alterations in global temperatures, precipitation patterns, ocean chemistry, currents, and frequency of extreme climatic events (IPCC 2019). Distribution range shifts are a widely accepted consequence of such changes (Bellard et al. 2013; Hulme 2017; Kuczynski et al. 2018), but the implications for alien biota are not straightforward as their ranges are linked not only to their physiological tolerances, but also to the processes through which they are translocated by humans. However, the invasion process is complex, moving through various stages (Blackburn et al. 2011) which may each be affected by a changing environment in different ways. Thus, it is clear that to anticipate the implications of climate change on invasions, there is a need to consider the consequences of a changing climate for how biota cross the various barriers and move through the invasion stages from transport to spread (*sensu* Blackburn et al. 2011). Importantly, as management approaches differ among these stages, an understanding of the specific implications of climate change for the various stages is needed to support management actions aimed at minimising introductions and mitigating the negative impacts of those that do occur.

The implications of climate change along the invasion process

Climate change is likely to affect invasions via three mechanisms (Fig. 1). Firstly, by changing the nature of vectors and pathways, secondly by altering the abiotic nature of the recipient environment, and thirdly through changes to biotic interactions in recipient communities. While the first of these mechanisms acts on the transport and introduction stages, the second two act simultaneously on the stages of establishment and spread.

Changes in the nature of pathways and the implications for the transport and introduction of alien taxa

Climate change is expected to increasingly affect the movement of people and due to the link between human movement and the introduction of alien biota, biological invasions will in turn be impacted. Notably, these changes are expected to take place as a result of changes in transport routes, destinations, altered traffic volume and changes in transit time. Presently, over 90% of the world's trade is moved by shipping (IMO 2019). This important pathway is expected to be influenced by the melting of the Arctic ice-cap, a process that will open new shipping routes. It is estimated that 5% of the world's trade could pass through these new routes, effectively increasing connectivity between Europe and Asia and decreasing transit times by up to 40% (Yumashev et al. 2017). From an invasion perspective, these changes in shipping have important implications (Miller and Ruiz 2014). For example, previously unconnected ports will act as sources and sinks for alien species and propagule pressure will increase between Europe

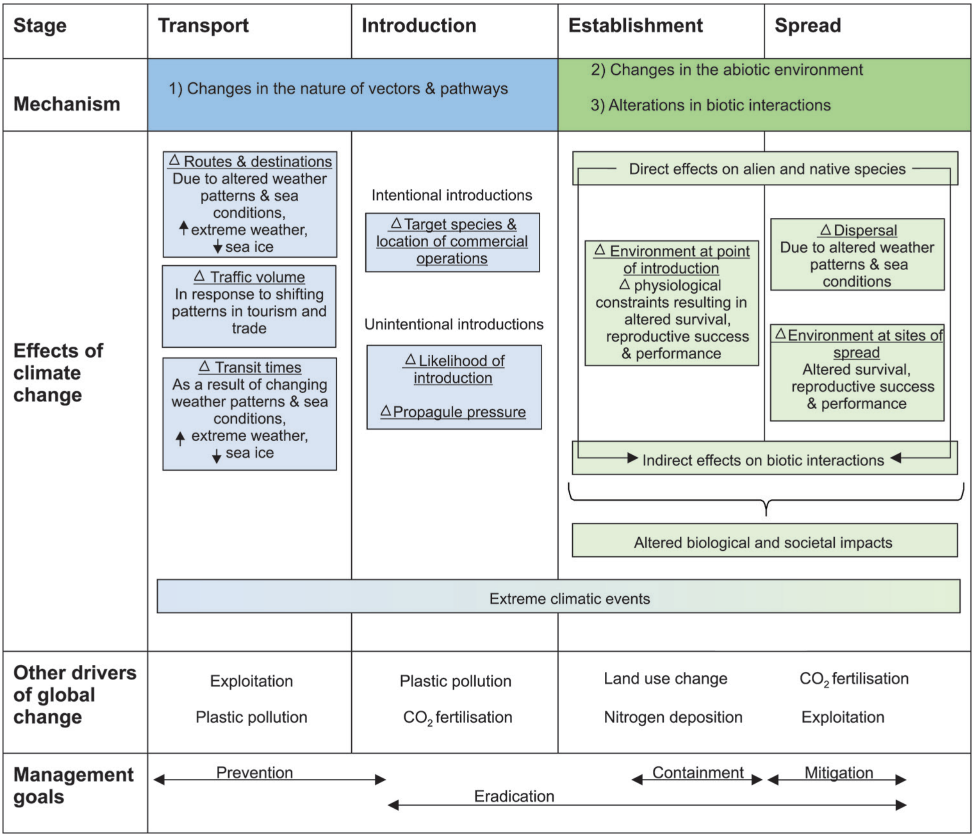


Figure 1. The effects of climate change on invasions and the mechanisms through which they act mapped onto the Blackburn Unified Framework for biological invasions (Blackburn et al. 2011). Examples of where other drivers of change may influence the invasion process are also indicated.

and Asia as fouling and ballast water associated species could experience increased survival due to shortened transit times (although the potential of the low water temperatures associated with the colder northern route to mitigate this effect has not yet been assessed). The shipment of goods through rivers and lakes is also expected to be affected by climate change. Lower water levels due to changes in rain patterns, droughts, and elevated temperatures might require a reduction on cargo weight, smaller vessels, and increased number of trips (Millerd 2011).

Besides direct impacts on transportation, future changes in climate are expected to alter where commodities are produced and where they are transported to. For example, salt transport in the Mediterranean Sea has revived due to decreased rainfall and increased winds raising the salinity in some regions (Raitsos et al. 2010), while the production of various fruits and vegetables is expected to shift in response to altered precipitation patterns (Parajuli et al. 2019). These sorts of shifts in agricultural production will serve to increase connectivity between presently disconnected regions and thus elevate the associated invasion risk. When accounting for changes in global trade patterns and predicted changes in climate it is anticipated that numbers of naturalised plant invasions will increase in northern-hemisphere temperate countries while declining in tropical and sub-tropical regions (Seebens et al. 2015). This pattern reflects warming in the north, increasing climate matching between dominant trade partners, while elevated temperatures in the tropics will have the opposite effect. Importantly though, increased trade volumes could offset climate driven declines in plant naturalisations (Seebens et al. 2015).

As the character of vectors and pathways change, so will the processes by which biota are introduced. Patterns in unintentional introductions are likely to closely follow changes in transport as described above. These shifts in trade, culture-based industries, and tourism (Hoogendoorn and Fitchett 2016; Yumashev et al. 2017) will see some regions become new recipients of stowaway species, while others may experience elevated propagule pressure due to increased traffic and more hospitable conditions during transit along with shorter transit times. In contrast, it is possible that some regions will experience reduced invasion risk if historically important pathways become less important.

Intentional introductions are often linked to agriculture, agroforestry, horticulture, aquaculture, and fisheries (Richardson and Rejmánek 2011; Saul et al. 2017; van Kleunen et al. 2018). Thus, as the climate shifts and regions become less optimal for growing traditional crops and target species, these industries may begin growing new taxa or varieties that are better suited to the novel conditions. This could require the importation of species for culture from other regions, thus resulting in a new invasion threat. Such implications have already been seen in response to extreme weather events. During the recent devastating drought in Cape Town, South Africa, nurseries saw an increased demand for drought-resistant garden plants (Goodness 2018). Notably, this pertained not only to native plants but also to potted cacti, despite the recognition of cacti as an invasion threat in South Africa (Novoa et al. 2015). The potential for a new wave of plant invasions has also been highlighted in in the United States where the demand for ornamental plant species that are tolerant of warmer and drier conditions has increased in response to recent climate change (Bradley et al. 2012). Notably, potted plants are an important though unintentional vector for arthropods (Nentwig 2015) and thus an increased demand for ornamental plants is likely to result in increased introductions of associated species.

Interestingly, crop choice may also change in an effort to reduce carbon emissions and address climate change. For example, Switchgrass *Panicum virgatum* has been identified as a potential carbon-negative biofuel that could be grown outside of its native range (Tilman et al. 2006), although the risk of it becoming a problematic invader has been highlighted (Hartman et al. 2011). Plant species that are introduced as biofuels could become invasive as many of the attributes that make these species suitable as biofuels also make them potentially successful invaders (Chimera et al. 2010). Management responses to climate change could result in new invasion pathways. For example, assisted migration, which is the intentional translocation of species for conservation purposes, often in response to climate change, could result in invasions (Mueller and Hellmann 2008).

For the above it is clear that climate change may completely alter the global biogeography of invasions, routes, and propagule pressure as well as redefining the species targeted for translocation due to a change in human needs.

The implications of a changing environment for the establishment and spread of alien biota

Establishment success and ensuing spread of alien species are influenced by an interplay between the abiotic and biotic nature of the recipient environment (Soberón and Arroyo-Peña 2017). As such, climate change could have direct impacts on native and alien species that could indirectly affect native-alien species interactions, and ultimately invasion success (Hellmann et al. 2008).

For an alien species to establish it needs firstly to survive and reproduce at the point of introduction, while spread requires the same outcome at the invasion front. Because physiological processes are often regulated by environmental factors such as temperature (Levitt 1980; Charnov and Gillooly 2003), changes in climate will affect the performance and success of both native and alien species. Presently, most literature implies that alien biota will be favoured or at least not negatively affected by climate change, while native species will be disadvantaged (Vilà et al. 2007; Hellmann et al. 2008; Thuiller et al. 2008). However, this is premised on the idea that native species ranges represent optimal conditions and environmental change will represent a challenge. This assumption, however, remains largely untested. With limited knowledge held on the physiological tolerance ranges of most species, especially in relation to the interactive effects of multiple environmental changes (e.g. ocean temperature and pH), generalisations about the directionality of effects on alien vs native biota and the implications for establishment and spread cannot be made with much certainty. An added complexity comes from the fact that hybridisation within invaded regions can lead to the emergence of lineages with differential tolerances to either parental line (Donovan et al. 2010). Hybrids might not only have higher plasticity to cope with climatic changes but changes in climate can lead to higher hybridization rates (Muhlfeld et al. 2014). Nonetheless, the vulnerability to warming of some tropical groups that are already living close to their thermal optima (e.g. terrestrial ectotherms (Deutsch et al. 2008) and many plants in tropical rain forests (Corlett 2011)) cannot be denied. Warming could thus favour invasion by other tropical taxa with higher thermal tolerances as native species are lost.

Presently many alien species are casual or are restricted to artificial habitats or modified urban environments (e.g. green houses, gardens, botanical gardens) (Hulme 2017; van Kleunen et al. 2018). In the northern hemisphere, cold winter conditions currently prevent survival in the wild, but future warming could facilitate their establishment and spread. Importantly, populations in protected microclimates could serve as persistent sources of high propagule pressure that could facilitate successful establishment in the wild and spread from urban areas under future conditions. In particular, this risk has been highlighted for garden plants (Dullinger et al. 2017) and spiders (Nentwig 2015) but is likely to also apply to other taxa that presently survive with assistance (e.g. those kept as pets; Lockwood et al. 2019).

While post-establishment spread in a poleward direction by various marine alien taxa is known to have been facilitated by ocean warming (Canning-Clode and Carlton 2017), evidence of such spread in freshwater and terrestrial species is less obvious (Rahel and Olden 2008; Hulme 2017). In freshwater systems, this is likely due to the fragmented nature of lentic and lotic inland waters that limits the ability of freshwater taxa to disperse when facing environmental change (Woodward et al. 2010). Such spread restriction will likely lead to species loss more than range shift, specifically when considering the high risk of extinctions for freshwater species when compared to their terrestrial counterparts (Collen et al. 2014). Nonetheless, predictions made using bioclimatic models suggest that spread in response to warming will occur for a variety of taxa (e.g. insects (Evans and Simpson 2010), freshwater fish (Rahel and Olden 2008), and plants (Bourdot et al. 2012)). Interestingly, such models suggest that while mountainous high elevation regions may be increasingly vulnerable to plant invasions under warming conditions, this response can be context specific (Petitpierre et al. 2016; Lamsal et al. 2018). Simultaneous increases in human disturbance and propagule pressure currently limit our ability to ascribe observed increased colonisation of mountainous environments over the last two centuries solely to climate change (Pysek et al. 2011). Notably, current predictions of how environmental change may affect alien species distributions are based primarily on realised niches, as reflected by current ranges. However, existing and fundamental niches can be larger than realised niches (Soberón and Arroyo-Peña 2017) and using only the latter as a proxy for tolerance ranges in predictive models can underestimate the environmental conditions under which species can persist. Additionally, genetic admixture between previously isolated lineages may increase genetic diversity in alien populations (Krehenwinkel and Tautz 2013), potentially enabling the hybrid to occur in conditions unfavourable to either parent species (Donovan et al. 2010). This may, at least partially, explain why niche conservation is not always observed between native and alien ranges (Beaumont et al. 2009; Gallagher et al. 2010) and highlights a challenge to predicting how climate change may affect the spread of both new and established alien species. Although species distribution models may be conservative, they can still be useful in identifying groups that could invade under future climatic conditions (e.g. ornamental plants in Europe (Dullinger et al. 2017) and marine zoobenthos in the Canadian Arctic (Goldsmit et al. 2020)). With such warning, policy makers and managers can take targeted steps to prevent introductions.

By altering physiological performance and population dynamics of alien and native species, changes in climate can ultimately indirectly affect invasion success through changes to alien-native species interactions (Zarnetske et al. 2012). As the outcomes of such interactions can be highly context dependant (Lord 2017; Skein et al. 2018) and our understanding of the implications of climate change even at the species level is relatively poor, our ability to predict indirect community effects remains limited (Lord et al. 2017). While these shortcomings in foundational biodiversity knowledge have been highlighted before (Zarnetske et al. 2012), they continue to hamper our ability to anticipate and manage interactions between climate change and invasions.

The role of extreme climatic events

An important aspect of climate change is the increasing frequency and intensity of extreme events such as droughts, floods, storms, and heat waves (Rahel and Olden 2008; Mal et al. 2018). Unlike the mechanisms described above, extreme climatic events can influence invasions in any of the stages of the invasion process (Diez et al. 2012). In terrestrial systems, storm winds have been implicated in the movement of insects and plants (Burt 2002), while flooding has spread both aquatic invertebrate and vertebrate taxa (Cohen 1994; Canonico et al. 2005). Additionally, the disturbance associated with extreme events can dampen competition for resources, ultimately facilitating establishment and spread of alien taxa (Diez et al. 2012). This process has been observed in forests where removal of tree canopy cover by hurricanes can enable invasions by understorey plants (Horvitz et al. 1998) and on rocky shores where invasive mussels have been shown to dominate primary space following storms, despite the presence of native comparators (Erlandsson et al. 2006). An additional mechanism through which extreme events affect biological invasions relates to the broad physiological tolerance of many alien taxa. This characteristic can enhance survival of alien vs native taxa during droughts and heatwaves (Larson et al. 2009; Sorte et al. 2010), facilitating establishment, spread, and potentially increasing impacts (Diez et al. 2012). It is notable that while climatic events can interact with all stages of invasions, a single event (e.g. a hurricane or flood) could introduce and aid the establishment of an alien species.

Interactions with other drivers of change

Besides biological invasions and climate change, other drivers of global change such as land-use change, CO_2 enrichment, exploitation, and pollution have negative consequences for biodiversity and society (Sala et al. 2000). However, none of these drivers act in isolation and interactions among them can compound their impacts (Burgiel and Muir 2010). Thus, while the focus of this paper is on the nexus between invasions and climate change, it is important to acknowledge that invasions will also be affected by other agents of change and that these too can be plotted onto the invasion process (Fig. 1). For example, the exploitation of forest resources can facilitate the transport of alien taxa into pristine areas (Walsh et al. 2004) while plastic pollution in the oceans represents an increasingly prevalent, though unintentional vector with increasing propagule pressure of fouling biota (Avio et al. 2017). Other drivers of change are recognised to affect the establishment and spread of alien taxa by effecting native communities. In particular, elevated atmospheric CO_2, and nitrogen deposition tend to provide invasive plants with a competitive advantage over native comparators (Liu and van Kleunen 2017) although this advantage can be moderated by temperature and rainfall (Bradley et al 2010). In turn, changes in land-use disturb natural systems resulting in increased resource availability and invasibility by reducing competition for previously limited resources (Lear et al. 2020). In marine systems, overfishing can reduce predator driven biotic resistance by removing predators (Skein et al. 2020), leaving systems vulnerable to invasive prey. Although the above examples are illustrative of how various drivers of change may interact with invasions, it is important to acknowledge that studies simultaneously considering multiple drivers of change are not yet common place and our ability to anticipate biological responses to suites of agents of change remains limited (Bradley et al. 2010).

Impacts of alien species in novel ranges under changing climatic conditions

Impacts can manifest at any point after introduction and are not limited to any particular stage in the invasion process. These can be biological, socio-economic, or human-health related and, in some instances, species can have impacts in more than one of these spheres (Blackburn et al. 2014; Mazza et al. 2014; Bacher et al. 2018). As the impacts associated with many alien species provide the impetus for their management, understanding how climate change may affect impacts is of scientific and practical interest.

How a changing climate might affect biological impacts of alien species can be conceptualised in terms of the relative impact potential of alien and native comparators (Dick et al. 2017). This approach posits that changes in the per capita impact and relative abundance of these biota in response to environmental changes will alter the severity of impacts. Ultimately, these responses will be governed by the direct effects of climate change on individuals at the physiological level and the indirect effects on biotic interactions described above. While the theoretical framework for understanding biological impacts is well developed, on a practical level impacts are not routinely quantified with biases among ecosystems, across taxonomic groups, and between geographic regions (Jeschke et al. 2012; Ojaveer et al. 2015; Bellard et al. 2018). While more studies are clearly needed on the impacts of alien taxa in general, there is a particularly pressing need to assess impacts on resources that are likely to become scarcer under climate change. For example, alien plants increase transpiration and evaporation losses, reducing mean annual runoff by >5% in the Western Cape, South Africa (Le Maitre et al. 2020). In the absence of remedial action, this loss is expected to double (Le Maitre et al. 2020), posing a significant risk to water security in an area predicted to face reduced precipitation in the future.

Predicting how economic impacts associated with invasions might be affected by climate change is challenging, as these effects are often linked to biological processes. It has been suggested that to estimate the future economic impact of alien species, information on current impact, future potential distribution, and the likelihood of impacts remaining similar under predicted environmental conditions is required (Hulme 2017). Considering the level of uncertainty embedded in each of these aspects, accurate predictions remain elusive for most alien taxa. However, for well-studied invasions in areas for which present environmental conditions are well understood and models of future conditions are well developed (e.g. *Drosophila suzukii* in Europe (Gutierrez et al.

2016; Shearer et al. 2016; Mazzi et al. 2017) local knowledge could provide valuable insight into expected economic impacts.

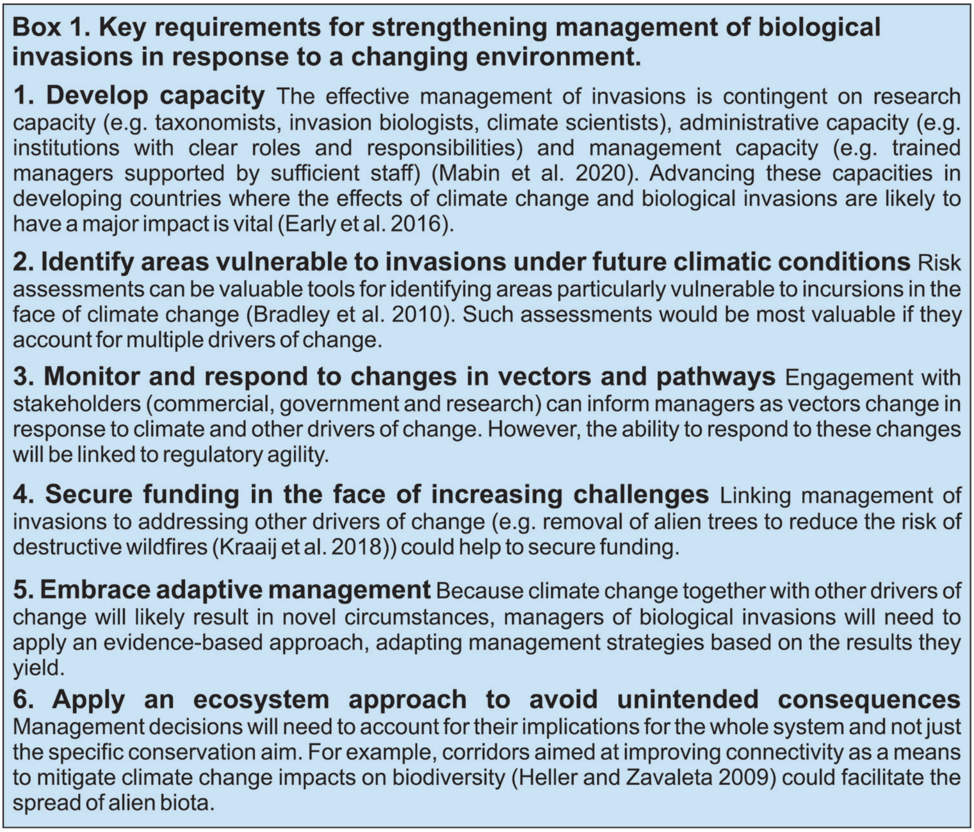
Impacts on human health under climate change are likely to be affected by shifting distribution and abundance of disease vectors (e.g. mosquitoes) and biota that are venomous or result in non-communicable diseases (e.g. allergenic reactions) (Fischer et al. 2011; Schindler et al. 2015). Although data remain scarce for many regions, in Europe alone more than 60 mammal, 70 bird, and 40 reptile species have been introduced along with their disease causing agents (Hulme 2014). Despite the obvious threat to human health and the potential implications for native taxa, the lack of dedicated risk assessment tools and the requisite data to implement them, challenges our ability to anticipate and prevent such introductions (Hulme 2014).

What does this mean for management?

Because management approaches are linked to the various invasion stages (Fig. 1) these will face new challenges as the climate alters and other drivers of change progress. Despite much uncertainty, the prospects of successful management of incursions could be greatly improved by proactively addressing key management needs (Box 1). A major challenge will be to strengthen proactive response capabilities in countries that currently have low biosecurity capacity. The ability to meet this challenge will be intricately linked to capacity development in multiple fields including research, administration, and management (Mabin et al. 2020). Such advancements in developing nations will be particularly important, as these countries are often particularly vulnerable to multiple drivers of change, including biological invasions.

The use of risk assessments to identify areas particularly at risk to invasion (Bradley et al. 2010) can help to focus monitoring in susceptible areas. In turn monitoring in high risk areas can facilitate early detection and swift management responses, ultimately maximising the probably of management success (Genovesi 2005). This approach could be particularly important in relation to protected areas that are charged with protecting diversity and associated ecosystem services. In Europe, only a quarter of marine and terrestrial protected areas were known to support any of the "100 of the most invasive species in Europe" species (Vilà et al. 2009) between 1920 and 2015 (Gallardo et al. 2017). However, future climate facilitated species range shifts could alter this and compromise the ability of these protected areas to meet their conservation mandates (Gallardo et al. 2017). Although the invasion risk faced by protected areas remains to be considered in many regions, an increasing number of studies have highlighted an anticipated rise in risk in marine, terrestrial and freshwater systems (e.g. Markovic et al. 2014; Iacarella et al. 2020; Liu et al. 2020).

As the climate changes biosecurity will be confronted by changes in vectors and pathways that will require engagement with stakeholders, adaptation of present protocols, and potentially, new legislative tools (Seebens et al. 2015). As such measures can be slow to institute, a proactive approach is likely to be important in ensuring that



Box 1. Key requirements for strengthening management of biological invasions in response to a changing environment.

1. Develop capacity The effective management of invasions is contingent on research capacity (e.g. taxonomists, invasion biologists, climate scientists), administrative capacity (e.g. institutions with clear roles and responsibilities) and management capacity (e.g. trained managers supported by sufficient staff) (Mabin et al. 2020). Advancing these capacities in developing countries where the effects of climate change and biological invasions are likely to have a major impact is vital (Early et al. 2016).

2. Identify areas vulnerable to invasions under future climatic conditions Risk assessments can be valuable tools for identifying areas particularly vulnerable to incursions in the face of climate change (Bradley et al. 2010). Such assessments would be most valuable if they account for multiple drivers of change.

3. Monitor and respond to changes in vectors and pathways Engagement with stakeholders (commercial, government and research) can inform managers as vectors change in response to climate and other drivers of change. However, the ability to respond to these changes will be linked to regulatory agility.

4. Secure funding in the face of increasing challenges Linking management of invasions to addressing other drivers of change (e.g. removal of alien trees to reduce the risk of destructive wildfires (Kraaij et al. 2018)) could help to secure funding.

5. Embrace adaptive management Because climate change together with other drivers of change will likely result in novel circumstances, managers of biological invasions will need to apply an evidence-based approach, adapting management strategies based on the results they yield.

6. Apply an ecosystem approach to avoid unintended consequences Management decisions will need to account for their implications for the whole system and not just the specific conservation aim. For example, corridors aimed at improving connectivity as a means to mitigate climate change impacts on biodiversity (Heller and Zavaleta 2009) could facilitate the spread of alien biota.

Box 1. Key requirements for strengthening management of biological invasions in response to a changing environment.

biosecurity keeps pace with evolving vectors and pathways. Attempts to standardise pathway classification and reporting of pathway importance (CBD 2014) is promising for managing changes in pathways, but not without its challenges (Faulkner et al. 2020). It is notable that not only will managers have to contend with new introductions, but many species that have been introduced or are naturalised could become invasive under future conditions. For example, much of Europe faces a high naturalisation risk from ornamental garden plants (Dullinger et al. 2017) with future climate change expected to increase this risk for many species (Haeuser et al. 2018). This invasion debt (Essl et al. 2011) will place a further burden on management resources. In addition, competing demands from other drivers of global change are likely to place a strain on resources available for biosecurity. For example, responding to extreme events such as floods will likely mean that fewer resources will be available for management of alien taxa. However, linking management of invasions to efforts to address other drivers of change (e.g. removal of alien trees to reduce the risk of destructive wildfires (Kraaij et al. 2018)) could help to secure and efficiently use scare resources.

Importantly, eradication, containment, and mitigation efforts are likely to be affected by how environmental changes affect alien species performance and the outcomes of biotic interactions with native biota (Bellard et al. 2018). As highlighted above, these will depend on the relative physiological tolerances of the different taxa. As such, an adaptive management approach that draws on previous knowledge but responds to observed outcomes is likely to offer a sound evidence-based approach to managing invasions in a changing world. Such an approach is likely to be particularly relevant with respect to the use of biological control agents. Notably, climate change could have positive, negative, or neutral impacts on weed biocontrol agents (Sun et al. 2020). This highlights the need to account for predicted future environmental changes in pre-release trials of new biocontrol agents and the use of an adaptive approach to managing ongoing biocontrol programs.

Although management actions aim for specific outcomes, the interconnected nature of ecological systems means that targeted actions can have ecosystem level implications. For example, corridors aimed at mitigating climate change impacts on biodiversity by improving connectivity (Heller and Zavaleta 2009) could enable the spread of alien biota, while assisted migration applied as a restoration tool may facilitate invasions (Derham et al. 2018). The application of an ecosystem approach to interventions could help to avoid unintended consequences. While this and the other measures discussed above could facilitate effective management of invasions in general, they will be particularly important in helping managers to navigate challenges in the face of climate change.

Challenges to a consolidated understanding of the implications of climate change for biological invasions

From the above it is clear that although numerous interactions between climate change and biological invasions have been recorded and we are able to make theoretical predictions about such outcomes in other instances, we do not have a consolidated understanding of the interplay between these drivers of global change (Bradley et al. 2010). This situation can be improved by addressing the following key challenges.

Gaps in knowledge

Probably the greatest obstacle to our understanding of how climate change will affect biological invasions stems from a lack of foundational knowledge (Zarnetske et al. 2012). Such gaps are evident in biological fields spanning taxonomy (e.g. cryptic invasions often go unrecognised (Morais and Reichard 2018)), natural history (e.g. life-history traits are seldom quantified, even for taxa considered to be well studied (Swart et al. 2018)), ecology (e.g. species ranges are often not georeferenced or routinely monitored (Pereira and Cooper 2006)), and even invasion biology (e.g. the inability to assign cryptogenic species as alien or native (Mead et al. 2011)). However, just as important is the lack of foundational environmental data in many regions, even for key parameters such as temperature and ocean pH (e.g. coastal carbonate chemistry remains unknown along the South African coast). An important avenue for addressing such data deficiency is to establish long-term monitoring programs that match data on the distribution and relative abundance of native and alien biota with environmental data. Additionally, to gain a mechanistic understanding of how establishment, spread, and impacts of alien biota may be affected by a changing climate, it is vital to assess physiological tolerances of native and alien taxa and how these may be altered through adaptation. However, in recognition of the complexities of climate change it is vital that future research considers how multiple environmental stressors may interact to affect such physiological outcomes (Todgham and Stillman 2013).

Inherent in the above gaps is a geographic bias in our understanding of biological invasions (Turbelin et al. 2017) and biotic responses to recent climate change (Bellard et al. 2018). In general, few alien species are reported from Africa and Asia (Turbelin et al. 2017), and in Africa at least, this likely reflects low capacity to detect and report on invasions rather than few invasions (McGeoch et al. 2010). It is notable that studies considering the ecological and evolutionary consequences of climate change are also sparse in these regions (Parmesan 2006), highlighting that our ability to understand the confluence of invasions and climate change will remain constrained until this bias is addressed. Addressing these gaps in knowledge should be prioritised as these regions support numerous biodiversity hotspots (Myers et al. 2000).

Transparent and reproducible taxonomy

A pillar of good science is reproducibility. While most publications uphold high standards with regards to reporting of methods, evidence of correct species identifications (e.g. citation of species descriptions used) is seldom provided (Bortolus 2008). While this issue is pervasive in ecology in general (Vink et al. 2012), it is particularly problematic in invasion biology, as the correct identification of study taxa underpins the essence of the field (Pysek et al. 2013). In order to improve the rigor of primary studies and enhance their value in terms of understanding how biological invasions may be effected by climate change, it is essential that the species descriptions used be cited (Meier 2016). This will facilitate reproducibility while also enabling researchers to track the use of species names, even when taxonomic assignments change through time.

Context dependency

Variability in invasions is well recognised and poses a particular challenge to our understanding of the processes driving incursions and our ability to manage them (Kueffer et al. 2013). This has led to attempts to use generalisations at a broad-scale to enhance understanding (e.g. Hui et al. 2013), but this can oversimplify patterns and have many exceptions (Novoa et al. 2020). A contrasting approach has been to focus on detailed case studies that comprehensively document individual invasions, but such results can lack generality (Robinson et al. 2017). Invasion syndromes (*sensu* Novoa et al. 2020) offer an approach for identifying generalities in invasions that are evident when grouping pathways, alien species traits and ecosystem characteristics that display predictable dynamics and impacts. The implication is that specific management approaches are thus identifiable per syndrome. This conceptual leap is an important step towards accounting for context dependency of invasions in light of climate change, as pathways, species traits and recipient environments could all be affected into the future. While some invasion syndromes have been identified (Novoa et al. 2020), for this approach to be fully tested, it needs to be applied to more systems. In the context of future climate change, invasion syndromes provide a theoretical foundation for hypothesis testing research. Depending on which of the three characteristics (pathways, alien species traits, or recipient environments) are affected and the nature of the effects, syndromes may remain intact, be partially dissolved or may no longer be valid. In any event, this offers a mechanism for incorporating climate driven changes into the human, biotic, and abiotic aspects of biological invasions. Invasion syndromes that hold, even under climatic change would vastly improve our ability to manage alien taxa in a dynamic world.

Valuable yet problematic databases

Because of the transboundary nature of both invasions and climate change, it is vital to place foundational data on well-maintained open access databases. Such broad-scale datasets could be pivotal in developing a spatial understanding of climate induced impacts on native and alien biota and providing inputs in support of environmental policy (Groom et al. 2017). To some degree this already happens through numerous international databases including GBIF, WoRMS, WRiMS, and the Encyclopaedia of Life. However, despite the value that these databases offer as expert-driven, collaborative, and centralised open-access sources of species occurrence data (Costello et al. 2018), they can face challenges in ensuring that data is accurate, up-to-date, and, importantly in the current context, georeferenced (Yesson et al. 2007). These challenges are aggravated by the fact that direct funding for the maintenance of foundational databases such as these is often limited, requiring researchers to volunteer their time. However, should these challenges be addressed, open access databases could provide a valuable source of information to researchers and managers alike.

A problem of scale

Future climate predictions are generally made at a global spatial scale. While this approach certainly has value, it can obscure important regional trends. For example, while at a global scale the present trend of ocean warming is predicted to continue (IPCC 2019), some regions along the South African west coast are in fact cooling (Rouault et al. 2010). This highlights the need for research considering the biological implications of climate change to account for both regional and local scale changes. Although theoretically sound, this approach may pose a practical challenge, as collection of data at a regional scale is linked to scientific capacity and funding and these practical constraints are notoriously uneven among regions (Costello et al. 2010). Ultimately, this results in geographic bias in fine-scale environmental data and regional understanding of the impacts of climate change (Pasgaard et al. 2015). While the collection of remotely sensed data may offset this challenge in some instances (Pettorelli et al. 2014), some environmental variables require the collection of physical samples (e.g. alkalinity when quantifying ocean carbonate chemistry to understand ocean acidification). Thus, until the scale at which environmental data are collected matches the spatial scale at which biological impacts manifest, our ability to fully understand the repercussions of climate change for alien and native biota will remain limited.

Caveats associated with analytical tools

The accurate forecasting of invasions, their rate of spread and potential range in novel regions are key requirements for effective management of invasions (Meyerson et al. 2019). Ecological niche models are a commonly applied predictive tool that use species traits (e.g. environmental tolerance) to map the potential range of alien species under current and predicted climates (Bellard et al. 2013). This is done by using the environmental conditions within a species known range (i.e. realised niche) as a proxy for physiological tolerances, which are then mapped onto the area of interest. While the benefit of this approach is that it enables pre-emptive assessment of invasions, it can fail to identify areas suitable for invasions as the fundamental niche may not be fully captured within the known range (de Andrade et al. 2019). Additionally, this approach assumes that processes controlling species distribution remain the same through time and space, and neglect novel interactions among biotic and abiotic variables (Elith and Leathwick 2009; Evans et al. 2015). Calibrating models with information from native and known alien ranges and reassessing niche changes as invasions progress can help to address these challenges (Pili et al. 2020). Unfortunately, models inherently become more accurate as species move towards occupying their full niche, but the predictive and applied value of models in such late stages of invasion are limited. Nonetheless, applying a mechanistic approach underpinned by a knowledge of physiology and life history traits where data allows can increase the value of predictive models (Meyerson et al. 2019).

Interdisciplinarity

Due to the multifaceted nature of biological invasions and the human dimension at the core of the problem, it is clear that interdisciplinarity is key to improving our understanding of the intersection between climate change and biological invasions. The emergence of invasion science out of ecology has been suggested as the reason for strong interdisciplinary interactions within the natural sciences but the need for meaningful engagement with social science is increasingly being recognised (Vaz et al. 2017). In terms of climate change and invasions, resolving questions around future changes in pathways and how best to manage them are likely to benefit immensely from an interdisciplinary approach. For example, understanding how agriculture might shift in response to changes in climate will enable early engagement with stakeholders and hence better biosecurity planning.

Conclusion

Unprecedented changes in climate will alter the nature of biological invasions and pose new challenges to their management. Changes in vectors and pathways will be largely directly human related and thus can be managed. However, the effectiveness of preventative measures and adaptive management will be greatly enhanced if they are proactive. For example, adaptation of importation permitting processes that anticipate import requests for new species or cultivars that may be better suited for culture under new environmental conditions will improve biosecurity outcomes in the face of climate change. In contrast to introduction and transport that are related to human actions, establishment and spread of alien biota are outcomes of ecological processes. Thus, our ability to effectively manage incursions through control, mitigation, and eradication will depend largely on our understanding of how climate change affects fitness at the species level and interactions among taxa. To this end, it is important that we address current knowledge gaps and invest in foundational understanding that will support informed management decisions into the future. Long-term monitoring of alien and native taxa offers an important tool for tracking invasions and gaining first insights into impacts. While context dependency in invasions already poses a notable challenge to their effective and efficient management (Novoa et al. in 2020), this is likely to be exacerbated by a changing climate. However, through proactive and adaptive management our ability to prevent and manage invasions under these challenging circumstances will be enhanced.

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REVIEW ARTICLE

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Reciprocal human-natural system feedback loops within the invasion process

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Abstract

Biological invasions are inextricably linked to how people collect, move, interact with and perceive non-native species. However, invasion frameworks generally do not consider reciprocal interactions between non-native species and people. Non-native species can shape human actions via beneficial or detrimental ecological and socioeconomic effects and people, in turn, shape invasions through their movements, behaviour and how they respond to the collection, transport, introduction and spread of non-natives. The feedbacks that stem from this 'coupled human and natural system' (CHANS) could therefore play a key role in mitigating (i.e. negative feedback loops) or exacerbating (i.e. positive feedback loops) ongoing and future invasions. We posit that the invasion process could be subdivided into three CHANS that span from the source region from which non-natives originate to the recipient region in which they establish and spread. We also provide specific examples of feedback loops that occur within each CHANS that have either reduced or facilitated new introductions and spread of established non-native species. In so doing, we add to exisiting invasion frameworks to generate new hypotheses about human-based drivers of biological invasions and further efforts to determine how ecological outcomes feed back into human actions.

Keywords

coupled human and natural systems, coupled social-ecological systems, feedback loop, invasive, negative feedback, non-native, positive feedback

Introduction

Humans are the principal drivers of biological invasions (see the Glossary in Box 1 for the definition of 'invasive'), evinced by the much higher rate of invasions in the modern era (Ricciardi 2007) and the wealth of literature detailing how people aid the establishment and spread of non-native species (e.g. Suarez et al. 2001; Wilson et al. 2009; Capinha et al. 2015). The invasion process could, therefore, be considered as a 'coupled human and natural system' (CHANS; defined by Liu et al. 2007) because natural components (i.e. non-native species and the environments or communities they impact) interact with and are affected by human behaviour and socioeconomic activity. However, none of the major hypotheses in invasion ecology (summarised by Catford et al. 2009) and few conceptual frameworks of the invasion process (e.g. Richardson et al. 2000; Colautti et al. 2006; Blackburn et al. 2011) explicitly considers reciprocal feedbacks (hereafter termed 'feedback loops') between humans and non-native species

Box 1. Glossary of terms.

Impact: Observable effects of non-native species, which can include ecological, economic and human health effects and changes in the provisioning of ecosystem services

Intentional: The intentional human-mediated transport and introduction of non-natives, such as for horticulture, the pet trade or biocontrol

Invasive: A non-native species with demonstrable impacts

Negative feedback loop: A human-natural feedback that continually stabilises or reduces ongoing or future invasions (also known as a 'balancing' feedback loop)

Non-native: Species moved outside their native range by human actions

Positive feedback loop: A human-natural feedback that continually increases ongoing or future invasions (also known as 'exacerbating' or 'reinforcing' feedback loops)

Recipient region: The specific location or region into which non-natives are introduced

Source region: The specific location or region from which a non-native originates

Unintentional: Non-natives whose human-mediated transport and introduction is entirely accidental, such as via hitchhiking on vehicles or through constructed corridors (but see Lodge et al. 2009; Howard 2019). Feedback loops are a distinguishing feature of CHANS because they are indicative of two, fully linked systems in which one system both drives and responds to changes in the other. These types of human-ecological feedback loops often produce unexpected interactive effects, such as sudden threshold shifts or lagged responses (Parker et al. 2008; Kramer et al. 2017). If these feedback loops exist for biological invasions, then identifying and incorporating them within invasion frameworks is essential to understanding how people can slow invasion rates, reduce negative invader impacts or accelerate stages of the invasion process.

We posit that three CHANS feedback loops can manifest within different stages of the invasion process, spanning from the initial source region where non-native species originate to the recipient region where non-natives establish and spread (Fig. 1). Each of these CHANS can produce 'negative' feedback loops that slow the rate of new species invasions over time and 'positive' feedback loops that accelerate invasion rates or exacerbate the impacts of previously-established invasive species (see examples in Fig. 2). Explicitly recognising the potential for multiple socioecological feedback loops within the invasion process elevates the relevance of existing published evidence that humans play a strong role in invasions. Additionally, recognising CHANS within the invasion process shifts the role of humans away from being simply vectors or unidirectional interactors with ecosystems that prime the way for invasions (Gurevitch and Padilla 2004) to one where people and non-native species are continually experiencing reciprocal feedback interactions in ways that can further control, sustain or even magnify invasion rates.

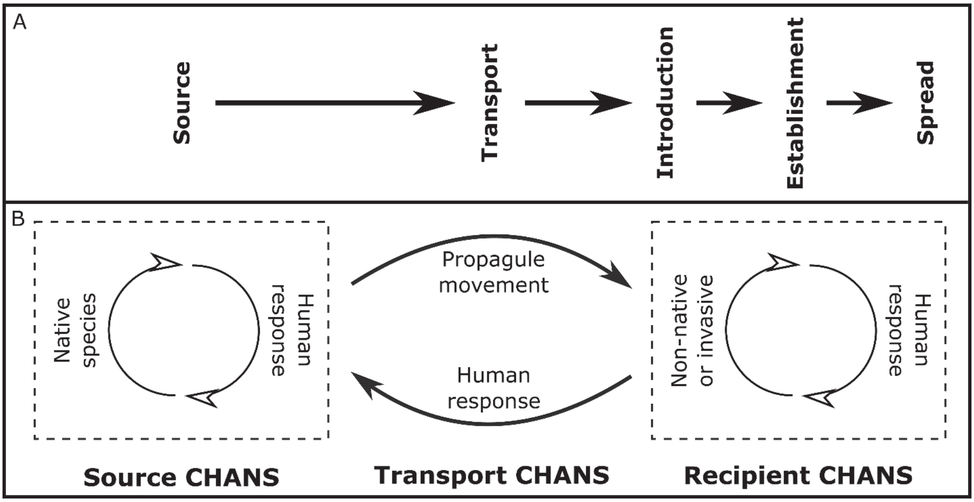
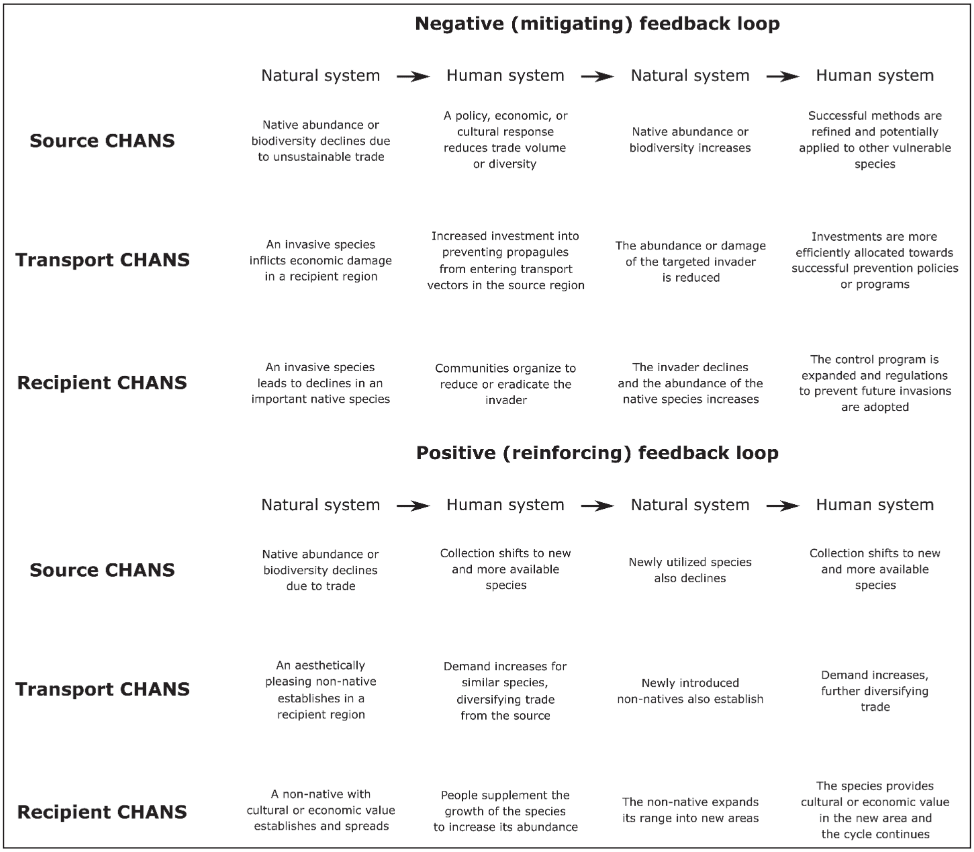


Figure 1. Comparison of (**A**) the different stages of the invasion process (based on Colautti et al. 2006) to (**B**) the three, linked coupled human-natural systems (CHANS) that potentially overlap these stages. The 'Source' CHANS encompassess the response of people in the region from which non-natives originate (i.e. the human system) to changes in and the collection of their own native biodiversity (i.e. the natural system). The 'Recipient' CHANS captures interactions between people and the introduction, establishment and spread of non-natives.The 'Transport' CHANS links the response of people to non-natives in the recipient region to the ongoing and future transport of organisms from the source region.

The first of our three CHANS (the 'source' coupling; Fig. 1A) acknowledges that there are human-natural feedback loops entirely localised within the region from which non-native species are sourced. Source region feedback loops can determine which and how many organisms are collected and transported to a new location (the 'recipient' region). Here, the CHANS is driven by how people in the source region perceive and respond to their local biodiversity, particularly in terms of the availability of species to exploit in trade. This feedback loop also recognises that local environmental or trade regulations can profoundly influence the quantity and diversity of species that enter the invasion process. These regulations may either prohibit the intentional transport of potentially invasive species or limit activities that tend to unintentionally transport individuals of species that may be invasive.

The second feedback loop (the 'transport' coupling; Fig. 2) encompasses interactions between source and recipient regions resulting from the transport of non-native species. Introduced non-native species can influence the ecology, culture, policy, economics or human health of the recipient region. These effects can then feed back to the source



Negative (mitigating) feedback loop

	Natural system →	Human system →	Natural system →	Human system
Source CHANS	Native abundance or biodiversity declines due to unsustainable trade	A policy, economic, or cultural response reduces trade volume or diversity	Native abundance or biodiversity increases	Successful methods are refined and potentially applied to other vulnerable species
Transport CHANS	An invasive species inflicts economic damage in a recipient region	Increased investment into preventing propagules from entering transport vectors in the source region	The abundance or damage of the targeted invader is reduced	Investments are more efficiently allocated towards successful prevention policies or programs
Recipient CHANS	An invasive species leads to declines in an important native species	Communities organize to reduce or eradicate the invader	The invader declines and the abundance of the native species increases	The control program is expanded and regulations to prevent future invasions are adopted

Positive (reinforcing) feedback loop

	Natural system →	Human system →	Natural system →	Human system
Source CHANS	Native abundance or biodiversity declines due to trade	Collection shifts to new and more available species	Newly utilized species also declines	Collection shifts to new and more available species
Transport CHANS	An aesthetically pleasing non-native establishes in a recipient region	Demand increases for similar species, diversifying trade from the source	Newly introduced non-natives also establish	Demand increases, further diversifying trade
Recipient CHANS	A non-native with cultural or economic value establishes and spreads	People supplement the growth of the species to increase its abundance	The non-native expands its range into new areas	The species provides cultural or economic value in the new area and the cycle continues

Figure 2. Examples of potential negative and positive feedback loops. Negative feedback loops can mitigate or balance invasions, whereas positive feedback loops can reinforce or exacerbate invasions. Examples are presented for each of the three proposed CHANS (source, transport, and recipient; Fig. 1) involved in the invasion process and are discussed further in the text.

region, such as through new prevention policies or shifting consumer demand. The transport feedback loop can span global scales, driven by inter-country travel and trade, but can also include local-scale interactions within a single region, provided propagules are being moved outside their native range (Faulkner et al. 2020; Pergl et al. 2020).

The final CHANS (the 'recipient' coupling; Fig. 2) encompasses local-scale feedbacks in the recipient region between humans and the effects of established non-native or spreading invasive species. This CHANS emphasises that how people respond to non-native populations and associated impacts in the recipient region is driven by local culture, demographics and economics, as well as the traits of the non-native species themselves. The response of local people can be a key driver for mitigating or further exacerbating potential new introductions, as well as promoting or preventing the continued spread of already-established non-native species.

In what follows, we highlight literature that supports key aspects of these three couplings and outline examples that show how human-nature linkages at each of these invasion stages can create both negative and positive feedback loops.

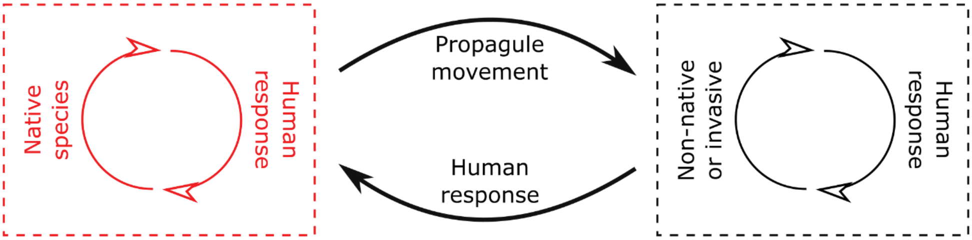
Source coupling

Drivers of source feedback loops

Invasion feedback loops that originate from the source coupling are driven by how people in the source region (i.e. the human system) respond to changes in that region's native species (i.e. the natural system) and how native species are, in turn, affected by these human responses. The key consideration in the source CHANS is whether these human-natural couplings can act to mitigate or exacerbate the rate at which the source region's native species are transported to one or more regions as non-natives.

Source region negative feedbacks

Source region negative feedback loops slow the rate of transport of non-native species into one or more recipient regions. The clearest examples of such feedbacks are locally-instituted quotas or harvest bans associated with the trade of live animals or plants. These top-down



Scheme 1.

regulatory measures are a human response to declining native species abundances that can reduce the exportation rate of the source region's native species (e.g. Rabemananjara et al. 2008). These measures reduce the diversity of species transported as non-natives or the propagule pressures associated with any one of these transported species. This feedback would, however, only form a complete loop if these regulations lead to an increase in the abundance or overall biodiversity of species native to the source region. If so, an additional strengthening of regulations or the adoption of new ones may follow (e.g. building 'legitimacy' in resource management; Pinkerton and John 2008), which may further slow the rate of organism collection and transport. A similar negative feedback loop can occur via bottom-up community interventions to conserve biodiversity by reducing unsustainable or illegal native species collection practices (Cooney et al. 2017). For example, by voluntarily reducing trade to protect a source region's biodiversity or to ensure sustainable trade, the number of species transported as non-natives out of a source location will slow and successful programmes could lead to the refinement or adoption of further interventions.

Negative feedback loops may also arise when people or agencies in the source region become more aware that their native species are considered invasive elsewhere. In this instance, people in the source region respond of their own volition by reducing the intentional or unintentional transport of known invaders. If the impacts of invasion are well-understood or economic incentives are provided to reduce the collection or accidental transport of known invaders out of the source region, the result could be improved detection and removal of hitchhikers before transport or a shift towards trading less harmful species. Cooperative international trade agreements that seek to reduce the further spread of known-invasive species, such as those contained within the International Plant Protection Convention or the Ballast Water Management Convention, embody this shift in international trade and reduction of hitchhikers. Cooperative international trade agreements encourage member nations to commit to actions that reduce the chances that vectors that emanate from their country transport invasive species to others (Keller and Perrings 2011). In this context, a negative feedback loop can result if the removal programmes or types of behaviour enacted in the source region succeed in reducing the number or diversity of transported organisms and these successes, in turn, provide information to reinforce or refine future efforts.

Source region positive feedbacks

Positive feedback source loops result in a continual increase in the quantity or diversity of species native to the source region being transported as non-natives to recipient regions. For example, similar in practice to 'fishing down the food web' (Pauly et al. 1998), if people in the source region respond to declines in their native species by continually shifting the base of exploitation to supply the live-animal or plant trade with the next most abundant or easily accessed species (Harfoot et al. 2018), then their actions ensure a continual increase in the pool of native species transported to recipient regions as non-natives. The same type of feedback loop can result from regulations in the source region that inhibit the collection or use of their declining native species if it drives commercial diversification towards the exploitation of new native species (e.g. Schroth and Ruf 2014). The loop continues if the abundances of newly-exploited species also decline, requiring new protective regulations which could again shift trade towards new species.

With the creation or continuation of a positive feedback loop for species that are intentionally transported, the resulting diversification in the native species transported from a source region will also diversify the transport of hitchhiking organisms associated with these species (e.g. the increasing diversity of zoonotic diseases as the global wildlife trade expands; Chomel et al. 2007). Beyond this example, however, it seems unlikely that positive feedback loops could arise for unintentionally collected organisms, such as plant seeds on clothing or arthropods within wooden pallets. Such feedbacks seem implausible given that people in the source region would have to purposefully increase their ability or propensity to collect and transport such species unintentionally based on changes in local biodiversity.

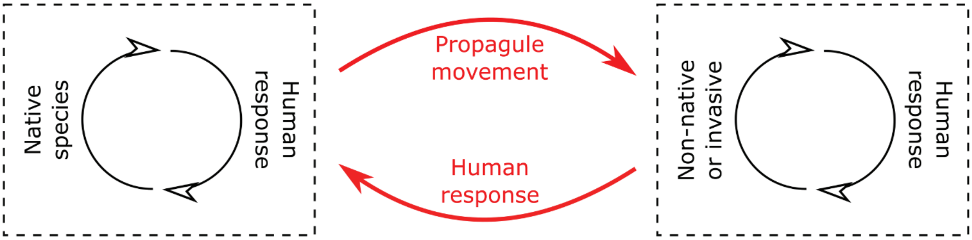
Transport coupling

Drivers of transport feedback loops

There is a well-established association between trade and travel intensity from source to recipient regions and the rate at which non-native species accumulate within recipient regions (Perrings et al. 2005; Hulme 2009; Seebens et al. 2017; Pyšek et al. 2020). A feedback loop can arise in this context if the effects of non-native species in the recipient region drive changes in policy, economics or human behaviour so that trade and travel from the source region either decreases (negative loop) or increases (positive loop). These feedbacks result in a concomitant reduction or acceleration of non-native introduction diversity or rates to the recipient region.

Transport negative feedbacks

Negative transport feedback loops occur when the economic, ecological or cultural costs of invasions in the recipient region incite a human response that reduces the diversity or quantity of species transported out of the source region. A full feedback loop results when this response is then adapted based on how effectively it prevented further



Scheme 2.

invasions or invader effects. For example, the damage caused by multiple invasive species in New Zealand led to government adoption of strict biosecurity measures that limit the importation of novel non-native species from a variety of source regions (Jay et al. 2003). These measures, in turn, prompted industry and government agencies in source regions to impose or strengthen their own pre- or within-transport biosecurity measures, such as adoption of cargo or ballast treatment, so that their products can successfully pass border inspections. The feedback loop was completed when these regulations or incentives were further revised, depending upon whether non-native establishment and spread declined or when a new invader arose (Hayden and Whyte 2003).

Economic feedbacks from the recipient region could also affect non-native species transport if the damage caused by an invader shifts investments towards funding prevention methods that reduce the quantity or diversity of propagules that enter, survive or exit transport vectors (Lodge et al. 2009; Latombe et al. 2020). This feedback loop hinges on the relative costs and benefits of investing in measures that prevent initial introduction compared to focusing on control of already established non-natives or even not managing the invasion process at all. Biosecurity preventative measures could be favoured if, for instance, the costs of pre-introduction treatments are low (Hyytiäinen et al. 2013), the projected or known damage of an invader is high (Marbuah et al. 2014) and if policy-makers are willing to accept the uncertainties of preventing potential invaders over controlling known invaders (Finnoff et al. 2007). There is also a clear potential for a shift in the strength of this negative feedback loop over time. Prevention can be favoured if damage increases as an invasive species' population increases or could be disfavoured if the invasive population declines. New technologies or refined risk assessments (e.g. Kumschick et al. 2020) could also alter the perceived costs versus benefits of investing in preventing non-native transport.

Awareness campaigns or stigmatising trade in particular species (Fischer 2004) provides an alternative type of cultural negative feedback loop that can reduce demand for live species or products that commonly result in the establishment of non-native species in the recipient region. Consumer preferences in the recipient region are a key driver of both intentional trade and unintentional transport of non-native species (Sinclair et al. 2020). Campaigns that target consumers of goods associated with high rates of species invasion can therefore reduce the diversity or volume of species transported from a source region, such as by altering preferences to favour native or non-invasive species (e.g. Drew et al. 2010; Patoka et al. 2018) or by encouraging the use of more sustainable or locally-sourced goods (e.g. Barlow et al. 2014). However, it is unclear whether changes in consumer demand can, in turn, be affected by elevated rates in the introduction and establishment of non-native species, thus completing the full feedback loop. Such a feedback loop might occur if consumer demand continues to decline in response to the success of awareness programmes at controlling non-native introduction rates.

Transport positive feedbacks

Non-native species introductions and subsequent invasion impacts in a recipient region can drive socioeconomic- or policy-based feedback loops that continually increase non-native species transport out of source regions over time. Increasing introductions of non-native pets and horticultural plants, for example (Mack 2003; Lockwood et al. 2019), has served to increase consumer demand for such products. This increased demand has subsequently elevated trade volume and diversified the number of species within these trades (e.g. Drew et al. 2010; Seebens et al. 2017; Scheffers et al. 2019), creating a potential feedback loop. A similar feedback could result from biocontrol introductions in which the human response to the effects of a non-native species is to introduce another non-native, natural enemy, which could subsequently become invasive and require further control (Simberloff and Stiling 1996). Culturally-driven import and release of traditional live food plants and animals by human communities (e.g. snakehead fish; Cagauan 2007) could also create a positive feedback loop in which the initial successful introduction of desired non-native species to re-create a cultural 'sense of place' can increase the appeal of further introductions (Brook 2003). All of these examples of potential positive feedback loops can produce a socioeconomic version of invasional meltdown (invasive species facilitating further invasions; Simberloff and Von Holle 1999), whereby the human response to non-native species introductions or the effects of these introductions is to desire that more non-native species be introduced, which could in turn spur further introductions (Fig. 3).

Regulation can also create positive feedback loops if the response of the people living in a source region to a policy change enacted in the recipient region is avoidance, rather than compliance. Avoidance behaviour can expand transport into new regions, subsequently increasing the spatial dispersion of transport vectors and thus associated introductions of non-native species. An agent-based model by Ameden et al. (2009) provides an example of such avoidance by showing that importers might respond to increases in invasive species border inspections with 'port-shopping' behaviour by seeking out ports with lower inspection standards. Non-native species blacklists can similarly drive avoidance responses by shifting transport towards as-yet unlisted taxa, subsequently increasing the probability of introducing new non-native species in recipient locations (García-de-Lomas and Vilà 2015). There are also examples in which travel fees in recipient regions can alter human movements rather than prevent or control them (e.g. Chivers et al. 2017) and this same principle could apply to transport vectors travelling between source and recipient regions. A full positive feedback loop can then arise when regulatory efforts subsequently expand to encompass the new regions into which vectors are now travelling, creating an 'arms race' between regulatory policy and avoidance responses.

Recipient region coupling

Drivers of recipient feedback loops

Once non-native species establish within a recipient region, the population abundance or geographical distribution of these species can be reduced or augmented via our final CHANS feedback loop. Here, reciprocal loops are generated by the cultures within a

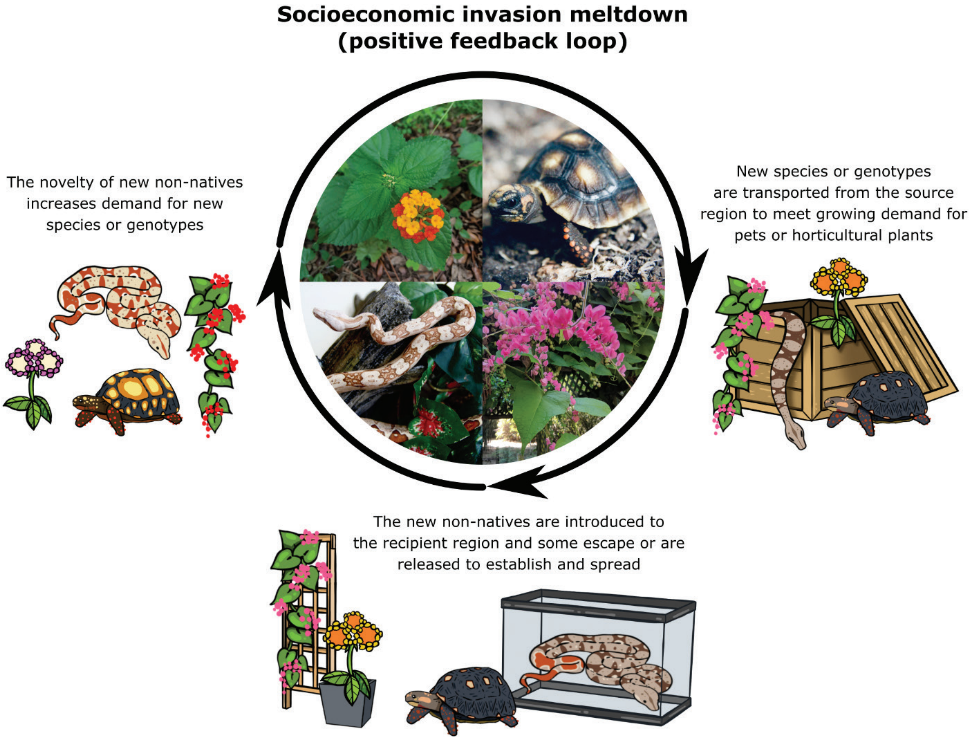
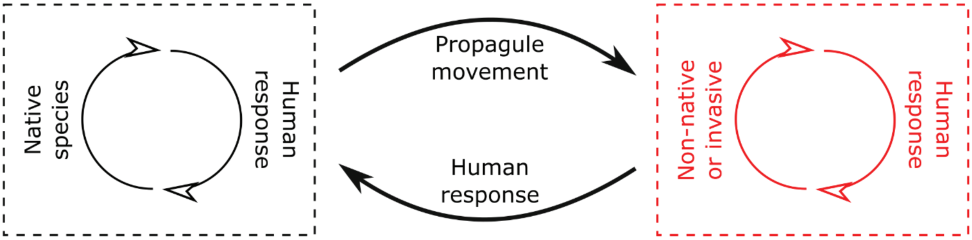


Figure 3. A conceptualisation of an invasion positive feedback loop driven by intentional introductions of non-native species for the horticulture or pet trades. The example species used are, from the top left of the centre photograph and moving clockwise, Lantana (*Lantana camara*), the red-footed tortoise (*Chelonoidis carbonarius*), coral vine (*Antigonon leptopus*) and the red-tailed boa (*Boa constrictor*). Each species has a history of intentional introduction and successful establishment in recipient regions. Drawings with different colours are based on actual colour varieties or morphs of these species. The plant photographs were provided by James Sinclair (the first author), the animal photographs were provided by Keara Clancy (Department of Wildlife Ecology and Conservation at the University of Florida) and the drawings were commissioned from Marie-Josée Létourneau for use in this manuscript.

recipient region and the perceptions of risks and benefits that established non-native species present (Trigger 2008; Gaertner et al. 2017; Vimercati et al. 2017; Polák et al. 2019; Potgeiter and Cadotte 2020). These perceptions will feed back towards either inhibiting or accelerating the population growth rate, geographical range expansion and/or secondary spread of established non-native species and, thus, their impacts which, in turn, will affect how the non-native is perceived (Shackleton et al. 2019).

Recipient region negative feedbacks

Non-native species that cause ecological or economic damage or that disrupt cultural and recreational activities can instigate a negative feedback loop via instigating control or eradication efforts or incentivising the use of native species or products that do not



Scheme 3.

facilitate secondary spread of non-native species. A full negative feedback loop occurs if self-, community- or government-enforced initiatives against harmful non-native species successfully limits their abundance or distribution or promotes awareness that facilitates management and reduces further spread (e.g. Klapwijk et al. 2016). These successes are then used to refine or inspire future efforts (e.g. Simberloff 2009). In this way, the human system is continually responding to ongoing changes in the natural system to better balance or mitigate invasions. An example of this feedback loop is when invasive trees or grasses restrict homeowner site lines or invasive aquatic plants limit boating and fishing opportunities and individual homeowners respond by actively reducing the population abundance of the non-native on their property (Charles and Dukes 2007; Niemiec et al. 2017). Invasive species can also pose risks to the persistence of culturally-valuable native species, such as the risk that the invasive emerald ash borer will result in the near-total loss of native ash trees that feature in the origin of stories about Native American tribes (Poland et al. 2017). When such damage to cultural or aesthetic amenities occurs, there is often a strong desire by residents to restore a 'natural' aesthetic by managing the invasive species or imposing stricter regulation of invasive and non-native species use or related goods (Dickie et al. 2014; Kueffer and Kull 2017). These individual responses can create full feedback loops when communities organise to form self-promoting groups to control several non-native species. Often membership in these groups or the social acknowledgement people receive from these groups, leads to more individuals joining, thus creating a social expectation of further engagement in non-native species management (Niemiec et al. 2016). This feedback can be reinforced when community groups exert considerable pressure on local governments to initiate management actions, which often happens due to local media attention or when the communities feel the potential threat of a growing invasion (Crowley et al. 2017).

Recipient region positive feedbacks

Many non-native species can elicit sympathetic reactions from people who have a historical relationship with these taxa or who are not aware of the issues presented by invasive species. Non-natives can also become more positively perceived through time as people may view pest species positively or novel if population sizes decline (Shackleton et al. 2019) and fear of non-natives can decrease with increased familiarity to the damage they can cause (Schüttler et al. 2011). Sympathetic or positive reactions to established non-native species can drive their increased population growth rates or enhanced dispersal potential via the human desire for their further establishment and spread. These actions can, in turn, expose new people to the non-native species and reinforce secondary spread through positive associations with the non-native, creating a positive feedback loop. For example, people in many regions have intentionally introduced non-native species for aesthetic or cultural purposes and, in some cases, these species have become culturally significant, resulting in a cultural desire for continued population growth or range expansion of the non-native species (Nuñez and Simberloff 2005). Due to this connection, non-native species that may be economically detrimental, but elicit sympathy through the human-animal bond (e.g. deer) or have charismatic features, such as song or colouration, may enjoy little to no reductions in their individual survival or reproduction rates due to push-back from citizens to proposed control measures (e.g. common lionfish; Jimenez et al. 2017). In fact, for many such species, people will actively promote survival and spread rates of non-natives through supplemental feeding and other protection (Robinson et al. 2005; Bonter et al. 2010). Even with invasive species, particularly horticulture plants introduced for aesthetics that have significant ecological impacts but limited negative or positive economic impacts (e.g. bamboo and tallow tree), invasive populations may be spread prolifically through continued local transport and intentional planting or release. This feedback occurs because, as populations of these invasive species spread, more people encounter the species which, in turn, fosters the desire for people to further the species' spread via intentional planting (e.g. Bradley et al. 2010).

Positive feedback loops can also occur when an invader becomes integrated with human communities in the recipient region as a resource (Robinson et al. 2005; dos Santos et al. 2014; Vilá and Hulme 2017), subsequently leading to human actions that promote further spread or that oppose control or eradication efforts. Many non-native species, for instance, have become key targets for hunting or provide essential food sources for local communities (Jean Desbiez et al. 2011). In several such circumstances, traditionally-hunted native species have declined as a result of past over-exploitation or the ecological impacts of other invasive species, resulting in a cultural shift in hunting practices towards exploitation of a non-native (Robinson et al. 2005; Jean Desbiez et al. 2011). Over time, responding to ongoing declines in native species by continually spreading a non-native, may become the cultural norm and the perception of the new species as 'non-native' may be lost (Semenya et al. 2012; Shackleton et al. 2015). People may also facilitate the secondary spread of established and valuable non-natives to new areas in response to its growing value as a resource (Nuñez et al. 2012), creating a full feedback loop.

Lastly, management responses to non-natives that do not account for human behaviour could drive positive feedback loops through an arms race between regulation and non-compliance. These types of feedbacks are more thoroughly discussed in the source and transport CHANS sections above, so we will not delve into them too deeply again, but it is important to acknowledge their localised role in the recipient region. Examples of potential positive feedbacks include access or cleaning fees levied to reduce unintentional non-native spread, which can instead drive the secondary spread of non-natives into new locations (Chivers et al. 2017). Similarly, localised restrictions on the sale or purchase of non-native species can drive customers to seek out nearby, unregulated vendors (e.g. shifting the within-state US trade of horticultural plants to out-of-state sources; Maki and Galatowitsch 2004). Efforts aimed at collecting non-natives from the broader public, such as pet or plant surrender programmes, could also perversely cause non-native species releases if people do not perceive participation to be personally cost effective or convenient (Drake et al. 2015). These examples can become fully realised positive feedback loops if the result of the human response is an increase in non-native species establishment, spread or impacts which, in turn, drives the adoption of further management responses that are again avoided.

Implications for Invasion Science

There is extensive literature on human responses to non-native and invasive species, but rarely are feedback loops within or across invasion stages explicitly considered (cf. Lodge et al. 2009; Howard 2019; and Hulme et al. 2020 for parallels with epidemiology). The recognition that three distinct CHANS can occur across the invasion process and that each can create negative and positive feedback loops, provides three key insights to invasion science.

Firstly, a CHANS perspective highlights that recipient region invasions are inextricably linked to interactions with the source region and that human-nature feedbacks, localised solely within the source, can drive invasion dynamics. This is a key insight because many invasion frameworks overlook processes that occur prior to non-native species introduction as potential drivers of accelerating global invasion rates (Sinclair et al. 2020). Considering how policy, economic and cultural feedback loops within the source region subsequently affect the invasion process and human-nature interactions in the recipient region could therefore be crucial for predicting how introductions may change in the future and for improving invader management (i.e. the same implications of a better focus on the 'supply-side' of invasions discussed by Verling et al. 2005).

Secondly, the continual feedback between people and native or non-native species in the CHANS we have outlined could produce unexpected or unpredictable interactions that may continue to change over time as humans respond and adapt to the presence of non-native species. These types of emergent effects are discussed more fully in other literature (e.g. CHANS or social-ecological systems; Liu et al. 2007; Preiser et al. 2018) and include: (i) legacy or lagged responses; (ii) thresholds and resiliency between alternate states; and (iii) indirect effects. Though not discussed from a CHANS perspective, there is evidence that these types of interactions can manifest in the invasion process. Examples include current invasions that are a legacy of past human-nature interactions (Essl et al. 2011), introductions that drive regime shifts in how people interact with non-native species (Shackleton et al. 2018), and indirect human responses to non-natives of changing demand for goods or services rather than direct control of local populations (Drew et al. 2010). This potential for complex and surprising human-nature interactions in invasions highlights a need to re-examine (and potentially revise) current hypotheses about the major drivers of invasion rates to address how humans might be shaping the ecological processes involved. Efforts to understand invasions that lack a consideration of human components will increase the likelihood that surprising, interactive effects will arise (Pyšek et al. 2020) and interventions, based on such incomplete knowledge, could generate new problems or even exacerbate invasions (e.g. control policies that drive a positive feedback loop).

Thirdly and finally, the potential existence of the three CHANS we have outlined highlights that there is still a great deal we do not know about how people and non-native species interact. Many of the example feedback loops we reviewed are theorised, simplified representations of complex interactions. We have supported our ideas where we can with background literature, but there is simply not enough research to fully specify the complete feedback loop for any one example. Further work is thus required to confirm that these CHANS exist as we have outlined and, if so, to fill in the complexities within each. Examples of such complexities include potential variability in the strength and relevance of each CHANS amongst different types of intentional and unintentional invasion pathways (e.g. intentionally released versus escaped non-natives; Hulme 2009). Feedback relevance may also shift across stages of the invasion process, such as accidental escapees or hitchhikers that are initially affected by policy or economic feedbacks, but cultural feedbacks may become more relevant as people become aware of the invader's impacts in the recipient environment. The prevalence of the non-native species-to-people portion of invasion feedback loops is also potentially complex. Examples of one-way feedbacks in which people respond to non-native species abound in the invasion literature (e.g. intentional introductions to encourage establishment or eradication programmes to remove spreading invaders), but less is known about how readily this human response is affected by subsequent changes in the non-native species themselves (but see examples in Howard 2019). Therefore, while our approach serves to deepen continuing efforts in invasion science and ecology as a whole to better account for the role of humans in natural processes, we have only scratched the surface of the milieu of potential interactions that likely exist between people and non-native species.

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Comparing the IUCN's EICAT and Red List to improve assessments of the impact of biological invasions

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Abstract

The IUCN recommends the use of two distinct schemes to assess the impacts of biological invasions on biodiversity at the species level. The IUCN Red List of Threatened Species (Red List) categorises native species based on their risk of extinction. Such assessments evaluate the extent to which different pressures, including alien species, threaten native species. The much newer IUCN Environmental Impact Classification for Alien Taxa (EICAT) categorises alien species on the degree to which they have impacted native species. Conceptually, the schemes are related. One would expect that: 1) if a native species is assessed as threatened under the Red List due to the impacts of alien species, then at least one alien species involved should be classified as harmful under EICAT; and 2) if an alien species is assessed as harmful under EICAT, then at least one native species impacted should be assessed as threatened by alien species under the Red List. Here we test this by comparing the impacts of alien gastropods, assessed using EICAT, to the impact on native species as assessed based on the Red List. We found a weak positive correlation, but it is clear there is not a simple one-to-one relationship. We hypothesise that the relationship between EICAT and the Red List statuses will follow one of three forms: i) the EICAT status of an alien species is closely correlated to the Red List status of the impacted native species; ii) the alien species is classed as 'harmful' under EICAT, but it does not threaten the native species with extinction as per the Red List (for example, the impacted native species is still widespread or abundant despite significant negative impacts from the alien species); or iii) the native species is classified as threatened under the Red List regardless of the impacts of the alien species (threatened species are impacted by other pressures with alien species potentially a passenger and not a driver of change). We conclude that the two schemes are complementary rather than equivalent, and provide some recommendations for how categorisations and data can be used in concert.

Keywords
Aichi Target 9, documenting impacts, Gastropods, invasive alien species, invasion frameworks, species population declines, threatened species

Introduction

The role of biological invasion as a driver of global change (Vitousek 1994; UNEP 2011; Simberloff et al. 2013; Sage 2020) is recognised by the UN Convention on Biological Diversity (CBD) in its Strategic Plan for Biodiversity 2011–2020 (Aichi Target 9; see Essl et al. 2020 for a proposal of targets for 2030 and 2050) and the UN Sustainable Development Goals (SDG Target 15.8, IUCN 2016). Amongst the many negative impacts of biological invasions are their roles in species extinctions. Data from the IUCN Red List of Threatened Species (Red List), in particular, have been used to determine the impact of biological invasions as a threatening process (Bellard et al. 2016). However, the mechanisms through which biological invasions threaten species and the extent to which they place species on a trajectory towards extinction are not always clearly documented (Kumschick et al. 2015; Downey and Richardson 2016). The threat of alien species requires well-tailored tools for objectively documenting, monitoring, and reporting their impacts (Latombe et al. 2017). In response to the need to understand the impacts of alien species, the Environmental Impact Classification for Alien Taxa (EICAT) was developed by Blackburn et al. (2014) based on the structure of the Red List. Comprehensive guidelines for EICAT were subsequently developed by Hawkins et al. (2015) and, after various trials, wide-ranging consultation, and further developments of the scheme, EICAT was adopted as a standard of the International Union for Conservation of Nature (IUCN) in 2020 (IUCN 2020).

EICAT provides a simple, objective, and transparent tool for systematically documenting the impacts of alien species that occur anywhere in the world (IUCN 2020), thus facilitating the monitoring of SDG and CBD goals. The EICAT definition of alien species includes “all taxa moved intentionally or unintentionally by human activities beyond the limits of their native geographic range, or resulting from breeding or hybridisation and being released into an area in which they do not naturally occur” (IUCN 2020). EICAT enables the categorisation of alien species based on the magnitude of impacts on native species (Table 1). The magnitude of impact varies from a reduction in the performance of individuals to the loss of individuals, the loss of populations, the loss of species locally, and, in the worst case, to the global extinction of species (Hawkins et al. 2015; IUCN 2020). Alien species are then classified as harmful (reduction of population sizes or worse) or non-harmful (reduction in performance of individuals or no reduction) based on the highest recorded impact seen anywhere in the world. This will facilitate the comparison of alien species across regions and taxonomic groups, enable the tracking of invasion impacts over time, facilitate the prediction of impacts of alien species introduced to new regions, and allow for the prediction of current impacts where such impacts have not yet been monitored, but have been recorded elsewhere in the world (Blackburn 2014; Hawkins et al. 2015; Latombe et al. 2017; Kumschick et al. 2020).

The Red List assigns species to categories of extinction risk using quantitative criteria and relevant species information, enabling species to be classed as threatened or not-threatened (IUCN 2019). As part of the process of assigning an extinction risk, the Red List identifies and documents the pressures on native species. These pressures include the five major biotic and abiotic pressures as defined by the CBD, namely invasive alien species, habitat loss and degradation, climate change, over-exploitation, and pollution (Global Biodiversity Outlook 2010). Information about the timing and nature of impacts [termed 'stresses' as per IUCN guidelines (IUCN 2019)] are recorded, as well as whether such impacts occur at the species or ecosystem-level (IUCN 2019). Pressures are also classified, where possible, by the scope (proportion of the population impacted) and severity (proportion of population decline over a set period) of impacts. The similarities and differences between the Red List and EICAT are outlined in Table 1.

In this paper, we examine the relationship between EICAT and the Red List using alien gastropods as a case study. We predict that: 1) if a native species is assessed as threatened under the Red List due to the impact of alien species, then at least one alien species involved should be classified as harmful under EICAT; and 2) if an alien species is assessed as harmful under EICAT, then at least one native species impacted should be assessed as threatened by alien species under the Red List. We then consider the relationship between the two schemes more broadly, responding to the World Conservation Congress (Hawaii 2016) resolution (WCC-2016-Res-018-EN) which urges the incorporation of EICAT assessment results into Red List assessments (IUCN 2016).

Methods

The choice of which taxa to use for comparison purposes was limited primarily by the availability of EICAT assessments (as a relatively new scheme, there are far fewer EICAT assessments than species with Red List assessments). EICAT assessments are available for alien birds (Evans et al. 2016), amphibians (Kumschick et al. 2018), and bamboos (Canavan et al. 2019), but we focussed on an assessment of 34 species of gastropods identified as alien species present in South Africa by Kesner and Kumschick (2018). The EICAT assessments by Kesner and Kumschick (2018), unlike the others, provide information on the specific impacted species and associated evidence sources. Moreover, the assessments looked at impacts anywhere in the world (the study aimed to identify potential impacts in South Africa). We used these assessments to create a database describing interactions between the alien gastropods and native species (only cases where the impacted native species was identified were included). This gave 192 records. We then excluded interactions where the alien species under EICAT, or the native species under the Red List, was scored as Data Deficient (DD) or Not Evaluated (NE). The final dataset consisted of 101 records of interactions [details of the full

Table 1. A summary of the IUCN Red List and the IUCN EICAT schemes showing areas of potential interaction between them. These are based largely on direct comparisons between the Red List guidelines (IUCN 2019) and EICAT standards and guidelines (IUCN 2020), see also Probert et al. (2020) for a discussion on uncertainty.

Sections	Red List	EICAT	Interaction between schemes
Purpose	To estimate the risk of extinction of specific native species and the drivers contributing to this risk.	To identify the type and magnitude of impacts that specific alien species have on native species.	The schemes have different purposes but share some outputs, for example, documenting alien species impacts.
Scheme categories	Not Evaluated (NE) Data Deficient (DD) **Not-threatened** Least Concerned (LC) Near Threatened (NT) **Threatened** Vulnerable (VU) Endangered (EN) Critically Endangered (CR) **Extinct** Extinct in the Wild (EW) Extinct (EX)	Not Evaluated (NE) No Alien Populations (NA) Data Deficient (DD) **Non-Harmful** Minor (MN) Minimal Concern (MC) **Harmful** Moderate (MO) Major (MR) Massive (MV)	With increasing threat levels of the impacted species on the Red List, the impact severity of the alien may also increase on EICAT. This may not be true for all cases.
Geographical scope	Global, regional or national.	Global, regional or national.	For the Red List, the global population is the entire distribution of the species within its native range. All levels of assessment are related to the global population (e.g., regional adjustments). For EICAT, the global scope refers to impacts recorded where there are alien populations present, and impacts are not related to the global population of the impacted native species.
Population declines	Population decline is recorded against specific thresholds per category. It is also assessed across different time frames (past, present, and future).	Harmful categories indicate decline, MO is for a population; MR is a reversible loss of a population; MV is an irreversible loss of a population. Only past declines are considered.	There are different thresholds of decline and methods and time frames of recording population decline.
Which species are explicitly specified	Native species and the species causing impacts (e.g., alien species, unless the native species is LC).	Alien species and native species being impacted.	Need to identify the same impacted taxa to enable the linkage of schemes.
Evidence sources	Projected, inferred, estimated or suspected.	Observed (estimated) and inferred.	The Red List makes allowance for the use of projections and suspected evidence, while these are not included on EICAT. Data included in Red List assessments may not be accepted under EICAT.
Responsiveness of schemes	Assessments are due every 10 years or as resources and/or new information becomes available. Additionally, new species are described regularly, so there are always more assessments to be conducted.	As a new scheme, only few groups have been assessed. Additionally, impacts must have been recorded before an assessment can be conducted or the species will be assessed DD or NE.	Two sources of delays in detecting change. First is due to processes of the assessment schemes (e.g. resource availability, expert time, assessment information). Second is the role of invasion debt resulting in, for example, delay in the detection of impacts.
Taxonomy	An updated taxonomic backbone is used, but is dependent on the experts to prompt updates.	Uses the same taxonomic backbone as the Red List; however, primary references may include outdated taxonomy of alien and impacted native species.	Both schemes are in principle using the same taxonomic backbone; however, primary literature sources may differ. This is a procedural difference and will need management as assessments are conducted.
Final status selection	The highest threat status selected based on supporting data as a precautionary method.	The highest impact status selected corresponding to the maximum threat level.	Both schemes make use of the highest status obtained.
Measure of uncertainty	No specific categories. Specify best estimate or range of plausible values and document all information used and process of calculation.	Three different levels: high, medium, and low.	Not directly comparable. Primary literature needs to be examined to determine how the uncertainties relate.
Sources of uncertainty	Natural variability and semantic uncertainty (vagueness in terms and definitions used in the criteria).	Presence of confounding effects, study design, data quality and type, spatial and temporal scale, and coherence of evidence.	Not directly comparable. Primary literature needs to be examined to determine how the uncertainties relate.
Threshold bases	Quantitative (e.g. range size, number of individuals).	Qualitative (e.g. categories of decline from individual performance to populations and species).	Not applicable.

range of individual impacts taken from Kesner and Kumschick (2018)], with information on the risk of extinction, year of assessment, population trend, and stresses (attributes of a taxon that are impaired due to the impacts of a pressure) taken from the Red List (IUCN 2019).

Given that the data are categorical, we used a Pearson Chi-squared test to assess, across all species interactions, whether harmful or non-harmful alien species tended to be associated with threatened or not-threatened native species (see Table 1 for details of the scheme categories). A Monte Carlo simulation was used with 1000 replicates, as the frequency of one of the variables was less than 5 (Hope 1968). We then compared EICAT statuses in order of increasing magnitude of impact (MC < MN < MO < MR < MV) to Red List statuses with increasing level of extinction risk (LC < NT < VU < EN < CR < EW or EX) using logistic ordered regression implemented in the R package polr (R Core Team 2019), with EICAT status as the predictor variable.

Results

Most impact evidence was recorded in Australia (n = 48), Hawaii (n = 12), and New Zealand (n = 10). The publication dates of the impact studies ranged from 1976 to 2016. All threatened species that were impacted had small distribution ranges and were endemic to the Hawaiian Islands, except for the fountain darter *Etheostoma fonticola* (EN), which is restricted to two locations in central Texas (extent of occurrence less than 100 km^2) (NatureServe 2013).

Of the 101 interaction records, only 18 had harmful EICAT statuses (17 Moderate impacts and one Major). This is not surprising as few alien species cause severe negative impacts and biological invasions is one of several interacting threats (Simberloff 2011; Hulme 2012; Russell 2012). Similarly, only a few of the interactions (13) were on threatened native species. However, almost all (10) of the threatened native species were impacted by harmful alien species. The majority of alien species assessed as having a Minor impact (MN) were impacting native species that were of least concern of extinction (LC), with one exception, the impacted native species, Poʻouli (*Melamprosops phaeosoma*), which was listed as Extinct (EX) (BirdLife 2019). There were only seven interactions where the same impacting alien species or group of species were identified in both schemes. In these seven interactions, the same mechanism of impact was scored in both schemes for the majority of interactions. Evidence for a large number of interactions was from laboratory experiments (n = 58). These interactions are scored as non-harmful under EICAT as per EICAT guidelines for evidence from laboratory experiments.

Harmful alien species tended to be associated with threatened native species, and non-harmful alien species with not-threatened species (chi-squared value = 35.6, $P < 0.001$). Similarly, an increase in Red List status was associated with an increase in the EICAT status (LR test = 28.0, df = 3, $P < 0.05$), although none of the individual transitions was significant (e.g. MO–MR or EN–CR), probably due to the low sample sizes (Fig. 1).

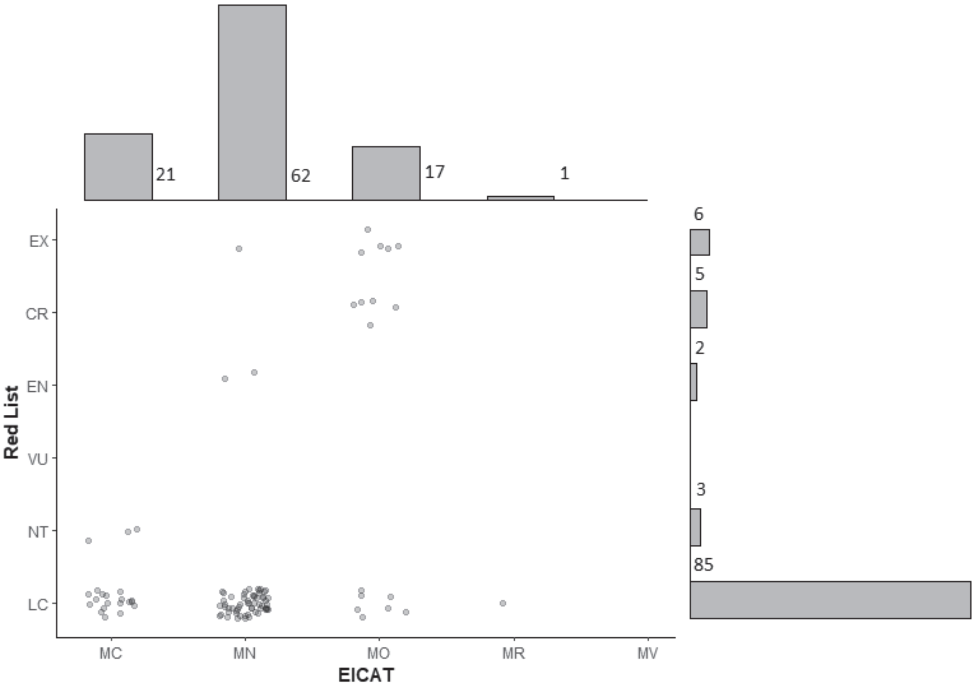

Figure 1. The relationship between EICAT and Red List assessments for interactions between alien gastropods and native species that were recorded as impacted (n = 102). In order of increasing impact, the EICAT categories are: Minimal Concern (MC), Minor (MN), Moderate (MO), Major (MR), and Massive (MV). In order of increasing extinction risk, the Red List categories are: Least Concern (LC), Near Threatened (NT), Vulnerable (VU), Endangered (EN), Critically Endangered (CR), and Extinct (EX). Extinct in the Wild is included in the EX category. Points are jittered to avoid overplotting. Margin bars indicate the numbers of interactions per Red List and EICAT category. The EICAT scores are based on the study by Kesner and Kumschick (2018), who assessed the global impacts of 34 gastropod species present as alien to South Africa.

Discussion

We found a positive but weak correlation between the EICAT status of alien species and the Red List status of impacted native species. However, the relationship between the two schemes is not a simple one-to-one correlation. We hypothesise that the relationship between Red List and EICAT statuses will follow one of three general forms.

Firstly, a linear relationship will occur when there is a positive correlation between the EICAT status of an alien species and the Red List status of an impacted native species (general form i in Fig. 2). Based on the analysis on alien gastropods, the schemes will align when: 1) they identify the same native species as impacted by the same alien species; 2) there is documented evidence of impact in at least one of the schemes; 3) the impacted native species has a small distribution range; and 4) the impacted native species shows a population decline that is caused by the alien species. However, a native species might not be threatened under the Red List regardless of the severity of the impact under EICAT (general form ii on Fig. 2). If a native species is widespread and abundant, then there might be large and significant negative impacts from alien species, but such

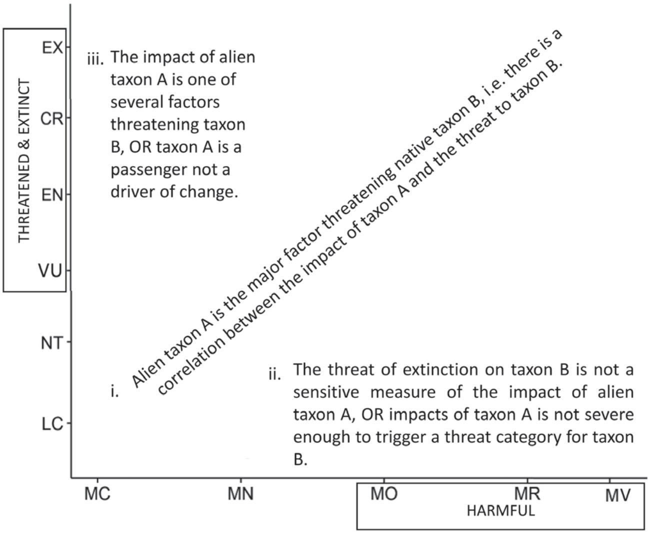

Figure 2. The proposed three forms of the relationship between assessments using the EICAT and the Red List schemes.

impacts do not threaten the native species with extinction. Finally, native species might experience various levels of threat despite there being little, if any, impact from an alien species (general form iii on Fig. 2). Native species are threatened by multiple interacting threats, of which alien species is but one. In particular, alien species can respond as a "passenger" to other drivers of change that directly threaten native species with extinction (MacDougall and Turkington 2005), for example, habitat transformation.

The different forms of the relationship arise, we argue, due to structural differences between the Red List and EICAT. Specifically, the schemes differ in the geographic coverage of assessments, the type of evidence used in assessments, their responsiveness to change, the mechanisms of impact, the specification of the alien species causing the impact, and the approach to taxonomic changes. We discuss these in turn.

Geographical coverage of assessments

Both assessment schemes have a global scope, but how underlying assessment data are interpreted is very different. EICAT assessments make use of all known impacts of an alien within its introduced range(s). However, impacts are recorded at the scale of a specific subpopulation or locality and the impacts often relate to only part of the global population of the impacted native species (Volery et al 2020). By contrast, for all levels of assessment on the Red List (national, regional, and global), the measured impacts and the resulting population declines are related to the entire global native population of the assessed species (e.g., regional adjustments, see IUCN guidelines, IUCN 2019).

The final Red List status of the species is adjusted when related to the global population if assessments are below the global scope. This has two consequences.

First, there is likely to be a closer correlation between EICAT and the Red List for alien species that impact native species that are range-restricted. For example, *Cyanea grimesiana* is an island endemic plant assessed as Critically Endangered (CR) in 2015, with biological invasion listed as a major pressure (Keir 2015). This species has a very restricted native range, an extremely small population (it is only known from 16 individuals), and is experiencing population decline (Keir 2015). Herbivory by two alien slug species, *Limax maximus* and *Limacus flavus*, is one of the pressures on *C. grimesiana*, and the evidence is that *L. maximus* and *L. flavus* are having a Moderate (MO) impact as per EICAT (Kesner and Kumschick 2018). In this case, the impact will likely be directly correlated to the threat status.

Second, native species that are widespread and assessed as of Least Concern (LC) in the Red List can be impacted by alien species with a wide range of EICAT statuses. This can be due to the range of scales at which impacts are recorded in EICAT and/or higher impacts relative to the local populations, not global ones, as in the Red List [e.g. Major (MR) impacts are described as reversible local population extinction]. An alternative explanation is that the native species might have a large global population, and a decline in the local populations is not sufficient to trigger a threatened category on the Red List. For example, the attenuate fossaria snail (*Galba truncatula*) is widespread across southwest Asia, southern Europe, and Mediterranean North Africa, and is predated upon by Draparnaud's glass snail (*Oxychilus draparnaudi*) (Rondelaud 1977). The attenuate fossaria snail was assessed as Least Concern (LC) on the Red List and there are no recorded declines or threats to this species (Seddon et al. 2014). Nonetheless, the alien Draparnaud's glass snail is still recorded to have Major (MR) impact, given its impacts on particular native populations of the attenuate fossaria snail (Kesner and Kumschick 2018).

Even though the native species was not threatened overall, such impact information is valuable for inclusion in a Red List assessment. It can become useful, for example, if the widespread species becomes threatened and can be used as evidence to track impacts over time. Additionally, this information can be used to highlight potential future threats to a species, even if it is currently not threatened (IUCN 2019). When including this information in the Red List the threat score would most likely be low, with severity classified as negligible. However, an assessor can also decide on the impact score by considering the primary source of the EICAT assessment, particularly the date of assessment and the type of evidence. This information can be used to determine the timing, severity, and scope of the impact, which determine the threat score in the Red List. Similarly, data collected on impacts of aliens identified in the Red List without an EICAT assessment could be used as a starting point for the EICAT assessment.

Type of evidence used in assessments

Despite our expectations, the schemes did not consistently draw from the same evidence sources in our case study on gastropods. This was partly an issue of timing (see responsiveness to change below), but the schemes also differ in the types of evidence considered. The Red List includes evidence that is observed, estimated, projected, inferred or suspected (IUCN 2019). When conducting Red List assessments, detailed data are not always available across the entire global range of a species, but the Red List allows the use of different data sources, enabling assessments to be conducted in the absence of complete data (IUCN 2019). For EICAT, only observed and inferred evidence from the introduced range of alien species may be included, while projected and suspected sources are excluded (IUCN 2020). The type of evidence EICAT uses is strongly linked to its purpose, providing a systematic method of collating evidence of the impact of alien species in their introduced range. In this study, the Red List evidence was based mostly on expert observations. Moreover, 58 of the interactions were based on laboratory experiments on EICAT. These were assessed as Minor (MN) or of Minimal Concern (MC). All EICAT assessed interactions classified as harmful were based on evidence sources from field experiments in this study as the protocol for EICAT states that declines due to alien species impact as measured by laboratory experiments cannot be considered as of Moderate (MO), Major (MR) or Massive (MV) impact (Table 1).

Responsiveness to change

Given the two systems are currently independent, updates of assessments might happen at different times and so scores may diverge. For example, Pua ʻala (*Brighamia rockii*), a Critically Endangered (CR) plant species, is only known from three subpopulations within the Hawaiian Islands and is currently experiencing population declines (Bruegmann and Caraway 2003). A study by Joe (2006) found that populations of *B. rockii* were impacted by *Limacus flavus* (the alien cellar slug). Therefore, *L. flavus* was assigned an impact status of Moderate (MO) under EICAT in Kesner and Kumschick (2018). However, the Red List assessment for *B. rockii* was published in 2003 and did not (or rather could not) incorporate the findings of Joe (2006): *L. flavus* was not mentioned in the Red List assessment as a pressure. The collection dates of primary source data on EICAT and the Red List are crucial. If this information is available, it can be used to resolve discrepancies between the schemes or even potentially determine the timing of the threat (IUCN 2019).

Under both schemes, there will be time lags between impacts occurring, the recording of impacts, and the incorporation of such data into assessments (IUCN 2019; IUCN 2020). Neither scheme deals explicitly with such lagged biodiversity responses (Crooks 2005; Essl et al. 2015) or, more specifically, invasion debt (Rouget et al. 2016). However, the schemes also differ in how they respond to new information. EICAT assessments can be easily updated on the publication of a single impact report. The Red List, on the other hand, does not require information to be formally published before it can be incorporated into an assessment, and can incorporate observed information, as well as projected and suspected evidence. This reduces the need to wait for evidence to be collected and reported before assessment (IUCN 2019; IUCN 2020). However, the Red List is dependent on experts' time and resource availability to finalise assessments, so updates may take longer.

Moreover, the status of a species on the Red List can improve or deteriorate from assessment to assessment (IUCN 2019). For EICAT, however, the impact status of alien species can only ever be up-listed to a more severe impact level. Thus, even if an alien species is no longer threatening a particular native species, it can still be categorised as harmful due to past impacts recorded (IUCN 2020). Therefore, the two schemes should exchange data with care. Coding the timing of the impacts would support this process; the Red List records this information and this should also be the case for EICAT (IUCN 2019).

Mechanisms of impact

Classification of the mechanisms of impact is similar between the schemes, but there are some key differences (Fig. 3). The underlying information and evidence used in the assessments must, therefore, be examined if the mechanisms are to be compared. For example, chemical, structural or physical ecosystem impacts recorded on EICAT could potentially be linked to either ecosystem conversion or ecosystem degradation on the Red List. Understanding the mechanisms of impact between the systems will assist in understanding the impact magnitude when linking the schemes.

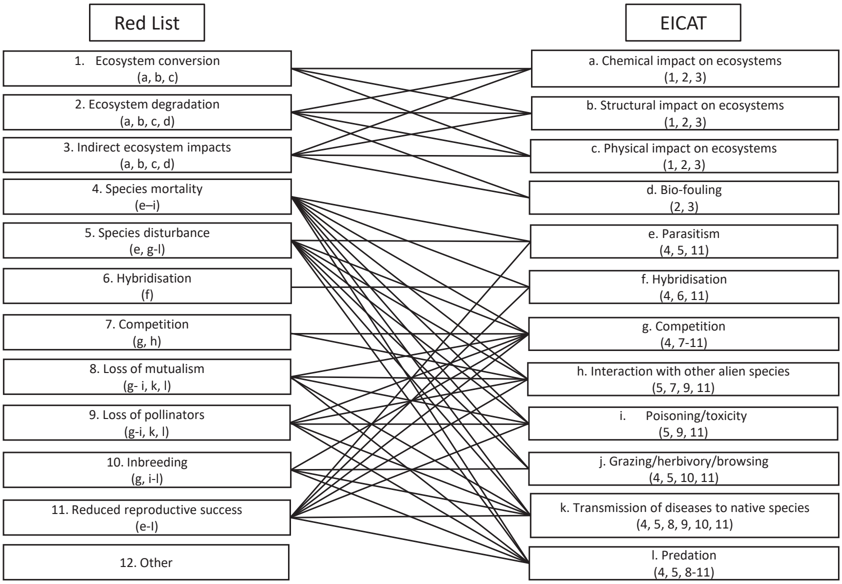

Figure 3. Proposed links between the mechanisms by which alien species impact native species as identified under the Red List and EICAT schemes. The description of each mechanism has been modified slightly to align the two schemes.

Specification of the alien species causing the impact

As part of an EICAT assessment, impacted native species are identified, and supporting documentation is recorded. By contrast, in the Red List, the alien species affecting native species are only required to be identified and recorded if the native species are assessed as threatened or Near Threatened (NT). For other classifications this information is optional.

Both schemes allow for the impacting species to be identified at whatever taxonomic level is appropriate or available. If a specific alien species is not identified in the assessment (e.g., only as a "slug" rather than as *L. flavus*), then further information is needed to improve the assessment. In this study, we found seven interactions for which the same alien species or groups of species were identified in both schemes. The majority of these assessments were for threatened species, with the exception of a single native species that was categorised as of Least Concern (LC) (Kesner and Kumschick 2018). The Red List assessment of this native species (*Lymnaea natalensis*) identified a congeneric alien species (*Lymnaea columella*) as having a minor impact scope, similar to its EICAT status of Minor (MN) (Kesner and Kumschcik 2018). We would strongly encourage the specification of impacting aliens, even for native species that are of Least Concern (LC), and that consideration is given to appropriately scoring their impact levels (Albrecht et al. 2018b).

Approach to taxonomic changes

The Red List's taxonomy is updated regularly when new classifications become available and when prompted by experts. EICAT refers to the Red List for taxonomy. However, the taxonomy used in primary references can differ. This may be particularly relevant for species with many synonyms that result from different taxonomic revisions. Information on synonyms captured in the Red List helps maintain this link, though the situation can be complicated. For example, *Bulinus natalensis* is part of a species complex that is widespread across Africa. It was assessed as Least Concern (LC) on the Red List under the currently-accepted name *Bulinus truncatus* (Albrecht et al. 2018a). Before *B. natalensis* was included in the species complex, it was recorded to have a small range size (de Kock and Wolmarans 2006), and, if pressures impacted it, then it might have been assessed as threatened in the Red List. This illustrates how changes in the taxonomy can influence the Red List status of a species and potentially an aliens species' EICAT status.

Conclusions and recommendations

The EICAT and Red List schemes will benefit each other if information underpinning their assessments is made available and shared. Making such supporting information available in appropriate formats will improve the generation of sound evidence-based assessments, and help to identify data gaps and research needs. For example, alien species noted to cause impacts under the Red List which are assessed on EICAT as Data Deficient (DD) or are Not Evaluated (NE) should be prioritised for further research and EICAT evaluation (and vice versa).

Each scheme should link to relevant corresponding data in the other. The Red List uses a well-organised data management platform, the Species Information System (SIS), to gather, organise, and store data. The development and use of a similar data management platform for EICAT would aid assessments and could be tailored to enable data exchange between the two schemes. Our study shows that the types, extent, and frequency of information overlap between the two schemes depend on a range of factors, including geographical scope, population trends, evidence sources, scheme responsiveness, mechanisms of impact, and the taxonomic systems used. Further, as assessments under either scheme are updated, corresponding assessments need to be examined and potentially revisited.

In summary, while the Red List and EICAT are conceptually related, they have different purposes and methods. We are keen to see similar evaluations for other taxonomic groups and habitats, but we predict that the results will be similar to those outlined in Fig. 2. EICAT and the Red List will not always align, nor should they. This means that while the EICAT and Red List schemes might be complementary and information can and should be shared between the schemes, they are not interchangeable.

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RESEARCH ARTICLE

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The importance of assessing positive and beneficial impacts of alien species

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Abstract

Extensive literature is available on the diversity and magnitude of impacts that alien species cause on recipient systems. Alien species may decrease or increase attributes of ecosystems (e.g. total biomass or species diversity), thus causing negative and positive environmental impacts. Alien species may also negatively or positively impact attributes linked to local human communities (e.g. the number of people involved in a given activity). Ethical and societal values contribute to define these environmental and socio-economic impacts as deleterious or beneficial. Whilst most of the literature focuses on the deleterious effects of alien taxa, some recognise their beneficial impacts on ecosystems and human activities. Impact assessment frameworks show a similar tendency to evaluate mainly deleterious impacts: only relatively few, and not widely applied, frameworks incorporate the beneficial impacts of alien species. Here, we provide a summary of the frameworks assessing beneficial impacts and briefly discuss why they might have been less frequently cited and applied than frameworks assessing exclusively deleterious impacts. Then, we review arguments that invoke a greater consideration of positive and beneficial impacts caused by alien species across the invasion science literature. We collate and describe arguments from a set of 47 papers, grouping them in two categories (value-free and value-laden), which span from a theoretical, basic science perspective to an applied science perspective. We also provide example cases associated with each argument. We advocate that the development of transparent and evidence-based frameworks assessing positive and beneficial impacts might advance our scientific understanding of impact dynamics and better inform management and prioritisation decisions. We also advise that this development should be achieved by recognising the underlying ethical and societal values of the frameworks and their intrinsic limitations. The evaluation of positive and beneficial impacts through impact assessment frameworks should not be seen as an attempt to outweigh or to discount deleterious impacts of alien taxa but rather as an opportunity to provide additional information for scientists, managers and policymakers.

Keywords
Biological invasions, environmental impacts, human well-being, impact assessment frameworks, nature conservation, prioritisation, socio-economic impacts

Introduction

The number of species which are introduced beyond their native ranges (i.e. alien species) continues to rise among geographic regions and taxonomic groups (Essl et al. 2011; Seebens et al. 2017). A vast literature is now available on the variety and magnitude of impacts (here defined as measurable changes as in Ricciardi et al. 2013) that alien species cause in native biodiversity and human well-being (Pimentel et al. 2001; Mazza et al. 2014; Shackleton et al. 2019a). Alien species may decrease and/or increase attributes of their recipient ecosystem (e.g. total biomass or species diversity), thus causing negative and positive environmental impacts. Alien species may also negatively and/or positively impact attributes linked to humans (e.g. the number or income of people involved in a given activity). Ethical and societal values, for instance, associated with nature conservation and human well-being, define whether these environmental and socio-economic impacts are perceived as deleterious or beneficial (Kumschick et al. 2012; Shackleton et al. 2019b). The majority of studies in the field of invasion science have focused on deleterious impacts only (Goodenough 2010; Guerin et al. 2018). The general focus on the deleterious effects of alien species has been motivated by the necessity and urgency to study the serious consequences that some have on native communities and human activities (Richardson et al. 2000; Pyšek et al. 2008; Guerin et al. 2018). The research focus on deleterious impacts has resulted in detailed descriptions of the mechanisms through which alien animals, plants and pathogens may damage recipient ecological and socio-economic systems (Vilà et al. 2010; Ricciardi et al. 2013; Blackburn et al. 2014; Vaz et al. 2017; Bacher et al. 2018). Such knowledge has been used to prioritise the most deleterious alien species and adopt management countermeasures (Oreska and Aldridge 2011; McGeoch et al. 2016; Roy et al. 2017). However, sustained attention on deleterious impacts could have led to an unwarranted disregard for their beneficial impacts, thus resulting in a simplified, if not misleading, understanding of impact dynamics (Goodenough 2010; Boltovskoy et al. 2018). As a result, there has been some disagreement over the use of terminology and the interpretation of data among invasion scientists (Boltovskoy et al. 2018). Guerin et al. (2018), for example, suggested that meta-analyses quantifying the impact of alien species might not be fully objective, as these studies are often characterised by selection bias toward highly deleterious taxa (but see also Kuebbing and Nuñez 2018, who argued that potential publication biases do not necessarily invalidate findings). Another potential consequence is the risk of implementing controversial management policies: management decisions based only on deleterious impacts ignore the fact that there might be conflicts of interest among stakeholders (Zengeya et al. 2017; Potgieter et al. 2019a; Kumschick et al. 2020a).

The general tendency to focus mainly on the deleterious impacts of alien taxa can also be observed in the impact assessment frameworks developed over the last decades. These frameworks adopt science-based approaches to estimate impact magnitude, describe mechanisms underlying impacts and facilitate comparisons across different taxonomic groups and geographic regions. However, only a subset of these impact assessment frameworks evaluate beneficial impacts. Of nine impact assessment frameworks developed in the last two decades, only three frameworks include strategies to incorporate beneficial impacts of alien species into the impact assessment process (Table 1). Frameworks focusing exclusively on deleterious impacts have been cited more often than those incorporating beneficial impacts, which may indicate that the latter are relatively less applied in the scientific community. Although we acknowledge that using the number of citations as a proxy for frequency of application might not always be appropriate, we found that this index reflects well with how often the different frameworks have been applied.

The conceptual framework proposed by Kumschick et al. (2012) uses a bidirectional ranking scale to estimate socio-economic and environmental impacts of alien taxa. In such a scheme, negative and positive socio-economic impacts mirror each other, with the former describing decreases in a measured variable that is relevant to humans (such as forestry and animal production) and the latter describing increases of the same variable. Environmental benefits, on the contrary, are evaluated by assessing the capacity of alien taxa to modify the ecosystem towards a hypothesised historical functional state. Despite the novel approach and insights provided, this framework is less frequently cited (Table 1), and applied than other schemes that exclusively assess negative impacts such as GISS (Generic Impact Scoring System, Nentwig et al. 2016) and EICAT (Environmental Impact Classification for Alien Taxa, Blackburn et al. 2014). This relatively low number of citations can be due to a variety of factors, including the high structural complexity of the framework, which requires to weigh impacts according to their importance for various stakeholders, or the successive development of other, more detailed, impact assessment frameworks such as EICAT. The framework proposed by Katsanevakis et al. (2014) describes multiple mechanisms by which marine alien species affect biodiversity (e.g. by habitat engineering) and ecosystem services (e.g. by ocean nourishment), both beneficially and deleteriously. Although the impact magnitude was not considered (i.e. local-, small-, and large-scale impacts were all treated equally) such a framework allowed the screening of a high number of marine species (87), finding most (67) cause both deleterious and beneficial impacts. Although the framework is highly cited within the scientific community (Table 1), most of the citations arise because of the large documentation on impact variation of alien species in the European seas. On the contrary, the same framework has been very rarely applied to assess deleterious and beneficial impacts of

Table 1. List of impact assessment frameworks which assess environmental and/or socio-economic impacts developed in the last 30 years. The list has been compiled following Roy et al. 2007, Bartz and Kowarik 2019, Srebaliene et al. 2019, Strubbe et al. 2019 and Vilà et al. 2019. The total number of citations per article corrected by year has been obtained from Google Scholar in June 2020.

General name	Target spatial area	Target taxa	References	Explicit assessment of beneficial impacts	Type of impact (E = Environmental, SE = Socio-Economic)	Number of citations / year (total number of citations)
Invasive species assessment protocol: evaluating non-native plants for their impact on biodiversity	USA	Plants	Morse et al. (2004)	No	E	2.6 (42)
Biopollution assessment scheme	Baltic Sea	Aquatic taxa	Olenin et al. (2007)	No	E	16.2 (211)
Conceptual framework for prioritisation of invasive alien species for management according to their impact	Global	Generic	Kumschick et al. (2012)	Yes	E /SE	14.1 (113)
Generic ecological impact assessments of alien species in Norway	Norway	Generic	Sandvik et al. (2013)	No	E	5.9 (41)
Review of impacts of invasive alien marine species on ecosystem services and biodiversity	Europe	Marine taxa	Katsanevakis et al. (2014)	Yes	E / SE	55.3 (332)
EICAT (Environmental Impact Classification for Alien Taxa)	Global	Generic	Blackburn et al. (2014), Hawkins et al. (2015)	No	E	81.2 (487)
GISS (Generic Impact Scoring System)	Europe	Generic	Nentwig et al. (2016)	No	E / SE	16.8 (67)
SEICAT (Socio-Economic Impact Classification of Alien Taxa)	Global	Generic	Bacher et al. (2018)	No	SE	39.5 (79)
InSEAT (INvasive Species Effects Assessment Tool)	Global	Generic	Martinez-Cillero et al. (2019)	Yes	E / SE	4 (4)

alien species on other ecosystems or geographic areas. The INSEAT framework (INvasive Species Effects Assessment Tool) developed by Martinez-Cillero et al. (2019) adopts a bidirectional scoring system to quantify ecosystem service gains and losses caused by alien species. To date, the INSEAT scheme has been tested on 18 alien species in Great Britain (Martinez-Cillero et al. 2019). The renewed attention paid toward ecosystem services and disservices linked to alien species (Vaz et al. 2017; Vilà and Hulme 2017; Potgieter et al. 2019b; Shackleton et al. 2019a; Milanović et al. 2020) might promote the future application of the scheme across different regions and taxonomic groups.

Several frameworks focusing on deleterious impacts still explicitly recognise the existence of beneficial impacts caused by alien species (Bomford et al. 2008; Blackburn et al. 2014; Copp et al. 2016). For instance, the EFSA risk assessment framework developed by the European Food Safety Authority (2011) suggests identifying and describing any beneficial effect caused by aliens on the provisioning and regulation of ecosystem services but specifies that such impacts should not be scored. The absence of a scoring system for beneficial impacts was not only motivated by the intrinsic scope of risk assessment frameworks, which consider multiple factors, such as introduction pathways or establishment probability, to estimate whether an alien species can become deleterious (Leung et al. 2012; Kumschick et al. 2020b). The EFSA members also stressed that "assessing positive impacts is extremely difficult and may also be inappropriate or cause a potential conflict of interest for risk assessors if introductions are intentional". Both conceptual and methodological reasons could thus explain why frameworks assessing both beneficial and deleterious impacts are less frequently cited, and applied, than those assessing deleterious impacts only. The latter are used to a greater extent not only because they specifically help to prioritise alien species according to the magnitude of deleterious impacts, but also because unidirectional frameworks might have reached a higher level of acceptance, clarity and understanding over time. The relatively limited attention given to beneficial effects of alien species across impact assessment frameworks seems thus to reflect a general tendency in invasion science to consciously exclude beneficial impacts for various reasons rather than an attempt to deny their existence.

Below we review arguments for a greater consideration of positive and beneficial impacts caused by alien species. We collected the arguments from a set of 47 papers and illustrate each argument with examples. We grouped the arguments into two categories (value-free and value-laden) that reflect whether each argument has been formulated independently from, or in combination with, ethical and societal values. Arguments grouped in the value-free category consider negative and positive impacts as numerical decrease or increase of an attribute (e.g. the concentration of soil nutrients; Jeschke et al. 2014). Positive and negative impacts do not denote human values (Kumschick et al. 2012), but rather quantify bi-directional changes caused by alien species "as neutrally as possible" (Jeschke et al. 2014). In accordance with this value-free perspective, in our manuscript we strictly define positive impacts as quantitative increases in attributes of the recipient systems. Arguments grouped in the value-laden category, on the contrary, refer to how impacts are perceived according to ethical and societal values (Jeschke et al. 2014). Impacts are generally considered deleterious or beneficial if they damage or benefit attributes linked to ethical and societal values (human well-being). In accordance to this value-laden perspective, in our manuscript we strictly define beneficial impacts as bi-directional quantitative changes (i.e. including both increases and decreases) in attributes of the recipient systems that are associated with benefits based on human values. Therefore, although negative and positive impacts are often considered as deleterious and beneficial, respectively (examples 1, 3 and 4 in Fig. 1), under our definitions, some negative impacts can less intuitively be perceived as beneficial (example 2 in Fig. 1), and some positive impacts as deleterious (example 3 in Fig. 1).

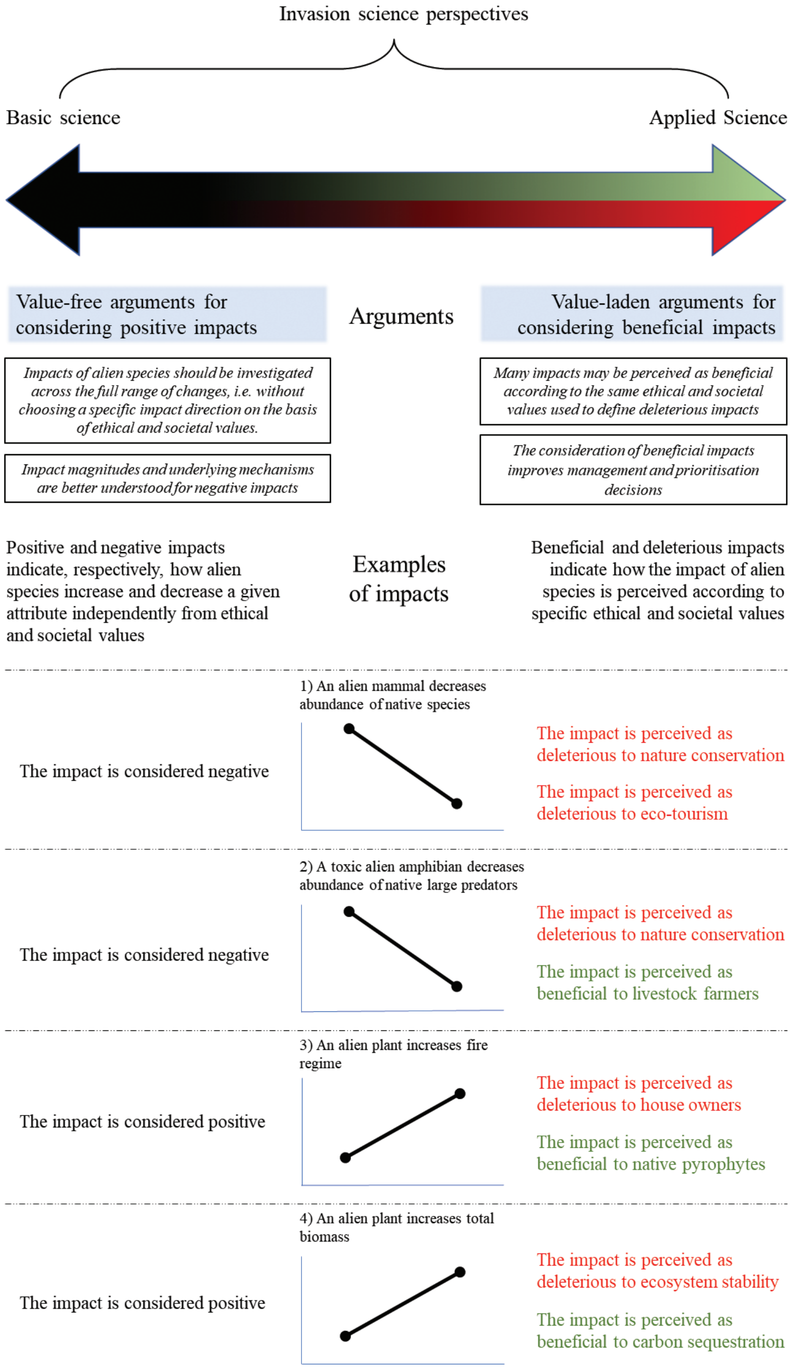

Figure 1. Schematic representation of the gradient of perspectives in invasion science. These perspectives i) contribute to the formulation of general arguments that invoke a greater consideration of positive and beneficial impacts; ii) help to distinguish between negative/positive impacts and deleterious/beneficial impacts. Four examples (1–4) are also provided to illustrate a conceptual distinction between positive/negative impacts (black text) and beneficial/deleterious impacts (red and green text).

We show how the development of impact assessment frameworks assessing positive and beneficial impacts can benefit the field of invasion science and we offer suggestions on how this development should be carried out.

Collection and value-based classification of arguments

We conducted a thorough, but non-exhaustive, literature review to identify arguments for considering positive and beneficial impacts of alien species. We started with papers on the topic that were already known to us and followed up on other papers that referred to them or were cited in them. Articles were selected only if they had broad aims, i.e. they were not restricted to a single case study or taxonomic group. The purpose of this review was to exemplify arguments why authors invoke greater consideration of positive and beneficial impacts in invasion science. However, we do not aim to make quantitative statements about the frequency of these arguments in the field.

In the papers selected, arguments stem from the different perspectives and interests of authors. Like in related disciplines, such as conservation biology (Scott et al. 2007), invasion scientists have disparate standpoints and interests that span from a basic science perspective to an applied science perspective (Humair et al. 2014; Estévez et al. 2015). The former perspective suggests that similarly to any other natural phenomenon, impacts of alien species should be investigated as neutrally as possible (Slobodkin 2001; Brown and Sax 2005). Therefore, the influence of ethical and societal values on the investigation of impacts needs to be minimised in order to adopt a value-free, scientific approach (Slobodkin 2001; Brown and Sax 2005; Sagoff 2018). At the other extreme, the applied science perspective recommends that invasion science “must serve and be relevant to communities” (Munro et al. 2019). Thus, since invasion science concerns, among others, “costs and benefits of the presence and abundance of introduced organisms with reference to human value systems” (Richardson et al. 2007), a value-laden scientific approach could be adopted in the study of alien species. We are aware that a complete distinction between these two perspectives is a simplification of the broad spectrum of the existing views in invasion science (Fig.1) (Humair et al. 2014; Estévez et al. 2015; Bartz and Kowarik 2019). However, such a distinction is still useful here for illustrating the key arguments (Fig. 1) that invoke a greater consideration of positive impacts (value-free arguments), and those which invoke a greater consideration of beneficial impacts (value-laden arguments).

Value-free arguments for considering positive impacts

Impacts of alien species should be investigated across the full range of changes, i.e. without choosing a specific impact direction on the basis of ethical and societal values.

All alien species will cause changes, i.e. impacts, to some attributes of their recipient systems (Ricciardi et al. 2013; Jeschke et al. 2014). These attributes may describe different aspects of the recipient ecosystem, such as species diversity, total biomass, carbon sequestration capacity, fire intensity, pollination frequency, etc. Impacted attributes may also be associated with both human well-being and socio-economic aspects, such as the number of people employed in forestry or fishing, food security, livelihood and human connection to nature. Basic scientific arguments advocate that changes in attributes should be investigated independently from ethical values in order to be objective (Slobodkin 2001). Authors strictly supporting these arguments state that value judgements cannot be empirically tested and that some ecologists fallaciously confuse these judgements with descriptions of environmental changes (Brown and Sax 2005; Sagoff 2018). In other words, one should measure the increase of a given attribute (positive impact) and the decrease of the same attribute (negative impact) along the full spectrum of changes, without any specific focus on one of the two directions (Jeschke et al. 2014, Fig.1). Value-laden terms such as "beneficial" or "deleterious" should be avoided whereas terms such as "positive" or "negative" should be only used from a numerical standpoint, as in the increase or decrease in the value of a property (Brown and Sax 2005). Furthermore, this argument posits that invasion scientists should act similarly to astronomers or particle physicists, who analyse scientific phenomena without considering moral values or practical consequences of their scientific research (Slobodkin 2001; Brown and Sax 2004).

Impact magnitudes and underlying mechanisms are better understood for negative impacts

Under a value-free perspective, value judgement should not interfere with the study of impacts; it is theoretically expected that studies targeting alien species assess their impacts on the recipient system independently and unbiasedly from impact directions (e.g. meta-analyses which use effect size, such as in Castro-Díez et al. 2019). However, biases towards negative impacts on native biota have been reported, i.e. predominantly reporting on native biota suffering from aliens and ignoring native biota that profit from the presence of alien species (Goodenough 2010; Schlaepfer et al. 2011; Fig.2). Furthermore, it is difficult to judge how large this alleged bias is because it is unknown if alien species more often cause a decrease (i.e. generate negative impacts), rather than an increase (i.e. generate positive impacts), to the attributes of their recipient systems (Charles and Dukes 2007; Vitule et al. 2012). An example of a negative impact may be the decrease of species diversity caused by alien populations of rodents introduced to islands (see also example 1, Fig.1), whereas an example of a positive impact may be the increase of local species diversity caused by the establishment of an alien invertebrate that acts as ecosystem engineer (Castilla et al. 2004).

Alternatively, there may be a bias toward studying and reporting negative impacts (Guerin et al. 2018). Multiple negative impacts of alien species (e.g. decrease in native population size) were considered as deleterious based on ethical and societal values (Jeschke et al. 2014; Bartz and Kowarik 2019). The urgency to investigate the conspicuous deleterious impacts that some aliens cause to native communities and human activities

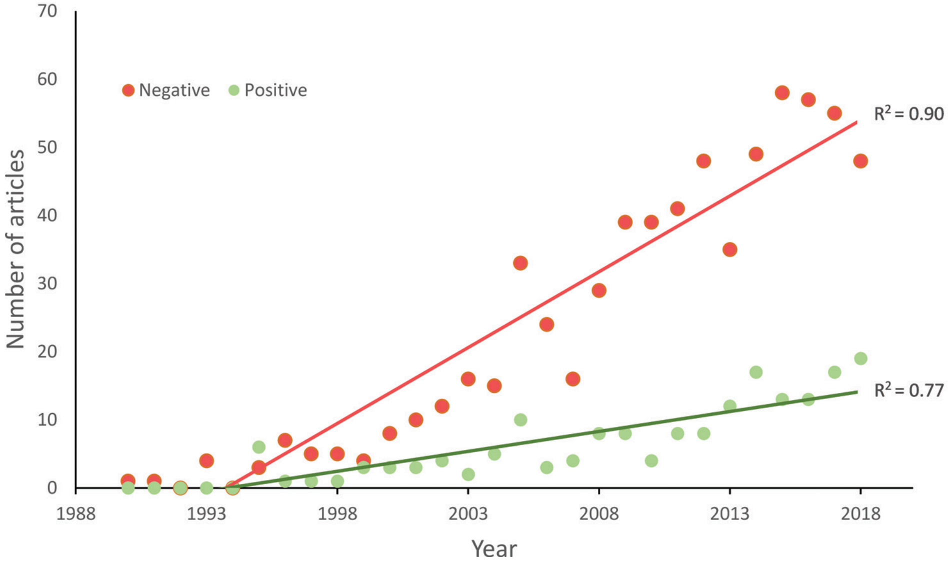

Figure 2. Plot reporting the number of articles and fitted linear regression obtained using the following search strings in Google Scholar at the end of October 2019: ***In red***: "negative * of alien species " OR "negative * of non-native species " OR "negative * of exotic species" OR "costs of alien species " OR "costs of non-native species " OR "costs of exotic species"; ***In green***: "positive * of alien species " OR "positive * of non-native species " OR "positive * of exotic species" OR "benefits of alien species " OR "benefits of non-native species " OR "benefits of exotic species".

(Richardson et al. 2000; Pyšek et al. 2008; Simberloff et al. 2012) might have contributed to this bias even among natural scientists. Such urgency was, for instance, emphasised during the Fourth Meeting of the Conference of the Parties to the Convention on Biological Diversity held in Slovakia in 1998, which first considered "including the subject of alien invasive species in its longer-term programme of work". The report of the meeting specifically noted "the significant adverse ecological and economic effects of certain alien species on biological diversity and human health" and "the importance of taking a precautionary and ecosystem approach when dealing with issues related to alien species" (UNEP 1998). The following editions of the conference considered "alien species that threaten ecosystems, habitat or species" as a cross-cutting and priority issue relevant to biological diversity, and advocated for the prevention and mitigation of their deleterious impacts, which has become a major cornerstone of invasion science. In addition to this, since many alien species were deliberately introduced to provide benefits to humans, such benefits might have seemed obvious, thereby preventing their systematic study. Many invasion scientists might also have investigated the unwanted deleterious consequences of alien taxa introductions in order to counterbalance a favourable attitude from many stakeholders towards alien taxa intentionally introduced for agriculture and forestry (Simberloff and Stiling 1996; Louda et al. 2003; Pyšek et al. 2008).

As most research assessing the impacts of alien species has been directed toward negative impacts, the magnitude of positive impacts has been rarely systematically assessed and quantified by using statistical or semi-quantitative tools (Goodenough 2010). Instead, the literature record of positive impacts seems rather anecdotal, with impacts usually defined according to human values (Vilà et al 2010; Schlaepfer et al. 2011). Thus, there are not only fewer studies that report positive impacts, but these studies often lack a systematic and evidence-based approach to classify and compare these impacts (Vilà et al 2010). Consequently, detailed descriptions of the mechanisms by which alien species can benefit their recipient ecological and the socio-economic systems are also scarce. Some mechanisms by which aliens positively affect the diversity and abundance of native taxa by providing food and refuge have been identified by Robinson et al. (2007), Goodenough (2010), Schlaepfer et al. (2011), McQuaid and Griffiths (2014) and Tassin and Kull (2015). Additionally, Kumschick et al. (2012) described mechanisms such as herbivory, competition or predation by which aliens may affect species that are degrading the ecosystem and thereby restore its historical functional state. Further studies on these underlying mechanisms may provide eco-evolutionary insights around alien-native coevolution, rapid adaptation, biotic resistance and niche vacancy. Greater knowledge has probably been gained around socio-economic benefits to human-well-being, as multiple authors identified mechanisms by which aliens increase ecosystem services and decrease ecosystem disservices (Katsanevakis et al. 2014; Vaz et al. 2017; Knapp et al. 2019; Shackleton et al. 2019a; Milanović et al. 2020). Despite these efforts, unified systematic approaches to capture the diversity of positive and beneficial impacts of aliens across taxa and geographic regions are still lacking.

Value-laden arguments for considering beneficial impacts

Many impacts may be perceived as beneficial according to the same ethical and societal values used to define deleterious impacts

Although impacts cannot be defined as deleterious or beneficial in an absolute way, changes caused by alien species may still be perceived as deleterious or beneficial according to societal and ethical values (Fig.1, Vilà et al. 2010; Kumschick et al. 2012; Jeschke et al. 2014; Bartz and Kowarik 2019). Alien species can alter the demography of endangered populations and permanently modify native communities (Doherty et al. 2008, Gurevitch and Padilla 2004). Since native populations and communities have high conservation value, their decrease (i.e. negative impact) can be considered deleterious from a value-laden perspective (example 1, Fig.1). This nature conservation perspective guided the development of some impact assessment frameworks frequently used (Vilà et al. 2019), such as the GISS framework (Nentwig et al. 2016) and the EICAT framework (Blackburn et al. 2014; Hawkins et al 2015; IUCN 2020), which both assess the deleterious impacts of alien species on native taxa. Alien species may also be perceived as deleterious to socio-economic systems and human well-being. For example, when alien species impede human activities such as fishing and farming or impair human health (Mazza et al. 2014; Rai and Singh 2020), personal safety or material and immaterial assets (Bacher et. al. 2018). Deleterious impacts on the social and economic sectors have been captured in the SEICAT framework (Socio-Economic Impact Classification of Alien Taxa), which adopts a scoring system analogous to EICAT to assess how human activities are affected by alien species (Bacher et al. 2018). Some impact assessment frameworks such as GISS (Nentwig et al. 2016) and INSEAT (Martinez-Cillero 2019), and many risk assessment frameworks, evaluate deleterious socio-economic impacts (for a review of impact assessment frameworks see Strubbe et al. 2019 and Vilà et al. 2019; for a review of risk assessment frameworks see Leung et al. 2012 and Kumschick and Richardson 2013).

Analogously to negative impacts that are perceived as deleterious to native communities and humans, many positive impacts can be considered beneficial according to values associated with nature conservation and human well-being. For example, some alien species may moderately increase fire frequency in their introduced range, thus providing benefits to native pyrophytes which require fire for germination (example 3 in Fig. 1). Alien plants can also increase the biomass of a recipient ecosystem, thus being beneficial to global carbon sequestration (example 4 in Fig. 1). Additionally, many alien species increase attributes that are relevant to societal values and human well-being. In other words, they increase existent, or provide additional, ecosystem services or beneficial contributions to people's quality of life (Díaz et al. 2018) such as food and water provision, soil and sand stabilisation and nitrogen fixation (Vaz et al. 2017; Milanović et al. 2019; Shackleton et al. 2019a). In a world of increasing environmental issues, aliens can also help to reduce the impact of other stressors. Examples include alien plants which mitigate the effects of climate change by facilitating coastal protection from erosion and favouring carbon sequestration (example 4 in Fig. 1, Essl. et al. 2017, in Castro-Díez et al. 2019). However, not all environmental and socio-economic beneficial impacts coincide with positive impacts; for example, in the impact scoring framework proposed by Kumschick et al. (2012), beneficial impacts of alien animals are quantified by measuring to what extent they reduce the population density of species degrading the ecosystem (e.g. pest species). In other words, a negative impact (e.g. decrease of pest species abundance), may thus be considered beneficial from a nature conservation standpoint or according to other values and interests (example 2, Fig.1). An alien bio-control agent (e.g. a parasitoid wasp) that reduces the abundance of an agricultural pest can be similarly considered beneficial to farmers and other stakeholders. Such species can thus provide additional benefits to humans by reducing ecosystem disservices (Vaz et al. 2017; Knapp et al. 2019; Milanović et al. 2019).

The consideration of beneficial impacts improves management and prioritisation decisions

Human values and interests associated with the impacts of alien species affect whether and how these species can be managed. Some alien species have been intentionally introduced because of the benefits they can provide to people (Castro-Díez et al. 2019). Additionally, many aliens cause low or insignificant impacts to their recipient systems and can be simply considered inconsequential for ecosystems and society (Zengeya et al. 2017). Beneficial and inconsequential species do not generally require management interventions, and their prompt identification facilitates the allocation of management resources elsewhere (van Wilgen and Richardson 2004; Zengeya et al. 2017). Aliens that provide beneficial impacts to human well-being might, however, decrease the demography of native populations, thus being deleterious from a nature conservation standpoint (Doherty et al. 2008). More generally, stakeholders may have such disparate values and interests that their perception toward alien species can be simultaneously favourable and unfavourable (Novoa et al. 2018; Shackleton et al 2019b). Such disparate values (examples 2,3 and 4, Fig.1) may cause a conflict of interests among different stakeholders and hamper management implementation (Jeschke et al. 2014; Crowley et al. 2017; Essl et al. 2017; Zengeya et al. 2017). For instance, van Wilgen and Wilson (2018) showed that control and regulation of a few alien taxa such as pine trees (*Pinus* spp.) and the rainbow trout (*Oncorhynchus mykiss*) were extremely controversial in South Africa, given these species cause both beneficial and deleterious impacts on different sectors of society. Analogously, the control of Paterson's curse (*Echium plantagineum*), an alien plant that is highly toxic to livestock, has generated conflicts between Australian farmers and beekeepers, with the latter benefiting from the nectar produced by the plant (Messing 2000). Transparent and evidence-based descriptions of beneficial and deleterious impacts of alien species may thus help to support prioritisation, clarify and motivate values underlying management, identify conflicts of interests and advance dialogue among stakeholders.

Reasons and suggestions to develop frameworks assessing positive and beneficial impacts

We show that arguments from different perspectives invoke a greater consideration of positive and beneficial impacts in invasion science. The development of assessment frameworks that classify deleterious and negative impacts through a standardised and evidence-based approach (e.g. EICAT and SEICAT) has improved our understanding of such impacts. These frameworks describe the different ways in which alien taxa deleteriously interact with native taxa (impact mechanisms), and quantify the severity of such interactions (impact magnitude) (Blackburn et al. 2014; Nentwig et al. 2016; Bacher et al. 2018). The application of these frameworks to different taxa and ecosystems has allowed for the investigation of factors driving impact magnitude (e.g., Kumschick et al. 2013; Measey et al. 2016; Novoa et al. 2016; Evans et al. 2018) and the ranking of hundreds of alien species based on their deleterious impacts (e.g. Kumschick et al. 2015; Nentwig et al. 2018). Given the above considerations, some of these frameworks might be adapted to assess beneficial impacts. Detailed descriptions provided by these frameworks around mechanisms by which alien species cause deleterious impacts can be extended to capture mechanisms linked to beneficial impacts (i.e. Blackburn et al. 2014; Nentwig et al. 2016). Approaches adopted by existing frameworks to evaluate assessment uncertainty can also be followed because they might help to overcome methodological limitations associated with transparency, clarity and reproducibility (Vilà et al. 2019; Probert et al. 2020). However, some conceptual and methodological aspects should be considered when developing frameworks that assess positive and beneficial impacts.

Impact assessment frameworks classify deleterious impacts according to their magnitudes, i.e. by measuring to what extent alien taxa affect reference attributes. This facilitates comparison among taxonomically distant alien species and across spatial scale and habitats. However, several different strategies have been adopted to measure impact magnitudes. Frameworks such as those proposed by Sandvik et al. (2013) and Martinez-Cillero et al. (2019) use ranking scales which distinguish between low (or noticeable), substantial (or medium), and high (intense) impacts. The scales may be associated with parameters that can be numerically quantified such as the spatial extent of the non-native range, genetic diversity, fitness and abundance of native individuals or provision of ecosystem services (Bartz and Kowarik 2019; Crystal-Ornelas and Lockwood 2020). As a consequence, such scoring scales could be easily adapted to assess bidirectional changes (Martinez-Cillero et al. 2019). Although general scaling approaches may allow the assessment of many alien species and adopt a fully symmetrical bidirectional approach (Zengeya et al. 2017), they may still be prone to subjectivity, especially when the distinction between the magnitude levels is not accurately described. The EICAT framework (Blackburn et al. 2014), on the contrary, clarifies differences between magnitude levels by assuming that with each level of impact magnitude (from minimal concern to massive), a different level of organisation is affected (from native individuals to native communities). Clarity in describing distinct levels of impact magnitude might have contributed to the increasing use of EICAT among scientists and practitioners (Kumschick et al. 2020a). An analogous scoring approach that assesses ecological impacts based on organisation level has been also developed by Olenin et al. (2007). Such approaches, however, define the highest levels of impact magnitude according to the capacity of alien species to cause the extinction of a native species (Olenin et al. 2007; Blackburn et al. 2014). As extinction cannot be exactly mirrored by any other positive ecological phenomenon, the development of a perfectly symmetrical bidirectional adaptation of these schemes might be difficult to achieve. As a consequence, not all impact assessment frameworks can, or need to, adopt a fully symmetric bidirectional scoring scale to assess impact magnitudes. This limitation should be recognised in any conceptual attempt to adapt existing frameworks in order to assess the benefits of alien species.

Impact assessment frameworks are generally developed based on different values that should be recognised and explicitly stated. Values and perspectives influence how we select the attributes of ecosystems or human activities that will be assessed (Bartz and Kowarik 2019; Strubbe et al. 2019) and must be considered when making management recommendations and in final decision making (Probert et al. 2020). However, values and perspectives also define the aims and the intrinsic limitations of each framework. For example, when evaluating the changes caused by an alien species to the community of the recipient environment, we should choose and specify which taxa are taken into consideration. Scientists embracing a conservation standpoint might consider only native, or even endangered taxa, as they aim to quantify alien impacts on species of conservation interest. Scientists who follow a more basic science approach, however, could consider all taxa independently of their origin, as their aim is to measure the negative or positive impacts of aliens from a value-free perspective. The development of a framework that assesses deleterious and beneficial impacts should thus disclose which values underlie the framework and whether the framework distinguishes between deleterious/beneficial impacts and negative/positive impacts. Such a disclosure of values can also be facilitated by the development, and adoption, of a more neutral and transparent terminology in invasion science. The distinction we have drawn in our manuscript between positive/negative and beneficial/deleterious impacts, for example, has been instrumental in defining impacts regardless of whether they were associated with human values. Both terms “positive” and “negative”, however, have in general an intrinsic value connotation and are often used as synonyms of “beneficial” or “favourable” and “detrimental” or “deleterious” in invasion science and other scientific disciplines. Given this lack of linguistic consistency, there might be the necessity to develop a more neutral and transparent terminology in invasion science that unequivocally clarifies whether an impact is defined in accordance to human values or only from a mathematical and value-free perspective.

Conclusion

When underlying values are explicitly stated and intrinsic limitations are openly recognised, the development of frameworks that assess positive and beneficial impacts might advance our scientific understanding of impact dynamics and generate reliable information for management and prioritisation. Adapting existing or developing novel frameworks to quantify these impacts should not be seen as an attempt to outweigh or discount deleterious impacts of alien taxa (EFSA 2011) but rather as an opportunity to provide an additional piece of information for scientists, managers and policymakers.

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Improving the Environmental Impact Classification for Alien Taxa (EICAT): a summary of revisions to the framework and guidelines

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Abstract

The Environmental Impact Classification for Alien Taxa (EICAT) classifies the impacts caused by alien species in their introduced range in standardised terms across taxa and recipient environments. Impacts are classified into one of five levels of severity, from Minimal Concern to Massive, via one of 12 impact mechanisms. Here, we explain revisions based on an IUCN-wide consultation process to the previously-published EICAT framework and guidelines, to clarify why these changes were necessary. These changes mainly concern: the distinction between the two highest levels of impact severity (Major and Massive impacts), the scenarios of the five levels of severity for the hybridisation and disease transmission mechanisms, the broadening of existing impact mechanisms to capture overlooked mechanisms, the Current (Maximum) Impact, and the way uncertainty of individual impact assessments is evaluated. Our aim in explaining this revision process is to ensure consistency of EICAT assessments, by improving the understanding of the framework.

Keywords
Alien species, impact assessment, impact mechanism, IUCN, non-indigenous species

Introduction

The Environmental Impact Classification for Alien Taxa (EICAT: Blackburn et al. 2014; Hawkins et al. 2015; IUCN 2020a, b) has been developed to quantify variation in the severity and type of environmental impacts generated by alien species. Semi-quantitative scenarios are used to categorise impacts caused by alien taxa on native species into one of five levels of severity – Minimal Concern (**MC**), Minor (**MN**), Moderate (**MO**), Major (**MR**), Massive (**MV**) (Fig. 1) – via one of 12 EICAT impact mechanisms: (1) Competition, (2) Predation, (3) Hybridisation, (4) Transmission of diseases to native species, (5) Parasitism, (6) Poisoning / toxicity, (7) Biofouling or other direct physical disturbance, (8) Grazing / herbivory / browsing, (9, 10, 11) Chemical, physical, or structural impact on ecosystem, (12) Indirect impacts through interaction with other species (see Table 1 in IUCN 2020a: Criteria used to classify alien taxa by EICAT impact category). Non-native species residing in the recipient environment can be negatively affected by the alien taxon as well, but EICAT only classifies impacts on the native biota. This classification system facilitates comparisons between impacts generated by alien species across geographic regions and taxonomic groups. Hawkins et al. (2015) provided guidelines for the application of the framework inspired by the IUCN Red List of Threatened Species (IUCN 2012, 2019).

EICAT has been used to undertake assessments of the environmental impacts of alien birds (Evans et al. 2016), amphibians (Kumschick et al. 2017; Measey et al. 2020), bamboos (Canavan et al. 2019), marine fishes (Galanidi et al. 2018), feral mammals (Hagen and Kumschick 2018) and gastropods (Kesner and Kumschick 2018), among others. Whilst these assessments demonstrated that EICAT can be effectively used to quantify and categorise the environmental impacts of alien species from different taxonomic groups, they also highlighted that aspects of the existing guidelines require refinement in order to improve the assessment process. In 2020, EICAT was officially adopted as the IUCN standard for classifying alien species in terms of their environmental impact. A new standard classification of the impacts of invasive alien taxa (IUCN 2020a), as well as new guidelines for using this standard classification (IUCN 2020b) have been developed based on an IUCN-wide consultation process to solve the

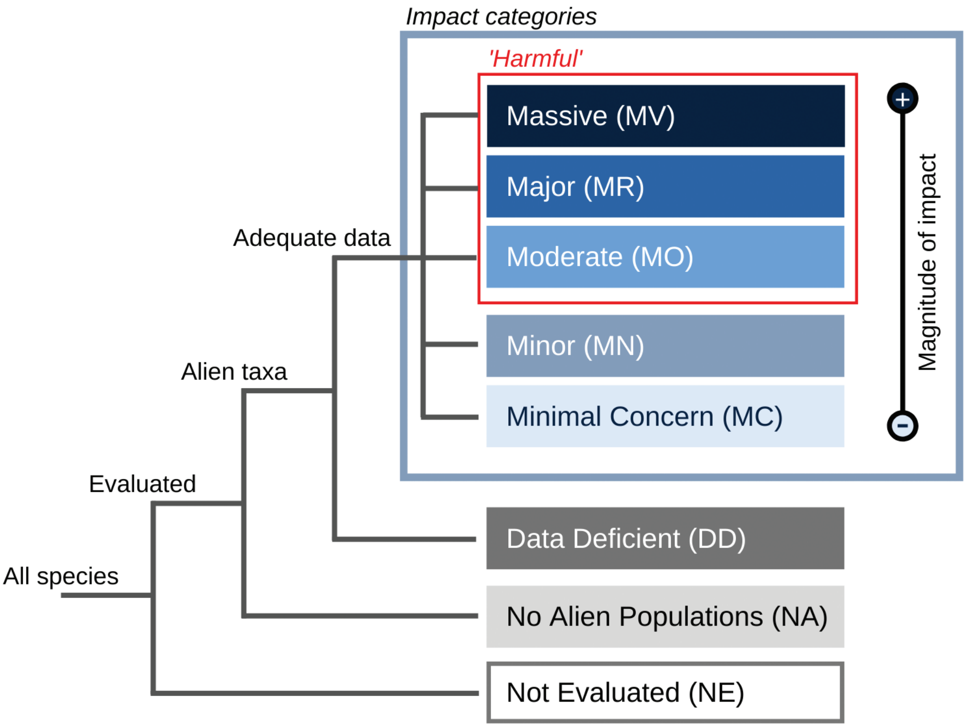


Figure 1. The different EICAT categories and the relationship between them. Reproduced from IUCN (2020a) IUCN EICAT Categories and Criteria, IUCN (Gland): page 10, https://doi.org/10.2305/IUCN.CH.2020.05.en, with permission from IUCN.

problematic aspects and improve the process: these documents update and replace the existing guidance documentation (Hawkins et al. 2015).

Here, we have explained the major changes made to the previous EICAT guidance and the reasons for these changes, so that the revision process is transparent. By detailing the reasoning behind the changes, we also aim to improve the general understanding of the framework, which is likely to result in an increased consistency in its use by different assessors. Therefore, while this guidance will be particularly useful to assessors already familiar with EICAT, we would also recommend it to assessors intending to use EICAT for the first time.

Definitions

'Fitness' has been replaced by 'Performance'

In the description of the **MN** impact magnitude and throughout, the term 'fitness' has been replaced by the term 'performance'. As fitness is usually defined as the number of descendants provided by an individual to the next generations, changes in the individual fitness lead per definition to changes in native population sizes (**MO** impact) (Krimbas 2004, Hunt and Hodgson 2010). This is problematic, as in EICAT, **MN** impacts explicitly do not involve population level impacts. Performance, on the contrary, does not necessarily relate to offspring production and therefore does not imply **MO** impacts: it includes changes in the individual growth, reproduction, fecundity, survival, defense, immunocompetence, etc. **MN** impacts (i.e. impacts on the individual performance) can lead to population level impacts (**MO**, **MR** and **MV** impacts), but do not necessarily do so.

Population, sub-population, local population

The three most severe EICAT impact categories (**MO**, **MR** and **MV**) involve population level impacts to native taxon [causing declining populations of native taxon (**MO** impacts), or reversible and irreversible population extinctions (**MR** and **MV** impacts, respectively)]. To reflect the severe nature of these impacts and to assist efficient communication of high impacts, **MO**, **MR** and **MV** impacts have been grouped together under the term 'harmful' (Fig. 1). This follows a similar approach adopted by the IUCN Red List of Threatened Species (https://www.iucnredlist.org/), where native species in the three of the Red List categories [Vulnerable (VU), Endangered (EN) and Critically Endangered (CR)] are grouped under the term 'threatened'. The terms 'population', 'local population', 'sub-population' and 'global population' are widely used terms which might not always be understood in the same way (Wells and Richmond 1995): to avoid any confusion on what is meant in EICAT by 'population level impacts', these different terms have been clearly defined in the revised guidance.

Revised guidance

The relationship between a global population, a sub-population and a local population has been clarified (IUCN 2020a):

- A global population includes all individuals of a taxon
- A sub-population is a geographically or otherwise distinct group in the global population of a taxon
- A local population is a group of individuals within a sub-population of a taxon

Sub-populations are largely isolated from each other, whereas local populations within a sub-population are connected by frequent movements of individuals (Fig. 2). For EICAT assessments, population decline and extinction should be evaluated at least at the level of a local population (but can also happen at higher levels, such as sub-population or global population levels).

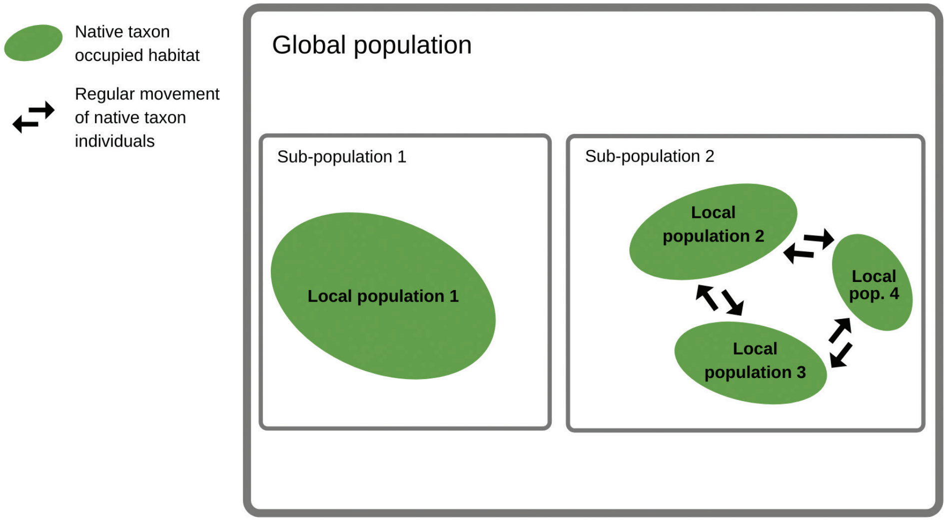


Figure 2. The relationship between a global population, sub-population and local population for the purposes of EICAT assessments. The global population includes all individuals of a taxon, a sub-population is a geographically or otherwise distinct group in the population, and a local population is a group of individuals within a sub-population. In this example, local population 1 includes all individuals within sub-population 1. Local populations 2, 3 and 4 are connected by frequent natural immigration, whereas sub-populations 1 and 2 are largely isolated from each other. Reproduced from IUCN (2020a) IUCN EICAT Categories and Criteria, IUCN (Gland): page 4, https://doi.org/10.2305/IUCN.CH.2020.05.en, with permission from IUCN.

To show impacts at the native population level (**MO**, **MR** or **MV**), studies should understand the structure and dynamics of the populations being considered through the assessment. The individuals comprising a local population are often spatially grouped into smaller units (termed patches, aggregates, clusters, herds, etc.), which are naturally dynamic (i.e. appearance of new patches and disappearance or expansion of existing patches; Hanski 1994). Impact studies and EICAT assessors should be careful not to consider individual patches as local populations when evaluating the magnitude of the impact caused by the alien taxon. Studies should also ideally have attempted to understand the natural dynamics of the native local populations, to avoid incorrectly interpreting changes due to natural variation as impacts of the alien taxon (e.g. Schooley and Branch 2009; Hanski et al. 2017; the guidelines of the IUCN Red List of Threatened Species (IUCN 2012, 2019) provide examples of different population dynamics, such as extreme fluctuations or severely fragmented populations).

Observations or experiments are sometimes carried out on native local 'populations' that are not reproducing (e.g. common garden experiments for plants or mesocosm experiments). In EICAT, impacts can be reported at the population level (**MO**, **MR** or **MV**) only when observations or experiments are carried out on native self-sustaining populations. Ideally, changes in native population dynamics should have been happening over several generations to conclude population level impacts (**MO**, **MR** or **MV**):

for instance, to confidently detect population level impacts, it might not be sufficient to observe fewer native plant individuals in the same generation, as these losses could be compensated for by seedling recruitment. Therefore, in the cases of non-self-sustaining native populations, one can only infer impacts on individual performance (**MN**).

Impact categories

Determining whether an impact is Major (MR) or Massive (MV) under EICAT

Determining whether the impact of an alien taxon on a native taxon is **MR** or **MV** under EICAT is established by assessing whether the impact is reversible. Both **MR** and **MV** impacts result in native taxon extinctions: a local population extinction that is reversible is classified as an **MR** impact, whilst an irreversible local population extinction is an **MV** impact. Under the previous EICAT guidance, the assessor is required to determine whether the impact of the alien taxon is likely to be reversible through management actions (for example by considering the logistics associated with extirpating or eradicating the alien taxon, re-introducing the native taxon and / or restoring native habitats). In cases where the effort or cost required to reverse the changes caused by the alien taxon were beyond capabilities, the impact would be judged irreversible (i.e. it would be assessed as an **MV** impact), even if in theory it might be possible to re-establish the native local population.

Determining whether management actions are likely to enable the native taxon to re-colonise the area is an unrealistic demand of the assessor. This is very difficult to establish in an EICAT assessment procedure and is usually not discussed in the original impact reports used in the EICAT process: it would inevitably introduce new causes of uncertainty and subjectivity.

Revised guidance

The requirement to evaluate the reversibility of a native taxon extirpation through management actions has been removed from the guidance documentation. To determine whether an impact is **MR** or **MV**, the assessor must instead apply the hypothetical scenario which assumes that the alien taxon is eradicated from the location where it caused the extinction of a native local population, regardless of whether this eradication is feasible or if the native taxon could be re-established with additional effort:

- A local population extinction is reversible (an **MR** impact) if the native taxon would most likely return to the community from which it was extirpated within 10 years or 3 generations of the native taxon, whichever is longer, under either of the following conditions; (1) naturally [e.g. individuals migrating from another local population (of the same sub-population) recolonising the area], or (2) assisted by human re-introductions, either intentionally or unintentionally, but only where the re-introductions were occurring at a similar rate before the alien taxon led to the native taxon local population extinction, and the re-introductions are not for conservation purposes. Examples for the second condition include cases where individuals of a native mussel are frequently (unintentionally) transported via boats to the place where the local population of this native mussel went extinct, or cases where a native fish is periodically (and intentionally) restocked for fishing in the lake where the local population of this fish went extinct. Therefore, re-introductions assisted by humans that were not already in place at the time the alien taxon led to the local population extinction and would require extra effort (e.g. re-introductions from captivity or from other areas) are not considered as reversible changes.

- A local population extinction is irreversible (an **MV** impact) if the native taxon is not likely to return to the community within 10 years or 3 generations of the native taxon, whichever is longer, without additional human assistance that was not already in place at the time the alien taxon led to the local population extinction. Local extinctions are irreversible when there is no propagule influx of the native taxon (e.g. global extinction, disconnection of the local population), or when the alien population changes the environment, making it unsuitable for the native taxon.

Local extinctions which, under the previous guidance, were considered irreversible (**MV**) because of practical constraints or inability to either eradicate the alien or restore the native habitats, should be re-classified as **MR** impacts, if it is possible for the native taxon to return to the community naturally or assisted by human re-introductions already in place before the alien taxon led to its local population extinction. Local extinctions which were considered irreversible (**MV**) because the native taxon was globally extinct, because of a disconnection of the local population, or because of changes in the habitat characteristics due to the alien, should remain classified as **MV** under the revised guidance. Local extinctions which were classified as **MR** because it was judged logistically feasible to re-introduce the native taxon with extra effort (i.e. with measures not already in place before the alien taxon led to the native taxon extinction) or by restoring the habitat modified by the alien, should be considered irreversible and re-classified as **MV** under the revised guidance.

Impact mechanisms

Broadening of impact mechanisms in order to capture all types of impacts

EICAT considers that impacts caused by alien taxon to a native taxon can occur through 12 EICAT impact mechanisms, which align with those identified in the IUCN Global Invasive Species Database (GISD) (http://www.iucngisd.org/gisd). In the previous EICAT guidance, these mechanisms were: (1) Competition, (2) Predation, (3) Hybridisation, (4) Transmission of diseases to native species, (5) Parasitism, (6) Poisoning / toxicity, (7) Biofouling, (8) Grazing / herbivory / browsing, (9, 10, 11) Chemical, physical, or structural impact on ecosystem, (12) Interaction with other alien species (Hawkins et al. 2015). Impact mechanisms describe the way a native taxon is affected by an alien taxon: e.g. by feeding on plants, alien herbivores can affect native plants through 'Grazing', and at the same time they can affect native insects or ground-nesting birds through 'Chemical, physical, or structural impact on ecosystem', because of above-ground plant biomass removal.

Indirect impacts to native taxon were not completely captured by these 12 mechanisms. In indirect impacts, the alien taxon does not directly interact with the impacted native taxon: it affects the native taxon by modifying another factor of the environment, which can be biotic (a population of another alien or native taxon), or abiotic (e.g. water or soil composition). In the 12 mechanisms, indirect impacts occurring through changes in abiotic factors are captured by the mechanism 'Chemical, physical, or structural impact on ecosystem'. Indirect impacts through changes to biotic factors can occur **a)** when the alien taxon facilitates the negative effect of an intermediate species on the native taxon of interest. This is the case in the 'Transmission of disease' or in the 'Interaction with another alien species' mechanisms, where the alien facilitates the negative impact respectively of a parasite (by vectoring it) or of another alien species. However, other examples of such indirect impacts exist, and were not described by any mechanisms of the previous guidance: for instance, on San Miguel and Santa Cruz Islands (California Channel Islands), an introduced pig (*Sus scrofa*) population enabled the colonisation by mainland golden eagles (*Aquila chrysaetos*) and caused an increase in their population by providing a supplemental food source, leading the golden eagle population to start feeding on the native fox (*Urocyon littoralis*) population and causing its decline (Roemer et al. 2001, 2002). In this example, the alien pig had an indirect impact on the native fox, by facilitating the impact of the golden eagle. Indirect impacts can also occur when **b)** the alien taxon inhibits a positive effect of an intermediate species on the native taxon of interest. This is the case in the 'Competition' mechanism, where the alien taxon decreases the availability of a resource and thereby decreases the benefits brought by this resource to the native taxon. However, other mechanisms for this type of indirect impacts were previously ignored as well. In North American forests, for example, the European plant garlic mustard (*Alliaria petiolata*) has been found to release antifungal phytochemicals which eliminate the activity of native arbuscular mycorrhizal fungi and suppress the growth of native tree seedlings by disrupting their mutualistic associations (Stinson et al. 2006; Callaway et al. 2008). Such impacts are not described by any mechanism and cannot be systematically and consistently classified.

With respect to direct mechanisms, impacts occurring through direct physical disturbances, such as vegetation trampling or tree rubbing, were not captured either. Alien populations of ungulates often cause direct physical disturbances: for instance, an alien population of the Asian elephant (*Elephas maximus*) on the Andaman Islands (India) contributed to the declines of several native plant populations by heavily grazing upon them, but also by uprooting and debarking trees (Ali 2004). In such impacts, native individuals are not indirectly affected by a change in some environmental characteristics (impact on ecosystem), but are affected by their direct interaction with alien individuals.

Revised guidance

To capture all indirect impacts occurring through changes to biotic factors, the mechanism 'Interaction with other alien species' has been amended to 'Indirect impacts through interaction with other species' and the semi-quantitative scenarios updated accordingly (see Table 1).

Unlike the direct mechanisms of 'Predation', 'Grazing / herbivory / browsing' or 'Parasitism', the direct impacts caused by physical disturbances (e.g. vegetation trampling) do not concern trophic interactions. The existing 'Biofouling' mechanism is also a direct mechanism not concerning trophic interactions but occurring through a physical disturbance of native individuals: therefore, the mechanism 'Biofouling' has been amended to 'Biofouling or other direct physical disturbance', to capture all types of impacts occurring through direct physical disturbances.

These extensions of two mechanism definitions allow the classification of impacts that were not captured in a systematic way under the previous guidance: impacts falling into these new definitions, and previously classified into unsuited mechanisms, should be re-classified into one of these two extended mechanisms.

Refinement and clarification of the criteria for the mechanism 'Transmission of disease'

In the 'Transmission of disease' mechanism, the alien taxon acts as a vector of a (native or alien) disease agent (e.g. virus, bacteria or prion) or parasite which impacts upon native taxa. When we evaluate the impact of the alien taxon through 'Transmission of disease', we evaluate its impact as a vector [i.e. the increase in the spread of the disease agent/parasite (hereafter, parasite) caused by the alien vector impacts the native taxon]. However, evidence of the alien taxon being a host is more frequently available than evidence of the alien taxon being a vector. For instance, the chytrid fungus (*Batrachochytrium dendrobatidis*), which has contributed to global amphibian declines, has been shown to be transmitted by alien amphibians populations to the native ones (e.g. Fisher and Garner 2007; Miaud et al. 2016); yet, most studies only show that alien amphibian populations are reservoirs for the chytrid fungus instead of showing that they transmit the disease to the native populations (Measey et al. 2016). The responsibility of the alien taxon for disease spread and observed impact is difficult to evaluate from such evidence.

Revised guidance

Based on the available types of evidence for this mechanism, the information required to classify impacts through 'Transmission of disease' has been clarified. For an impact to be classified as **MO**, **MR** or **MV**, the following information is needed: an impact on the native population [e.g. a decline (**MO**) or a local extinction (**MR/MV**)] has to be observed and the alien taxon has to be shown to be a host of the parasite at the same time and space as the native population (based on Kumschick et al. 2017). When the only available evidence is that the alien taxon is a host (or a vector) of a disease that affects individuals, the impact should be scored as **MN**: the extent of the impact on the native population is not shown or studied, so we can only suppose that the performance of the infected individuals has been affected. Impacts are classified as **MC** when the disease or parasite carried by the alien taxon was not found in the native taxa, or when the disease or parasite was found in the native taxa but shown to be harmless to the native individuals. The semi-quantitative scenarios of the 'Transmission of disease' mechanism have been updated accordingly (see Table 1).

Establishing whether the alien taxon is the only (or main) vector of the parasite in the recipient environment, or whether multiple vectors are present and are aiding the spread of the parasite, helps to evaluate the impact of the alien vector. If the alien taxon is the only vector, the impact of the alien taxon equates to the impact of the parasite. If the alien taxon is not the only vector of the parasite, the impact of the alien taxon equates to the impact caused by the increase in the spread of the parasite due to the alien taxon.

If the parasite vectored by the alien taxon is also an alien in the area of interest, separate EICAT assessments need to be performed for it, under the mechanism 'Parasitism'. In cases where the alien vector is the only vector present in the recipient environment, the same impact magnitude would be recorded for the alien vector and for the alien parasite (because if either of them were absent, the observed impact would not occur). In cases where the alien vector is increasing the spread of an alien parasite, the impacts of the alien parasite and of the alien vector might be of different magnitudes (but the impact of the alien parasite will always be the same or higher than the impact of the alien vector in this specific mechanism).

These updates show how to apply the information usually available regarding the 'Transmission of disease' mechanism: impact reports showing that the alien is a host of a parasite causing damage to the individual performance or population of a native species can now be classified in a consistent way. Such impact reports might have been classified differently under the previous guidance, because of a lack of solid evidence showing that the alien taxon was transmitting the parasite to native species: these reports should be re-classified based on the new criteria.

Revised scenarios to describe the severity of 'Hybridisation' impacts

For all impact mechanisms, the five semi-quantitative scenarios categorising severity should follow the same general logic. However, the semi-quantitative scenarios used to describe the severity of 'Hybridisation' impacts are not in-line with those used to describe the severity of impacts associated with other mechanisms, because they focus on the viability of the hybrid offspring, rather than on the native individuals. The semi-quantitative scenarios are also based on hypothetical (projected) impacts, instead of on observed impacts. Indeed, these scenarios assume that as soon as hybrids can reproduce with the native population, the latter is inevitably lost. In so doing, they ignore the possibilities that hybrid individuals may be removed from the population, that hybrids may only reproduce with other hybrids (assortative mating), that stable hybrid and native populations may coexist, that backcrossing processes may occur, or simply that hybridisation may not have been happening for long enough for the native population to go extinct. For example, the ruddy duck (*Oxyura jamaicensis*) hybridises with the endangered white-headed duck (*Oxyura leucocephala*) in Spain, but even though hybrids are fertile and produce viable offspring, early control programmes of the alien population and the hybrids allowed to avoid a decline in the white-headed duck population (Muñoz-Fuentes et al. 2007). The Asian sika deer (*Cervus nippon*) is known to hybridise with the native red deer (*Cervus elaphus*) in Scotland and England, but local red deer populations show very different levels of hybridisation. The sika deer have led to population declines in some locations where high proportions of hybrids were detected (e.g. in Kintyre Peninsula), but not in others, where a low frequency of hybrids was detected in large sample sizes, revealing past hybridisation followed by extensive backcrossing (e.g. in Lake District and North Highlands) (Smith et al. 2018).

Revised guidance

Each hybridisation event between native and alien or hybrid individuals reduces the reproduction rate of the pure native taxon, which can lead to a decline in population size or to local extinction, depending on the frequency of the hybridisation events and on whether hybrids are fertile. The criteria are now based on observed instead of projected impacts: hence, cases where hybrids are fertile but did not lead to local extinctions would no longer be classified as **MR** or **MV** (but maximum as **MO**). With increasing impact severity, the reproduction rate of the pure native taxon reduces, which may lead to declining populations of a native taxon (**MO** impacts) or to reversible and irreversible species extinctions (**MR** and **MV** impacts), depending on the frequency of the hybridisation events (see Table 1).

'Hybridisation' impacts classified using the previous guidance can be adapted to the revised guidance as follows:

- Impacts initially classified in the **MC** or **MN** categories can remain classified in the **MC** or **MN** categories, respectively;
- Impacts initially classified in the **MO** category because hybridisation is regularly observed in the wild and has led to a decline of the pure native population can remain classified in the **MO** category. In contrast, impacts initially classified in the **MO** category only because hybrids are vigorous but sterile, but with no decline of the pure native population observed, should be re-classified in the **MN** category;
- Because, in the previous guidance, the criteria of the **MR** category did not describe any replacement of the pure native population, impacts initially classified in the **MR** category should be re-classified in the **MO** category;

Table 1. Criteria used to classify alien taxa by EICAT impact category (**MC**, **MN**, **MO**, **MR**, **MV**) for the three modified mechanisms: Indirect impacts through interaction with other species, Transmission of disease to native species and Hybridisation. Reproduced from IUCN (2020a) IUCN EICAT Categories and Criteria, IUCN (Gland): pages 13–16, https://doi.org/10.2305/IUCN.CH.2020.05.en, with permission from IUCN.

	Massive (MV)	**Major (MR)**	**Moderate (MO)**	**Minor (MN)**	**Minimal Concern (MC)**
Categories should adhere to the following general meaning	Causes local extinction of at least one native taxon (i.e., taxa vanish from communities at sites where they occurred before the alien arrived), which is naturally irreversible; even if the alien taxon is no longer present the native taxon cannot recolonise the area	Causes local or subpopulation extinction of at least one native taxon (i.e., taxa vanish from communities at sites where they occurred before the alien arrived); which is naturally reversible if the alien taxon is no longer present	Causes population decline in at least one native taxon, but no local population extinction	Causes reduction in individual performance (e.g., growth, reproduction, defence, immunocompetence), but no decline in local native population sizes	Negligible level of impact; no reduction in performance (e.g., growth, reproduction, defence, immunocompetence) of individuals of native taxa
Mechanisms					
Indirect impacts through interaction with other species	Interaction of an alien taxon with other taxa leading to indirect impacts (e.g., pollination, seed dispersal, apparent competition) causing local extinction of one or several native taxa, leading to naturally irreversible changes that would not have occurred in the absence of the alien taxon	Interaction of an alien taxon with other taxa leading to indirect impacts (e.g., pollination, seed dispersal, apparent competition) causing local population extinction of at least one native taxon; changes are naturally reversible but would not have occurred in the absence of the alien taxon	Interaction of an alien taxon with other taxa leading to indirect impacts (e.g., pollination, seed dispersal, apparent competition) causing a decline of population size of at least one native taxon, but no local population extinction; impacts would not have occurred in the absence of the alien taxon	Interaction of an alien taxon with other taxa leading to indirect impacts (e.g., pollination, seed dispersal, apparent competition) affecting performance of native individuals without decline of their populations; impacts would not have occurred in the absence of the alien taxon	Interaction of an alien taxon with other taxa leading to indirect impacts (e.g., pollination, seed dispersal, apparent competition) but reduction in performance of native individuals is not detectable
Transmission of disease to native species	Transmission of disease to native taxa resulting in local extinction of at least one native taxon; changes are naturally irreversible	Transmission of disease to native taxa resulting in local population extinction of at least one native taxon; naturally reversible when the alien taxon is no longer present	Transmission of disease to native taxa resulting in a decline of population size of at least one native taxon, but no local population extinction; disease is severely affecting native taxa, including mortality of individuals, and it has been found in native and alien co-occurring individuals (same time and space)	Transmission of disease to native taxa affects performance of native individuals without leading to a decline of their populations; alien taxon is a host of a disease which has also been detected in native taxa and affects the performance of native taxa	The alien taxon is a host or vector of a disease transmissible to native taxa but disease not detected in native taxa; reduction in performance of native individuals is not detectable
Hybridisation	Hybridisation between the alien taxon and native taxa leading to the loss of at least one pure native local population (genomic extinction); pure native taxa cannot be recovered even if the alien and hybrids are no longer present	Hybridisation between the alien taxon and native taxa leading to the loss of at least one pure native local population (genomic extinction); naturally reversible when the alien taxon and hybrids are no longer present	Hybridisation between the alien taxon and native taxa is regularly observed in the wild; local decline of populations of at least one pure native taxon, but pure native taxa persist	Hybridisation between the alien taxon and native taxa is observed in the wild, but rare; no decline of pure local native populations	No hybridisation between the alien taxon and native taxa observed in the wild (prezygotic barriers), hybridisation with a native taxon is possible in captivity

- Impacts initially classified in the **MV** category because hybridisation is common in the wild and /or because hybrids are fully vigorous and fertile should be:

- re-classified in the **MO** category if hybridisation has led to a decline in the pure native taxon but no replacement of the pure native population;
- re-classified in the **MR** category if hybridisation has led to the replacement of the local pure native population, but the native pure bred population can recover (either naturally or assisted by human re-introductions already in place before the alien taxon led to the local population extinction) if the alien and hybrids are no longer present;
- remain classified in the **MV** category if hybridisation has led to the replacement of the local pure native population, and the native pure bred population cannot recover (either naturally or assisted by human re-introductions already in place before the alien taxon led to the local population extinction) even if the alien and hybrids are no longer present.

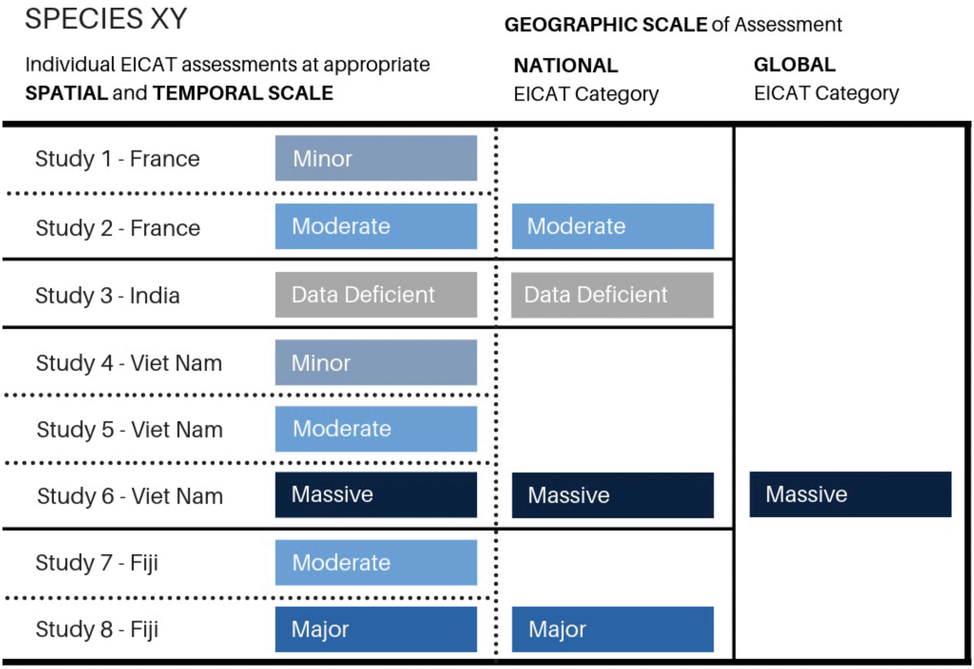
Overall impact of an alien taxon

Distinction between spatial scale of assessments and geographic scale of assessments

The previous guidelines independently addressed the concepts of spatial scale of assessments and geographic scale of assessments. The term 'spatial scale of assessments' is used in the context of an individual EICAT assessment (based on one impact observation, or study), whereas the term 'geographic scale of assessments' is used in the context of the overall classification of an alien taxon. While these terms are used at different stages of the assessment process, they might be confused, as they both involve spatial aspects of assessments. The distinction between the two terms is made clear in the revised guidance.

Spatial scale of assessments: The term spatial scale of assessments relates to the evidence of impacts being assessed using the EICAT Categories and Criteria. Impacts caused by alien taxa need to be observed or investigated at an appropriate spatial and temporal scale, over which the original native communities can be characterised. Assessments based on evidence generated at spatial or temporal scales that are very different to the scales over which the local native population can be characterised are likely to be subject to greater uncertainty.

Geographic scale of assessments: Where impacts are assessed based on evidence from across an alien taxon's global introduced range, the geographic scale of the maximum recorded impact would be 'Global'. However, where impacts are assessed based on evidence from a single country to which an alien taxon has been introduced (excluding impacts from areas of its alien range in other countries), the geographic scale of the maximum recorded impact would be 'National' (Fig. 3). IUCN will only review and display global EICAT assessments on their website.



SPECIES XY

Individual EICAT assessments at appropriate **SPATIAL** and **TEMPORAL SCALE**		**GEOGRAPHIC SCALE** of Assessment **NATIONAL** EICAT Category	**GLOBAL** EICAT Category
Study 1 - France	Minor		
Study 2 - France	Moderate	Moderate	
Study 3 - India	Data Deficient	Data Deficient	
Study 4 - Viet Nam	Minor		
Study 5 - Viet Nam	Moderate		
Study 6 - Viet Nam	Massive	Massive	Massive
Study 7 - Fiji	Moderate		
Study 8 - Fiji	Major	Major	

Figure 3. How data from individual EICAT assessments of the impacts of a hypothetical alien taxon (species XY) inform the EICAT Category to which the taxon is assigned at national and global scales. The global assessment categorises the taxon based on its highest impact anywhere [in this case, a Massive (**MV**) impact in Vietnam]. National scale assessments are based only on impacts reported from those countries [e.g. Major (**MR**) for Fiji]. Data Deficient (**DD**) in India indicates that the alien taxon was assessed but no impact reports from India were found. Reproduced from IUCN (2020a) IUCN EICAT Categories and Criteria, IUCN (Gland): page 20, https://doi.org/10.2305/IUCN.CH.2020.05.en, with permission from IUCN.

No longer recording Current (Maximum) Impact

Under the previous guidance, a dual assessment of the alien taxon's impacts was required (Hawkins et al. 2015):

- Maximum Recorded Impact (**MC**, **MN**, **MO**, **MR** or **MV**)
- Current (Maximum) Impact: the severity of impacts associated with an alien taxon's current impacts on a native species (at the time of the EICAT assessment) (**MC**, **MN**, **MO**, **MR** or **MV**)

The rationale here was that the two measures of impact severity could be compared to demonstrate whether the impacts of an alien taxon were increasing or decreasing over time. For instance, an impact could be downgraded to a lower magnitude once management practices had been established to control the alien population.

While downgrading or upgrading an impact to lower or higher magnitudes can be informative for the impact caused by a specific alien population, downgrading or upgrading the overall impact of an alien taxon with multiple introduced populations is not straightforward and might lead to the loss of information on impacts, for the following reasons:

- Different introduced populations of the alien taxon are likely to vary over time in different ways: the same reduction or increase in the impact magnitude will probably not be observed in all its introduced populations. It is difficult to define in such cases how to treat the different scenarios with one global Current Impact score.
- Moreover, it is unclear when an impact should be considered as 'current' when considering the overall impact of an alien taxon (i.e. it is difficult to define a reasonable time scale over which impact magnitudes should be re-evaluated).
- Finally, information on the variation of impacts over time will likely not be available for most of the introduced populations of the alien taxon. It is unclear if potential differences in recent impact reports are the result of temporal changes in impact magnitudes.

Revised guidance

The requirement to assess an alien taxon's Current Impact has been removed: an assessment of the alien taxon's Maximum Recorded Impact is still required, which equals the taxon's EICAT Classification (as in Kumschick et al. 2020). EICAT is an evidence-based scheme: the classification of an alien taxon is only based on its observed impacts (or impacts inferred based on evidence), but potential, hypothetical or projected impacts are not assessed by the framework (IUCN 2020a).

Dealing with uncertainty

The assessor should assign each (relevant) impact report to its most likely impact category and assign a level of confidence to this assessment (high, medium or low), depending on the likelihood of the assigned impact category being correct. In the previous guidance, the factors listed as potentially reducing the assessors' confidence in the impact magnitude assigned to an impact observation included: the availability, reliability and type of data used as evidence of impacts, the spatial scale over which data were collected, the ease of interpretation of the available data, and whether or not all available data were in agreement with respect to the magnitude of recorded impacts.

The previous guidance did not address three important sources of uncertainty in EICAT assessments (see also Probert et al. 2020):

- **Confounding effects:** The presence of confounding effects is a frequent source of uncertainty in impact reports when changes are happening at the local population level (**MO**, **MR** or **MV**). Large-scale phenomena such as changes in native population dynamics usually do not allow an 'ideal' experimental set-up with control situations to exclude the possibility that other biotic or abiotic factors have caused or contributed to the observed impact (Kumschick et al. 2015, Christie et al. 2019). It is therefore often difficult to distinguish whether an alien taxon is the driver of these changes, or whether confounding effects are at play. For instance, when a decline of a native taxon is observed but multiple stressors – including the alien taxon – act on that species, it is possible that the observed decline would have happened in the absence of the alien taxon. The impact caused by the alien taxon might therefore be lower than the one assigned (e.g. **MO**), if the decline would have happened anyway: the presence of other stressors can reduce the confidence in the assigned impact category. Conversely, when no other stressor is known to act on the impacted native taxon, the alien taxon is more likely to be responsible for the observed change.

- **Study design:** Impact studies are rarely designed to determine which impact magnitude is caused by the alien taxon based on the EICAT criteria (i.e. at which level of organisation are the native taxa affected by the alien taxon). Therefore, even in well-designed impact studies, uncertainty can exist regarding the impact magnitude that has been assigned to the impacts they report. For instance, some studies focus only on one particular level of impact (e.g. the individual performance) and are not investigating higher levels of impact (e.g. whether the impact on the individual performance is affecting the size of the population) even when these are likely (Probert et al. 2020). In such cases, the assessor should be aware that the study design creates uncertainty: the 'true' impact magnitude could be higher than the one assigned, if the alien causes a decline in the native population. Hence, these impacts cannot be classified as **MN** impacts with high confidence, as the **MN** category corresponds to impacts at the individual performance level and no impact at the population level (IUCN 2020b). In contrast, impact reports from study designs that describe an impact at the individual performance level, and which would have allowed detection of an impact at higher levels, can be classified as **MN** with high confidence regarding the 'Study design'.
- **Temporal scale:** Studies performed over time periods that are too short to capture the changes in a native population might lead to an over- or under-estimation of the severity of an impact. As previously explained, a study investigating impacts at the native population level (**MO**, **MR** or **MV**) should be performed at a temporal scale that allows changes in the dynamics of native populations to be captured, over several generations.

Revised guidance

The revised guidance for the confidence classification distinguishes between five sources of uncertainty in EICAT assessments: confounding effects, study design, data quality and type, spatial and temporal scales, and coherence of evidence (see Probert et al. 2020). The source 'Data quality and type' addresses the uncertainty associated with the use of inferred information in the assessment, but also the uncertainty associated with the way the impact observation is communicated in the report. For instance, if no detail is provided on the way the observation or experiment has been performed in the report, the assessor cannot evaluate the relevance of the spatial/temporal scale or of the study design. The guidance also specifies how each of these sources can affect the assessor's level of confidence in their assessment, and in which circumstances these sources would lead to a high, medium or low score (Table 2).

Table 2. Guidance for confidence classification (from IUCN 2020b).

Sources of uncertainty that influence the confidence rating	Presence of confounding effects	Study design	Data quality and type	Spatial and temporal scale	Coherence of evidence
High confidence: it is likely (approximately 90% chance) that the true impact category is equal to the assigned one	The likelihood of including confounding effects is low (i.e. it is unlikely that the level of impact would have been observed if the alien taxon was not introduced)	The study design would have allowed the detection of higher/lower impact magnitudes than the one assigned	There is relevant direct observational evidence to support the assessment; the data are reliable and of good quality	Impacts are recorded at the typical spatial and temporal scales at which the local native population can be characterised	All evidence points in the same direction (no contradictory evidence)
Medium confidence: there is potential for the true impact category to be different from the assigned one (approximately 65–75% chance of the assigned impact category being correct)	Confounding effects may be at least partly responsible for the observed impact (i.e. potentially the observed level of impact would still have happened if the alien taxon was not introduced)	The study design would not have allowed the detection of higher/lower impact magnitudes than the one assigned (i.e. it cannot be reasonably excluded)	There is some direct observational evidence to support the assessment, but some of the data are inferred	Impacts are recorded at a spatial or temporal scale which may not be relevant to the scale over which the local native population can be characterised, but extrapolation or downscaling of the data to relevant scales is considered reliable or embraces little uncertainty	Most evidence points in the same direction, but some is contradictory or ambiguous
Low confidence: it is likely that the true impact category is different from the assigned one (approximately 35% change of the assigned impact category being correct)	The likelihood of including confounding effects is high (i.e. it is likely that the observed level of impact would have happened if the alien taxon was not introduced)	The study design does not allow any conclusions about higher or lower impact magnitudes and it is likely that the true impact magnitude is higher or lower	There is no direct observational evidence to support the assessment; data are of low quality	Impacts are recorded at a spatial or temporal scale which is unlikely to be relevant to the scale at which the local native population can be characterised, and extrapolation or downscaling of the data to relevant scales is considered unreliable or embraces significant uncertainties	Data are strongly ambiguous, or contradictory

Conclusions

Here we have provided clarifications to improve the understanding of the EICAT framework. We highlighted the problematic aspects of the initial EICAT framework and guidelines (Blackburn et al. 2014; Hawkins et al. 2015), which have been modified, but not explained, in the revised versions (IUCN 2020a, b). We also provided concrete examples and additional explanations on the impact assessment process.

It is, however, impossible to completely avoid differences in interpretation amongst assessors for some aspects of the framework. Therefore, we stress the importance of following the recommendations given by González-Moreno et al. (2019): assessors should be adequately trained, and continuously discuss and exchange their work with other assessors for feedback and review.

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RESEARCH ARTICLE

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Is invasion science moving towards agreed standards? The influence of selected frameworks

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Abstract

The need to understand and manage biological invasions has driven the development of frameworks to circumscribe, classify, and elucidate aspects of the phenomenon. But how influential have these frameworks really been? To test this, we evaluated the impact of a pathway classification framework, a framework focussing on the introduction-naturalisation-invasion continuum, and two papers that outline an impact classification framework. We analysed how these framework papers are cited and by whom, conducted a survey to determine why people have cited the frameworks, and explored the degree to which the frameworks are implemented. The four papers outlining these frameworks are amongst the most-cited in their respective journals, are highly regarded in the field, and are already seen as citation classics (although citations are overwhelmingly within the field of invasion science). The number of citations to the frameworks has increased over time, and, while a significant proportion of these are self-citations (20–40%), this rate is decreasing. The frameworks were cited by studies conducted and authored by researchers from across the world. However, relative to a previous citation analysis of invasion science as a whole, the frameworks are particularly used in Europe and South Africa and less so in North America. There is an increasing number of examples of uptake into invasion policy and management (e.g., the pathway classification framework has been adapted and adopted into EU legislation and CBD targets, and the impact classification framework has been adopted by the IUCN).

However, we found that few of the citing papers (6–8%) specifically implemented or interrogated the frameworks; roughly half of all citations might be viewed as frivolous ("citation fluff"); there were several clear cases of erroneous citation; and some survey respondents felt that they have not been rigorously tested yet. Although our analyses suggest that invasion science is moving towards a more systematic and standardised approach to recording invasions and their impacts, it appears that the proposed standards are still not applied consistently. For this to be achieved, we argue that frameworks in invasion science need to be revised or adapted to particular contexts in response to the needs and experiences of users (e.g., so they are relevant to pathologists, plant ecologists, and practitioners), the standards should be easier to apply in practice (e.g., through the development of guidelines for management), and there should be incentives for their usage (e.g., recognition for completing an EICAT assessment).

Keywords

Biological invasions, EICAT, introduction pathways, invasion science, Pathway Classification, Unified Framework

Introduction

The field of invasion science has grown rapidly (Pyšek et al. 2006; Richardson and Pyšek 2008). However, despite major advances on many fronts, there are ongoing debates about how the phenomenon of biological invasions should be circumscribed and classified (Latombe et al. 2019). Such differences in definitions hamper our ability to develop robust generalisations, consistently monitor the phenomenon across different scales, and report on it to multiple stakeholders. To facilitate generalisations, and to improve the link between science, policy, and management, numerous frameworks have been developed in an attempt to unify different concepts and definitions. For these frameworks to allow for generalisations and to have value in decision-making, they need to be applicable across taxonomic groups and environments and be accepted by different end users.

These issues were discussed as part of a workshop on "Frameworks in Invasion Science" in November 2019 (Wilson et al. 2020). As background to this workshop, and to understand the role of frameworks in invasion science generally, this paper explores the degree to which existing frameworks have been accepted and adopted. For this purpose, we selected three of what we consider amongst the most influential recent frameworks in invasion science: the pathway classification framework first outlined by Hulme et al. (2008); the proposed Unified Framework for Biological Invasions describing the introduction-naturalisation-invasion continuum (Blackburn et al. 2011); and the Environmental Impact Classification for Alien Taxa [the rationale was introduced by Blackburn et al. 2014; and guidance as to how to apply it in practice (with slight modification) was provided by Hawkins et al. 2015]. These are hereafter referred to as the "Pathway Classification", the "Unified Framework", and "EICAT", respectively (and where data are presented for all three frameworks, they are presented in this order, with a combined/single figure for the two papers that outline EICAT). This is a biased selection. Many more frameworks have been proposed, some of which are very similar to those selected (Catford et al. 2009; Leung et al. 2012; Wilson et al. 2020), and several others paved the way for the frameworks selected here (Nentwig et al. 2010; Richardson et al. 2000; Williamson and Fitter 1996). However, we selected these frameworks as they capture the phenomenon of invasion in its entirety (i.e., introduction dynamics, establishment, spread, and impact) and they were all explicitly designed to be generalisable across taxa and contexts. They are also amongst the most widespread and widely adopted frameworks, for example, the Pathway Classification has been modified and adopted into EU regulations and by the Convention on Biological Diversity (Scalera et al. 2016), and EICAT was adopted by the IUCN (IUCN 2020). Both the Unified Framework and the Pathway Classification have been proposed for use in international biodiversity standards, and EICAT is under consideration for a future proposal (Groom et al. 2019). Therefore, they arguably represent the frameworks that are closest to being standards in invasion science, and see Box 1 for how they have been adopted policy and management settings in South Africa as an example.

Box 1. How the frameworks have influenced policy and management in South Africa.

All three frameworks–the Pathway Classification (Hulme et al. 2008), the Unified Framework (Blackburn et al. 2011), and EICAT (Blackburn et al. 2014; modified by Hawkins et al. 2015)–have been implemented to different degrees in South Africa. While these frameworks are not formally part of South African legislation, they are incorporated into national reporting on biological invasions and in a recently-developed risk analysis framework (see details below). There is, therefore, an incentive for South African researchers to explicitly use the coding of the frameworks.

Status report on biological invasion in South Africa

South African regulations on biological invasions require that, every three years, a report on the status of biological invasions and the effectiveness of control measures and regulations is produced. The primary aim of the status report is to strengthen the links between basic research, policy, and management by detailing the current status and providing support to decision-makers. The first report was released in October 2018 and it was the first effort globally to report on the status of biological invasion at a national level (van Wilgen and Wilson 2018). The report is based around 20 indicators covering pathways, species, sites, and interventions (Wilson et al. 2018). Of these, six indicators require the direct application of the invasion frameworks, and a further two are related to the frameworks.

Risk analysis framework

The South African regulatory lists (Department of Environmental Affairs 2014a; b) were initially developed through a series of stakeholder engagements and expert panel meetings (Kumschick et al. 2020-b). However, this has been contested in some cases. In response to the need for transparent and repeatable evidence to underpin the list, a risk analysis framework was developed. (Kumschick et al. 2020-c) As with the status report, the framework explicitly tries to align with the proposed frameworks.

Due to the way we selected the three frameworks, our analysis is somewhat circular. For example, the frameworks were selected on the basis that there has been some uptake into policy, so it is unsurprising that we found some uptake by policy-makers. However, we feel it is important to: (i) establish whether these frameworks are used broadly by people interested in invasion science or used just by a subset (e.g., only researchers based in Europe or only people studying marine invasions); (ii) determine whether the frameworks are being used as they were intended or only used to justify working on biological invasions; (iii) to assess how users perceive the frameworks; and (iv) to draw insights on how the field could move forward.

Methods

To evaluate the impact of the frameworks, we conducted an analysis of the citations of the papers, surveyed the authors of citing papers, and explored the extent to which the frameworks have been used in policy and management documents.

Citation analysis

The impact of a research publication is often measured by where it is published and how often it is cited (Biagioli 2016). By aggregating across publications, metrics have been developed to provide a measure of the impact of individual scientists and institutions (Hirsch 2005) that is incorporated into decisions around recruitment, promotions, and research funding (Hicks et al. 2015). While such metrics are simple and transparent, they create perverse incentives. For example, researchers, in an attempt to increase their h-scores, might inappropriately or egregiously promote their own work when reviewing or editing other people's manuscripts (Biagioli 2016; Zaggl 2017). Nonetheless, and acknowledging that impact as measured by citations is a different concept from research quality (Bornmann and Haunschild 2017), citations are a useful starting point to evaluate impact.

We explored four main aspects. First, we assessed the proportion of self-citations to gauge the degree to which the frameworks were only used by those who constructed them. Second, we evaluated whether the geographic and taxonomic biases apparent in the scientific literature in general (cf. Wilson et al. 2007; Wuestman et al. 2019) and invasion science in particular (Pyšek et al. 2006; Pyšek et al. 2008) were also apparent in the papers citing the frameworks. Our expectation was that the selected frameworks would be used across taxa as they were designed to be generally applicable. For example, an explicit rationale for the development of the Unified Framework was to merge a scheme predominately used by zoologists (Williamson and Fitter 1996) with a scheme used predominately by botanists (Richardson et al. 2000). Third, we wanted to explore whether the citing papers actually implemented the frameworks or simply cited the papers to back up general comments about biological invasions. And finally, we wanted to assess the degree to which the citations were from studies focussing on biological invasions or whether the frameworks had impact beyond their originally-intended field of study.

We downloaded bibliographic information from the ISI Web of Science Core Collection (https://www.webofknowledge.com) on 1 July 2019 for all the publications listed as citing one of the four papers considered here (Blackburn et al. 2014; Blackburn et al. 2011; Hawkins et al. 2015; Hulme et al. 2008), and obtained copies of the citing publications if possible (books and book chapters were omitted if a digital copy could not be readily obtained – 3.2, 1.6, 2.8% of cases for the Pathway Classification, the Unified Framework, and EICAT respectively; Suppl. material 1). We developed an initial protocol to score the articles according to set criteria. Ten of the authors scored 10 papers to look at consistency in scoring (i.e., inter-rater reliability). For most categories, it was found to be consistent, but in a few cases (e.g., the discipline), we found there was some disagreement that could be reduced by refining the protocol. However, when attempting to score papers in terms of the degree of influence the frameworks had on the paper there was substantial disagreement, even after discussion to refine the categories [Fleiss' Kappa of 0.179 in R package irr (Gamer et al. 2019)]. As a result, the extent of influence of each framework was scored by only one person for consistency (JRUW scored the Pathway Classification and SK scored the Unified Framework and EICAT, after discussing and aligning the scoring categories, see Suppl. material 2: Table S2.1). Most authors did some scoring of the other sections. We then adapted the protocol (see Suppl. material 2.1) and scored each paper accordingly (see Table 1 for details of the data extracted). It took 2–10 minutes to score each paper once it was downloaded.

The list of journals that cited each framework was extracted. To determine whether the frameworks had impact beyond their originally-intended field of study, we assigned each citing journal to one of three categories – those that explicitly included biological invasions as a subject area; those that published other aspects of ecology or were more general in scope; and those that did not include ecology as a subject area.

To evaluate geographic biases in the papers citing the frameworks, we used the results of a previous analysis of the geographic pattern of invasion science as a whole (Pyšek et al. 2008) as a point of comparison. We identified the corresponding author of studies that had cited the frameworks and assigned their primary affiliation to a geographic region as per the regions used by Pyšek et al. (2008). We then compared the number of studies in each region relative to the number of studies noted in Pyšek et al. (2008) against the expectation based on the rest of the world. After adjusting for multiple comparisons, regions that tended to have cited one of the frameworks either more often or less often than expected were identified (see Suppl. material 2.5).

Survey of citing authors

Because it was difficult to be sure how the frameworks had influenced publications, we surveyed the corresponding authors of papers that cited any one of the four papers. The survey was conducted under ethical clearance (SU project number: 14445) issued by Stellenbosch University.

The questionnaire (Suppl. material 2.2) was structured to assess how the frameworks are viewed and why they were cited in the authors' works. We used structured questions that were adopted and modified from a framework that has been applied to survey authors in citation analyses (Case and Higgins 2000; Harwood 2008; Prabha 1983; Shadish et al. 1995). The questionnaire consisted of 35 questions in four sections: eight proximity questions that assess the relationship between the person who cited a publication and any authors of that publication; 21 questions that seek reasons why authors might cite a paper; four semi-structured questions to gauge whether the frameworks are used in research or to implement policy and management strategies; and two questions that provided an opportunity to list any suggestions for or proposed improvements to the frameworks (Suppl. material 2.2). The questions that elicit reasons why authors might cite a paper can be grouped into five broad citation categories – classic citations, negative citations, creative citations, personal influence citations, and supportive citations – and the results were interpreted in the context of these groupings. A cover letter and a link to the questionnaire were emailed to a total of 958 corresponding authors, with a reminder sent to non-responders after one week. The survey ran for three weeks, from 13 March to 6 April 2020.

Influence on policy and management

Policy papers and strategies, unlike journal articles, often do not have a comprehensive list of references, are not indexed by academic databases, and many are published in languages other than English. Therefore, we read a selection of national and international policy documents. These documents included national strategies, status reports, national and international guidelines, and documents published by the Convention on Biological Diversity, International Union for Conservation of Nature, and the European Union. We then qualitatively assessed the degree to which the documents explicitly or implicitly referred to or implemented the frameworks. For this purpose, we only considered documents dated more recently than 2008, i.e., after the Pathway Classification was published.

Results

Citation analysis

The results of the citation analysis are summarised in Table 1. As of 1 July 2019, the Pathway Classification had 436 citations recorded on the ISI Web of Science database, the Unified Framework 729 citations, and the two papers that present and refine EICAT 249 citations. This puts them in the top ten most cited papers in their respective journals amongst articles published in the same year or more recently. The vast majority of these citations are from papers that can be classified as invasion science. In fact, about a third of all papers published in the journal Biological Invasions in 2018 cite the Unified Framework. The numbers of citations are increasing annually, with no indication of any plateaus (Figure 1). The number of self-citations has also increased over time, but their relative proportion has declined. Twelve percent of the papers cited more than one of the frameworks (Suppl. material 2.3).

Table 1. Summary of the results of the citation analysis of frameworks in invasion science. Where numbers are given, they are for the Pathway Classification framework (Hulme et al. 2008), the Unified Framework (Blackburn et al. 2011), and EICAT (Blackburn et al. 2014; Hawkins et al. 2015) in that order.

Variable	Type	Description	Expectation	Results
Discipline	Factor with three levels (invasion, ecology, other)	A rough indication of what the topic of the paper is.	No specific expectation, but provides an indication of the extent to which the frameworks have been used beyond invasion science.	The vast majority of citing papers were directly related to biological invasions (96, 93, 92%), but all of the frameworks were cited by some broader ecological (or evolutionary) papers (4, 6, 7%), and a handful of papers in other disciplines (< 1% in each case, including some in journals with apparently no link to ecology, for example, the *American Journal of Roentgenology*).
Extent of influence	Ordered factor with four levels (general, definition, broad, specific)	An interpretation of how the citation is actually used (i.e., the degree to which the paper implements the framework). This provided a response variable for testing other variables against.	Papers citing the frameworks should tend to implement specific aspects of the proposed frameworks, although they might also be used to make general points about biological invasions.	The level of frivolous citations was surprisingly high ~ 50% of all citations were classed as general (i.e. "citation fluff"), with only 6–8% of citing papers actually implementing the frameworks. This pattern was similar across the frameworks studied here. (see Figure 2, cf. the bar widths from left to right).
Self-citation	Factor with two levels (TRUE, FALSE)	Whether authors of the original paper were also authors of the citing article.	There should be a significant number of self-citations, but this should decline over-time as other people start using the framework. Authors of the framework would be more likely to specifically utilise the framework.	Confirmed (Figure 1) There were a large number of self-citations, (25, 22, 39%), but the relative proportion of self-citation is declining over time (generalised linear model with binomial errors, with year as an explanatory variable and whether a reference was a self-citation as the response using Chi-squared test of the change of variance: $p = 0.02$; $p < 0.01$; $p = 0.11$). Self-citations were more likely to implement the frameworks in detail than use them as "citation fluff" (analysis based on an ordered factor of the *extent of influence* versus *self-citation*: $F_{3,417} = 6.1$, $p < 0.01$; $F_{3,708} = 4.0$, $p < 0.01$; $F_{3,240} = 4.8$, $p < 0.01$).
Realm	Factor with six levels (freshwater, marine, terrestrial, other, multiple, NA)	The scope of the paper in terms of the environment. For laboratory-based studies, this is based on the taxa used.	A core rationale for the development of the frameworks was to make them generalisable across different environments (cf. Ojaveer et al. 2018). As such, the expectation was the frameworks are used consistently across realms.	Largely confirmed, but with notable biases (Figure 2). All three frameworks are cited by studies across different realms and taxa, though most were terrestrial studies and most on animals. However, it is notable that, when implemented in detail, the Pathway Classification was particularly used for comparisons across taxa and realms (i.e. multiple), while the Unified Framework tended to focus on particular realms (freshwater or terrestrial) and particular taxa (animals or plants) rather than for comparisons.
Taxon	Factor with five levels (animals, plants, other, multiple, NA)	The taxonomic scope of the organisms studied in the paper.	A core rationale for the development of the frameworks was to make them generalisable across different taxa. As such, the expectation was the frameworks are used consistently across taxa.	Largely confirmed, but with notable biases (Figure 2). See results for realms above. Studies on animals that cited EICAT tended to have implemented the framework more than other studies and there were no fungal or microbial studies as yet.
Number of citations	Integer	The number of times the framework is cited in the paper.	Papers that cite a framework multiple times would be more influenced by those frameworks.	Confirmed, but there is a large amount of variation. The extent of influence tended to increase with number of citations, but this factor on its own did not explain much of the variance in number of citations (31, 23, 30%); and some papers that specifically implemented the frameworks only cited the frameworks once, while other papers that used the frameworks as "citation fluff" still had numerous citations (maximums of 4, 9, 5). In conclusion, the amount of variance explained was not enough to suggest that the number of times the framework is cited in text is a reliable proxy for the extent of influence of the framework on a paper.

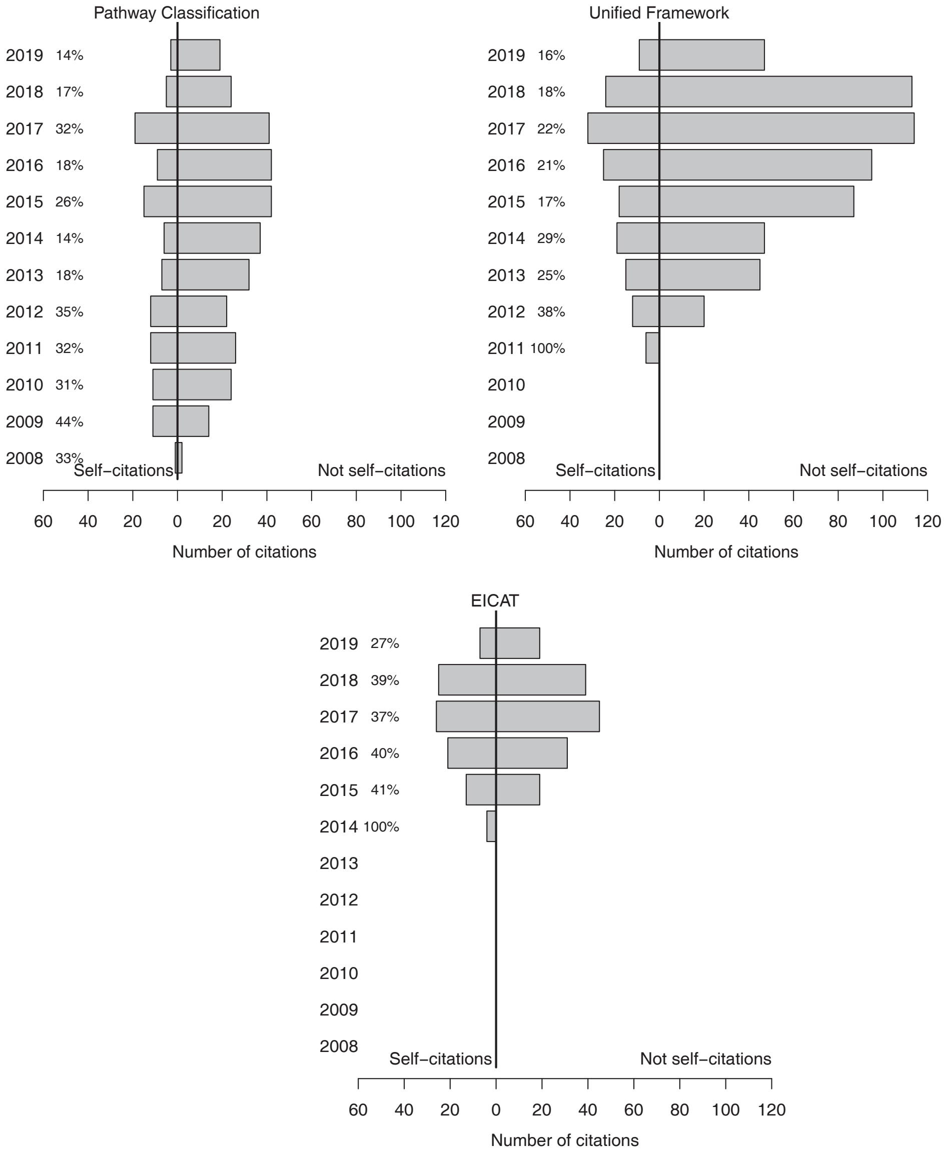

Figure 1. The number of times each framework paper was cited since publication until 1 July 2019. The frameworks are the Pathway Classification (Hulme et al. 2008), the Unified Framework (Blackburn et al. 2011), and EICAT (\Blackburn et al. 2014; Hawkins et al. 2015). Values from 2019 only include a portion of the year and even the number of citations by articles published in 2018 is a slight underestimate as it has also increased in the time since July 2019. Each framework has shown a general increase in citations per year since publication, and a decrease in the proportion of self-citations (Table 1).

Almost half of the citing papers only cited the frameworks to justify general comments about biological invasions. Importantly, however, the citing papers covered a wide range of realms and taxa, and the frameworks were implemented in detail in a similar wide range of studies (Figure 2).

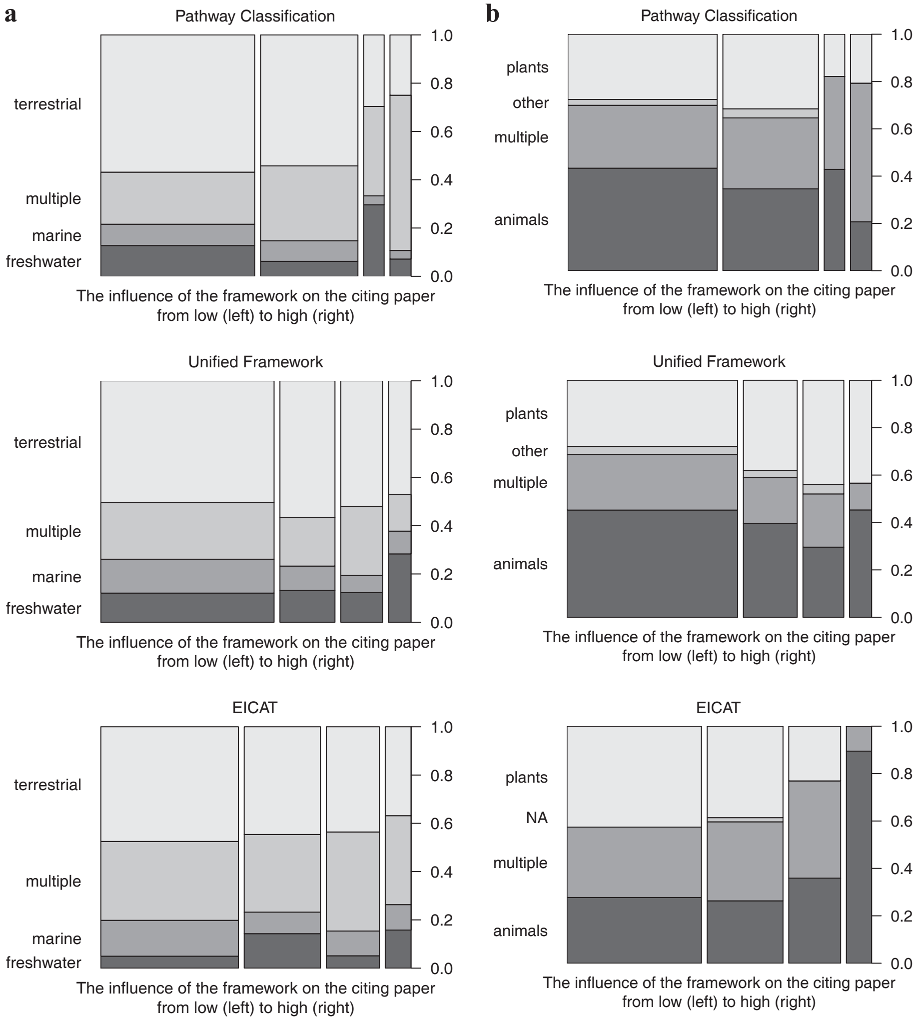

Figure 2. The extent to which the frameworks have influenced citing papers broken down by (**a**) environment and (**b**) taxonomic groups. The frameworks are the Pathway Classification (Hulme et al. 2008), the Unified Framework (Blackburn et al. 2011), and EICAT (Blackburn et al. 2014; Hawkins et al. 2015). The widths of the bars are proportional to the number of citations. The degree to which the framework was used in the citing paper increases from left to right on each figure [from general, to definition, to broad (application), to specific (application)]. The data are in Suppl. material 1, and the methodology used for scoring in Suppl. material 2.1.

The frameworks were cited by articles published in a wide range of journals (151, 223, and 108 journals, see Suppl. material 2.4). Unsurprisingly, the majority of these journals (70, 68, and 79%) have invasions as one of or their main subject area. Similarly, the majority of articles citing each framework (83, 85, and 87%) were explicitly on invasion science. All three frameworks have a global reach and have been cited by authors from around the world working on invasions in a similar global range of sites (Suppl.

material 2.5). However, when compared with the analysis of citation patterns in invasion biology (Pyšek et al. 2008), all the frameworks are more frequently cited by researchers based in Europe or South Africa and less often by those based in North America [49, 44, and 52% of all citations to the respective frameworks were from research led by European based authors vs. 22% of all studies in Pyšek et al. (2008); for South Africa: 9, 16, 18% vs. 2%; for North America: 20, 17, 12% vs. 50%; (the probability from a Chi-squared test was < 0.01 in all these cases)]. See Suppl. material 2.5 for the full details.

Survey of citing authors

We received responses from 84 people contacted (~ 9% of the 905 e-mails that did not bounce) from 20 countries (including 14 responses from North America, a slight over-representation). Responses were split fairly evenly across the frameworks (20 of 256; 51 of 589, and 13 of 113 respectively). The statement that respondents tended to most agree with was "This reference is authored by recognized authorities in the field" followed by "This is a classic reference in the field". The most common reason for citing the frameworks was that they are "classic citations" (Fig. 3, Shadish et al. 1995). Importantly, of the six statements that suggest a paper is viewed as a "classic citation", the two questions that were not widely supported (in fact more respondents disagreed than agreed) were "There have been substantial efforts to show that the framework is wrong" and "The framework has withstood many efforts to show that it is wrong". Therefore, while the papers are undoubtedly viewed and used as classic citations, there is a general feeling that the frameworks have not been adequately investigated. This was borne out by various suggestions of how the frameworks could (and in some cases have) been modified or where other frameworks are more appropriate (Suppl. material 2.6).

In terms of the link between the citing authors and the authors of the frameworks, over half have spoken to one of the authors (64, 51, 95%) and a substantial number of these consider one of the authors a personal friend (35, 13, 41%). While the respondents often recommended the citation to others during review (40, 27, 46%), it was not suggested to them often (5, 6, 0%). Of course, the respondents are a small section of the invasion science community who have actively cited the framework and who were willing to respond to a survey concerning the framework.

Influence on policy and management

All three frameworks seem to have had some impact on policy and management (Suppl. material 2.6 and 2.7; Box 1). The Pathway Classification framework has arguably had the most impact. The CBD's Aichi Biodiversity Target 9 specifies (amongst other things) the need to identify and prioritise pathways by 2020 and a modification of the pathway framework was proposed for use by the CBD itself (Scalera et al. 2016). Other examples of its adoption include the guidelines for invasive species planning

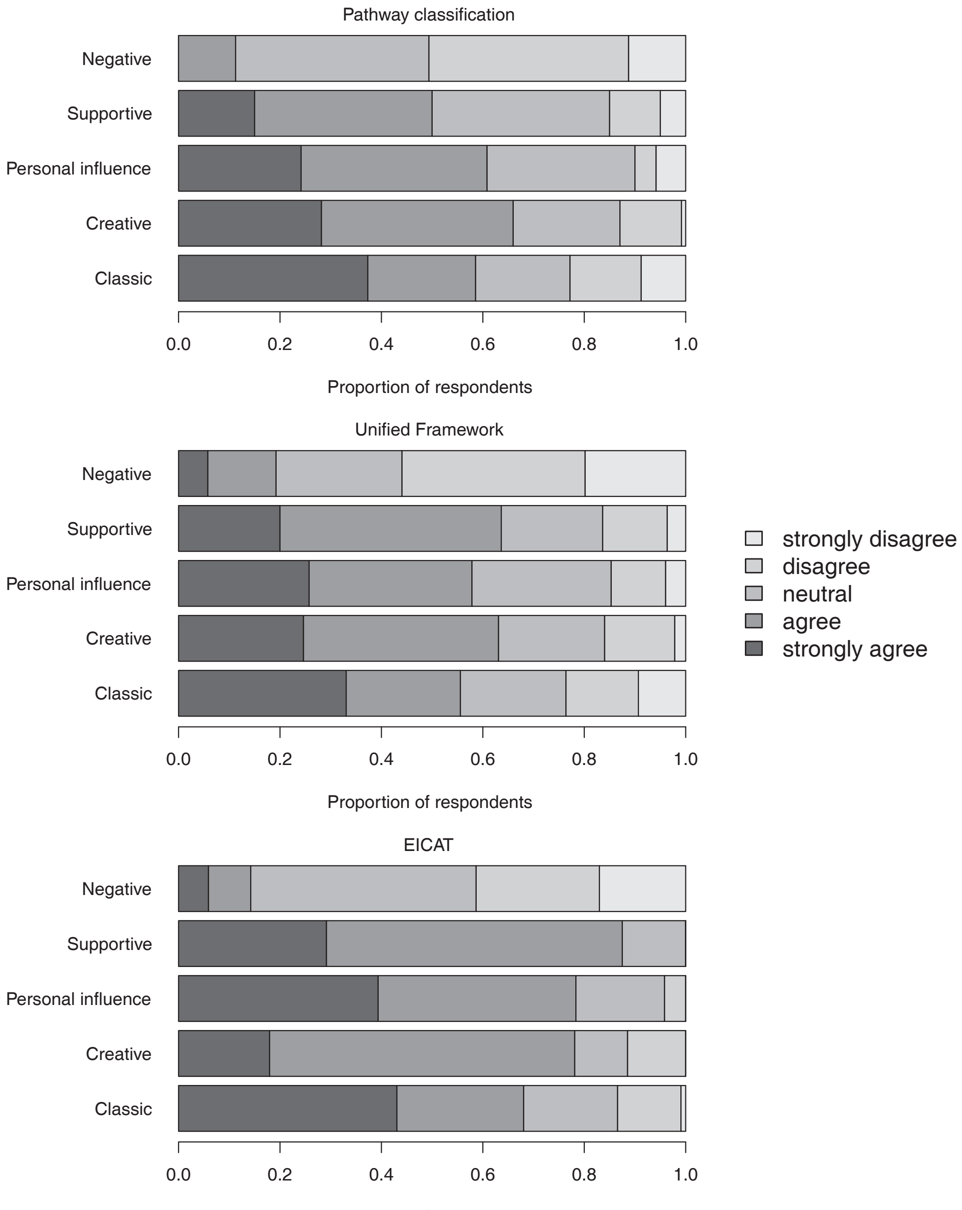

Figure 3. Reasons for citing the frameworks based on the response to a questionnaire sent to corresponding authors. The frameworks are the Pathway Classification (Hulme et al. 2008), the Unified Framework (Blackburn et al. 2011), and EICAT (Blackburn et al. 2014; Hawkins et al. 2015). The categories Negative, Supportive, Personal Influence, Creative, and Classic are based on Shadish et al. (1995). See Suppl. material 2.2 for a copy of the questionnaire and Suppl. material 2.6 for the full results and how the questions map on to different categories.

and management on islands published by IUCN and the European Union Regulation on the prevention and management of the introduction and spread of invasive alien species. More recently, EICAT has been adopted as an IUCN standard (IUCN 2020) and is anticipated to play an important role in future biodiversity targets and as part of an indicator to track impact (Essl et al. 2020; GEO BON 2015; Latombe et al. 2017). By contrast, we found little evidence that the Unified Framework (the most cited framework investigated here) has been used in policy and management. This could in part be due to differences in how the phenomenon of biological invasions is defined (Wilson et al. 2016). Policy-orientated definitions of invasive organisms often include the impact of the organism, while the biogeographic definition also represented in the Unified Framework (Richardson et al. 2000) seems to be more common in science.

Importantly, once a scientific framework has been widely accepted by an international body like the CBD or the IUCN, it is very likely that the original references are no longer cited. Therefore, caution must be observed in interpreting the policy influence of scientific documents.

Discussion

We found that the invasion frameworks assessed here are widely cited by studies focussing on different realms and taxa, and from many different parts of the world. While many citations might be viewed as frivolous ("citation fluff"), there is a substantial number where the frameworks have been implemented in detail. There are different possible explanations for these trends. Invasion science might be coalescing temporarily; it might be settling down to adopt standard and widely-agreed practices; a particular 'school' of invasion science that uses particular frameworks might be emerging; or there might always be a suite of papers that are core papers for citing, but that do not actually influence the direction of the field. We discuss some of these issues here.

Frameworks are temporary, concepts are permanent, but where ideas come from can have long-lasting effects

The Unified Framework and EICAT owe substantial intellectual debts to previous papers and frameworks. Indeed, some of the original frameworks are arguably still more influential. The Unified Framework is based partly on a framework for plants outlined by Richardson et al. (2000), and this earlier paper still tends to be more widely cited. Richardson et al. (2000) had a huge effect on the study of biological invasions. By creating standards that were widely adopted by the research community, data on biological invasions have been increasingly based on a common set of criteria, and are therefore directly comparable. This has facilitated a wide range of comparative analyses [e.g., the Global Naturalized Alien Flora (GloNAF) project (Pyšek et al. 2017)].

Frameworks also evolve and develop over time and in some cases are superseded. The Pathway Classification has been expanded and subcategories developed as part of its proposed uptake by the CBD (Harrower et al. 2017; Scalera et al. 2016). It is noticeable that some more recent journal articles and policy documents implement the CBD pathway classification scheme without citing the original paper on which it is based. This might be quite typical, i.e., once a framework is adopted into a policy or adapted into a guideline, there is a step-change in the impact it has, but conversely, the original paper might no longer be cited. Papers applying EICAT often use it in combination with the Generic Impact Scoring System (GISS; Nentwig et al. 2016; Nentwig et al. 2010) upon which EICAT is based or they use a modification using aspects of both schemes. GISS has probably been more often applied to date and to a wider taxonomic range than EICAT (e.g., Kumschick et al. 2015), but due to EICAT's adoption as an IUCN Standard, EICAT is rapidly gaining momentum.

Frameworks often need to be adapted in light of practical experience. For example, several adaptations to the Unified Framework have been proposed based on experiences of implementing it in Europe (Groom et al. 2019), Hawaii (Brock and Daehler 2020), and South Africa (Wilson et al. 2018). Similarly, Pergl et al. (2020) and Faulkner et al. (2020) provide proposals to refine the CBD pathway classification scheme based on applying it in different contexts, and Volery et al. (2020) document changes made to EICAT after stakeholder consultation. All three frameworks have, to different extents, been incorporated in developing biodiversity data standards, and this will provide a more formalised process for revising them.

Importantly, however, our results show that the extent of influence of the frameworks is still somewhat affected by how they were originally developed. There is, unsurprisingly, a high level of self-citations, and this likely explains part of the apparent European and South African bias in uptake (cf. Fig. 1 and Suppl. material 2.5). The Pathway Classification was a direct product of the European Union Funded ALARM project (Settele et al. 2005); the idea to develop the Unified Framework arose at a workshop in Switzerland and was further elaborated at a meeting in South Africa; and EICAT resulted from a workshop in Germany. Moreover, of the 33 original authors of the frameworks, 26 are based in Europe, three in South Africa, and one each in Australia, Canada, New Zealand, and the USA. In this context, the global influence of the frameworks has been impressive, but it will be important for the utility of the frameworks to be assessed in more depth and in different contexts. For example, introduction pathways have changed over time (Faulkner et al. 2016; Hulme 2009), and the importance of different pathways varies across the world. Faulkner et al. (2020) highlight one such case, where the trade in traditional medicines is a potentially important introduction pathway in Africa, but is not considered explicitly in the current (arguably Eurocentric) Pathway Classification. Similarly, the Unified Framework originated from combing zoological and botanical frameworks, and there are several practical issues applying both it and the Pathway Classification to fungi and microbes (Paap et al. 2020).

Nonetheless we believe that our results provide some indication that invasion science is beginning to coalesce around systematic schema for classification and understanding that are applicable across taxa and realms.

Comparisons with other frameworks?

Given the lack of points of comparison, it is difficult to gauge whether the results seen here are surprising or not. Ideally, we would have looked at the uptake of other important frameworks in invasion science (including historical and more contemporary schemes) and compared with highly-cited framework papers from related disciplines. Unfortunately, the methodology we developed was time-consuming. We found no reasonable proxy for a manual analysis of the extent of influence of the frameworks on the citing papers. There was a broad correlation between our manual scoring of the extent of influence and the number of times a framework was cited, but there were many exceptions (Table 1). Similarly, simply noting whether a citation was in the methods, discussion, or introduction provided some indication of whether the frameworks were used, but not enough to reliably predict that the frameworks were actually implemented (results not shown, but data presented in Suppl. material 1). We concluded that conducting such a citation analysis requires careful examination of at least the sentences that include the citation, and often an evaluation of the whole manuscript. Machine-learning techniques might offer a solution to this issue in future.

We did, however, identify some comparisons that would be particularly interesting and some important research gaps. As mentioned previously, most of the frameworks presented here had progenitors [for example, the Unified Framework explicitly built upon Williamson and Fitter (1996) and Richardson et al. (2000)], an explicit evaluation of how these have been used over time would provide a benchmark against which our results could be assessed. Similarly, while the frameworks chosen reflect pathways, species, and impacts, it would be important to consider frameworks centred around sites of invasion or the effectiveness of interventions (McGeoch et al. 2016; Wilson et al. 2018), or to consider how invasion hypotheses are cited (Catford et al. 2009; Jeschke and Heger 2018). Finally, it might be instructive to track recent frameworks [e.g., SEICAT, the socio-economic impact classification of alien taxa scheme (Bacher et al. 2018), although there has not been much time for uptake].

Insights into citation practices

Our research did not primarily set out to evaluate citation practices, but several insights were apparent. Many of the citations were what we considered frivolous (and informally dubbed “citation fluff”). The introduction of most papers starts with a generic catch-all statement about invasions, and the frameworks were often used to support these, often inappropriately [e.g., citing the Unified Framework as evidence that invasions have impact, or EICAT as a risk assessment protocol (Kumschick et al. 2020-a)]. Arguably “citation fluff” provides an indication of influence, i.e., the frameworks are not directly and explicitly used, but play a role in shaping the overall mental model of the processes at play. However, there were many errors in the way in which the frameworks are cited (see Suppl. material 2.3). Should there be a greater onus on authors, reviewers, and editors to purge “citation fluff” or at least to ensure such references really support the general statements made?

The fact that 20–40% of all citations are self-citations is not necessarily indicative of nepotistic or insular research practices (Seeber et al. 2019). The frameworks were the products of highly productive scientists with the intention of producing seminal papers in a research field in which they were amongst the research leaders. The rapid uptake and declining proportion of self-citations are arguably, healthy signs, as is the geographic spread of the citations. This is borne out by the respondents to the survey where the authors were considered well respected, and the framework papers were, by and large, considered classic papers in the field.

However, the papers analysed and the people surveyed were very biased. The results are, therefore, consistent with the notion of a distinct school of thought amongst certain (particularly European and South African) invasion scientists for whom these frameworks are valuable (cf. the MAFIA framework of Pyšek et al. 2020). A study of researchers who did not cite or use these frameworks despite the framework being relevant to (or even designed to assist) their research would do much to further our understanding of the limitations of the frameworks. As an analogue, it is difficult to understand why some invasions are successful if we lack data on failed invasions (Zenni and Nuñez 2013).

A suggestion to journals – avoid numbered citations

Finally, as a side note, in our experience papers with numeric citations are harder to read, comment on as editors and reviewers, and make analyses, like the one here, much more cumbersome. It is not clear to us why online-only publishers (e.g. the Public Library of Science) persist with this format (cf. https://svpow.com/2011/01/07/an-open-letter-to-plos-one-a-pox-on-your-numbered-references/).

Conclusion

The selected frameworks are influential and widely cited. They are being used to provide information about explicit efforts at monitoring and reporting biological invasions and the development of internationally-agreed data standards. Nonetheless, they are not yet widely implemented as they were originally formulated. We believe that our ability to understand and manage biological invasions will improve as we move increasingly towards agreed standards in the field (Wilson et al. 2020). Invasion frameworks will need to both provide information about such change and be flexible, so they can be modified in the light of the experience and needs of users.

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Supplementary material 1

Data used in a citation analysis of frameworks in invasion science

Authors: John R. U. Wilson, Arunava Datta, Heidi Hirsch, Jan-Hendrik Keet, Tumeka Mbobo, Khensani V. Nkuna, Mlungele M. Nsikani, Petr Pyšek, David M. Richardson, Tsungai A. Zengeya, Sabrina Kumschick

Data type: Excel spreadsheet

Explanation note: Information on the papers that cited the three frameworks under investigation here (see Suppl. Material 2 for details).

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Supplementary material 2

Supplementary material to a citation analysis of frameworks in invasion science

Authors: John R. U. Wilson, Arunava Datta, Heidi Hirsch, Jan-Hendrik Keet, Tumeka Mbobo, Khensani V. Nkuna, Mlungele M. Nsikani, Petr Pyšek, David M. Richardson, Tsungai A. Zengeya, Sabrina Kumschick

Data type: explanatory text and additional analyses

Explanation note: **2.1** The protocol used to score publications that had cited the selected invasion framework papers (including **Table S2.1.** An ordinal categorical four point-scale used to score the extent to which the papers were directly or indirectly influenced by or applied the invasion frameworks). **2.2** The questionnaire used to evaluate the opinion of invasion scientists as to how fundamental the frameworks have been to invasion science, policy, and management. **2.3** Citations to the frameworks as at 1 July 2019 showing frequency with which papers shared citations. **2.4** The journals in which papers citing the invasions framework were published, and number of citing papers published in each. **2.5** The location of the corresponding authors when they completed their study (i.e. their primary address) of papers that cited each framework compared to the number of studies reported from different geographical regions by Pyšek et al. (2008). **2.6** The results of the survey of corresponding authors of papers who have cited one of the papers that outline the Pathway Classification framework; the Unified Framework or EICAT. **2.7** Examples of documents showing the influence of the selected framework papers beyond scientific audience.

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RESEARCH ARTICLE

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A priority-setting scheme for the management of invasive non-native species in protected areas

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Abstract

Invasion by non-native species is one of the major threats to the conservation of biodiversity and to the provision of ecosystem services by protected areas. Invasive species often co-occur in protected areas, represented by sparse, isolated individuals or populations in different stages in the process of invasion. Species invasiveness, habitat invasibility and impact also differ between ecosystems, so the risk of invasion varies. Besides, prioritization is required due to constraints on time, financial and other resources. Priority-setting is therefore key to help protected area managers invest efforts on biological invasions that offer the best chances of producing large-scale positive results at the lowest cost possible. A priority-setting scheme for the control of invasive non-native species in natural areas is presented in this paper. The scheme, based on field observations of species occurrences, was applied to the Itatiaia National Park (Brazil). Priorities are calculated from a combination of three criteria attributed to each occurrence: species risk of invasion considering local ecosystems, invasion stage, and species frequency. Data collected in the field in the Itatiaia National Park were used to calculate priorities for 50 non-native species (six animals and 44 plants) in four locations in the Park. The highest priorities were attributed to species of high risk in an early stage of invasion occurring in one site, whereas a few widespread species of low risk were given lower priority. The scheme has proven functional for setting priorities for the control of non-native species in the Itatiaia National Park and in many other protected areas in Brazil.

Keywords
Invasion risk, invasive alien species, invasive species control, invasive species management, Itatiaia National Park, prioritization framework, priority-setting scheme, protected areas

Introduction

Invasion by non-native species is one of the major threats to the conservation of biodiversity and to the provision of ecosystem services by protected areas (Foxcroft et al. 2013; Hulme 2018; IPBES 2019). Although the quantification of impacts of invasive species focused on protected areas is still poor in most places (Hulme et al. 2014; Hulme 2018), studies have reported impacts ranging from predation and displacement of native species to changes in community structure and composition, as well as on disturbance regimes and ecosystem functioning (Turner et al. 1997; Loope et al. 2013; Ballari et al. 2015; Lessa et al. 2016; Schmidt et al. 2020).

The importance of protected areas in providing refugia for native species might be even more prominent under climate change (Gallardo et al. 2017). Thus, the control and eradication of invasive species in protected areas must be incorporated as a fundamental component of protected area management. In fact, international agreements and national regulations acknowledge the importance of this issue in different countries. For instance, targets are established in international agreements such as the Convention on Biological Diversity. National regulations, such as the Law 9985/2000 in Brazil, prohibit the introduction of non-native species in certain protected areas and define protected areas as priorities for invasive species control (Dechoum et al. 2018).

Invasive species often co-occur in protected areas, represented by sparse, isolated individuals or populations in different stages in the process of invasion (McGeoch and Latombe 2016). Species invasiveness, habitat invasibility and impact also differ between ecosystems, so the risk of invasion varies. At the same time, the opportunities to effectively eradicate or control invasive species are limited due to constraints on time, financial and other resources, lost opportunity costs and conflicting priorities (Robertson et al. 2003; Cheney et al. 2018). Therefore, priority-setting is key to help natural area managers invest efforts on biological invasions that offer the best chances of producing large scale positive results at the lowest cost possible (Gallardo and Aldridge 2013). A prioritization scheme is any structured system that produces a ranking or ordered set of risk categories (McGeoch et al. 2016). An effective priority-setting system should produce a list of priorities that enables managers to cover more area in less time to manage the best eradication or effective control opportunities first. This has been shown to be more efficient as a management strategy because small invasions have a higher potential to spread than large invasions that have been established longer (Moody and Mack 1988; Emry et al. 2011). This approach is also preventative, especially when addressing populations that are somehow contained, and considers the relevance of early detection and rapid response strategies (National Research Council 2002; Reaser et al. 2020) to avoid future impacts. Individuals that are isolated, especially before reaching reproductive age, are therefore the highest priority especially in relation to those requiring long-term control (Moody and Mack 1988; Hoffmann et al. 2016). This approach also tends to translate into best cost-efficiency.

Priority-setting requires an appropriate evidence base for the definition of control and/or eradication targets (Gallardo and Aldridge 2013). In protected areas, a local assessment of invasive non-native species occurrences and invasion stage is essential for establishing management priorities, considering a preventative approach for the control of individuals or populations, and for actions aimed at eradication. Several prioritization methods have been used in other contexts to date. For example, Robertson et al. (2003) developed a scheme that used a multi-assessor approach for questions that resemble risk assessments. This scheme was used to define priorities based on species. Nel et al. (2004) derived lists of priority species for South Africa using available quantitative data on species distribution and expert knowledge. Later schemes, such as Forsyth et al. (2012) prioritized species first, then combined spatial data with stakeholder input to identify priority catchments for control in South Africa. Cheney et al. (2018) showed that systematic surveys are the best option to generate reliable data for priority-setting schemes, although the cost may be high. Available schemes such as these were however considered too complex for application by managers or field practitioners, too costly, or too time-consuming. In addition, while the majority of existing schemes focus solely on species, the scheme presented here focuses on species, populations and sites with the aim of identifying the best control opportunities of high-risk species, as in the reasoning of early detection and rapid response, and listing the remaining invasions in order of priority.

In this paper, we describe a priority-setting framework for the control of invasive non-native species in natural areas that essentially includes the knowledge of managers. This priority-setting scheme was initially developed in 2007 by the Horus Institute for Environmental Conservation and Development for application in protected areas in the state of Espírito Santo, in southeastern Brazil, and has never been published in the scientific literature. Priorities were defined for occurrences of invasive species in order to optimize control work and the use of financial resources. The scheme has since been used over the last 13 years to develop invasive plant species management plans for approximately 20 protected areas in Brazil. Managers receive training during the development of the plans and technical support to begin practical management. The resulting prioritization is adjusted for each protected area based on the knowledge of managers on local conditions, accessibility, costs, and the existence of susceptible or sensitive sites where control is urgent. A case study applied in the Itatiaia National Park (Brazil) using systematic sampling techniques for plants and mammals is included in this paper.

Methods

Priority-setting

The scheme used to define priorities for the non-native species observed in the Itatiaia National Park was applied to several protected areas over the years and a user-guide is available from the Horus Institute (Instituto Hórus 2008). The scheme is based on field observations of occurrences registered as individuals or populations of non-native invasive species in the area of interest. Priorities are calculated from a combination of three criteria attributed to each occurrence: species risk of invasion (R), invasion stage (S), and species frequency for each occurrence (F) (Fig. 1).

Risk of invasion by a species (R) is defined considering the non-native species' propensity to invade habitats in the area of interest, and can be (1) high, (2) moderate or (3) low. Species ranked as high risk are those with the largest potential to invade, and therefore the greatest potential for future impact. Evaluations of impact are not required for application of this scheme because this would create a level of complexity that would mostly hinder its practical use. The three levels of risk were defined as: (1) high – species recognized as invasive in many areas beyond the area of interest that tend to repeat the history of invasion locally due to environmental or climatic similarities; (2) moderate – species with a lower level of invasiveness which also tend to impact biodiversity at the local level and have a known history of invasion elsewhere, but less expressive than high-risk species, and; (3) low – species with scarce or no history of invasion that most often occur in degraded or agricultural areas and seldom become dominant. For our case study, the level of risk was defined by verifying whether the species was listed in the Database of Invasive Non-Native Species in Brazil managed by the Horus Institute (http://bd.institutohorus.org.br), which only includes non-native species that are invasive in natural ecosystems in Brazil. If the species was not listed, the Global Invasive Species Database (www.issg.org/database) and the CABI Invasive Species Compendium (www.cabi.org/isc) were consulted. The history of invasion across the world and records of impacts on natural areas were used to define the level of risk in the case study. Complementarily, the expert knowledge of the assessor, and especially of the protected area managers, was considered to ponder decisions on invasion risk.

The invasion stage (S) at each species occurrence is defined as: (0) contained, when individuals are under controlled conditions (e.g. greenhouse, pond or in cultivation), therefore not in direct contact with the natural environment; (1) casual, apparently not reproducing locally; (2) naturalized, when reproducing locally; or (3) invasive, involving reproduction and spread (sensu Blackburn et al. 2011).

Frequency (F) represents the spatial distribution of the species in each point of occurrence. It is registered as occurring in one single site (1), a few sites (2) or widely distributed in the sector or area considered (3). Distribution has to be considered in accordance with the scale of application. As this method can be applied at very different scales, attempts to define distribution in hectares or other units of measurement have not proven useful.

Combining the three criteria, the formula for calculating the level of priority is:

$$Pr = (R + S + F) - 2, \text{ where:}$$

Pr = level of priority,
R = species risk of invasion (1 = high, 2 = moderate, 3 = low),
S = invasion stage (0 = contained, 1 = casual, 2 = naturalized, 3 = invasive),
F = frequency (1 = one site, 2 = a few sites, 3 = widely distributed).

The highest priorities are attributed to species of high risk in early stages of invasion (contained or casual) that occur in one site (Fig. 1). The subtraction was included so that the highest priorities result as level 1. In the case of species contained in a laboratory, pond or in cultivation, the highest priority will result in zero (contained high-risk species in one site).

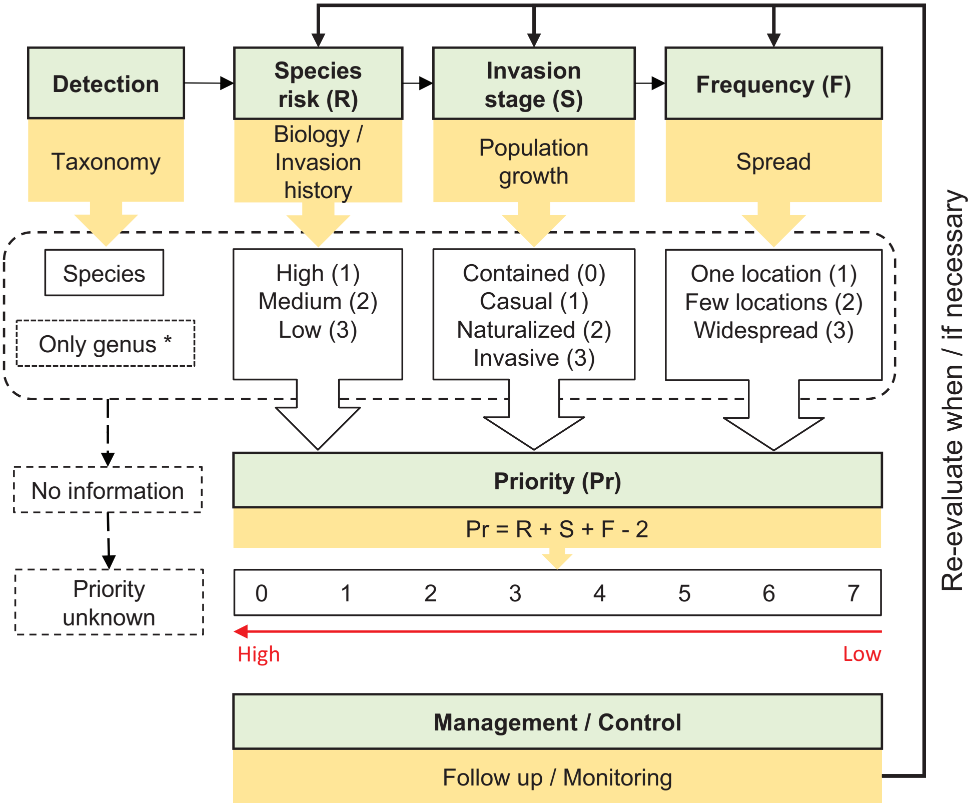

Figure 1. Conceptual framework of the priority-setting scheme for invasive non-native species control in protected areas. Priorities are determined for each species at each location in the protected area. (*) When an organism is not identified at the species-level, but the genus is known, the highest level of risk for a known species in the genus should be applied.

If the information for any of the criteria is not available, the priority cannot be calculated. This tends to happen if the species cannot be identified, as the level of risk would be difficult to estimate. Species from genera with several known invasive species, often difficult to distinguish at the species level, such as pines (*Pinus* spp.), eucalyptus (*Eucalyptus* spp. or *Corymbia* spp.), privet (*Ligustrum* spp.) or brachiaria (*Urochloa* spp.), none of which are native in Brazil, would have been included at the genus level. In this case, the precautionary principle is used to eliminate non-native species even if the precise identity is not known, and the highest level of risk for a known species in the genus should be applied.

Once species and populations have been scored, more nuanced factors (e.g. sensitivity of the area invaded, presence of threatened or endemic native species, invasiveness of the species in the protected area, and operational logistics) can be used to further refine priorities in close collaboration with local managers. Further details are provided in the discussion.

Study area

To test the prioritization scheme and determine its applicability to protected areas, the scheme was applied to the non-native flora and fauna of the Itatiaia National Park, Brazil (22°22'31"S, 44°39'44"W). The Itatiaia NP covers 28,084 ha and is located in the municipalities of Itamonte and Bocaina de Minas in Minas Gerais state, and Itatiaia and Resende in Rio de Janeiro state. The Park protects part of the Serra da Mantiqueira in the Atlantic Forest hotspot (Myers et al. 2000). According to the Köppen classification, there are two types of climate in the Itatiaia NP region: Cwb (temperate climate with dry winter and warm summer) and Cwa (temperate climate with dry winter and hot summer) (Arnfield 2019). The altitude ranges from 540 m to 2,791 m above sea level, with mean temperatures between 13 °C and 21 °C, and annual precipitation around 2500 mm (ICMBio 2014).

As in other protected areas classified as strict protection in Brazil, private properties whose landowners have not been compensated by the federal government remain within the Park limits. These properties include summer homes, hotels and hostels (mainly in the lowlands) as well as small rural properties (in the highlands) where the main economic activity is cattle farming (ICMBio 2014).

Data collection

The study area was subdivided in sectors identified by the Park staff: Serra Negra, Santa Clara, highland and lowland. Within each sector, sampling points where non-native species were present were considered an occurrence, while sampling efforts were conducted to determine invasion stage (S) and frequency (F) for each occurrence.

Mammals

To measure the presence and frequency of non-native mammals in the Park, camera traps were installed in 25 sampling points: four in Serra Negra, two in Santa Clara, nine in the highland and ten in the lowland (Fig. 2). Each sampling point was set at a minimum distance of 500 m from the next to ensure independence between samples. Three data collecting efforts of about three months each were conducted between September 2018 and July 2019. Cameras were installed by trails and inside forests. One camera-trap (Bushnell, Digital Hunting Camera, and Trail Camera) was placed in each sampling area, tied to a tree at approximately 30 cm above the ground. The cameras remained active day and night and were configured to take three pictures every 30 seconds once the sensor was triggered. In order to avoid data repetition, we computed the photographs discarding consecutive shots of the same individuals by the same camera at intervals shorter than one hour (Srbek-Araujo et al. 2012). The photographic records were analyzed to define the invasion stage for each mammal occurrence. Species were considered contained if on a leash or inside a cage or behind a fence in private properties (invasion stage = 0); casual, if only adults with no offspring were registered (1); naturalized, if offspring was present in only one photograph (2); and invasive, when offspring was registered in more than one photograph or by more than one camera (3).

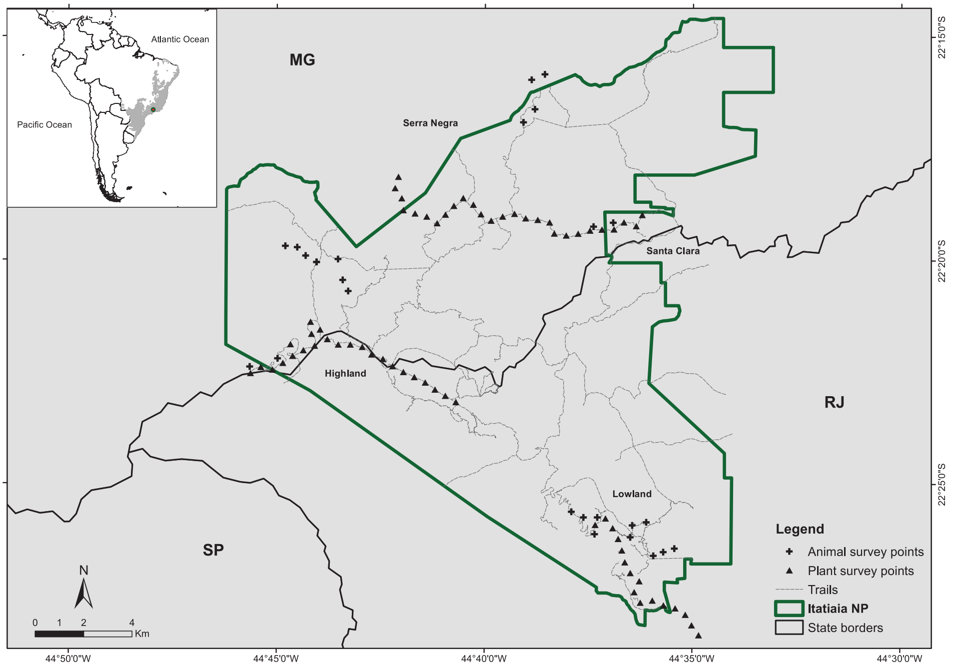

Figure 2. Map of the Itatiaia National Park with existing trails and sampling areas used for the survey of non-native mammals (crosses) and plants (triangles).

Plants

Non-native plants were surveyed in the four sectors of the Itatiaia NP along two roads and one trail, totaling *ca*. 25 km of linear area (Fig. 2). The road starting in the city of Itatiaia and continuing across the lowland for about 8.5 km to the Park headquarters was used to survey the lowland sector. The road accessible from Garganta do Registro continuing for about 25 km to the Rebouças shelter was used to survey the highland sector. The trail crosses two sectors of the park. Half of the trail is located on the northeastern face in the sector called Serra Negra. The other half of the trail is located on the northwestern face in the sector, Santa Clara. The ridgeline separates the two faces and, consequently, the two sectors.

Along the selected roads and trail, we marked sampling points every 500 m in a straight line. Each sampling point was comprised of three subplots for herbaceous plants and one transect for trees. The three subplots of 1 × 10 m each were installed parallel to the road or trail, the first by the edge of the road or trail, the second at a five-meter distance, and the third at a ten-meter distance. One 100 m transect parallel to the road or trail was set at each sampling point. We walked along the transect performing a visual search for non-native trees on only one side of the road or trail. If a non-native tree species was observed, we walked towards the plant to check for other plants of the same species or the presence of a population. If a population was present, offspring were counted and registered. In total, 24, 16, 14 and 13 sampling points were established in the highland, lowland, Serra Negra and Santa Clara, respectively. Additionally, other non-native species observed in the Itatiaia NP, but not registered in the plots or transects, were listed separately. Information on non-native species obtained from a literature review using the combination "alien" or "exotic" or "non-native" species and "Itatiaia National Park" on Google Scholar, from the Park management plan (ICMBio 2014), and from official newsletters available from the Park website (http://www.icmbio.gov.br/parnaitatiaia/) was also included.

The plant samples collected were identified at the Bioinvasion and Conservation Laboratory and at the ESAL Herbarium of the Federal University of Lavras. Species identifications were confirmed by the RB Herbarium of the Rio de Janeiro Botanical Garden. We also consulted the scientific literature to ensure that the species identified were not native in the Itatiaia NP. We classified species invasion stage in each sector using the definitions proposed by Richardson et al. (2000) and Blackburn et al. (2011). Plant populations of herbaceous species occurring in a few points on the edge of the road or trail or in cultivation, not spreading into native vegetation, were classified as casual (invasion stage =1); plant populations with self-sustaining populations of individuals occurring in the first and second subplots across several points were considered naturalized (2); and plant populations present in all three subplots in numerous sampling points were considered invasive (3). Trees occurring in a few points on the edge of the road or trail or in cultivation, not spreading into native vegetation, were classified as casual (invasion stage =1); plant populations with self-sustaining populations of individuals occurring only in the surroundings of adult plants with no detectable signs of spread were considered naturalized (2); and tree populations spreading farther than 100 m from adult plants in numerous sampling points were considered invasive (3).

Results

Four non-native mammal species were recorded in the Itatiaia NP after a total of 298 camera trap*day: domestic cattle (*Bos taurus*, n = 97), wild boar (*Sus scrofa*, n = 72), domestic dog (*Canis lupus familiaris*, n = 10), and European hare (*Lepus europaeus*, n = 1). Domestic cattle and wild boar were observed in six of the 15 sampling areas, domestic dogs in four, and European hare in one. Three species were observed in Serra Negra (*C. lupus familiaris*, *S. scrofa*, and *L. europaeus*) and three in the highland (*C. lupus familiaris*, *S. scrofa*, and *B. taurus*). No records of non-native mammals were obtained in Santa Clara or in the lowland. Invasion stage (S) was determined as casual for *B. taurus* and *C. lupus familiaris* in the highland, and for *C. lupus familiaris* and *L. europaeus* in Serra Negra. The invasion stage of *Sus scrofa* was determined as invasive in the highland and in Serra Negra. In terms of frequency, *L. europaeus* was observed in one point in Serra Negra, *C. lupus familiaris* in a few points in the highland and in Serra Negra, *S. scrofa* in many points in the highland and in Serra Negra, and *B. taurus* in many points in the highland. Based on the history of invasion of these species and considering the ecosystems in the Park, risk was rated low for *B. taurus*, moderate for *L. europaeus* and high for *C. lupus familiaris* and *S. scrofa*. Priorities were calculated based on risk, abundance, and spread, resulting in assignment of level 2 for *C. lupus familiaris* in both Serra Negra and the highland, level 2 for *L. europaeus* in Serra Negra and level 5 for *B. taurus* in the highland and *S. scrofa* in both Serra Negra and the highland (Table 1). The invasion risk factor can be considered as the most important factor to separate species/populations that have the same priority score. As such, because *B. taurus* does not have a significant history of invasion, the final adjustment on the scheme would place it as the last population to be managed unless other evidence indicated the need for urgent action.

A total of 36 non-native plant species were registered at the sampling points along roads and trails (Table 2). Of the 12 plant species in the highland, three species occurred only in casual populations, one in naturalized populations, and eight in invasive populations. In the lowland we registered 25 non-native species: 14 species in only casual populations, seven naturalized, and four invasive. In Santa Clara we registered

Table 1. List of non-native mammal species registered in the Itatiaia National Park, Brazil, and priority levels for management based on species invasion risk: 1 – high, 2 – moderate, 3 – low; Invasion stage: 1 – casual, 2 – naturalized, 3 – invasive; and frequency of occurrence: 1 – one location; 2 – few locations, 3 – widespread (Fig. 1). Priorities vary from 1 (highest priority) to 5 (lowest priority). The table is sorted by priority level, then invasion risk, then by family and Latin name except when species considered more relevant for control are shifted up within the same level of priority and risk based on expert knowledge.

Order	Family	Latin name	Area of occurrence	Invasion risk	Invasion stage	Frequency	Priority level
Carnivora	Canidae	*Canis lupus*	Highland	1	1	2	2
Carnivora	Canidae	*Canis lupus*	Serra Negra	1	1	2	2
Rodentia	Leporidae	*Lepus europaeus*	Serra Negra	2	1	1	2
Artiodactyla	Suidae	*Sus scrofa*	Highland	1	3	3	5
Artiodactyla	Suidae	*Sus scrofa*	Serra Negra	1	3	3	5
Artiodactyla	Bovidae	*Bos taurus*	Highland	3	1	3	5

Table 2. List of plant non-native species registered in the Itatiaia National Park, Brazil. Priority levels for management based on species invasion risk: 1 – high, 2 – moderate, 3 – low; Invasion stage: 1 – casual, 2 – naturalized, 3 – invasive; and frequency of occurrence: 1 – one location; 2 – few locations, 3 – widespread (Fig. 1). Priorities vary from 1 (highest priority) to 7 (lowest priority). The table is sorted by priority level, then invasion risk, then by family and Latin name except when species considered more relevant for control are shifted up within the same level of priority and risk based on expert knowledge.

Family	Latin name	Area of occurrence	Invasion risk	Invasion stage	Frequency	Priority level
Araceae	*Epipremnum aureum*	Santa Clara	1	1	1	1
Balsaminaceae	*Impatiens walleriana*	Lowland	1	1	1	1
Poaceae	*Megathyrsus maximus*	Lowland	1	1	1	1
Poaceae	*Cynodon dactylon*	Lowland	1	1	1	1
Cupressaceae	*Cupressus lusitanica*	Highland	1	2	1	2
Asparagaceae	*Dracaena fragans*	Lowland	2	1	1	2
Iridaceae	*Crocosmia crocosmiiflora*	Highland	2	1	1	2
Poaceae	*Eleusine indica*	Lowland	2	1	1	2
Poaceae	*Eragrostis plana*	Lowland	1	2	2	3
Musaceae	*Musa rosacea*	Lowland	2	2	1	3
Poaceae	*Poa annua*	Lowland	2	1	2	3
Rutaceae	*Citrus × limon*	Santa Clara	3	1	1	3
Asteraceae	*Bidens pilosa*	Santa Clara	3	1	1	3
Asteraceae	*Bidens pilosa*	Serra Negra	3	1	1	3
Asteraceae	*Cosmos sulphureus*	Lowland	3	1	1	3
Asteraceae	*Youngia japonica*	Lowland	3	1	1	3
Cupressaceae	*Cunninghamia lanceolata*	Highland	3	1	1	3
Fagaceae	*Quercus robur*	Highland	3	1	1	3
Hydrangeaceae	*Hydrangea macrophylla*	Lowland	3	1	1	3
Moraceae	*Ficus auriculata*	Lowland	3	1	1	3
Zingiberaceae	*Curcuma longa*	Lowland	3	1	1	3
Zingiberaceae	*Hedychium coronarium*	Lowland	1	3	2	4
Rosaceae	*Rubus rosifolius*	Santa Clara	2	2	2	4
Moraceae	*Morus nigra*	Lowland	2	2	2	4
Moraceae	*Musa rosacea*	Lowland	2	2	2	4
Commelinaceae	*Commelina diffusa*	Lowland	2	2	2	4
Commelinaceae	*Tradescantia zebrina*	Lowland	1	3	3	5
Saururaceae	*Houttuynia cordata*	Lowland	1	3	3	5
Poaceae	*Poa annua*	Highland	2	3	2	5
Fabaceae	*Desmodium adscendens*	Lowland	3	2	2	5
Poaceae	*Eragrostis cilianensis*	Santa Clara	3	2	2	5
Lauraceae	*Persea americana*	Lowland	3	2	2	5
Rosaceae	*Rubus rosifolius*	Highland	2	3	3	6
Asteraceae	*Galinsoga parviflora*	Highland	2	3	3	6
Polygonaceae	*Rumex acetosella*	Highland	2	3	3	6
Apiaceae	*Centella asiatica*	Serra Negra	3	3	2	6
Hydrangeaceae	*Hydrangea macrophylla*	Highland	3	3	2	6
Poaceae	*Eragrostis cilianensis*	Serra Negra	3	3	2	6
Poaceae	*Eriochloa villosa*	Santa Clara	3	3	2	6
Apiaceae	*Centella asiatica*	Lowland	3	3	3	7
Apiaceae	*Centella asiatica*	Santa Clara	3	3	3	7
Fabaceae	*Trifolium repens*	Highland	3	3	3	7
Lamiaceae	*Prunella vulgaris*	Highland	3	3	3	7
Poaceae	*Anthoxanthum odoratum*	Highland	3	3	3	7

seven non-native plant species: three species in casual populations, two naturalized, and two invasive. In Serra Negra we registered three non-native plant species: one species in casual populations and two in invasive populations (Table 2).

Invasion risk was considered low for 17 of the 36 species, while ten were rated moderately invasive and nine highly invasive (Table 2). None of the non-native plants registered in our survey occurred both in the highland and in Serra Negra, whereas only one species was recorded both in the highland and lowland, or in the highland and in Santa Clara. In total, four species were assigned priority level 1, three species level 2, fourteen species level 3, five species level 4, six species level 5, seven species level 6 and five species level 7 (Table 2). The lowland was the area with the highest number of species in priority level 1 (*C. dactylon*, *I. walleriana* and *M. maximus*), and the highland was the area with the highest number of low priority species (category 7: *A. odoratum*, *P. vulgaris* and *T. repens*). The four species in priority level 1 only occur in casual populations in one location, but are species of high invasion risk in the ecosystems considered. On the other hand, the five species categorized as level 7 are species with populations widespread due to cattle farming prior to the establishment of the Park, but these are ruderal species of low risk without significant history of invasion (Table 2).

Discussion

Details on the usability and application of a simple priority-setting scheme are described in this paper to support the management of invasive non-native species in protected areas. As per the prioritization scheme, the highest priorities for control were attributed to species of high invasion risk in early stages of invasion restricted to one location (e.g. *C. dactylon* and *C. familiaris* in this case study), whereas widespread species of low risk were given lower priority (e.g. *C. asiatica* and *B. taurus* in this case study).

Among the three criteria used in the priority-setting scheme, classifying species risk, interpreted as the propensity of a species to invade the local ecosystems, may be the most challenging part given the general lack of training of natural area managers and other field practitioners on invasive non-native species, or knowledge of species and their behavior in local conditions. In these cases, invasive species databases (e.g. the Horus Institute in Brazil, CABI ISC and ISSG GISD) as well as the EICAT scheme (Environmental Impact Classification for Alien Taxa) (Hawkins et al. 2015; Evans et al. 2016), or available results of risk assessments (e.g., online sources, da Rosa et al. 2018; Ziller et al. 2018) can be used in addition to field observations to support decisions on the level of risk of each species. The disadvantage of using generic information is that although there may be records of invasion, impact, or results of high risk from assessments that refer to other parts of the world, the information may not apply well to local ecosystems. Additionally, present and future climate and habitat types should be considered when using these alternatives whenever possible, and especially, expert opinion and field observations. Quantitative risk assessments are often underused because they tend to be time-demanding or require data that is not readily available (McGeoch et al. 2016).

Although the scheme proved useful to define priorities for control in the Itatiaia NP, knowledge of invasive species and their potential or current behavior in the ecosystems considered is important for its application. For instance, in our case study, the inclusion of species such as *Hydrangea macrophylla*, *Bidens pilosa*, and *Quercus robur*, which are in turn cultivated (*H. macrophylla*) and ruderal, as well as species that require long-term, persistent control and have expanded beyond small and few patches, such as African grasses, pushed aggressive invasive species such as *Hedychium coronarium* and *Tradescantia zebrina* down the list because these have invaded larger areas in the Park. Species that are characterized as not invasive or ruderal, such as the ones mentioned above (*H. macrophylla*, *B. pilosa*, and *Q. robur*), should be placed in a separate table to ensure that all species with a history of invasion are treated first. An initial effort in separating species with and without invasive potential will help managers filter the most important populations and species for control. This information cannot be obtained from general data sources, as it refers to the local ecosystems under consideration, and requires expert opinion as well as field observations. For this reason, species referenced in global databases as ruderal or invasive only in agricultural areas should be considered of low risk unless invasive behavior is actually observed locally, or other evidence corroborates higher risk.

In this study, formal sampling techniques were applied for data collection on non-native species. Although systematic sampling will produce the best possible data set (Cheney et al. 2018), this is, however, not the only approach for data collection. With training and experience, protected area staff can conduct field surveys to register the occurrence of non-native species with a GPS, while noting down invasion stage and frequency, as well as inferring invasion risk. Furthermore, information can be obtained from published sources. Effective prioritization must consider not only invasive species and pathways, but also the sites most sensitive and susceptible to invasion (McGeoch et al. 2016). This information can only be obtained locally, therefore invasion patterns must be observed during the surveys and used in the attribution of invasion risk. Information from other references is useful to corroborate these assumptions, as mentioned before. Cheney et al. (2018) demonstrated how mistaken general perceptions can be, as there was substantive disagreement between datasets produced by managers and by systematic sampling, implying that field data has to be collected locally. The application of our scheme entails full cover of protected areas, or of entire sections in the case of former prioritization of sites for control, very large areas, or very limited financial resources. Input from protected area managers is key especially after an initial list of priorities is defined based on field surveys. Logistics, as well as potential impact on fragile areas or on areas with threatened or endemic species, are discussed to adjust the operational sequence. At this time, knowledge of the area, accessibility, transportation or walking time, and many other details are considered to adjust the sequence of priority areas and species populations. Still, it is the priority levels that guide implementation. This last phase in the application of the scheme allows for flexibility and incorporation of exceptional circumstances regarding threatened or endemic indigenous species, susceptible or sensitive sites that may justify shifting the order of some priorities.

It is always best to register species occurrences by sectors of a natural area that are well-known by those in charge of management (e.g. entrance, headquarters, bridge, specific trails and other names in use). Once the list of priorities is generated, local managers must decide which sectors should be treated first, for example, due to the presence of threatened native species, unique or fragile habitats combined with other complementary criteria such as accessibility. Resulting workplans will only be useful if taking local experience and knowledge of protected area staff into account, especially to define implementation.

Control efforts should begin by addressing the priorities with the lowest numbers (priorities listed as 0 or 1 first, then 2, and so on up to priority 7). Priority zero indicates the occurrence of a non-native invasive species which might not yet have spread, providing an opportunity for elimination before it invades, but contained species may in certain cases not require management either because they cannot escape or because they are not aggressive. These occurrences should be evaluated on a case-by-case basis. Species of higher risk should be treated first within the same level of priority. The operational sequence of the priority-setting scheme should respect the list of priorities as much as possible, but is flexible to be adjusted to optimize logistics.

Because control requires persistence to prevent species from reproducing in order to reduce existing populations, monitoring and control are part of a continuous cycle once management begins (Fig. 1). This cycle ends either when the invasion is eliminated or due to other reasons such as limited funds or personnel, or others that lead to the interruption of activities. Complementarily, capacity-building for invasive species management is a key component of efficiency in the control of invasive species, especially to avoid wasting time and resources and to avoid missing important opportunities of restoring natural areas or creating negative references.

Most protected areas around the world face the threat of multiple invasive species and managers are required to implement control practices to limit the spread and impact of invasive species. However, resources and time are often limited for controlling all invasions at once (Robertson et al. 2003; Forsyth et al. 2012). Thus, priority-setting is key for the effective management of invasive non-native species (McGeoch et al. 2016). The priority-setting scheme presented in our paper is intended to be simple and functional for prioritizing invasive non-native species for eradication or control. As it has been designed for application by protected area managers or field practitioners, it can be readily implemented in any protected area.

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