

The value of sentinel plants for risk assessment and surveillance to support biosecurity

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Abstract

Effective surveillance for early detection of invasive alien species in natural ecosystems, or on valued plants found in modified areas, could prevent potentially devastating and costly impacts (whether environmental, economic or cultural) of new invasions on the invaded country. Surveillance technologies are often constrained by a range of factors. Determining which species present a significant risk before they reach the border is an effective strategy to minimize the possibility of invasion and/or the impact of invasion. Surveillance of sentinel plants provides an important tool to strengthen biosecurity programs assisting with i) detecting and identifying insect pests, nematodes and plant diseases that could potentially invade uncolonized countries, and ii) developing pest risk analysis profiles to eliminate or mitigate the risk of arrival. This review examines some of the challenges and opportunities provided by sentinel plant research and discusses the factors that could affect the success of their use for biosecurity risk assessment and surveillance in the New Zealand context.

Keywords

Plant biosecurity, expatriate plant sentinels, IPSN, insects, plant pathogens, nematodes, pest surveillance, pest risk analysis

Introduction

Global mass transportation of trade and humans is a significant driver for movement of biota into new regions and ecosystems. Some of these biota thrive in the new environments and become invasive aliens. A key aim of invasion science is to predict which species will become invasive before an invasion occurs. Accurate prediction of potential invasiveness of an organism supports the risk assessment of that organism and the development of effective, targeted biosecurity measures, including surveillance, against it. In practice, the first invasion of a new species is frequently unanticipated because the invader is not a recognized pest in its country of origin (Poland and McCullough 2006; Paap et al. 2017) and/or the invader has jumped to a new host that is not attacked in its country of origin (Vettraino et al. 2017). New Zealand (Aotearoa) is an island nation with a high proportion of endemic plant and animal species (Miller 1971; Dugdale 1988; McGlone et al. 2001). It is heavily reliant on its natural landscapes for tourism, and primary industries for its economic wealth. Both natural ecosystems and primary production are at risk from the negative impacts of exotic invaders including loss of biodiversity, habitat modification, reduced growth or persistence, and cost of controls. So too are some taonga (things of value), in this case flora and fauna of significance for Māori, the indigenous population of New Zealand. Biosecurity strategies developed pre-border, border, and post-border, are New Zealand's defensive screen against invasive alien species that threaten species of cultural, environmental and economic importance. Sentinel plants (as defined below) can be a tool to detect potential plant pests, help indicate the degree of damage they could inflict on valued species and inform pest risk analyses, if there is a potential threat to New Zealand. They can therefore, play a significant role in border biosecurity.

Since the concept was formally proposed as a means of identifying the potential risk of invasive species offshore (Aalders et al. 2006; Fagan et al. 2008; Britton et al. 2010), sentinel plants have developed into an internationally recognized strategy for detecting potential invaders (Groenteman et al. 2015; Barham et al. 2016; Paap et al. 2017; Eschen et al. 2018). However, the sentinel plant concept has been interpreted in several different ways. This review describes the scope of the sentinel plants concept and presents examples of its implementation. We also consider ways in which the use of sentinel plants can be optimized for biosecurity purposes with particular reference to the enhancement of New Zealand's biosecurity.

What is a sentinel plant?

The simplest definition of a sentinel plant is “a plant that is monitored for the presence of species that have the potential to cause damage”. Examples of damaging species include herbivorous insects, plant parasitic nematodes and plant pathogens, and these will hereafter be referred to collectively as “pests”. Sentinel plants may be broadly classified into two types depending on the primary reason for monitoring, i.e. to identify new pest species of risk to determine their distribution (sentinel plants for risk as-

assessment) or to detect pest species of risk (sentinel plants for surveillance) (Figure 1). While the former is concerned with determining the potential pests of a particular host plant genus or species, which can then inform a pest risk assessment, sentinel plants for surveillance focus on detecting range expansion of particular pests or pest groups.

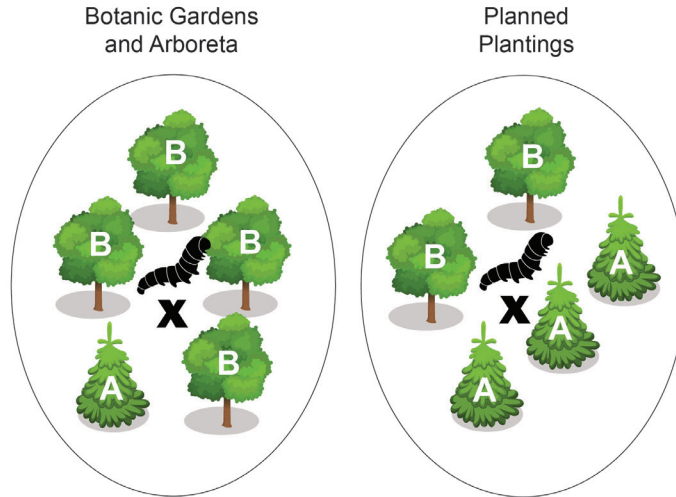
Sentinel plants for risk assessment

The purpose of sentinel plants for risk assessment is to detect new host associations of particular valued plants with pests with which they have not co-evolved. To do so, we monitor valued plants that have been grown outside their natural home range, i.e. expatriate plants (Britton et al. 2010; Eschen et al. 2018), where they are exposed to a suite of organisms from the country in which they are grown and determine whether any of those organisms feed or cause damage on the sentinel plants (Table 1 summarises recent examples of this approach).

An example of this is New Zealand native plants growing in botanic gardens or arboreta in other countries which provide the opportunity to identify species utilizing those plants and which could become pests if they established themselves in New Zealand (Fagan et al. 2008). Such observations can identify potential invaders and prompt risk analyses for those species to be conducted. Once the degree of invasion risk is estimated, the potentially affected economic sectors can be alerted to it, raising awareness and surveillance for the identified pest and risk managers can, if it is deemed necessary, employ strategies to block the pathways by which an invasion could occur. For instance, soil samples were taken from the root zones of a selection of expatriate New Zealand native plants growing at the Ventnor Botanic Gardens on the Isle of Wight (United Kingdom). Nematodes extracted from the soil revealed that the plant parasitic lesion nematode *Rotylenchus pumilus* (Perry), was associated with *Olearia pachyphylla* Cheeseman (Asterales: Asteraceae). This is a very rare and critically endangered endemic shrub in New Zealand (de Lange et al. 2017). While sampling at Ventnor Botanic Gardens did not ascertain the effect of the nematode on *O. pachyphylla*, the discovery suggests that if a pathway existed for long-distance transfer of *R. pumilus* to New Zealand (e.g. on soil contaminated footwear, McNeill et al. 2011), the few remaining wild populations of *O. pachyphylla* in New Zealand may be at risk.

While established expatriate sentinel plants can be used for monitoring (Scott-Brown et al. 2017), specific plantings of valued plants can also be undertaken. For example, trade in live plants from China to Europe provided a pathway, carrying significant risk, for the introduction of invasive alien species into Europe. As an early warning tool to identify potential impacts, European tree species were grown in China as sentinels to detect possible insect pests and pathogens originating from that region (Roques et al. 2015; Vettraiño et al. 2015). An invasion risk identified from this work was the box moth, *Cydalima perspectalis* (Walker) (Roques et al. 2015). Taking a similar strategy, native Asian plants that are commonly traded with Europe, were grown in 'sentinel plant nurseries' in China for the same purpose (Vettraiño et al. 2017; Kenis et al. 2018).

Risk Assessment



Surveillance

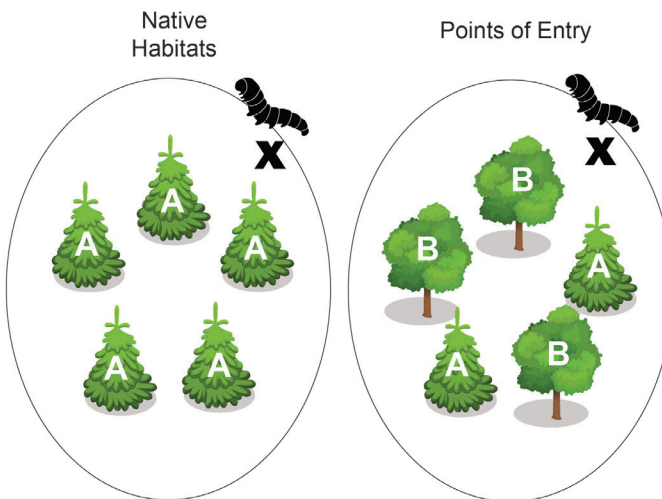


Figure 1. Different types of sentinel plants. **Risk Assessment:** monitoring expatriate plant A (*outside its native range*), can give information on exotic pests (pest X) associated with plant B that might attack Plant A should pest X become established in the home range of plant A. In this case, plant A acts as a sentinel plant for risk assessment. Sentinel plants may be *in situ* within existing botanic gardens and arboreta or planned plantings to record colonization and impacts. Risk assessment sites can be in the native range of plant B or regions outside plant B's native range where pest X is invasive. **Surveillance:** monitoring plant A and/or plant B in *the native range of plant A* may give information on the arrival and spread of pest X into that area. In this case, plants A and B act as sentinel plants for surveillance. Surveillance sites may be in native habitats for plant A or at likely points of entry for pest X.

The concept of growing plant species in exotic environments to detect known associate pests of those plant species, or similarly native species in their home range has been described as “*ex-patria*” and “*in-patria*” plantings respectively (Eschen et al. 2018). As defined by Eschen et al. (2018), *in-patria* plantings consist of young woody plants of species that are commonly exported to identify pests native to the exporting country. *Ex-patria* plantings consist of exotic young or mature woody plants and surveys may provide information about potential impacts of pests if these were to become established in a new country. However, this dichotomy fails to acknowledge that some invasions will not follow the most direct pathway from the country of origin to the invaded country. An invader may enter and colonize one (or more) countries outside its native range through bridgehead invasion (e.g. Lombaert et al. 2010) before reaching the country of concern. Figure 2 illustrates this from the New Zealand perspective: primary invasion represents the most direct route for invasion into New Zealand whereas bridgehead invasion and secondary invasion represent an indirect route via invasion of another country before reaching New Zealand.

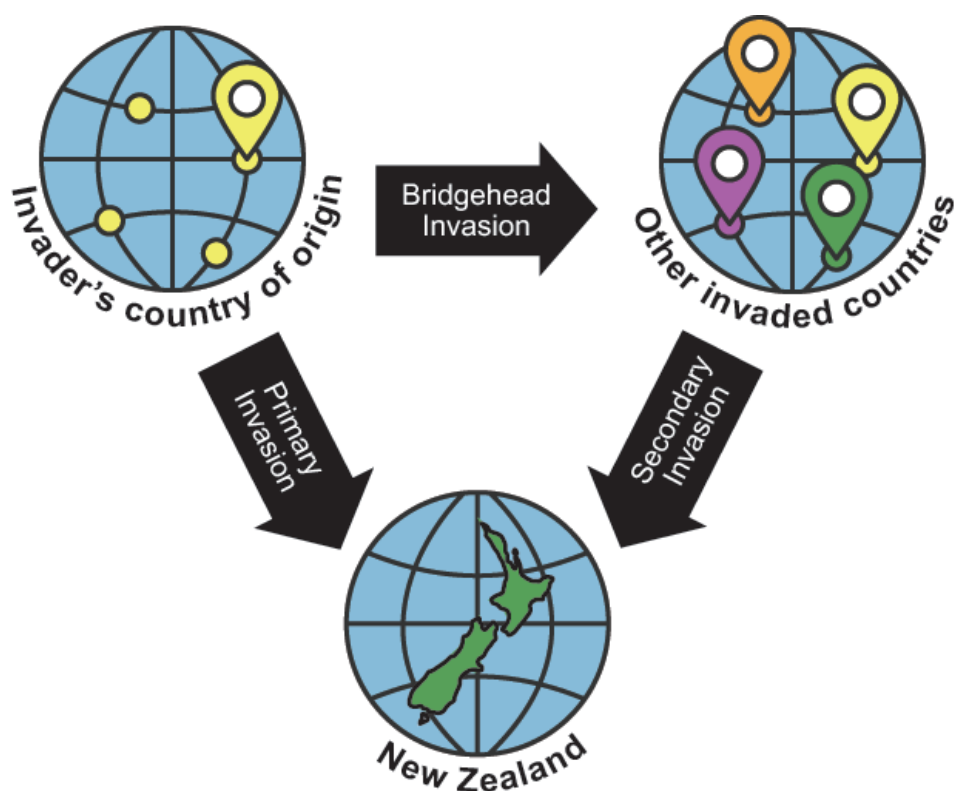


Figure 2. Invasion pathways into New Zealand in relation to the invasive species’ country of origin. In a primary invasion, an invader may enter New Zealand directly from its native range, while in a secondary invasion pathway, the pest colonizes one (or more) countries outside its native range through bridgehead invasion, before reaching New Zealand.

Sentinel plants for surveillance

Sentinel plants used for surveillance assume that a risk of pest invasion has been identified and possible entry and dispersal pathways determined. In this case, surveillance sites can be selected based on proximity to trade and tourism entry points, climate matching and other relevant criteria such as potential host-plant associations, historical interception records and logistics of accessing sites. Once the risk of a new host association has been identified, then sentinel plants for surveillance may be used to detect arrival or range expansion of particular pests (Table 1). Whether the host plant is native to the country potentially being invaded or exotic does not matter so long as it is susceptible to attack by the pest of interest. A defining feature of sentinel plants for surveillance is that they are used outside the known range of the target pest.

An obvious application of sentinel plants for surveillance is for detecting the invasion of new species into an area. For example, New Zealand's Ministry for Primary Industries (MPI) High Risk Site Surveillance System (HRSS), oversees the monitoring of arborescent plants near likely points of pest entry, such as airports, seaports and container devanning sites (Stevens 2008). Currently >10,000 inspections are carried out annually, each involving many individual sentinel plants along a predetermined walked transect. In 2005–06, its first year of operation, the HRSS reported 62 significant finds of pests new to New Zealand, new host records and new pest distributions (Stevens 2008). In the period 2013–2018, the system has detected a total of 22 species which are new to New Zealand (Stevens 2018). New Zealand's HRSS is clearly an effective application of the 'sentinel plants for surveillance' concept, though it is monitoring the vegetation as found at site. There may be potential to design sentinel systems for surveillance that include particular plants, not already present among *in situ* vegetation, to target a specific pest, but the authors are not aware of relevant published examples. Any planned planting of sentinel plants for surveillance near points of entry would need to balance the benefits of early detection and rapid response to invasion against the risk that such plants may act as habitat that supports colonization by invasive species.

Biosecurity applications for the use of sentinel plants

The efficacy of a biosecurity program that uses sentinel plants, either for risk assessment or surveillance will be affected by several factors and these need to be considered when designing the program. These include: i) is there a scientific aim for the program; ii) the selection of sentinel plant species; iii) attributes of the potential invasive species/taxa of interest; iv) commonalities and differences between geographic origin/location of the sentinel plants and invaders, including habitat and environmental matches; v) appropriate technologies for detection of invasive species; vi) appropriate frequency of monitoring; and vii) effective communication of results to groups of interest. These factors may interact with each other. For example, the invasive species/taxa of interest will determine the most appropriate

Table 1. Examples of sentinel plant research for risk assessment and surveillance including use of *in situ* plants and planned plantings.

Sentinel type	Sentinel location	Target plants	Target pests	Outcome	Reference
Risk, <i>in situ</i>	Ventnor Botanic Garden, Isle of Wight	New Zealand species	Nematodes	New association found between root nematode and rare endemic species	Aalders et al. 2006
Risk, <i>in situ</i>	Siberian arboreta and cities	European and Eurasian woody broadleaved species	Fungal pathogens	29 new fungus-host plant associations detected, some with significant damage	Tomoshevich et al. 2013
Risk, <i>in situ</i>	Southern California	39 New Zealand perennial species	<i>Homalodisca vitripennis</i> , <i>Xylella fastidiosa</i>	28 species tested positive for <i>X. fastidiosa</i> ; 26 out of 102 individual plants showed <i>H. vitripennis</i> activity	Groenteman et al. 2015
Risk, <i>in situ</i>	Christchurch	62 exotic conifers	Exotic aphids	13 new aphid-plant associations detected	Redlich et al. 2019
Risk, planned	Riverside, California	12 Australian tree species	<i>H. vitripennis</i>	8 species supported at least one life stage; 5 species supported adults, nymphs and eggs	Rathe et al. 2014
Risk, planned	Beijing and Fuyang	European trees: 5 broadleaves, 2 conifers	Foliage-feeding insects	> 100 morphospecies including larvae of at least 6 species detected on trees	Roques et al. 2015
Risk, planned	Fuyang	3 <i>Quercus</i> species	Fungal pathogens	Four taxa associated with disease symptoms identified	Vettraino et al. 2015
Risk, planned	Beijing and Fuyang	5 ornamental woody plants from Asia	Insects	> 90 new insect-plant associations detected	Kenis et al. 2018
Surveillance, <i>in situ</i>	Palm House, Kew Gardens	181 species	<i>Scirtothrips dorsalis</i>	73 species had <i>S. dorsalis</i> adults, 44 species also had juveniles	Scott-Brown et al. 2017
Surveillance, <i>in situ</i>	New Zealand wide	Various native and exotic spp.	Exotic pests	22 exotic species detected 2013–2018	Stevens 2018

sampling methods for detection. Consideration of such factors, and their interactions, in the design phase of the biosecurity program will facilitate its successful implementation and ensure it achieves its purpose.

Scientific aim

A purely protective biosecurity program does not require a scientific goal but there are considerable benefits for such an inclusion, not least being the validation of the program and possible improvements to future programs based on the success, or otherwise, of the current program. Sentinel plants for risk assessment and surveillance can be used not only for the primary purpose of identifying and detecting new potential invaders (e.g. Stevens 2008; Tomoshevich et al. 2013; Vettraino et al. 2017; Kenis et al. 2018), but also to test either general ecological theories about biological invasions (Kirichenko et al. 2013; Kirichenko and Kenis 2016; Burgess and Wingfield 2017) or specific hypotheses about particular invasive species (Thu et al. 2009; Rathe et al. 2014; Kurose et al. 2015). Some sentinel plant programs address both purposes (Roques et al. 2015; Vettraino et al. 2015; Eschen et al. 2018). Programs designed to test theories or hypotheses can require deliberate planting of sentinel species to meet experimental requirements; as was carried out in China using European tree species (Roques et al. 2015; Vettraino et al. 2015) or Chinese species grown for the nursery trade into Eu-

rope (Kenis et al. 2018), and Australian tree species domiciled in California (Rathe et al. 2014). Deliberate planting has advantages such as the program design can be more robust than if relying on existing plants, plants can be selected for consistency (e.g., plant age, cultivar type), sample size can be pre-determined, and the investigation sites can be chosen to meet specific conditions (e.g. climate, habitat type, proximity to a source of potential invaders).

If the program's sole purpose is identification of potential new invaders, it is more common to monitor selected plants *in situ* from pre-existing botanic gardens or arboreta. The International Plant Sentinel Network (IPSN) was established to co-ordinate sentinel plant monitoring and data sharing across botanic gardens in multiple countries (described by Barham et al. 2016). The use of *in situ* plants, and long term monitoring, can have advantages where long-lived perennial species, particularly woody plants, are involved because a plant's susceptibility to attack may change during its lifespan (Eschen et al. 2018). Reliance on *in situ* plants, however, does limit the species and cultivars/ecotypes available to sentinel plant programs. Species that are either poorly represented or wholly absent in existing botanic gardens and arboreta will require deliberate planting if they are to be included in a sentinel plant program. Where deliberate planting is used to establish a sentinel plant program, it is essential that the plants themselves do not create a new invasion problem, either by becoming weeds or by inadvertent introduction of new pests. To minimize such risks, local biosecurity concerns need to be considered during selection of sentinel plant species and all plant material subject to screening for unwanted organisms before use in the program and destruction and disposal of plants at the conclusion of the experiment to prevent their establishment as weeds.

Selection of sentinel plant species

Sentinel plant programs choose plants of significant value to humans. That value may be environmental (endangered species, species that perform a valued non-economic service, or species that support key ecosystems); economic (plants grown for food and fibre), or cultural/aesthetic. New Zealand's long geographic isolation has led to a high level of endemism amongst its flora (Wilton and Breitwieser 2000). Of the many indigenous vascular plant taxa, 403 are classified as threatened and 851 as 'at risk' (de Lange et al. 2017), due to habitat loss or environmental changes (de Lange et al. 2010, 2017). For New Zealand's Department of Conservation, many of these species are considered high priority for inclusion in expatriate sentinel plant programs (C Green, Department of Conservation, pers. communication). Several New Zealand plants e.g. kaka beak (*Clianthus puniceus*) (G.Don) Sol. ex Lindl. (Fabales: Fabaceae), are classified as critically endangered in the wild but are grown in several Australian and European botanic gardens.

In New Zealand, the cultural/aesthetic aspect includes a wide range of significant species of value to Māori (Black et al. 2019), and under obligations relating to the

Treaty of Waitangi (a document of central importance to the history and political constitution of New Zealand), this aspect is an important consideration in selection of species for sentinel plant research. Therefore, species such as pōhutukawa (*Metrosideros excelsa* Sol. ex Gaertn.) (Myrtales: Myrtaceae), kauri (*Agathis australis* Salisb.) (Pinales: Araucariaceae) and harakeke (flax) (*Phormium tenax* J.R.Forst. & G.Forst.) (Asparagales: Asphodelaceae), have value for Māori because of their traditional utilisation for food, medicine, weaving, carving and construction.

When plants growing *in situ* are used as sentinels in programs with a research component, availability is an important criterion and can override other factors. If a sentinel plant program intends to test ecological theories about invasive species, as opposed to the empirical risk assessment described above, then the history of different taxa, or individual plants, may affect the results. For example, the rate of accumulation of new species has differed between plant taxa in Europe (Roques 2015), suggesting some plant taxa are more vulnerable to invasive species than others. Kirichenko and Kenis (2016) found residence time, i.e. the year an exotic species was first planted at the study site, influenced the rate of colonization by native leaf miners in a Siberian botanic garden. Such factors need to be considered explicitly during program design and subsequent data analysis because including plant groups with substantially different histories in the same program may create unintended bias. Any prior knowledge regarding the invasive species/taxa of interest to the program should be taken into account when selecting sentinel plant species (see next section), and there may be significant limitations to risk assessment if the invasive species cannot be identified using either morphological or molecular taxonomy (Roques et al. 2015).

Potential invasive species/taxa of interest

Expatriate sentinel plant programs may target particular pest species (e.g. glassy-winged sharpshooter, *Homalodisca vitripennis* (Germar), Groenteman et al. 2015), taxa (e.g. leaf chewers and leaf miners, Kirichenko and Kenis 2016) or insect herbivores and plant pathogens associated with specific plant taxa (e.g. oaks and conifers, Roques et al. 2015). If a potential invasive species is a recognized pest in its place of origin, knowledge of it and previous research on its native host plant range can assist development of expatriate sentinel plant programs.

If the pest of interest has invaded elsewhere, the impact of these invasions on plants in those locations may indicate vulnerable species that should be considered for inclusion in sentinel plant programs for surveillance in the country at risk of invasion. For example, studies of glassy-winged sharpshooter, *H. vitripennis*, on Australian and New Zealand native plant species growing in California, provided information on new insect-plant host associations of biosecurity concern to both countries (Rathe et al. 2014; Groenteman et al. 2015). For example, Groenteman et al. (2015) found 26 of 102 individual plants growing in Californian botanic gardens and arboreta showed signs of *H. vitripennis* activity (eggs, nymphs, adults, or presence of shed exuviae) while

the pathogen *Xylella fastidiosa* was present in 51% of the plant samples. Of particular concern to New Zealand, *X. fastidiosa* was detected in the culturally important species pōhutukawa, tītoki (*Alectryon excelsus* Gaertn.) and kauri.

In some cases, investigations are looking for the unknown – apparently harmless species that change hosts or that escape natural enemies in their native range to become significant pests in an invaded country. For example, the emerald ash borer, *Agilus planipennis* Fairmaire is not a pest within its native range in Asia but became a significant pest after invading North America (Poland and McCullough 2006). These unknown potentially invasive species are the most difficult to recognize prior to invasion. For example, a study carried out in China over a two-year period on five ornamental woody plants (*Acer palmatum* Thunb., *Ilex cornuta* Lindl., *Buxus microphylla* Siebold & Zucc., *Fraxinus chinensis* Roxb. and *Zelkovia schneideriana* Handel-Mazzetti) that are commonly exported from China to Europe, recorded 105 insect species and host associations on these sentinel plants with 90% of these associations not recorded in a previous literature review of insect pests of the five plants (Kenis et al. 2018). An earlier investigation that involved planting seven European tree species in China followed by three years of monitoring, found 38 unanticipated plant-insect associations in which the majority of identified species had switched from agricultural crops and fruit trees rather than from forest trees (Roques et al. 2015).

A possible clue to identifying a non-pest species that has the potential to become a significant risk in another country may be via examination of herbivorous invertebrate communities associated with plants native to that country and that are closely related to sentinel plant species of interest. Any herbivores associated with these closely related plant species, particularly where impacts are severe, should be investigated as risks and potential invaders if pathways, climate suitability, and hitchhiker potential enable long distance dispersal, survival and establishment of that species (e.g. Toy and Newfield 2010; Meurisse et al. 2018). Wylie and Floyd (2002) explored this concept in relation to Australian eucalypts and potential insect invaders from tropical Asia: seven of ten key pest genera or species associated with eucalypts native to Asia were rated as high or medium risk to Australian eucalypts. Conversely, Australian insects were identified as significant risks to eucalypt plantations in Asia, especially those that could occupy unfilled faunal niches should they invade (Wylie and Floyd 2002).

Insect pests and plant diseases generally have received the most attention within the sentinel plant context, in part because the signs and symptoms of damage are generally visible to both specialist researchers and casual observers. By comparison, indications of the presence of nematodes tend to be more cryptic, and their impacts overlooked. Of the nematode taxa, plant parasitic nematodes (PPN) provide the most concern to biosecurity officials and growers, because their effects on plant growth and production can be significant. PPN are small (generally less than 1 mm in length) and found mostly in and around plant roots, while a small number of important genera infect leaves and stems. Plant symptoms of nematode infection can often be mistaken for nutrient deficiency or attributed to other pests or diseases. Due to their small size, identification requires access to specialist equipment and expertise. Few species of PPN

are currently recognized as invasive but this is undoubtedly because of insufficient investigation and recognition of their presence (Singh et al. 2013). The importance of potential association of PPN with New Zealand expatriate native plants, and by inference in New Zealand, was shown by a study involving three overseas botanic gardens (Aalders et al. 2006; Aalders et al. 2012; Bell et al. 2013). While PPN impacts were not assessed, 17 plant feeding nematode genera or families were identified from all three sites, including root-knot (*Meloidogyne* spp.) and lesion (*Pratylenchus* and *Rotylenchus* spp.) nematodes (Fagan et al. 2009; Aalders et al. 2012).

Geographic origin, trade patterns and pathways

Central to the concept of sentinel plants is the question of geographic origins of potential invaders and selected sentinel plant species (Figure 2). For New Zealand, Australia (Close et al. 1978, Fox 1978) China and the United States (Paini et al. 2016) represent the greatest potential sources of invasive species. It seems logical, therefore, to deploy sentinel plant programs for risk assessment to these countries. Trade and tourism with all these countries provide invasion pathways that, if unmitigated, could enable invasive species to establish in New Zealand (McCullough et al. 2006; Anderson et al. 2015; Early et al. 2016; Paini et al. 2016; Chapman et al. 2017).

Floral similarities between countries also facilitate invasion by “new” pests. For New Zealand, sentinel pōhutukawa plants for risk assessment that are grown in countries with substantial Myrtaceae flora (e.g. Australia, Pacific Islands, South America) allow the identification of new potential invaders that may enter New Zealand directly (Figure 2, primary invasion). This approach is based on the hypothesis that exotic pests associated with plants closely related to the sentinel plant are an invasion risk (Ridley et al. 2000). For pōhutukawa, the taxonomic focus can be narrowed down from family to the genus *Metrosideros*, which is distributed across the Pacific, South America and South Africa, with its centre of biodiversity located in New Caledonia (Wright et al. 2000; Pillon et al. 2015). This narrowing of investigation from family to genus level could increase the accuracy of predictions that arise from it and is being used to reduce potential risk to pōhutukawa. Myrtle rust *Austropuccinia psidii* (G. Winter) Beenken, a pandemic neotropical rust strain associated with Myrtaceae (Carnegie and Pegg 2018) has recently established in New Zealand (Beresford et al. 2018; Large and Galbraith 2017). Other emerging threats include *Ceratocystis huliohia* and *C. lukuohia*, two recently identified pathogenic strains killing the endemic ōhi‘a tree (*Metrosideros polymorpha*) in Hawaii (Barnes et al. 2018). The obvious concern is that these strains also could have an impact on New Zealand *Metrosideros* species. The probability of *C. huliohia* and *C. lukuohia* reaching New Zealand is open to conjecture. Movement of infected plant material is believed to be the main pathway for introduction and spread of these plant pathogens (Barnes et al. 2018), and as no live plant material is permitted into New Zealand without a phytosanitary certificate and pre-release screening for unwanted organisms, the pathway risk appears minimal.

Nevertheless, in conjunction with the USDA, a follow-up project has been initiated to screen *M. excelsa* for resistance against both *C. huihiohia* and *C. lukuohia*.

As noted above, it is possible for potential invaders to switch hosts to unrelated plant species; this type of host shift is very difficult to predict. From New Zealand's perspective, an unexpected host shift may be detected after a 'bridgehead' invasion (Figure 2) that has the potential to act as a source of colonists for future invasions (Lombaert et al. 2010). Detections of possible risk from this pathway is likely to happen through networks like the IPSN that monitor *in situ* plants (Barham et al. 2016). Such a detection would also alert biosecurity scientists to the potential risk of secondary invasion (Figure 2) into New Zealand. Monitoring to detect bridgehead invasions is important because it identifies species that have already demonstrated invasiveness; sentinel plants for risk assessment are ideal for this purpose. It further provides an opportunity to investigate the invader's ecology in both its invaded range and country of origin (if known), before it reaches New Zealand. International research to assess impacts from known invasive species also may detect new associations unexpectedly e.g. *Metrosideros polymorpha* ('ōhi'a) seedlings sent from Hawaii to Viçosa University in Brazil for testing against multiple strains of myrtle rust fungus (*A. psidii*), became infested with the pathogenic fungus *Calonectria metrosideri* (Alfenas et al. 2013). This new association was described as another fungal pathogen of 'ōhi'a and listed as an "actionable" species for USDA-APHIS (Farr and Rossman 2016). It seems sensible to consider this fungal pathogen a potential risk to New Zealand's *Metrosideros* species.

Sampling methods, taxonomic identification and frequency of monitoring

The choice of sampling methods used in a sentinel plant program, for either risk assessment or surveillance, should be determined by what is known about the potential invader(s). If the target is a known species or taxon, then specific sampling techniques may be able to be adopted to maximise the probability of pest detection, e.g. Kirichenko and Kenis (2016) used different sampling methods for leaf chewers versus leaf miners. If the sentinel plant program is targeting unknown pests then a variety of sampling methods or techniques validated to detect a wide range of organisms should be used so that the probability of detecting a pest is maximized. For example, different methods are needed to detect insect herbivores to those needed for fungal pathogens.

A key step when dealing with unknown invaders is correct taxonomic identification based on morphological and/or molecular characteristics, at least to genus and preferably to species level (James et al. 2014; Kenis et al. 2018). The more precise the identification, the more accurate the risk predictions can be. The identification process may be particularly challenging for cryptic species, such as PPN and gall-forming insects. An important aim of the IPSN is enhanced early detection of new and emerging invasive species through initiatives to raise awareness of plant health issues, provide tools to aid early detection and identification, train stakeholders to develop their taxonomic skills, and develop electronic reporting systems (Barham et al. 2016, Roques et al. 2017).

Sentinel plants may be subject to a regular monitoring schedule or checks may be conducted intermittently, as time permits. In general, a regular and frequent schedule is likely to be more useful for biosecurity purposes, particularly when consistent sampling methods are used at each check (e.g. detection of *Thaumastocoris peregrinus* in New Zealand, Sopow et al. 2012), as the quality of data collected is likely to be better. However, even intermittent inspections may give early warning of potential new invaders. For example, Fagan et al. (2009) identified 10 potential invaders to New Zealand from 14 visits to overseas botanical gardens by researchers.

Communication of research results

An easily overlooked, but essential, aspect of sentinel plant research is the need to communicate results to the relevant biosecurity authorities and potentially affected stakeholders. These need early warning of both potential and actual new invaders, particularly if significant impacts are expected, so that mitigation can be planned and implemented to minimise pest impact. While publication in peer-reviewed journals is critical for scientific veracity and quality, this does not obviate the need for wider communication of new research findings. Communication must be timely and relevant with the information presented in a way that non-specialists in government and industry organisations can understand, yet it must also acknowledge the inevitable uncertainties in research findings.

In New Zealand's case, rapid communication is best directed to government agencies such as the Ministry for Primary Industries (MPI) (as New Zealand's National Plant Protection Organisation) and the Department of Conservation (DOC) as well as the appropriate Crown Research Institutes, depending on the sectors or environments most likely to be affected by the new invader. The most affected sectors will also determine which industry stakeholders should be involved with a risk assessment or an incursion response. In general, early communication with authorities and stakeholders informs pest risk and pathway analyses, as well as raising awareness and vigilance amongst the affected groups. As part of this process, there needs to be effective channels to share feedback from government authorities and stakeholder organizations with research providers. This is essential to confirm that useful information has been received by all parties, to share information, and to support co-development of important pest risk and pathway analyses.

Gaps in sentinel plant programs

Most research using sentinel plants, whether to detect new invasions or assess risks, involves perennial woody tree species. Plants of environmental and cultural value are more likely to be monitored through botanic gardens and arboreta, which presumably reflects the availability of such species in alien environments. Annual plants, short-lived perennials, and grasses are under-represented in the literature, yet there are valued

species within these groups e.g. snow tussock (*Chionochloa rigida*) is an iconic New Zealand species. It is not clear if these under-represented groups are less common in parks and botanic gardens and therefore simply unavailable for monitoring, or if these groups are actively excluded from sentinel plant programs either because the value of this approach is not recognized for such plants or research funding is unavailable.

The other significant group rarely included in sentinel plant programs for risk assessment are plants of economic importance. For example, many non-woody crop plants are grown outside of their native range where they are at risk of attack by local polyphagous pests (Singer et al. 1993). Once the local pest has colonized the novel crop plant within the pest's native range, there is potential for that pest to become invasive if a pathway exists for it to move to new countries. Conceptually, novel crops act as sentinel plants for detection of new pest associations and may provide early warning of new biosecurity risks. For example, Queensland fruit fly, *Bactrocera tryoni* (Froggatt), is a well-known biosecurity risk for New Zealand and other countries both because of its ability to damage a wide range of fruit crops that did not co-evolve with this pest and its history of detections at or post-border (Kean 2016; Haynes and Dominiak 2018). A barrier to the inclusion of economic crops in a sentinel programme may be that, whether expatriate or domestic, they are subject to regular harvesting and pest control; practices that are often incompatible with monitoring programs intended to detect biosecurity threats. In such cases dedicated sentinel crops may be required. Sentinel plant programs for risk assessment that target commercial crops in regions of biosecurity concern may provide useful insights on the diversity of potential invasive species, their associated impacts and biological control agents (as shown by Roques et al. 2015 and Kenis et al. 2018). For New Zealand, sentinel plant programs for risk assessment that target forage or horticultural crops in regions of biosecurity concern (e.g. Australia, China or USA, Paini et al. 2016), may provide useful insights on pest biodiversity, impacts and biological control agents from sowing to maturity. This would be augmented by research literature identifying specific pests to include in sentinel plant programs. In this respect, it is important to be able to access foreign language literature, as this can expand information on pest species and impacts (e.g. Xu et al. 2016).

Outside of programs focused strictly on biosecurity, but in many cases aligned to real or potential biosecurity breaches, sentinel plant programs for risk assessment can be used to develop pest control strategies, particularly where biological control of invasive plant species is considered. Sentinel plants may be used to identify potential biological control agents and/or to assess their efficacy (e.g. Groenteman et al. 2015) although such work is conducted more often in response to a successful invasion (e.g. Kurose et al. 2015), rather than before invasion occurs. Along similar lines, expatriate plants may be used to test for non-target impacts from potential weed biological control agents prior to introduction to the affected country. This approach is important to protecting commercial forestry from invasive pests (Showalter et al. 2018) and has been used previously to test the susceptibility of New Zealand's endemic *Sophora microphylla* Aiton (kowhai) to *Pirapion immune* Kirby, a phytophagous biological control agent of broom (*Cytisus scoparius*, (L.) Link) in the UK (Syrett and Harman 1995). The ability

of *P. immune* to develop successfully on *S. microphylla* under field conditions in the UK, led to the rejection of the weevil as a biological control agent for *C. scoparius* in New Zealand (Syrett and Harman 1995). More recently, the same approach was used to test susceptibility of the native passion vine, *Passiflora tetrandra* Banks ex DC., to biological control agents of the invasive weed, banana passionfruit (*Passiflora* spp.) in Colombia (Q. Paynter, Landcare Research, pers. comm.).

Sentinel plants and New Zealand's biosecurity

Ideally, both *in situ* plants (in botanic gardens and arboreta) and planned plantings (research plantings) should be incorporated in target sentinel plant programs, because no single approach can cover all potential invaders, particularly plant pathogens (Desprez-Loustau et al. 2007; Webber 2010). In this respect, home gardens near ports also provide another avenue for early detection of invasive pests (e.g. Barratt et al. 2015). The engagement of citizen scientists to support detection and reporting of new incursions may prove valuable to the overall aims of biosecurity (Thomas et al. 2017).

Regular monitoring of established specimens of plant species that are valuable to New Zealand, particularly expatriate specimens of endemic species, is the most practical strategy because it contributes information about recognized pests in their country of origin, new pests that emerge through bridgehead invasions into other countries, and potential new invasions into New Zealand (Figure 2, Table 2) while at the same time requiring relatively low monetary and capital resources. Alongside such monitoring, participation in the IPSN and similar collaborative networks can potentially leverage knowledge held by local staff in botanic gardens and arboreta, while increasing the number of 'eyes on the ground' (Britton et al. 2010, Barham et al. 2016). The report that pōhutukawa is susceptible to *X. fastidiosa* subsp. *multiplex* originated through this network (Anon. 2016). Participation also provides the opportunity to identify overseas locations of key plant species for *a posteriori* study to measure impacts from invasive species following their establishment in New Zealand (e.g. Marroni et al. 2018).

Planned planting programs of sentinel plants for risk assessment are best used to address specific questions that cannot be answered using *in situ* plants in the invader's country of origin and/or its invaded range or where robust data collection is required. The cost and logistics of sentinel plant programs will increase with complexity and inevitably there will be trade-offs between optimal data collection and manageability. However, such programs will be particularly important for plant taxa that are poorly represented in botanic gardens and arboreta, such as grasses, annuals and short-lived perennials and may also be justified in the case of economic crops. For example, ryegrasses (*Lolium* spp.) are New Zealand's most valuable crop (Nixon 2016) and its economic worth would justify planned plantings and extensive monitoring in countries where potential invaders occur, particularly as relatively few pests in New Zealand attack it. Plant selection can be strategic to assess impacts of selected invasive pests or pathogens not yet in New Zealand (e.g. exposing *Metrosideros* spp. to *C. huihioha* and *C. lukuohia*

Table 2. Strategies for use of sentinel plants to enhance New Zealand's (NZ) biosecurity.

Geographic location	<i>In situ</i> sentinel plants	Planned sentinel plantings
Invader's country of origin (sentinel plants for risk assessment)	Monitor 1) any plants damaged in country of origin that are valuable to NZ and 2) any valuable NZ species that are taxonomic relatives of plants damaged in country of origin.	Establish planned plantings of any potentially vulnerable species not already represented among <i>in situ</i> plants in the invader's native geographic range.
Other countries subject to a bridgehead invasion	Monitor 1) any plants damaged in the invaded range that are valuable to NZ and 2) any valuable NZ species that are taxonomic relatives of plants damaged in the invaded range. If the invader's country of origin can be identified, follow recommended sentinel plant strategy within the invader's native geographic range.	Establish planned plantings of any potentially vulnerable species not already represented among <i>in situ</i> plants in the invaded range and, if possible, the invader's native geographic range.
New Zealand (sentinel plants for surveillance)	Monitor 1) local specimens of any plant species damaged in the invader's country of origin (if known), 2) local specimens of any species valuable to NZ that are damaged in other invaded countries, and 3) any valuable NZ species that are taxonomic relatives of plants that are either damaged in the invader's country of origin (if known) or damaged in other invaded countries. Monitoring should include air and sea ports, botanical gardens, forestry plantations, home gardens etc., whose geographic location increases their likelihood of exposure to invaders.	Planned plantings may be less relevant in this context because rapid detection of a new invasion is best achieved through <i>in situ</i> plants occurring across a wider geographic landscape. At sites where biosecurity scientists can have input into long-term landscaping choices, it may be feasible to plant valuable species that augment <i>in situ</i> plants.

in Hawaii), or structured in order to assess colonization and impact from a range of pest taxa on selected valuable species (e.g. Rathe et al. 2014; Roques et al. 2015). The selection of plant species to be assessed faces differing requirements depending on their status. In New Zealand, assessment of commercial crop species requires little if any public approval but the use of native plant species requires consultation and agreement from Māori, particularly where seed is sourced from regions within hapū boundaries.

Challenges to implementation of planned sentinel plant programs include freedom to carry out research in overseas jurisdictions, remote management and monitoring of overseas field trials and data ownership as well as biosecurity, commercial and cultural considerations. Another significant challenge is that an 'absence of evidence is not evidence of absence', i.e., sentinel plants can provide positive evidence of a pest-plant interaction, but the lack of such interaction does not prove conclusively that the interaction will never occur. This is particularly important for plant pathogens, where the conditions supporting infection may be highly specific (Cleary et al. 2016). There is also no guarantee that a pest-plant host association that shows little impact in one environment or region will have a similar impact in another environment or region, because host generality and trophic position (Romanuk et al. 2009), natural enemy release (Colautti et al. 2004; Jeschke et al. 2012); new host plant-pathogen associations (Cleary et al. 2016), or a range of other variables determine the impact of invasive species (Desprez-Loustau et al. 2007; Tylianakis and Romo 2010; Enders et al. 2018).

Over and above these is the challenge of identifying the specimens collected in the studies, especially if they are undescribed, and the cost of carrying out the research. However, this approach may provide a better platform to assess impacts from invaders,

as it allows for experimental replication, site selection, and may give some control over the degree of exposure to the invasive species. Many crop and pasture species are grown worldwide so sentinel plant projects with such species may be easier to implement than for native or endemic species, due to fewer biosecurity and cultural concerns around planned planting of the chosen species at the experiment sites. For these economically important species, the cost of sentinel plant programs that enable pre-emptive mitigation of potential pest impact would undoubtedly result in a positive cost benefit analysis, where the cost of investigation is far exceeded by the economic savings gained from preventing an invasion.

As financial and logistic constraints are likely to limit the scope of sentinel plant programs, so collaboration and information sharing between countries is essential, as the IPSN demonstrates. Regular monitoring of valuable New Zealand species that are present in botanic gardens and arboreta is an important strategy for New Zealand's biosecurity; but particularly for commercial species and those with high cultural value, there is also a case for planned sentinel plant programs whereby these species are grown overseas and regularly monitored for evidence of colonization by exotic invertebrate pests and plant pathogens.

Closing remarks

Botanic gardens can act as early warnings of exotic pests and diseases as well as increasing knowledge of exotic species presence/absence (Barham et al. 2016). Through the IPSN there has been a concerted effort amongst botanic gardens and arboreta to improve expertise in identifying exotic species (Roques et al. 2017), raise awareness, and improve networking amongst botanic gardens and arboreta on a global scale.

Expatriate sentinel plant research using deliberate plantings has shown the potential to identify new insect-plant host associations, while also demonstrating that there can be significant challenges to identifying key phytophagous taxa when taxonomic databases or resources are lacking (Roques et al. 2015; Kenis et al. 2018). Expatriate sentinel plants can take a targeted approach for particular insect taxa (Groenteman et al. 2015) or potentially can target specific plant species or taxa, such as the project to screen *M. excelsa* against the pathogens *C. huliobia* and *C. lukuohia* in Hawaii.

As a working sentinel plants framework, Fagan et al. (2008) investigated various scenarios for selecting and monitoring overseas gardens including a ranking system based on climate matching, local site criteria, plant collection and pest parameters along with the willingness for collaboration. Planned visits by New Zealand biosecurity scientists to survey important plant species for potential invaders will complement participation in such networks, although the frequency and timing of visits should be managed to maximize their value for our national biosecurity goals. Such visits are also necessary to maintain reciprocal biosecurity networks and to identify new research opportunities. Fagan et al. (2008) developed a good template for operational research that may warrant greater investment, although refinements in site selection need to take into account major trading partners, the dynamics of invasion into new regions as well as climate change scenarios.

As a biosecurity pre-border strategy, expatriate sentinel plants provide the advantage of early warning of pest and disease attack, but selection criteria and desired outcomes need to be carefully planned as does a mechanism to prioritize risk. For New Zealand, an area that is lacking from the sentinel plant approach to border biosecurity is their use for commercial crops, particularly for the agricultural sector. The sentinel plant approach can be a component of New Zealand's biosecurity platform, but the global examples presented in this review demonstrate its potential to contribute to New Zealand's biosecurity preparedness. Continued monitoring of plants near likely invasion sites within New Zealand through the HRSS program (Stevens 2008) completes the chain of sentinel plant data, from country of origin to other invaded countries then to New Zealand (Table 2).

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Author contributions

MRM and SM carried out the literature search and wrote the paper, BIPB contributed to writing of the manuscript, and along with LA and NB contributed to collection of specimens and interpretation of data for the project; DT, KBW and JK contributed to the development of the project and review.

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Population responses of common carp *Cyprinus carpio* to floods and droughts in the Pampean wetlands of South America

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Abstract

Common carp (*Cyprinus carpio*) is a global invader that exhibits a wide distribution in Argentina, particularly in shallow lakes and wetlands of the Pampean region. The hydrological conditions of these environments are driven by variations in annual precipitation that determine inter annual changes in water levels leading to flood-drought cycles. The present study focused on understanding the *C. carpio* population responses to annual rainfall regime and long-term flood and drought events in the Ajó wetlands located in the east of the Pampean region. The results of a two-year biological sampling program showed that *C. carpio* feeding rate, reproduction, condition, and recruitment were associated with the hydrological cycle. Otolith derived age structure of the population and back-calculated recruitment strength revealed that extraordinary flooding events generated strong cohorts while dry years resulted in low recruitment. Its long-life span (maximum 14 years in Ajó) coupled with a high fecundity, and broad diet allows *C. carpio* to persist in refugia during dry years and capitalize on wet years when inundation of the floodplain enhances recruitment and facilitates spread. Management and control strategies for this invader should therefore incorporate hydrological variability by promoting intensive removal campaigns during dry years when populations are dominated by large fish confined in remnant water-bodies and, during wet years, carp harvest fisheries should be promoted to reduce population density when increased connectivity is likely to facilitate spread.

Keywords

Cyprinus carpio, exotic species, recruitments dynamics, Pampean region

Introduction

Common carp *Cyprinus carpio* Linnaeus, 1758 is a freshwater fish native to the Ponto-Caspian region (Balon 2004) that, as a result of human introductions, has invaded freshwater ecosystems on all continents except Antarctica (Zambrano et al. 2006; Vilizzi et al. 2015). The invasive success of *C. carpio* is strongly related to its high tolerance to environmental stress (e.g. Edwards and Twomey 1982; Weber et al. 2010; Maiztegui et al. 2016); a generalist feeding strategy (Sibbing 1988; Colautti and Remes Lenicov 2001; García-Berthou 2001); fast growth, high fecundity and early sexual maturation (PANEK 1987; Winker et al. 2011; Vilizzi and Copp 2017). Impacts are linked primarily to their bottom grubbing feeding mechanism which mobilizes sediments, increases turbidity and enhances nutrient availability which have been shown to alter aquatic food webs on multiple trophic levels (Vilizzi et al. 2015). As a result, *C. carpio* is considered to be one of the most pervasive and destructive of freshwater fish (Koehn 2004; Matsuzaki et al. 2009; Kloskowski 2011) and is listed amongst the world's worst 100 invasive alien species (Lowe et al. 2000) therefore controlling *C. carpio* populations is a high priority in many countries. Examples include legislative limitations to movement in South Africa (Ellender et al. 2014), viral biocontrol in Australia (McColl et al. 2018), and direct control using piscicides in the USA (Meronek et al. 1996; Bajer et al. 2009). Although approaches differ between regions and countries, it is widely accepted that an understanding of the biology and population dynamics of *C. carpio* in the invaded environment is critical to the efficacy of control measures (Driver et al. 2005; Bajer et al. 2012; Weber and Brown 2013; Koehn et al. 2017).

In Argentina, *C. carpio* were introduced for ornamental and aquaculture purposes in the second half of the 19th century and the species is currently distributed throughout the center and north of the country (Baigún and Quirós 1985; Maiztegui et al. 2016). In an assessment of environmental suitability, Maiztegui et al. (2016) concluded that more than half of the country, and especially the Pampean region, offered suitable climatic conditions for its establishment. Indeed, in this region *C. carpio* have expanded their distribution over the past 30 years and now occupy many eutrophic and vegetated shallow lakes. Pampean lakes provide considerable ecosystem services that include a valuable recreational fishery for native species (Baigún and Delfino 2003), but are subject to multiple stressors including catchment degradation, habitat modification by man-made infrastructure and species invasions (Baigún and Lombardo 2017). *Cyprinus carpio* are of particular concern as impacts on shallow lakes and floodplains are well-documented (Lougheed et al. 1998; Vilizzi and Tarkan 2015; Huser et al. 2016). Key to the effective management of *C. carpio* is understanding its population dynamics in invaded environments (Driver et al. 2005; Bajer et al. 2012; Weber and Brown 2013; Koehn et al. 2017).

In this study, the Ajó wetlands, located in the eastern Pampean region, were used as a natural experiment to assess how *C. carpio* populations respond to short and long-

term variations in inter annual flood-drought cycles. The Pampean region is characterized by the presence of irregular periods of persistent droughts, interspersed with periods of heavy rainfall that cause severe floods, as happened for example in 1980, 1985, 1993 and 2002 (Scarpati et al. 2011; Scarpati and Capriolo 2013). The hydrological dynamics of the wetlands and their shallow lakes are complex as they are linked to macro-scale episodic events such as El Niño and La Niña events (ENSO) (Bohn et al. 2016; Elisio et al. 2018), and to meso-scale climatic phenomena such as the South American low-level jet stream (Virji 1981), the South American monsoon (Zhou and Lau 1998) and the South American Convergence Zone (SACZ) (Barros et al. 2000). The retraction or expansion of water surface area in the Pampean wetlands is therefore dependent on the intensity and duration of these rainfall events, which in turn affect both the structure and abundance of Pampean fish assemblages (Colautti et al. 2015) and the expansion of alien species including *C. carpio* (Maiztegui et al. 2016).

One of the major areas occupied by *C. carpio* in this region is the Ajó wetlands, a complex and highly variable hydrologic system where *C. carpio* dominate the ichthyofauna both numerically and in biomass (Maiztegui 2016). This study is aimed at understanding how seasonal and inter-annual hydrological variations influence *C. carpio* biological responses and how extraordinary flooding years affect recruitment.

Methods

Study area

Fieldwork was carried out in the Ajó wetlands (36°36.89'S; 57°06.69'W), which are located in the east of the Pampean region (Fig. 1). According to the classification of Thornthwaite (1948), the climate is sub-humid to humid, mesothermal and with scarce to null water deficiency (Carol 2008). Annual average temperature is 15.2 °C and mean annual precipitation is 1078 mm y⁻¹, with 1634 and 421 mm y⁻¹ being the maximum and minimum registered between 1887 and 2002, respectively (Carol 2008). Rainfall is seasonal with peaks during the austral spring and summer (Carol 2008). Hydrologically, the area is a complex and heterogeneous system that includes an estuarine brackish water zone and an inland freshwater zone. In the estuarine zone, the Ajó River is the main natural water course that drains into the Río de la Plata estuary (200 km from Buenos Aires City). The main water courses of the freshwater portion are Canal Dos (C2) and Canal el Palenque (CP) (Fig. 1), which are flood-gate regulated man-made drainage canals for de-watering flooded lands during high rainfall conditions affecting the Ajó River. Both canals comprise a complex network of small creeks with semi-permanent water that are temporarily connected depending on water levels (Carol 2008). The floodgates are generally closed to prevent the inflow of brackish water from the Ajó River estuary, retaining freshwater in the wetlands regulating the flows towards the bay depending on the hydrologic period in the area (Carol et al. 2012; 2013).

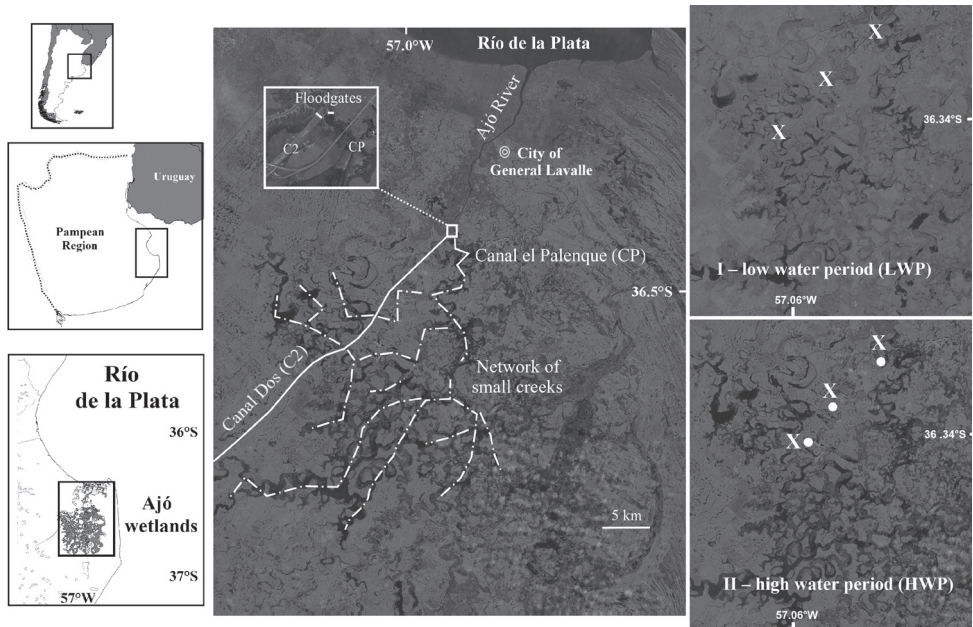


Figure 1. Geographical location of the Ajó wetlands in the Pampean region, indicating the main water courses: Ajó River, Canal Dos, Canal el Palenque (with detail of their respective flood gates) and the main streams of the network of small creeks. Satellite images from the Ajó wetlands during two contrasting hydrological scenarios: **I** low water period (LWP), sampling sites in Canal Dos (X) **II** high water period (HWP), sampling sites in Canal Dos (X) and the network of small creeks (white circle).

During drought periods, water levels in the C2 and CP are reduced and the network of small creeks becomes dry; meanwhile, during floods, the mean depth of the Ajó wetland increases up to 2.5 m (Carol 2008). In intermediate periods, the water level of the network of small creeks undergoes a periodic and unstable hydrologic pattern, connecting or disconnecting with the canals depending on the annual precipitation and evapotranspiration regime and the retained water in the wetland.

Water level periods and sampling program

Sampling was conducted monthly from April 2009 to March 2011. This included low water periods (LWP) from April to June 2009 and January to February 2010 during which water levels at the network of small creeks were below 0.2 m, and high water periods (HWP) from July to December 2009 and from March 2010 to March 2011 when the water level of these environments was above 0.2 m. During LWP *C. carpio* specimens were sampled only from C2 (Fig. 1I) but during the HWP they were collected in C2 and also in the network of small creeks (Fig. 1II). Monthly water balance was calculated as the difference between precipitation records provided by the mete-

orological station located in the city of General Lavalle (P) and the historic monthly evapotranspiration regime (EVT) (Carol et al. 2015).

Fish were collected using fyke nets (Colautti 1998) with a 5 mm mesh end, 1.2 m wide \times 0.8 m deep opening, and a 0.8 m height \times 20 m long guiding net. In addition, a 70 m long beach seine with a 35 mm bar mesh was used. Fyke nets were deployed at night while seine netting was conducted during the day; it is important to note the use of these fishing gears was applied with the aim to encompass the maximum possible range of L_T for *C. carpio*. All captured fish were measured (L_T , nearest mm) and weighed (W_T , nearest g). The total length frequency distribution (L_T) of each fishing gear was contrasted by means of the non-parametric *Kolmogorov-Smirnov* test. Monthly, a maximum of 40 specimens ($L_T > 350$ mm) were euthanised by severing the spinal cord and the asteriscus otoliths were removed and stored dry. The mass of the gonads (W_G , g), digestive tract (W_{DT} , g) and the eviscerated body (W_S , g) were obtained for each fish. The foregut (i.e. portion between the esophagus and the first major bend of the digestive tract) was then dissected out and the degree of fullness (DF) assessed according to the subjective scale recommended by Hyslop (1980) as either: empty (0), 1/3 full (1), 2/3 full (2) or full (3). Gut contents were preserved in buffered 10% formalin for later diet composition analysis.

Reproduction and condition

To describe the gonadal cycle and determine the length of the spawning season, the gonadosomatic index (GSI) was calculated as $GSI = W_G / W_T * 100$, and assessed within the context of water level (m) and temperature ($^{\circ}C$) measured at C2. The relative condition factor (K_N ; Le Cren 1951) was calculated as: $K_N = W_T / W_P$, where W_P is the length-specific mean weigh predicted by the population's W_T and L_T relationship and regressed against the monthly water level variation.

Gut contents

The repletion index (RI), calculated as $RI = W_{DT} / W_S * 100$, was used to determine monthly variation in feeding intensity throughout the study period. In the laboratory, monthly samples were assessed for diet composition. To this end, foregut contents were homogenized with a magnet shaker, and a sub-sample of 1 ml obtained by means of a pipette. This sub-sample was evaluated and analyzed under a stereomicroscope (Olympus SZ61, $\times 2$) in a Sedgwick-Rafter (APHA 1995) counting chamber. Consumed items were discriminated based on their origin (vegetal or animal). In the case of vegetal material, it was possible to differentiate between vegetal debris and remains of seeds; whereas animal items were classified into major taxonomic categories. All identifiable items were then quantified volumetrically through a graduated measuring capsule (Hellawell and Abel 1971; Hyslop 1980) and this procedure was performed

in triplicate for each stomach. Once all the dietary items were identified together with their respective volumes in the samples, their abundance was extrapolated to the rest of the known volume of the gut contents.

Average monthly values of RI and the percentages of DF assigned in each month (DF%) were plotted against time to determine annual variability in feeding intensity. In addition, analyses were also undertaken to assess for differences between samples obtained from C2 (LWP), C2 (HWP) and the network of small creeks, to assess whether site or water level influenced feeding intensity.

A General Linear Model (GLM) analysis was performed to assess the influence of water level, location and season (month) over RI. A Poisson distribution for response variable and logit-link function were used to develop the models. The adjustment of GLM parameters was evaluated using the Student's t-test.

In order to detect temporal trends in length structure and recruitment events during the sampling period, monthly L_T -frequencies distributions corresponding to each sample date were graphed in time sequence.

Ageing

Asteriscus otoliths (Vilizzi 2018) were embedded in clear epoxy resin blocks with their nuclei aligned and transversely sectioned along the dorso-ventral plane through the primordia using a cutting saw. Otolith sections (0.4 mm) were mounted on microscope slides and analyzed under a microscope using transmitted light by two individual readers without knowledge of the date of capture or fish length. The number of annuli was determined by counting the opaque zones along an aging transect from the nucleus to the edge of the ventral portion of the sectioned otolith (Brown et al. 2004). If age estimates between readers were identical, then the count of growth zones was accepted, but when they differed, a third reading was conducted.

As the rate at which growth zones are deposited in *C. carpio* otoliths can differ between localities (Winker et al. 2010) growth zone deposition rate in the Ajo wetlands population was validated using edge analysis (Campana 2001). To this end, the optical appearance of the edge of each otolith was assessed, and categorized as either optically opaque (1) or translucent (0) (Fig. 2). The proportion of otoliths with an opaque zone present at the edge was then arranged on a monthly basis, and the time of annulus formation was estimated using periodic logistic regression (See Winker et al. 2010).

Based on otolith readings and L_T measurements, an age-length key (ALK) for the *C. carpio* population under study was obtained ($n = 177$). The integrated L_T frequency distributions of the months of slow growth (according to edge analysis) for both years of sampling were transformed to age by means of the ALK, thereby obtaining two age structures for the population. These were analyzed to determine the mean relative representation of each year class (cohort) and then, based on the documented in-

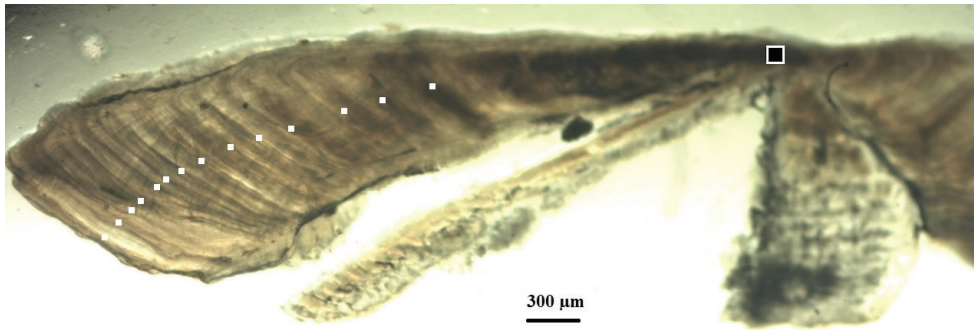


Figure 2. Photomicrograph of a sectioned asteriscus otolith, indicating the position of the nucleus (black square) and the marked annuli (white squares).

stantaneous natural mortality rate for *C. carpio* in Pampean region $M = -0.784 \text{ yr}^{-1}$ (Colautti 1997), the strength of each year-class was back-calculated as an estimator of each recruitment. Such calculation was obtained according to the following equation: $N_0 = N_t / e^{0.784t}$, where N_0 is the number of individuals at time $t = 0$, N_t is the number of individuals at time t and $t = \text{years}$. To demonstrate the response of *C. carpio* population to hydroperiods, estimated annual recruitment were regressed against the respective yearly precipitations in the region (Diovisalvi et al. 2010; Colautti et al. 2015).

Results

Water level variation

The monthly water level variation of C2 and the network of small creeks is presented together with the hydrological balance regime (P-EVT), evidencing the alternation, duration and timing of hydrological scenarios LWP and HWP (Fig. 3). It is important to note that during the sampling period precipitation was considered average.

Sampling results and fishing gear selectivity

A total of 2363 fish measuring between 90 and 800 mm L_T and weighing between 12 and 6820 g W_T were sampled during the study. Fyke nets collected 414 *C. carpio* individuals (90–715 mm L_T) and the beach seine nets captured 1949 specimens (125–800 mm L_T). Although fyke nets sampled juvenile fishes more effectively, the length frequency distributions fish of ≥ 300 mm L_T did not differ between gears (Kolmogorov-Smirnov, $D = 0.09$; $p = 0.098$). Most fish (81.9%) were obtained from C2 and the remainder (18.1%) from the network of small creeks.

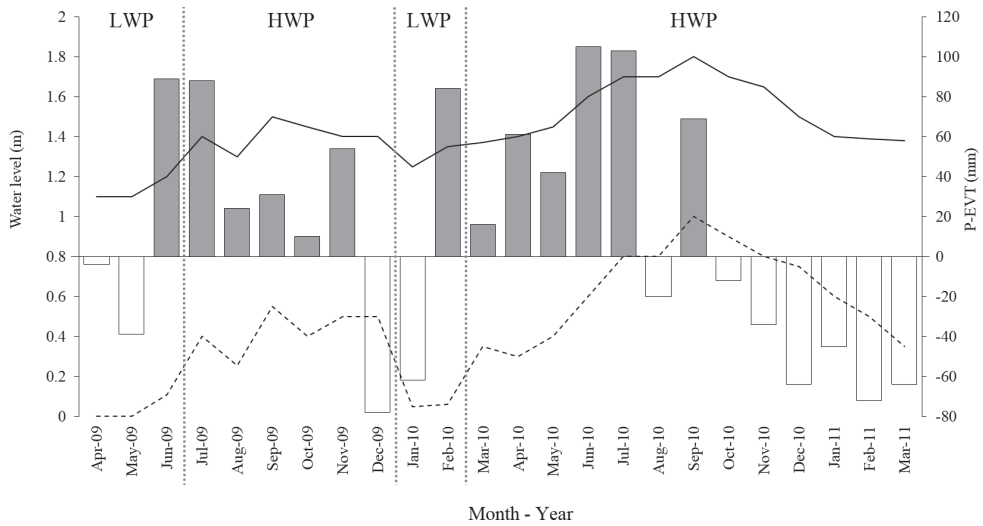


Figure 3. Monthly water level of Canal Dos (continuous line) and the network of small creeks (dotted line), indicating low water periods (LWP) and high water periods (HWP). Bars indicate the monthly water differences (mm) between precipitation (P) and evapotranspiration regime (EVT), grey bars represent months with hydrological excess and white bars represent months with hydrological deficit.

Reproduction

Female GSI values exhibited a wide range of monthly variation, showing a differential gonadal ripening through the study (Fig. 4a). Higher values of GSI were observed during the HWP's regardless of the year under consideration, but the development of GSI differed between years. During 2009, a seasonal pattern was observed whereby the average GSI values increased until reaching their maximum during early spring in concordance with water temperature of 16.3 °C. Thereafter, GSI decreased to a minimum in the late spring. In contrast, in 2010, two GSI peaks were noted, the first occurring in winter with water temperatures of 11.4 °C and the second in early summer at 23.3 °C (Fig. 4a).

Male GSI also showed wide monthly variation with peaks during autumn and winter (Fig. 4b). Differences between years were, however, not detected as clearly as with female fish. Male GSI typically increased during autumn (5–8) and winter (6–8) and decreased thereafter.

Gut contents

Cyprinus carpio feeding intensity (Fig. 4c) showed that they fed more actively during the months when the water levels were highest regardless of the season or year (Fig. 3). The 65% of analyzed digestive tracts ($n = 112$), corresponding to specimens with L_T that ranged between 400–800 mm, demonstrated that *C. carpio* had an omnivorous

Table 1. Diet of *Cyprinus carpio* in the Ajó wetlands: percent number in volume (Vol%) phylogenetically arranged, increasing in taxonomic complexity. Number of foreguts ($n = 73$, including specimens captured in Canal 2 during low water periods ($n = 16$), high water periods ($n = 38$) and in the network of small creeks ($n = 19$). Total volume of prey items = 20.45 ml.

Food categories	Vol%
Algae	1.9
Seeds	23.9
Plant debris	50.1
Rotifera	<0.1
Statoblasts of Bryozoa	<0.1
Remains of Mollusca	0.4
Copepoda	3.0
Cladocera	5.0
Ephipids of Cladocera	0.9
Ostracoda	0.9
Amphipoda	0.4
Decapoda	1.8
Remains of Crustacea	0.1
Larvae of Insecta	4.8
Remains of Insecta	0.5
Acari	<0.1
Remains of Arthropoda	5.4

diet with a broad trophic spectrum including both plant and animal prey (Table 1). In turn, the GLM analysis suggests that the RI was mainly influenced by the water level of C2 over location or time of the year, explaining 27 % of the RI variation ($p < 0.05$).

Changes in fish condition were closely linked to water level and feeding intensity, being detected the lower values of monthly average RI and K_N during LWP, and the higher values during HWP (Fig. 4.d). There was a positive linear relationship between the monthly K_N values and the water level in C2 ($y = 2.5804x - 1.2911$, $r^2 = 0.7138$). In addition, the analysis showed significant differences in K_N taking into account sites and water level periods (ANOVA, $F = 33.74$; $p < 0.05$), exhibiting fish from C2 (LWP) a lower K_N than C2 (HWP) and the network of small creeks ($p < 0.05$). During HWP, K_N did not differ between environments d ($p = 0.161$).

Monthly length structure

The structure of monthly length frequency distributions demonstrated that during 2009 the population consisted exclusively of adult specimens ($L_T > 350$ mm, Maiztegui 2016), and this was regardless of water level period or sampled location. In the summer of 2010, the length structure of the population experimented a change by inclusion of a large number of age-0 individuals ($L_T < 350$ mm) (Table 2; Fig. 5). This cohort

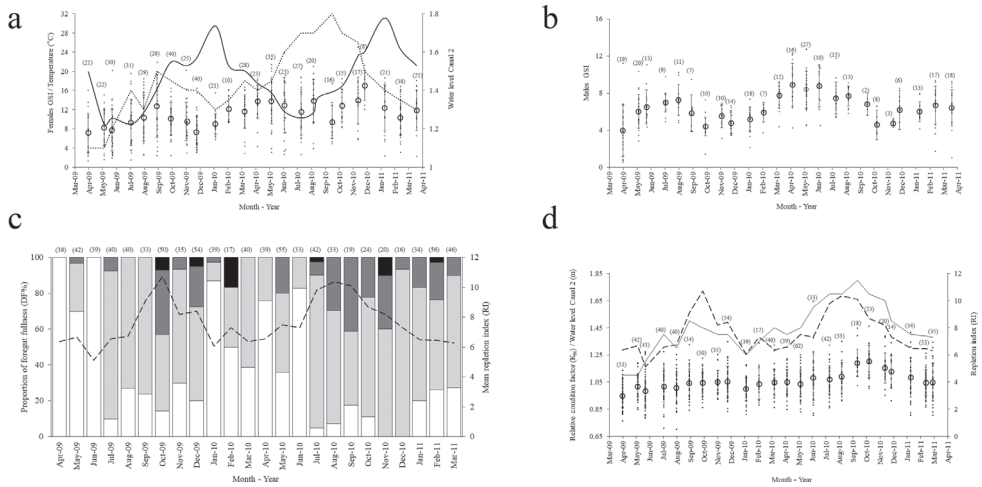


Figure 4. **a** Monthly changes in female GSI of *C. carpio*, presenting observed values (circles), mean (big circles) and standard deviations together with temperature (continuous line) and water level (dotted line). Numbers above (in parentheses) refer to the number of analyzed individuals in each month **b** Monthly changes in male GSI of *C. carpio*, presenting observed values (circles), mean (big circles) and standard deviations. Numbers above (in parentheses) refer to the number of analyzed individuals in each month **c** Monthly degree of fullness proportion (DF%) of *C. carpio*: white bar = 0 (empty), light grey bar = 1 (1/3 full), dark grey bar = 2 (2/3 full) and black bar = 3 (full); average monthly repletion index (RI) (dotted line). Numbers above bars (in parentheses) refer to the number of *C. carpio* analysed in each month for RI **d** Monthly changes in K_N of *C. carpio*, showing observed values (circles), mean (big circles) and standard deviations; water level variation in Canal Dos (continuous line) and the repletion index (RI) (dotted line). Numbers above (in parentheses) refer to the number of specimens analyzed every month.

was clearly identified through the end of our study (March 2011) using the length structure analysis. The lack of juvenile fish in the previous year indicated inter annual variability in recruitment success.

Age structure

The aging analysis using otoliths from 177 fish demonstrated that the population's age structure comprised age classes between 0 and 14 years. Two main groups were recognized as being the most dominant in the sample, the first from 0 to 1 years ($n = 47$) and the second comprised of fish aged between 6–9 years ($n = 83$) (Table 2). According to observed data of the monthly edge analysis asterici and the predicted model, fitted by the logistic periodic regression ($\hat{O}_i = -1.075 + 1.038 \sin(2\pi Mi/12 - 1) + 1.107 \cos(2\pi Mi/12 - 1)$, $r^2 = 0.78$; $p > 0.05$), the temporal proportion of opaque zone depositions (\hat{O}_i) for the monthly periods (Mi) reached maximum values once a year from May to July (Fig. 6).

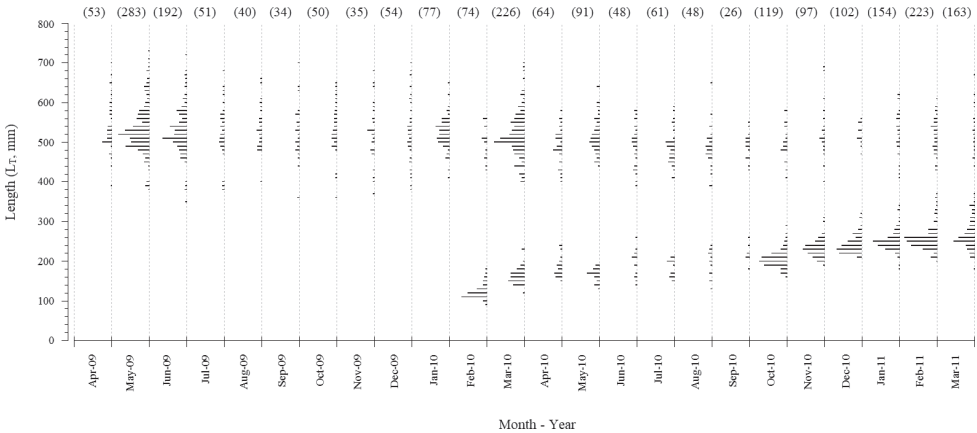


Figure 5. Monthly length-frequency distribution of the *C. carpio* population during the sampling period in the Ajó wetlands. In parentheses, the number of individuals captured in each month.

Table 2. Age length key (ALK) obtained for common carp *Cyprinus carpio* in the Ajó wetlands. Number of specimens analyzed ($n = 177$), discriminating the age assigned for a particular length category.

L ₁ (mm)	Cyprinus carpio age														
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14
150	3	1													
200	17	6													
250	7	7	1												
300	1	3													
350		1	4	1											
400		1	3	3	1	1									
450				6	1	1		1							
500				1	2	3	5	6	6	4					
550				1			5	6	8	3	1				
600					1	1	5	2	5	5		1		1	
650					1		1	2	6	1	2	3			1
700							2	1	2	6	4		1		1
750										1					

The relative strength of the annual cohorts of *C. carpio* in the population obtained by back-calculation based on population age structure, showed that an extraordinarily strong recruitment occurred during years of high annual precipitation, specially 2001–2002, while only weak cohorts were derived from years when rainfall was low (Fig. 7a). The regression between these variables from 2001 to 2009 (Fig. 7b) was portrayed by a positive linear relationship ($y = 0.0225x - 15.713$; $r^2 = 0.79$), demonstrating that the *C. carpio* recruitment dynamic in the region is indeed strongly regulated by the annual precipitation regime.

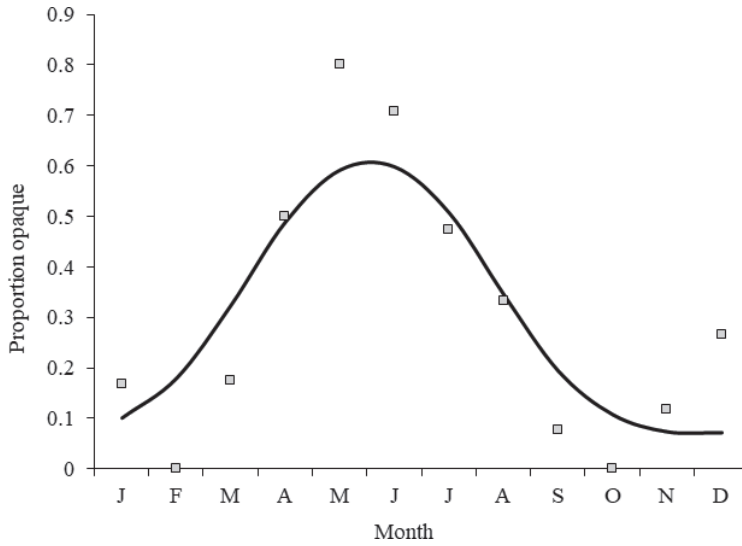


Figure 6. Monthly proportion of otoliths with an opaque zone on the margin for *C. carpio* in the Ajó wetlands (gray squares) and the predicted annual cycle of opaque deposition using logistic periodic regression (line).

Discussion

This study represents the first attempt to understand how *C. carpio* biological responses and population dynamics are synchronized with the yearly seasonality and modulated by multi-annual hydrological regime in temperate South American wetlands.

Here, as is the case elsewhere (e.g., Balon 1995; Stuart and Jones 2006; Penne and Pierce 2006), *C. carpio* spawning occurs between spring and summer when water temperature exceeds 15 °C and when shallow vegetated areas are available (Horvath 1985; Sivakumaran et al. 2003; Smith and Walker 2004; Winker et al. 2011). In the Ajó wetlands, female GSI followed a predictable seasonal pattern but the frequency, timing and synchronization of spawning differed between years (Fig. 4a). Spawning appears closely related to water levels during spring with more extended spawning during flood years and more protracted and dispersed spawning frequency during drought years. This was consistent with research conducted in the wetlands in the Camargue in France (Crivelli 1981), the Guadalquivir in Spain (Fernández-Delgado 1990), Victoria (Sivakumaran et al. 2003) and Barmah forest in Australia (Brown et al. 2005).

Cyprinus carpio diet in the present study was consistent with omnivorous feeding mostly associated with the benthos as observed elsewhere (e.g., Sibbing 1988; Sidorke-wicz et al. 1998; Colautti and Remes Lenicov 2001; García-Berthou 2001). Feeding activity was related to the water level, reaching maximum values during HWP, suggesting that adult *C. carpio* not only undertook lateral movements into recently inundated areas for spawning but also for access to new food resources. During low water levels, *C. carpio* were restricted to the C2 area where feeding opportunities were

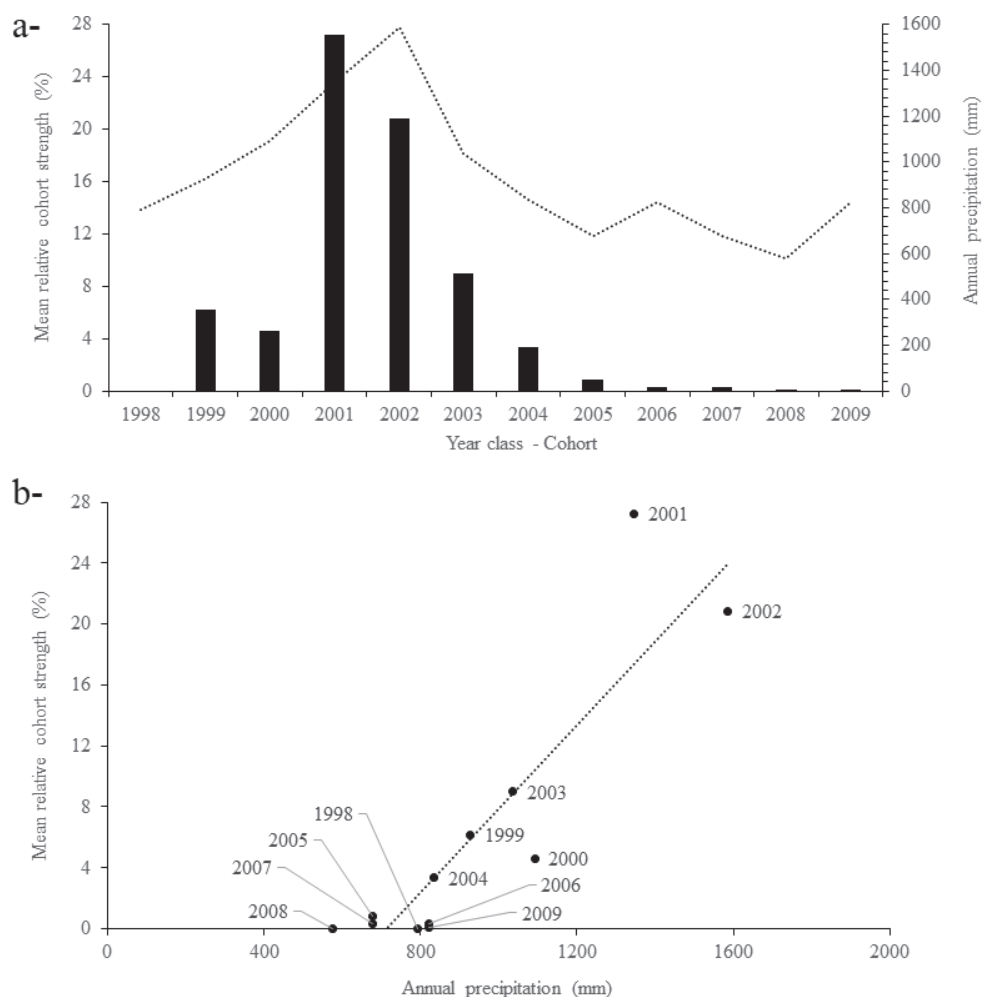


Figure 7. a Mean relative cohort strength (%) of *C. carpio* in the Ajó wetlands from 1998 to 2009 and annual precipitation in the Pampean region for the same time period (dotted line) **b** Regression between the annual precipitation of the Pampean region and the mean relative cohort strength (%) from the *C. carpio* population in the Ajó wetlands from 2001 to 2009. Dotted line indicates the model fitted to the dataset.

limited. Such observations are reinforced by the RI and DF% analysis which showed that *C. carpio* fed more intensely during HWP, in agreement with similar results showing the dependence of feeding activity on the hydrological regime (Jones and Stuart 2009; Daniel et al. 2011; Taylor et al. 2012). The influence of the habitat selection and water level was reflected by the variability of the repletion index, suggesting that food supply was at least partially dependent of entering into flooded habitats during regular high water levels. Increased feeding activity was reflected in body condition (K_N) which regressed positively with water level. On the other hand, during LWP, the gut content analysis also showed that feeding rate, and, by inference, food availability, was low.

During such periods *C. carpio* condition factor was the lowest documented during the study, probably associated with restriction to food resources in peripheral areas and the possible increase in intraspecific competition as the population was concentrated and restricted to C2. The connection between habitats facilitated by the HWP provided access to increased feeding opportunities that resulted in better condition, growth and increased recruitment success. As a result of the inherent climatic variability, the recruitment pattern in the Ajó wetland was more erratic than the regular patterns described in the Barmah Forest in Australia (Brown et al. 2005) and shallow lakes of South Dakota in USA (Weber and Brown 2013) but similar to the unstable interconnected aquatic environments of the Upper Mississippi River basin (Bajer et al. 2012).

Age data suggests that strong recruitment occurred during years of high annual precipitation (Fig. 7b). This study indicates that the pattern of regular and exceptional recruitment following rainfall and flooding events (Fig. 7a) is supported by age structure data which demonstrates that the population is dominated by individuals between 7 and 9 years of age, which is likely a result of strong recruitment during the exceptional flooding in 2002 (Scarpatti and Capriolo 2013; Colautti et al. 2015). *Cyprinus carpio* are periodic life-history strategists (Winemiller 1992; Winemiller and Rose 1992) that, as a result of their long life span and high fecundity (King et al. 2003; Bajer and Sorensen 2010; Weber and Brown 2013), are able to overcome recruitment limitations during unfavorable years by maximizing their reproductive output when conditions are favorable. This storage effect (Warner and Chesson 1985) has also facilitated the persistence of *C. carpio* population in Ajó wetlands where weak annual recruitment and long starvation periods associated with regional droughts are compensated by strong recruitment during wet years.

This study demonstrated that increasing water levels promoted lateral migrations of *C. carpio* into peripheral habitats to take advantage of the network of small creeks as a nursery area, predation refuge for juveniles, and as a spawning and feeding grounds ground for adults. In addition, macro-scale climatic events strongly modulate *C. carpio* population dynamics in the Ajó wetlands, with wet and dry years enhancing and restricting recruitment respectively. We conclude that the *C. carpio* life-history in relation to climatic conditions has relevance for the control of this species in the Pampean wetlands. Human demands for water have resulted in the increased construction of infrastructure and land use changes to support agricultural expansion in the Pampean wetlands (Baldi and Paruelo 2008; Gras 2009). Water infrastructure development in the Pampean plain could represent a major driver of *C. carpio* persistence and dispersal because man-made channels and reservoirs could provide suitable habitats during prolonged drought periods for the persistence of *C. carpio* (as observed in C2) and could act as stepping stones enhancing species dispersal when these environments become connected during large flood periods. Management and control strategies for this invader should therefore incorporate hydrological variability by promoting intensive removal campaigns during dry years when populations are dominated by large fish confined in remnant waterbodies and, during wet years *C. carpio* harvest fisheries should be promoted to reduce population density when increased connectivity is likely to facilitate spread.

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Assessing the ecological and societal impacts of alien parrots in Europe using a transparent and inclusive evidence-mapping scheme

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Abstract

Globally, the number of invasive alien species (IAS) continues to increase and management and policy responses typically need to be adopted before conclusive empirical evidence on their environmental and socioeconomic impacts are available. Consequently, numerous protocols exist for assessing IAS impacts and differ considerably in which evidence they include. However, inclusive strategies for building a transparent evidence base underlying IAS impact assessments are lacking, potentially affecting our ability to reliably identify priority IAS. Using alien parrots in Europe as a case study, here we apply an evidence-mapping scheme to classify impact evidence and evaluate the consequences of accepting different subsets of available evidence on impact assessment outcomes. We collected environmental and socioeconomic impact data in multiple languages using a “wiki-review” process, comprising a systematic evidence search and an online editing and consultation phase. Evidence was classified by parrot species, impact category (e.g. infrastructure), geographical area (e.g. native range), source type (e.g. peer-review), study design (e.g. experimental) and impact direction (deleterious, beneficial and no impact). Our comprehensive database comprised 386 impact entries from 233 sources. Most evidence was anecdotal (50%). A total of 42% of entries reported damage to agriculture (mainly in native ranges), while within Europe most entries concerned interspecific competition (39%). We demonstrate that the types of evidence included in assessments can strongly influence impact severity scores. For example, including evidence from the native range or anecdotal evidence resulted in an overall switch from minimal-moderate to moderate-major overall impact scores. We advise using such an evidence-mapping approach to create an inclusive and updatable database as the foundation for more transparent IAS impact assessments. When openly shared, such evidence-mapping can help better inform IAS research, management and policy.

Keywords

evidence base, impact assessment, invasive alien species, monk parakeet (*Myiopsitta monachus*), ring-necked parakeet (*Psittacula krameri*), Psittaciformes

Introduction

The number of human-mediated species introductions has been increasing worldwide (Seebens et al. 2017), with invasive alien species (IAS – the subset that cause negative impacts) identified as a significant environmental, societal and economic threat (Pimentel et al. 2005; Vilà et al. 2010; Bellard et al. 2016; Paini et al. 2016; Bacher et al. 2018). As an international response, Aichi Biodiversity Target 9 of the Convention on Biological Diversity (CBD) states that, by 2020, IAS and their pathways should be identified and prioritised and priority species controlled or eradicated (CBD 2010). Legal instruments have been established to meet this target, including European Union (EU) legislation (Regulation No. 1143/2014). This regulation aims to set a common standard for combatting IAS across political jurisdictions at a multinational scale, underpinned by a list of IAS of Union Concern (Tollington et al. 2017; Carboneras et al. 2018). Robust prioritisation tools are therefore essential to target the limited available resources towards the most relevant species (i.e. those that are or will likely become invasive). Consequently, the last decade has seen the development of a diverse range of IAS risk assessment protocols which, collectively, evaluate entry, establish-

ment, spread and impact – differing considerably in their scope, approach, strengths and limitations (Roy et al. 2018).

Quantifying the magnitude of IAS impacts remains particularly challenging for various reasons (see Jeschke et al. 2014; Courchamp et al. 2017; Bartz and Kowarik 2019). In practice, most impact assessment protocols rely on searching for evidence of previous records of invader impacts. However, one important, but arguably under-recognised, way in which available protocols differ is in the type of evidence they consider. Firstly, in some protocols impact evidence needs to originate from the invaded area under assessment, but in other protocols can also be derived from other non-native ranges, species' native ranges, or even from captivity/cultivation. Secondly, some protocols only accept peer-reviewed evidence, whereas others allow inclusion of grey literature or expert opinion. Thirdly, study design is rarely differentiated, risking largely anecdotal observations to be considered as equally informative as experimental studies. Finally, although impacts of IAS can be positive or negative (Ricciardi et al. 2013, Simberloff et al. 2013), the fact that a noticeable change has occurred is often viewed negatively. Accordingly, most protocols focus on deleterious impacts and only few acknowledge so-called 'beneficial impacts' (Bartz and Kowarik 2019), despite their importance for making informed management decisions (Schlaepfer et al. 2011; Branquart et al. 2016). Efforts are therefore being made to produce standardised and globally applicable impact assessment protocols; e.g. Environmental Impact Classification of Alien Taxa, EICAT (Blackburn et al. 2014). Although available protocols increasingly require assessors to carefully document which studies are selected to provide information for impact assessments (e.g. Hawkins et al. 2015), limited attention has been paid to developing strategies for collating, organising and structuring this evidence in a transparent, openly accessible, inclusive and standardised manner.

An assessment of the consequences of accepting different types of evidence data on impact assessment outputs has yet to be conducted. However, the current disparity in accepted evidence potentially leads to ambiguous, difficult-to-repeat and even contested impact assessment outcomes (Kumschick et al. 2017; Matthews et al. 2017), when instead, it is vital that IAS management and policy decisions are underpinned by a robust and transparent impact assessment (Courchamp et al. 2017; Vanderhoeven et al. 2017). This would, for example, help minimise stakeholder and societal conflicts arising from IAS control actions and is especially important for managing charismatic invaders (IAS with widespread popular appeal), such as many pet bird species, given the often strong public objection against their control (Crowley et al. 2019). Consequently, we suggest the implementation of a general scheme that allows for an inclusive, transparent and reproducible mapping and appraisal of the evidence entering any IAS impact assessment (Table 1, Suppl. material 1: Fig. B1). Briefly, this scheme arranges the evidence along four different axes of variation. First, it discriminates the geographical relevance of the area from which the evidence is taken ("geographical area"). Second, evidence is classified according to where it is published

Table 1. Impact evidence variables and metadata recorded for each evidence entry in this study. When assignment to a single category is difficult, this can be flagged in the comments column or the entry can be given a dual coding.

Impact evidence variable	Levels	Description
Species	11 parrot species	Any one of the 11 parrot species designated “alien” status in Europe by EASIN (see Table 2).
Impact category	GISS categories (see Suppl. material 1: Appendix B3 for descriptions)	Environmental: (1) competition, (2) transmission of diseases or parasites, (3) herbivory and (4) impacts on ecosystems. Socioeconomic: (5) agricultural production, (6) animal production, (7) forestry production, (8) human health, (9) human well-being, and (10) human infrastructure and administration.
Geographical area	European	Evidence from Europe (see Suppl. material 1: Appendix B2 for definition)
	Other non-native range	Evidence from any other non-native range
	Native range	Evidence from native range
	Captive	Evidence from captivity (regardless of country)
Actual / potential impact	Actual	Evidence from within assessment area (here: Europe).
	Potential	Evidence from native range, other non-native range or captivity.
Source type	Peer reviewed	Peer-reviewed publications, academic books and book sections.
	Not peer-reviewed (grey literature)	PhD/Master’s thesis, governmental/NGO reports, conference proceedings, magazine/newspaper article, webpage.
	Unpublished data	Personal communication, personal observation, unpublished data.
Study design	Experimental	Qualitative/quantitative study using a qualitative/quantitative experimental manipulation of the mechanisms by which the invader is presumed to have an effect (allows inference on magnitude and causality of impact).
	Non-experimental	A study that uses a qualitative/quantitative, but non-experimental, scientific sampling design (allows inference on magnitude but not causality of impact).
	Anecdotal	Casual observation acquired without a sampling design (only allows inferences on presence/absence of impact, not on magnitude or causality).
	Indirect report	Impact not observed by person reporting it or sources that do not report primary data (impacts cannot be verified).
Impact direction	Deleterious	Evidence entry explicitly reports deleterious impact.
	Beneficial	Evidence entry explicitly reports beneficial impact.
	No impact	Covers cases where no impact is explicitly reported.
Metadata	Source identifier; Evidence entry identifier (for entries coming from a source containing multiple pieces of evidence); Year in which evidence was made available; Source language; Geographical region; Country; Detailed location of reported impact (e.g. nearby city or coordinates); Full bibliographic reference of source; Expert assessor name; and a short written description of relevant evidence.	

(“source type”), in order to provide some structure along the gradient of reliability of sources. Third, it distinguishes the methodological approach that was used to obtain the impact evidence (“study design”), since these differ in what types of inferences

can be made with respect to causality and magnitude of impact. Finally, the scheme records whether the impact is deleterious, beneficial or no impact detected (“impact direction”). Such an initial classification of reported impacts subsequently allows stakeholders to apply different assessment protocols or other criteria to the evidence and then to evaluate how this affects the final impact scoring. Here, we explore the utility of classifying the evidence base in this manner using alien parrot species (Psittaciformes) within Europe.

Parrots are amongst the most prominent pet birds worldwide and the large volume of pet-trade driven exports followed by escape and release has resulted in the establishment of numerous alien populations worldwide (Reino et al. 2017). Alien parrots have repeatedly been listed as a cause for concern; e.g. the ring-necked parakeet (RNP, *Psittacula krameri*) is considered amongst the 100 worst IAS in Europe (DAISIE 2009). Parrots are also a charismatic species group and since alien parrots currently mainly concentrate in urban areas where they were first introduced (Pârâu et al. 2016; Mori et al. 2019), they are often encountered by the general public – attracting both concern and support. Thus, alien parrots represent a complex socio-environmental conflict (Luna et al. 2019).

The European Alien Species Information Network (EASIN) recognises 11 alien parrot species in the EU (Table 2) and only two of these species are currently listed as having “high impact” (RNP and monk parakeet: MP, *Myiopsitta monachus*), with the remainder designated “low/unknown impact”. Across Europe, the RNP has a minimum of 90 established breeding populations and has grown from several tens of individuals in the 1970s to at least 85,000 birds in 2015 (Strubbe and Matthysen 2009; Pârâu et al. 2016). The MP is found in 179 municipalities across Europe, with its stronghold in Madrid and Barcelona. The current population of 23,000 individuals originates from a few tens of individuals recorded breeding in the mid-1970s (Strubbe and Matthysen 2009; Postigo et al. 2019). There have been a number of studies which have assessed alien parrot impacts alongside other species (e.g. Evans et al. 2016) and several additional studies have reviewed (but not quantified) impacts of alien parrots (e.g. Menchetti and Mori 2014). The findings of these studies (Suppl. material 1: Table A2) demonstrate substantial uncertainties and conflicting results regarding the environmental and socioeconomic impacts of alien parrots, partly due to differing protocols and evidence bases.

Alien parrot species thus represent an excellent group to explore the added value of the above-mentioned evidence-mapping scheme for conducting impact assessments (Table 1 and Suppl. material 1: Appendix B1). Here, we conduct a systematic and comprehensive assessment of existing evidence of environmental and socioeconomic impacts by alien parrots, on a continental scale. The resulting evidence base was subsequently used to (1) provide insights on how the evidence-mapping scheme can be used to further improve impact assessments and (2) identify the main types of alien parrot impacts, whilst evaluating the quantity, quality, spatial distribution and severity of the underlying evidence.

Table 2. Current status of the 11 alien parrot species within Europe (as recognised by EASIN; <https://easin.jrc.ec.europa.eu/>). Information obtained from GAVIA database (Dyer et al. 2017) unless otherwise stated. Only countries where species have been assigned “Breeding” or “Established” status are included under “Other alien range”, whereas countries assigned “Unknown” or “Died Out” status are also included for European range.

Species name	Native range	Alien European range (<i>Unknown, Died out</i>)	Europe populations (size)	Other alien range: breeding/ established	Impact status (EASIN)
Yellow-collared lovebird (<i>Agapornis personatus</i>)	Tanzania	France, Spain	Unknown	Burundi, Kenya	Low/ unknown
Turquoise-fronted amazon (<i>Amazona aestiva</i>)	Argentina, Bolivia, Brazil, Paraguay	Italy, Spain (<i>Germany, Switzerland</i>)	Genoa, Milan, Valencia (Mori et al. 2013, 2017)	USA	Low/ unknown
Yellow-crowned amazon* (<i>Amazona ochrocephala</i>)	Central and South America	(<i>Germany, Italy</i> : Mori et al. (2013, 2017))	Genoa, Milan, Stuttgart (50 since 1984) (Mori et al. 2013, 2017)	Barbados, Cayman Islands, Mexico, Netherlands Antilles, Puerto Rico, Trinidad, USA	Low/ unknown
Blue-crowned parakeet (<i>Araucaria acuticaudata</i>)	South America	Spain, (<i>UK, Italy</i> : Mori et al. 2013)	Barcelona (8 pairs/25 birds) (Anton et al. 2017), Sabadell, Valencia. Less than 200 birds across Europe	USA	Low/ unknown
Red-masked parakeet (<i>Araucaria erythrogenys</i>)	Ecuador, Peru	Spain	Barcelona, Seville, Valencia	Cayman Islands, USA,	Low/ unknown
Mitred parakeet (<i>Araucaria mitrata</i>)	Argentina, Bolivia, Peru	Spain	Barcelona (100–150 birds) (Anton et al. 2017), Valencia, Mallorca.	Puerto Rico, USA	Low/ unknown
Budgerigar (<i>Melopsittacus undulatus</i>)	Australia	Greece (<i>Germany, Spain, Turkey, Austria, Belgium, Italy</i> (Biondi et al. 2005), <i>UK</i>)	Unknown	Cayman Islands, Dominican Republic, Guadeloupe, Hong Kong, Jamaica, Japan, Mexico, Namibia, Oman, Puerto Rico, Qatar, Spain (Canary Islands), Taiwan, USA, Venezuela	Low/ unknown
Monk parakeet (<i>Myiopsitta monachus</i>)	Argentina, Bolivia, Brazil, Paraguay, Uruguay	Austria, Belgium, Czech Republic, France, Germany, Italy, Netherlands, Portugal, Spain, UK (<i>Denmark, Slovakia</i>)	30 established populations. More than 22,000 individuals across Europe (Postigo J-L, pers. comm. 2018).	Australia, Canada, Cayman Islands, Chile, Dominican Republic, Guadeloupe, Israel, Japan, Kenya, Mexico, Puerto Rico, USA, Venezuela	High
Nanday parakeet (<i>Nandayus nenday</i>)	Argentina, Bolivia, Brazil, Paraguay	Spain	Barcelona (5 pairs) (Anton et al. 2017)	Israel, Puerto Rico, Spain (Canary Islands), USA	Low/ unknown
Alexandrine parakeet (<i>Psittacula eupatria</i>)	Southern Asia	Belgium, Germany, Italy, Turkey (<i>Greece, Netherlands, Spain, UK</i>) (Ancillotto et al. 2016).	A minimum of 1000 individuals in Europe (Ancillotto et al. 2016; Gedeon et al. 2014)	Bahrain, Israel, Japan, Jordan, Oman, UAE, Yemen	Low/ unknown [†]
Ring-necked parakeet (<i>Psittacula krameri</i>)	Southern Asia and sub-Saharan Africa	Austria, Belgium, France, Germany, Greece, Italy, Netherlands, Portugal, Slovenia, Spain, Turkey, UK (<i>Ireland, Switzerland, Ukraine</i>)	95 populations have established since the 1960s. At least 85,000 birds (Pärä et al. 2016).	Australia, Bahrain, Barbados, Cape Verde, Cayman Islands, China, Cuba, Egypt, Hong Kong, Iran, Iraq, Israel, Japan, Jordan, Kenya, Kuwait, Lebanon, Maldives, Malta, Mauritius, Oman, Philippines, Puerto Rico, Qatar, Reunion, Saudi Arabia, Singapore, South Africa, Thailand, UAE, USA, Venezuela, Yemen	High

* includes *belizensis* and *oratrix* subspecies (following the taxonomy used by EASIN).

[†] European Commission horizon-scanning identified it as a one of the 95 (very) high risk species across the EU within the next 10 years (Carboneras et al. 2018).

Materials and methods

Impact categories

We assessed the environmental and socioeconomic impacts of the eleven alien parrot species (Table 2) within Europe (see Suppl. material 1: Appendix B2 for countries included). We applied the impact categories proposed by the Generic Impact Scoring System (GISS; Kumschick and Nentwig 2010), with the following modifications. We omitted the ‘hybridisation’ category as there are no parrots native to Europe and the “predation” category, as all parrot species in this study are primarily herbivores (aggressive interactions whereby alien parrots kill or severely wound native species were categorised as ‘competition’, as these interactions are almost always related to food or nest-site conflicts). We therefore considered 10 impact categories (Table 1).

Building the impact evidence base

We utilised an innovative “wiki-review” process to facilitate comprehensive inclusion of sources and subsequent impact evidence into the evidence-mapping database. The process combined literature searches and preparation of impact review documents and databases by 15 selected experts from the EU collaborative network on alien parrots “ParrotNet” (COST Action ES1304), followed by an online editing and consultation phase conducted by a larger expert panel (open to ParrotNet participants and additional experts).

Each selected expert was first assigned an impact category and conducted a literature review to gather associated evidence on parrot impacts. Although a formal systematic review approach was not used due to the breadth of the study and its inclusive nature, experts conducted systematic keyword searches of the literature (i.e. using search terms pertinent to the respective impact category in combination with the scientific name of each species or either the term “parrot”, “parakeet”, “amazon”, “budgerigar” or “lovebird”). There was no restriction on publication year. Experts classified all evidence found on parrot impacts by *geographical area*, *source type*, *study design* and *impact direction* (see Table 1 and Suppl. material 1: Appendix B1 for definitions). Impact data was also distinguished as either being evidence of “actual impact” (i.e. from free-living individuals/populations within Europe) or “potential impact” (i.e. from outside Europe and/or in captivity). Where possible, primary sources were included, otherwise relevant data from reviews and other secondary sources were used and categorised as “indirect report” under *study design*. Experts were provided with a set of database fields in Excel wherein all evidence reports were entered. This database was designed such that each row comprised of a single record of evidence (i.e. evidence entry). If any given evidence source reported more than one impact, these were entered into the evidence database as separate entries. For example, if a source reported agricultural

damage caused by both RNP and MP, this would constitute two separate evidence entries (one per parrot species).

Upon completion, all impact reviews and associated evidence-mapping databases were placed online and the larger expert panel invited to review, edit and add information. Specifically, they read through one or more impact reviews and added any evidence not yet included, with a focus on evidence from grey literature, unpublished data and evidence in their native language and/or from their country of residence. This subsequent wider-consultation was open between March and December 2016, undertaken by 47 experts in (parrot) invasion biology and covered 17 languages (Bulgarian, Catalan, Dutch, English, Estonian, Finnish, French, German, Hebrew, Italian, Polish, Portuguese, Romanian, Russian, Slovenian, Spanish and Turkish). Several additional relevant sources, published between the end of the consultation period up to May 2017, were added by the lead authors.

Finally, to complement the “wiki-review”, we consulted stakeholders from locations across Europe where parrots have established in order to identify any additional evidence of socioeconomic impact. Stakeholders included representatives of farmer/landowner associations, government officials responsible for agricultural damage or public complaints officers, airport bird collision officials and bird or conservation NGOs. Altogether, 69 stakeholders were contacted between October and December 2015, from nine countries (Belgium, France, Germany, Italy, Netherlands, Portugal, Spain, Turkey and UK) and 41 responded (59% response rate), representing all aforementioned countries except Turkey. All stakeholders who responded to our survey provided anecdotal information on minor damage to crops (notably, by RNP) - information which was already well-captured in our “wiki-review”. Since these insights were not collected by stakeholders in a rigorous way and were mainly based on personal or anecdotal knowledge, these responses were not included in the database, but serve as a form of validation to the findings of the literature search and are summarised separately in Suppl. material 1: Table C1.

Impact severity scoring

Impact severity was assessed via the GISS impact assessment protocol (Kumschick and Nentwig 2010), which covers both environmental and socioeconomic impacts and has been extensively applied to birds (see Suppl. material 1: Table A2). During the evidence mapping and “wiki-review” stages, experts were not asked to assess the impact severity, as we believe that this process should be standardised to avoid biases resulting from, for example, utilising different thresholds. A single assessor systematically examined all evidence entries and attributed an impact score to each (independently reviewed for consistency by two other experts). The same score was obtained for the majority of evidence entries between the assessor and two independent reviewers. However, when there were disagreements, we discussed these objectively until a consensus was made. GISS scores invader impacts using a six-level scale ranging from 0 (‘no impact detect-

able') to 5 ('highest impact possible'). We added a "Not Assessable" ("NA") category, which was assigned to evidence entries where it was not possible to determine impact severity (due to the evidence being ambiguous, incomplete or failing to explicitly associate an impact as coming from a specific parrot species). Definitions of each impact category, scoring level and thresholds were set, following a workshop discussion with over 20 experts and are provided in Suppl. material 1: Appendix B3 (e.g. damage to crops that exceeds 5% was set as high damage in fields or fruit consumption). Finally, while there have been some attempts to score the strength of beneficial impacts created by alien species (Kumschick et al. 2012), there is currently no widely-adopted protocol. Consequently, although we included all beneficial impact evidence, we did not score their level of impact.

Data representation and analysis

In order to obtain a general overview of the evidence base, we first used descriptive statistics to synthesise and summarise how reported impacts were distributed across species, impact category, geographical area, source type, study design and direction of impact. Secondly, we mapped the spatial distribution of the evidence for deleterious impacts (Europe and worldwide) across impact categories, providing a visual representation of where different reported impacts originated. Finally, we investigated how criteria on evidence inclusion influenced the outcome of IAS impact assessments, for all alien parrots in Europe (combined and per species). Following Turbé et al. (2017), impact scores were summarised per impact category by taking both the average (using the full set of recorded impacts) and maximum (based on the most severe recorded impact only) scores. Entries that could not be assigned a numerical impact score, including all those reporting beneficial impacts, were excluded here. Specifically, we explored how impact severity scores (average and maximum) varied by species, impact category, geographical area, source type and study design.

Results

Evidence-mapping database

A total of 386 independent evidence entries were obtained from 233 sources, spanning from 1895 to 2017 (with a noticeable increase from the late 1990s onwards). Although peer-reviewed publications were the most common evidence source, 42% of entries came from grey literature or unpublished data. Entries spanned sources written in 10 different languages (predominantly English: 71%), from all continents (save Antarctica) and 32 countries (Europe: 39%; other invaded range: 20%; native range: 32%; captive: 9%; Suppl. material 1: Fig. C1a–b). Most entries reported potential (62%), not actual, impacts for Europe. All 11 alien parrot species within Europe were included

in the database, although the vast majority of entries (83%) referred to either the RNP (64%) or MP (19%). Regarding impact category, most entries referred to agriculture (42%), followed by competition (19%), herbivory (19%), disease (8%), human health (5%), infrastructure (4%) and human well-being (3%). In terms of study design, most entries were anecdotal (50%), followed by non-experimental (33%), indirect reports (11%) and experimental (6%). The vast majority of entries reported deleterious impact (82%), whilst 10% provided evidence of no impact and 8% beneficial impacts. The complete impact evidence-mapping database, including assigned impact scores, is provided in Suppl. material 1: Appendix D and can be consulted interactively online via an R Shiny application (<https://goo.gl/ZwWZPo>).

Deleterious and no impact evidence

Within Europe (Fig. 1a), most evidence of deleterious impact referred to populations in Spain (30%), the UK (18%) and Belgium (13%). Competition with native species and agricultural damage were the main impact categories (31% and 29%, respectively). Evidence of actual deleterious impact was found for six parrot species, but 93% of these entries related to RNP or MP (Suppl. material 1: Table C2). It is also important to note that 12% of impact entries from Europe were from captive populations, including all evidence from Poland (where currently no parrot populations are established). These entries were mostly related to disease transmission in captive populations and consequently only provide tentative evidence of potential impact of feral populations on human health. For non-native areas outside Europe (Fig. 1b), most evidence of deleterious impact came from Israel (39%; all referring to RNP and largely reporting agricultural damage) and the USA (36%; largely reporting socioeconomic impact by MP). Within the ‘native range’ impact category (Fig. 1b), most deleterious impact entries were reported from India (59%) or Pakistan (17%) and referred to agricultural damage by RNP. Overall, 39 entries (10%) found no evidence of impact (Suppl. material 1: Table C2).

Beneficial impact evidence

Overall, 29 entries reported evidence of beneficial impact (45%: competition, 41%: herbivory, and 14%: human well-being). Beneficial entries for indirect facilitation of conditions, either by providing resources or by competing with native species’ local competitors, were all anecdotal, with 18% of all competition evidence from Europe being beneficial (referring to nesting cavities made by RNP and *Psittacula eupatria*, use of MP nests as breeding sites and protection via RNP anti-predatory (‘mobbing’) behaviour). Evidence of beneficial impacts relating to herbivory reported that parrots can disperse seeds of native species or feed on and damage alien plants. Most of this evidence (82%) came from the native ranges of the six respective species and, except for one experimental study, were either anecdotal or non-

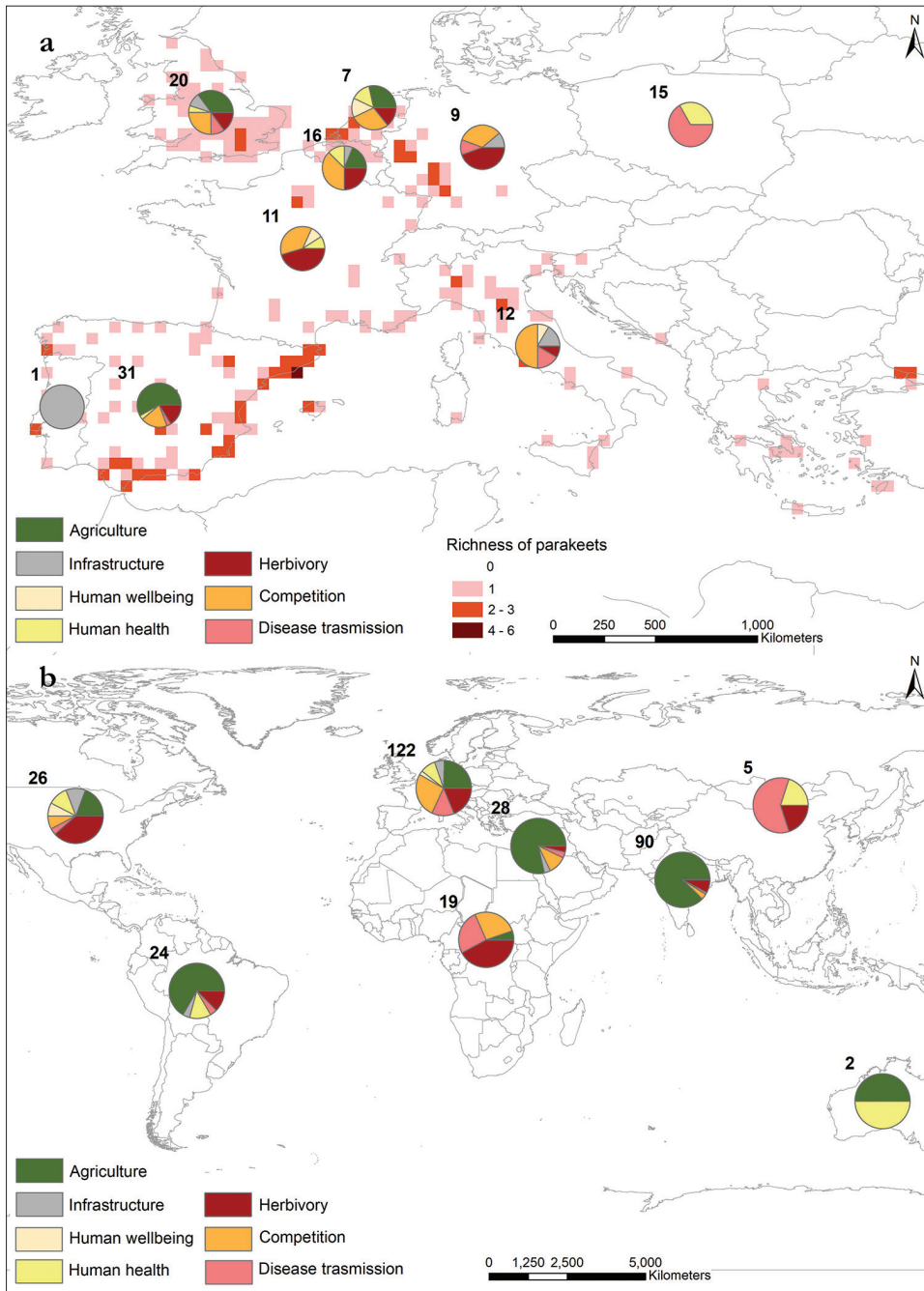


Figure 1. Spatial distribution of deleterious impact evidence for the 11 alien parrot species in Europe, by **a** countries within Europe ($n = 122$) and **b** regions across the world ($n = 316$; Africa, Australia, Europe, Far East, Indian-subcontinent, Latin America, Middle East, North America). Evidence is further split by GISS impact category. Numbers refer to corresponding number of evidence entries, which include those from captivity. Parrot species occurrence data used to derive parrot species richness maps were taken from the Global Biodiversity Information Facility (GBIF, www.gbif.org).

experimental. Finally, evidence on benefits to human well-being came largely from anecdotal sources, with 75% from Europe (all RNP), one entry from the USA (MP) and none from native ranges.

Impact severity scores and the effects of evidence selection criteria

Almost half (48%) of all evidence entries could not be assigned an impact score. Within the entire database (386 entries), 19 entries scored a “4” for impact severity; these reported potential impact (i.e. outside of Europe) and all but two related to agricultural impact. Only three entries obtained the maximum score of “5”: two reports (one anecdotal and one indirect) of competition between RNP and the endangered Echo parakeet (*Psittacula eques*) in Mauritius and an indirect report of the RNP being involved in bird-aircraft strikes in the UK. When using all collected evidence recorded in any geographical area, maximum impact across impact categories was highest for both competition and infrastructure (5), whereas mean impact was greatest for agriculture (2.35) and infrastructure (1.93) (see Suppl. material 1: Table C3, which also contains a breakdown per species).

Impact scores were separated by actual versus potential impact (i.e. recorded within or outside of Europe, respectively), source type and study design (Figs 2–3; per species: Suppl. material 1: Tables C4–5). Most actual impact scores were \leq “1” (72%), compared with 41% for potential impacts. For all species combined, both mean and maximum impact scores were higher for potential than for actual impacts, except for human health and human well-being (equal values) and maximum infrastructure impact (actual > potential, Fig. 2a–b). Both mean and maximum impact scores also varied with source type, but not in a consistent manner across impact categories (Fig. 2c–d). Finally, concerning study design, mean impact score generally increased from indirect report/anecdotal through to experimental (Fig. 3a); however, this was not the case for maximum impact scores (Fig. 3b).

Focusing on the RNP, most scores related to non-experimental evidence of agricultural impact from the native range (Fig. 4a), followed by non-experimental evidence about competition in Europe (Fig. 4b). Mean and maximum scores for actual impacts were highest for infrastructure, whereas the highest mean and maximum scores for potential impacts were for agriculture and competition, respectively (Suppl. material 1: Table C4). For the MP, most scores related to non-experimental evidence on agricultural impact in Europe and to anecdotal evidence on infrastructure damage in Europe (Fig. 4c–d). Both within and outside of Europe, mean and maximum impact scores were highest for evidence of agricultural impact (Suppl. material 1: Table C4).

Agricultural impact by parrots was reported for 16 crops within Europe (mainly maize, plums and tomatoes) and outside Europe for 33 crops (mainly maize and sunflower), although impact severity scores could only be assigned to 11 and 21 crop types, respectively. Although sample sizes were low, the highest actual (European) impact was reported for plums, pumpkin, sunflower, maize and tomato. Potential (non-European)

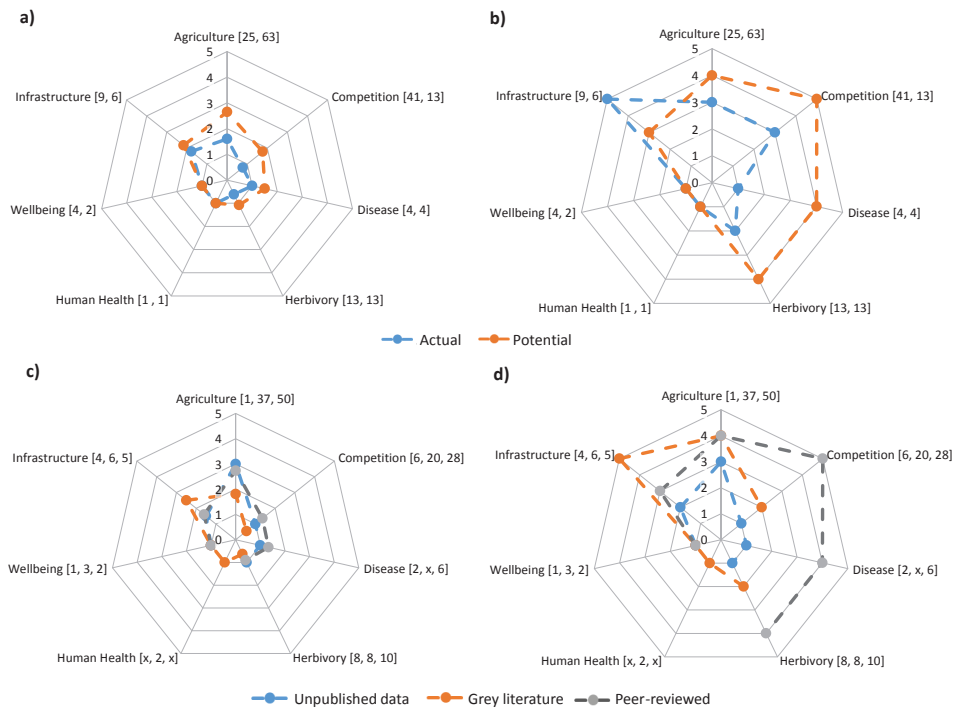


Figure 2. Impact scores for all 11 alien parrot species combined per impact category, broken down by actual versus potential impact (**a** mean **b** maximum) and source type (**c** mean **d** maximum). Sample sizes are shown in square brackets and relate to levels as ordered in the legend (x signifies no data with an impact score).

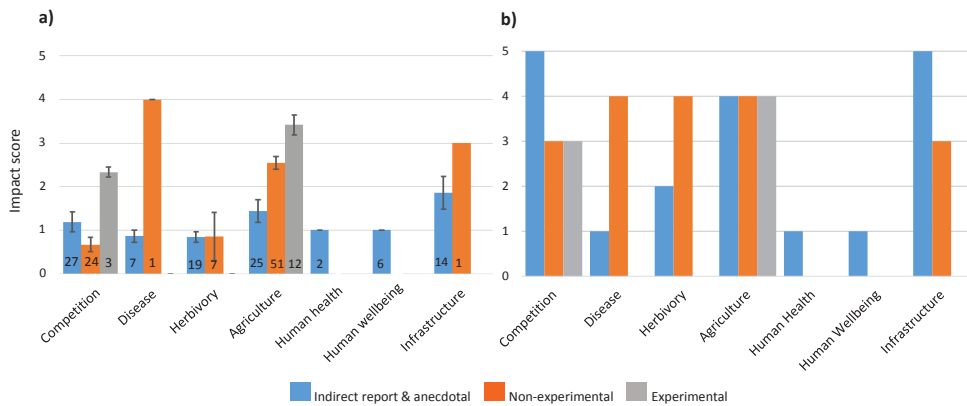


Figure 3. Impact scores for all 11 alien parrot species combined per impact category, broken down by study design (**a** mean \pm SE **b** maximum). Samples sizes for both plots are shown within the bars of the first plot.

crop impact was greatest for rice, mango, pomegranate, sunflower and maize. Within Europe, most evidence of MP agricultural damage comes from Spain, whereas the damage attributable to the RNP originates mainly from Belgium and the UK.

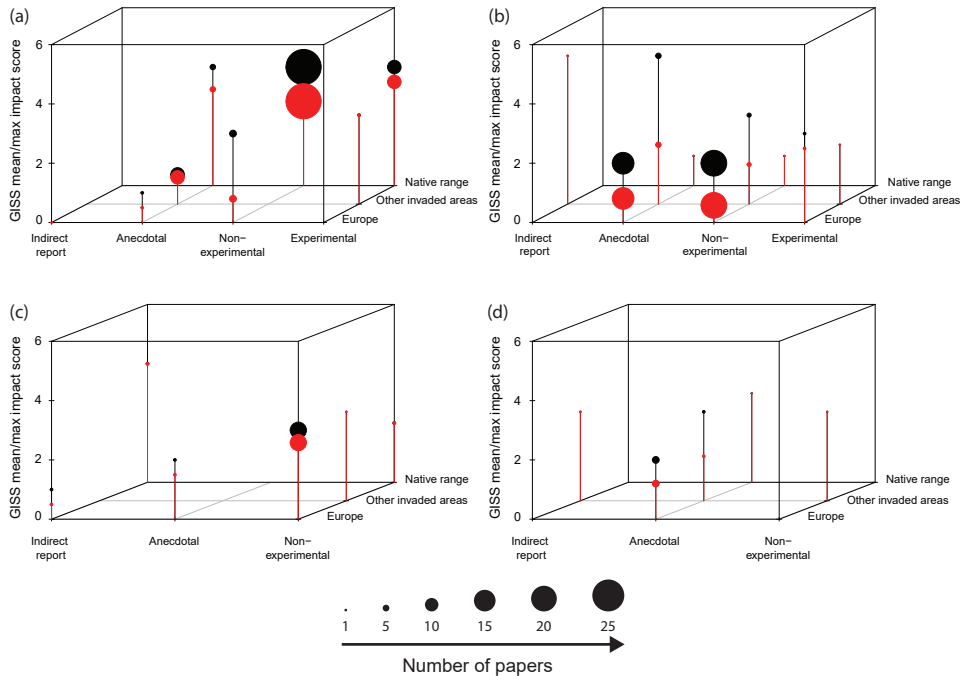


Figure 4. Mean (red) and maximum (black) impact scores broken down by study design and geographical area for **a** RNP agricultural impact **b** RNP competition impact **c** MP agricultural impact and **d** MP infrastructure impact. Highest possible impact score = 5.

Discussion

Evaluation of impact evidence-mapping scheme and “wiki-review”

A range of impact assessment protocols exist to assist necessary prioritisation of IAS management. However, protocols vary in the types of evidence included. Here, we argue that all impact records encountered during any IAS impact assessment should first be summarised into a transparent, openly-accessible, inclusive and standardised evidence base, allowing one to track how variation in accepted evidence influences the severity of final, overall impact scores. We believe doing this will strengthen the existing standards of IAS impact assessments and contribute towards scientifically, socially and politically acceptable IAS management decisions.

Both the evidence-mapping scheme and “wiki-review” used in this study facilitate the creation of such an evidence base. The former enables a more structured and transparent evaluation of impacts for any alien species within any geographical location. It can also allow the interchange or publication of datasets, potentially preventing unnecessary replication of literature review efforts, facilitate rapid updating and enable comparison of outcomes of assessments with respect to different protocols. The “wiki-review” process facilitates the collection of non-peer-reviewed information plus evidence from additional

(non-English) languages. Collectively, these two sequential approaches can help address some of the main challenges surrounding the reliability of IAS risk analysis, as highlighted by Vanderhoeven et al. (2017). Firstly, they facilitate improved quality control of impact assessments, by reducing the likelihood of “data laundering”, whereby the results of impact assessments are used to draw conclusions and make decisions without being aware of the potentially limited quality of the underlying evidence (Strubbe et al. 2011). Secondly, they can help formalise a peer-review process between assessors and reviewers, as advocated by Vanderhoeven et al. (2017). We do not believe that either our proposed evidence-mapping scheme or “wiki-review” represent a major additional burden for expert evaluators. However, it would be worthwhile exploring the extent to which non-experts could conduct them and so allow experts to focus on the subsequent IAS impact assessments.

The use of the impact evidence-mapping scheme here does not resolve some long-standing important issues, which are part of impact assessments. For instance, the use of anecdotal data, information from the native range, evidence on beneficial impacts, summarising methods for impact severity and setting up clear thresholds to what is considered high or low impact (Strubbe et al. 2011, Turbé et al. 2017, Bartz and Kowarik 2019). However, it does allow them to be explicitly identified and therefore accounted for in the subsequent risk management stage. Firstly, the quality of data across evidence entries is likely to vary considerably. Here, we classified the evidence by study design, as a proxy for evidence quality and reliability (on the basis of susceptibility to bias). Our database of alien parrot impacts in Europe showed important variation in impact scores with respect to study design. Although anecdotal data is, by definition, a poorer quality evidence type, it is not necessarily irrelevant and should be included in impact assessments. The reason for this is that there is a trade-off between impact detectability and management efficiency (Simberloff et al. 2013). When alien species start to establish, their impacts may be hard to detect due to small population sizes and low awareness. It also takes some time to establish a sound evidence base of impact for such novel alien species. However, from a management perspective, this early stage is critical, since populations are still small and any mitigation attempts will likely be most cost-effective. Anecdotal information can be valuable in directing both research and a fast response in the early stages of invasion. By explicitly classifying such variation in the evidence base, the evidence-mapping scheme draws attention to this matter and thereby increases transparency in the choices made during risk management.

A second outstanding issue is how to deal with evidence from the native range and other invaded areas. We argue that impacts from these geographical areas should be mapped but kept separate from evidence obtained from the focal study region, as extrapolation may not be straightforward (Kulhanek et al. 2011). It has previously been suggested that impacts in the introduced range are likely to be more severe than in the native range (Kumschick et al. 2011); however, we did not find this to be always true. Damage by RNP and MP to agriculture and infrastructure are limited within Europe, despite both species being locally abundant, with impact scores being greater in their native or other invaded ranges. Focusing on agriculture, it is important to highlight that, as a result of global climate change, farming practices within Europe will increasingly have to adapt to warmer

climates. For example, maize, sunflower, orchards and vineyards are sectors set to expand as the climate warms (Olesen et al. 2011) and for which evidence of parrot damage within Europe (albeit localised) and other invaded ranges already exists. Therefore, climate-driven expansion of certain crops across Europe, bringing them into contact with parrots, could place increasing pressure on farmers and the economy. Again, our scheme allows decision-makers to visualise the available evidence from the focal study region, other non-native ranges and native ranges and subsequently decide which and how to utilise it.

Lastly, evidence-mapping results in a set of recorded impacts, but these need to then be scored and summarised into a single, overall impact score to allow ranking IAS according to the magnitude of the threats they pose. The summarising method has strong implications on the magnitude of impacts assigned to alien species and our results clearly demonstrate that. Both scoring methods (maximum and mean) have strengths and weaknesses and we suggest that summarising impact based on both approaches is of inherent and complementary value for guiding management decisions (see also Turbé et al. 2017). Integrating beneficial impacts into the scoring system is even more challenging, as the direction of an impact depends on some sort of valuation relative to a desired situation and is therefore relative (if not subjective) (Bartz and Kowarik 2019). For example, we scored protection of heterospecifics from predators by mobbing parrots as beneficial, but it would be a deleterious impact from the point of view of the predators. Beneficial impacts attributed to IAS are an often ignored factor (Schlaepfer et al. 2011) and currently not a formal part of IAS impact assessment. Including direction of impacts as a category in the evidence-base will therefore also highlight that impacts (in either direction) are never fully objective and always “user-dependent”: some impacts may be valued differently by distinct sections of the scientific community and the general public. Including beneficial impacts into the evidence base, even when it is not (yet) an integral component of the impact score, enables relevant people to consider this evidence at the subsequent risk-management and risk-communication stages. Furthermore, our evidence-mapping scheme needs to be used in tandem with recent recommendations aimed at reducing disagreement between expert assessors (e.g. Turbé et al. 2017, Vanderhoeven et al. 2017; González-Moreno et al. 2019), to obtain more comprehensive impact assessments. Altogether, we argue that mapping all of the available evidence allows all the above-mentioned issues to be transparently considered during the decision-making phase of risk management.

Impacts of alien parrots in Europe, as a function of “admissible evidence”

The approach followed in this study has resulted in the most comprehensive and transparent assessment of alien parrot impacts within Europe to date. Allowing different levels of the evidence base (Table 1) to enter into the assessment can seriously affect not only evidence quantity, but also impact severity scores and identification of main impact mechanisms (e.g. as seen in both the MP and RNP). When considering only actual impact (and also excluding indirect and anecdotal reports), we find that RNP

mostly cause minimal and only rarely moderate impacts in Europe (i.e. GISS scores 1-3). These relate mainly to competition with native cavity nesting species. For instance, the threatened greater noctule bat (*Nyctalus lasiopterus*) in Seville (Spain) can be forced out of roosting cavities by RNP, which has only recently been found to contribute to declining bat populations (Hernández-Brito et al. 2018). Such long-term studies investigating the effect of competition on the local abundance of species are scarce in the invasion literature (Strayer et al. 2006). It is also important to highlight that roughly half of the entries for competition within Europe found explicit evidence of no impact. RNP are shown to damage crops and trees in Europe, but evidence is scarce and localised. When allowing impact evidence from other invaded ranges into the evidence base, RNP is considered both a more serious agricultural threat and competitor with threatened species (due to its competition with the threatened echo parakeet in Mauritius). If native-range impact information is considered, numerous studies have found the RNP to be a moderate to major agricultural pest, predominantly in India. Finally, indirect and anecdotal evidence indicate that RNP can cause minor herbivory, disease, human health and well-being impacts, but severe (GISS score 5) infrastructure impact, although it must be emphasised that the latter is based on one (indirect) report finding RNP to be involved in <1% of bird-aircraft strikes at Heathrow Airport (UK) (Fletcher and Askew 2007) and should therefore not be taken out of context.

Evidence of MP impact in Europe (excluding indirect and anecdotal reports) comes from only two studies reporting agricultural damage in Spain (Barcelona) (Senar and Domènech 2001; Senar et al. 2016), where they are shown to be a moderate threat to at least ten crop types. Only when indirect and anecdotal reports are included do we find some evidence of infrastructure damage via the communal stick nests they build and a few additional low impact cases relating to agriculture and herbivory. No evidence of deleterious competitive interactions with the MP could be found in Europe. In fact, 71% of the species' actual competition entries were beneficial (e.g. facilitating nesting conditions for other species). Allowing impact evidence from other invaded ranges into the evidence base causes the MP's damage to infrastructure score to increase, along with limited evidence of both minimal competition and human well-being impacts. Native range evidence suggests MP could be capable of causing major agricultural damage to both maize and sunflower.

For the remaining nine parrot species, either no or very little information on impacts within Europe were retrieved (mainly indirect reports or anecdotal). These species all have localised and (very) small European populations and negligible actual impact. Even when allowing impact evidence from other invaded ranges or the native range, assessments for these species remain unchanged, except for *Amazona aestiva* which is an agricultural pest in parts of its native range (e.g. Villalobos and Bagno 2013).

Knowledge gaps and biases in the evidence base

One of the benefits of the evidence-mapping scheme used here is that it facilitates identification of knowledge gaps and can potentially influence the direction of future

IAS research. Roughly half of all entries in our database did not allow assignment of an impact severity score, due to ambiguous evidence; e.g. a given source failing to explicitly associate an impact as coming from a specific parrot species. Although parrots are a relatively well-studied bird group which is at least partly attributable to their being noisy and conspicuous (Evans et al. 2016), there is a general paucity of published research on established parrot species impacts within Europe. For example, the majority of experimental studies in our evidence base relate to agricultural impacts by RNP in their native India, whereas we found only two experimental studies reporting impacts within Europe – both relating to competition by RNP (Strubbe and Matthysen 2009; Peck et al. 2014). We also lack studies that explicitly assess and/or quantify the general public's opinion on alien parrots, their impacts and their management, which is recognised to be complex and multifaceted (Crowley et al. 2019; Luna et al. 2019), but highly important to understand in order to promote effective management. Finally, within Europe, most impact categories are underpinned by only one or a few studies (even for RNP). Despite growth in the study of invasion biology (Richardson and Pysek 2008), empirical evidence of the impact of IAS can be difficult to obtain and, as a result, IAS impacts are generally poorly documented. Nonetheless, in Europe, at least in the case of RNP and MP, our study indicates minimal to locally moderate impacts based on the available evidence to date.

One broad reason to explain why little impact data exist for most alien bird species generally, is that some populations may be perceived to cause negligible or no harm (i.e. below the threshold) and, consequently, are not studied (Evans et al. 2016). Lack of data in this situation reflects a perceived (but perhaps unreal) lack of impact. Pysek et al. (2008) highlighted a tendency for studies to focus on species considered to have the most severe impacts (e.g. RNP and MP in our study) and neglect others (e.g. the remaining nine parrot species). This also raises an outstanding issue regarding what is the threshold beyond which an alien species becomes invasive or a negative impact becomes a significant negative impact (see Bartz and Kowarik 2019). This links with the issue that there will always be a time lag between initial introduction of an alien species and a detectable impact (Edelaar and Tella 2012). On the other hand, studies that fail to find a deleterious effect (e.g. Cardoso and Reino 2018) are likely not published and under-reported (Schlaepfer et al. 2011). Assembling a comprehensive database, which includes anecdotal evidence of deleterious impacts and evidence of no impact as suggested here, can potentially help direct research towards important possible impacts.

IAS management and policy implications

The outputs from impact assessments alone should not be used to prioritise alien species for management, as impact assessment is only one subcomponent of risk assessment, which in turn is only one subcomponent of risk analysis (Suppl. material 1: Fig. A1). However, our extensive impact evidence base and associated impact assessments suggest possible management and policy considerations for alien parrots in Europe.

We find limited evidence of widespread (severe) parrot impacts across Europe. Instead, impacts within Europe are predominantly localised and differ across countries/regions. Hence, it is unlikely to be necessary, at present, to put any of the 11 parrot species on the Union List. Most parrots in Europe are currently known from relatively few and disjunct populations and necessary management actions, if any, can be carried out at local or regional levels. RNP and MP are more widespread and populations may span national borders (e.g. across the lowlands of northern France, Belgium, the Netherlands and Germany or across parts of the Mediterranean seaboard; Pârâu et al. 2016; Postigo et al. 2019). Effective management of these species will likely benefit from designating them as “invasive species of local and regional concern”, as per Articles 11 and 12 of the EU regulation on IAS.

The rise of “invasive species denialism” (Ricciardi and Ryan 2018, Russell and Blackburn 2017) challenges invasion biologists to better present the available evidence, because disagreements often arise when uncertainty on impacts are confounded by differences in personal values. More broadly, there are concerns that a culture of “evidence complacency” may be prevalent in many areas of conservation amongst academics, practitioners and decision-makers (O’Connell and White 2017; Sutherland and Wordley 2017). Hence, especially in our contemporary “post-truth” world (Higgins 2016), we re-emphasise the importance of all IAS management and policy decisions to be made, based upon having access to impact assessments produced using a transparent, comprehensive and publicly available evidence base and for there to be a clear evidence audit trail.

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Supplementary material I

Supplementary background, methods and results

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Data type: background, description, measurement

Explanation note: Appendix A: Supplementary background, Appendix B: Supplementary methods, Appendix C: Supplementary results.

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Supplementary material 2

Impact evidence database

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Data type: description, measurement

Explanation note: Appendix D: Impact evidence database.

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Invasive alien plant species in unmanaged forest reserves, Austria

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Abstract

Invasive alien plant species (IAS) are one of the greatest threats to global biodiversity and the sustainable functioning of ecosystems and mitigating the threat posed by them is therefore of great importance. This study presents the results of a 15-year investigation into how IAS occur within natural forest reserves (NFR): unmanaged forest ecosystems within Austria, concluding that unmanaged forests are not resistant to plant invasions. The study comprised ground vegetation, regeneration, and stand structure surveys. The presence or absence of IAS in different forest types was assessed and the influencing variables for their presence or absence were determined. In addition, the study analysed whether the abundance of IAS has increased at the site level within the past decade. Significant differences in the probability of IAS presences between forest types (photosociological alliances) were found. The results of the study show that natural riparian and floodplain forests are among the forest types most vulnerable to biological invasions, which is reflected in elevation and soil type being determined as the main factors influencing the spread of IAS in unmanaged forests. The results of this study may be useful for persons responsible for sustainable forest management programmes or for managing forested areas within national parks. They provide a case study on non-intervention forest management policy in order to mitigate the impacts of IAS in protected areas. Forest areas, where IAS begin to spread can be identified, which in turn leads to measures in the early stages of invasion, and to optimise monitoring and control measures for relevant species in Central European forest types.

Keywords

Austria, biological invasions, forest ecosystems, floodplains, natural forest reserves, nature conservation, neophytes

Introduction

Invasive alien plant species (hereinafter “IAS”) are one of the greatest threats to global biodiversity and the sustainable functioning of ecosystems (Perrings et al. 2010). Mitigating the threats posed by IAS has therefore become a major topic for consideration by conventions, many international organisations, non-governmental organisations (NGOs), governments, and local communities (EU Regulation 2014; CBD 2016; IUCN 2018). Managing the spread of IAS in forest ecosystems requires action from stakeholders directly involved in the conservation of forests as well as from those using forests for trade, health, or tourism (Brundu and Richardson 2016).

Databases and platforms such as the Global Register of Introduced and Invasive Species (GRIIS) have been established to collate information on the distribution of IAS for use by decision makers to plan and manage the spread of IAS (CABI 2019; GBIF 2019; GISD 2019; GRIS 2019). Measures for controlling the spread of IAS are often an integral part of forest management plans that aim to sustain and develop biodiversity-rich forest ecosystems and sustainable timber production systems (Pagad et al. 2015; Brundu and Richardson 2016).

In total, 42% (167 million ha) of the land surface of the EU is covered in forests, and preventing, controlling at early stages of invasion, and managing the spread of IAS in Europe’s protected forest areas is therefore of particular importance for insuring ecosystem services of European forests (The EU Forest Strategy 2013). Approximately 21% (375,000 km²) of Europe’s forests are included in the NATURA 2000 network, the largest network of protected areas in the world extending across all 28 EU countries (EEA 2018). Structured forest management systems have shaped the development of forest ecosystems within the NATURA 2000 network for centuries (Bastian 2013; European Commission 2015). IAS are among the severest threats to the biodiversity and ecosystem functions of European protected forest areas (Chirici et al. 2014; Seidl et al. 2014; Guerra et al. 2018). Protected forests are well-established across Europe, whilst unmanaged woodlands and primary natural forests are very rare (FAO 2015; Potapov et al. 2017). It is estimated that primary forests constitute only 0.7% (1.4 million ha) of the total European forest cover (Sabatini et al. 2018), and very few data on the distribution of IAS in these unmanaged natural or primary forest are reported. For example, a study in the Białowież’a primeval forest in north-eastern Poland recorded the presence of the alien plant species *Impatiens parviflora* in similar abundance to managed forests in Lower Saxony and North Hesse, Germany (Chmura 2004; Chmura and Sierka 2007 ; Adamowski 2008; Schmidt 2012).

From previous studies we can conclude that alien species also occur in many unmanaged forests and that they are often invaded by similar sets of alien species (Foxcroft et al. 2013). Nevertheless, it was assumed that unmanaged forests are generally more resistant to invasion than managed forests with high levels of human disturbance

(Rejmánek and Richardson 1996; Levine et al. 2004). It is, however, difficult to compare the spread of IAS in managed and unmanaged forests, as almost all forests in Europe have been managed for centuries. The difficulties in comparing these two types regarding any species invasion should be addressed.

Looking at Austria in particular, the proportion of land surface covered in forests is 47.9% (4.02 million ha), well above the EU-wide proportion. About 88% of this area (3.53 million ha) consists of managed productive forest (BFW 2019). The Austrian National Forest Inventory reports an average proportion of alien tree species of less than 2% in Austria (NFI 2009). The alien tree species most commonly occurring in the forest inventory areas during the most recent inventory period (2007–2009) were hybrid poplars, Douglas fir, and *Robinia pseudoacacia*.

The study area comprises the Austrian natural forest reserves (hereinafter “NFR”) as historically managed and now unmanaged forest sites, which provide novel areas for research, training, and education on forests. The aim of the NFR programme is to conserve, enhance, and monitor forest biodiversity by abstaining from forest utilisation, logging of dead wood, and artificial regeneration of forest trees (Frank and Müller 2003; BFW 2018). The sites will be used to add further information on the spread of IAS in Central European forest ecosystems. This is highly relevant for the implementation of transnational early warning systems and local alert lists (Smith et al. 2008; Kettunen et al. 2009; National Pest Control Agencies 2015).

Few studies have been conducted with the aim of understanding how human activity in forests causes changes in the presence of IAS. Validated knowledge on forest regeneration and tending, tree species selection, regeneration procedures, production and regeneration periods, competition control, and natural selection and differentiation in particular is needed to be able to compare the production, protection and recreation provided by forests depending on their ecological conditions. This type of information would help forest managers to identify forest regions or stands where IAS start to spread, which in turn gives rise for action in the early stages of invasion and optimise monitoring and control measures concerning the relevant species for Central European forest types.

This paper develops the current literature on IAS by providing an analysis of the alien flora in unmanaged NFR in Austria. The aims are (i) to identify invasive plant species in NFR and (ii) to analyse which variables are important for determining the presence or absence of IAS across multiple NFR, with particular reference to (iii) the composition of native plant species in those NFR. Additionally, the paper analyses at the site level (iv) whether the abundance of invasive alien plant species has increased within the past 15 years. The results of this paper are particularly useful for assessing “zero-IAS-management-scenarios” in forests, which is an ongoing challenge for persons responsible for sustainable forest management programmes or managing forested areas within national parks, by providing information on the spread of IAS in different unmanaged forest types.

Method

Study area

The NFR analysed for this study are part of the Austrian Natural Forest Reserve Programme established in 1995. Sites in formerly managed forest areas were selected according to a set of criteria including naturalness of tree species composition. Today, the NFR network comprises 192 reserves in Austria with a total area of 8,355 ha. The aim of the programme is to represent the 118 forest communities (out of 159 known forest and shrub communities) found in 22 growth zones within Austria (Kilian et al. 1994; Frank 2003; Willner and Grabherr 2007); it currently covers 84 of the 118 relevant forest communities. It is important to realise that the investigated NFR sites are unique observational plots representing unmanaged natural forest ecosystems and therefore not representative of the typical Austrian forest cover - 47.9% (4.02 million ha) of the area of Austria are covered in forests, with 88% of this area (3.53 million ha) consisting of managed productive forest (BFW 2019).

Data sampling

a) Vegetation sampling

The ground vegetation was recorded in 2,344 sample plots with sizes varying from 50 to 700 m² (average size: 240 m²) across all 192 NFR sites using the Braun-Blanquet cover abundance scale with 7 to 9 classes (Braun-Blanquet 1928, 1932; Moore 1962; Londo 1976). The sample plots were distributed representatively across the occurring forest communities of each NFR site. For the analysis of the presence or absence of IAS in each of the 2,344 sample plots, forest communities were summarized into forest associations according to the classification by Willner and Grabherr (2007).

b) Tree sampling

The composition and development of tree species was systematically determined for the sampling plots within the NFR using Bitterlich's angle count (AC) sampling with a basal area factor (BAF) of 4 (Bitterlich 1984). No threshold was defined for the diameter at breast height (DBH). Only NFR with repeated surveys were relevant for the analysis (784 AC plots in 36 NFR). The only sample areas with a proportion of IAS in the AC sampling were those in the floodplain forest community *Fraxino pannonicae-Ulmetum* (Soó in Aszód 1936 corr. Soó 1963) located alongside the river March in Lower Austria. Accordingly, the analysis of tree species development focused on floodplain forests. This March floodplain study site covers an area of 91 hectares (64 plots in 6 NFR) at an elevation of 140 to 150 m above sea level. The *Fraxino pannonicae-Ulmetum* community typically occurs in the broad floodplains of lowland rivers and is dominated by *Fraxinus angustifolia*, with *Acer campestre*, *Carpinus betulus*, *Ulmus laevis*, and *Ulmus minor* also commonly appearing (Douda et al. 2016).

The first data collection took place between 1997 and 1999 (period 1), and the survey was repeated 15 years later between 2013 and 2014 (period 2). The collected data included tree-related information like species, DBH, tree height, crown height, and location within the plot (distance and direction). For the analysis of tree species composition and development, the stem number (N) and basal area (G) per hectare were determined. The number of trees per hectare (N) was calculated by dividing the BAF (BAF = 4) by the circular area represented by each tree. The basal area per hectare (G) was calculated by summing up the trees in the AC and multiplying them with the BAF.

c) Regeneration sampling

Natural regeneration in the NFR was investigated from 2013 onward, and information is available for 36 NFR (784 samples). On each sample plot, 4 satellite samples of 1 m² in size (4 m² per plot) were collected to document the regeneration of tree species. Tree species, height (in 10 cm increments) and browsing damage were determined for each recorded plant. For the analysis of tree species regeneration, the number of regeneration trees per hectare was calculated by multiplying the number of trees with 2,500.

Data processing and analysis

Each of the alien plant species found in the 192 NFR was evaluated to determine its invasive potential in Austrian bioregions as well as at the European level and to estimate the likelihood of its future spread and negative ecological impact in Austrian forests (Essl et al. 2002; Fischer 2008; Lauber and Wagner 2008; GISD 2018; Landolt et al. 2010; CABI 2019; European Commission 2019; GRIS 2019). This approach yielded two groups of alien plant species in Austria (Table 1): invasive alien plant species (IAS) and non-invasive alien plant species (AS). The variables correlating with the presence of IAS and AS in NFR were documented for each sample plot ($n = 2,344$, Table 2) and subsequently added in based on their importance according to literature (Mucina 1993; Essl et al. 2002; Willner and Grabherr 2007; Fischer 2008). Only IAS were considered for further statistical analysis.

To prevent possible autocorrelations between the sometimes heavily spatially clustered vegetation recordings, neighbouring vegetation recordings were conflated into a single unit, with a threshold distance of 2 km defined for this purpose. This distance is based on the close proximity of six NFR located in the lower March floodplains in a 4.5 km radius. Although the distances between some individual areas is nearly 2 km, their specific species composition, especially that of alien species, is owed to their spatial proximity according to expert opinion. They were therefore aggregated into a single NFR site. This aggregation of neighbouring NFR was pragmatically extended to all other NFR as well, which provides the additional advantage of increasing the number of observations per NFR unit of area. In all, 21 groups of two NFR, five groups of three NFR, three groups of five NFR, two groups of six NFR, and one group of seven

Table 1. List of invasive alien plant species (IAS) and non-invasive alien plant species (AS) in NFR. The 16 invasive alien plant species with their family, life form (Raunkiaer system), native range, number of NFR with occurrence.

#	Family	Species	Life form (Raunkiaer system)	Native range	number of NFR
Invasive alien species					
1	Balsaminaceae	<i>Impatiens parviflora</i> DC.	Therophyte	Asia	42
2	Fabaceae	<i>Robinia pseudoacacia</i> L.	Phanaerophyte	Northern America	16
3	Compositae	<i>Solidago gigantea</i> Aiton	Hemikryptophyte	Northern America	11
4	Balsaminaceae	<i>Impatiens glandulifera</i> Royle	Therophyte	Asia	6
5	Sapindaceae	<i>Acer negundo</i> L.	Phanaerophyte	Northern America	4
6	Compositae	<i>Bidens frondosa</i> L.	Therophyte	Northern America	4
7	Oleaceae	<i>Fraxinus pennsylvanica</i> Marshall	Phanaerophyte	Northern America	4
8	Compositae	<i>Symphytrichum lanceolatum</i> (Willd.) G.L.Nesom	Geophyte	Northern America	2
9	Simaroubaceae	<i>Ailanthus altissima</i> (Mill.) Swingle	Phanaerophyte	Asia	1
10	Elaeagnaceae	<i>Elaeagnus angustifolia</i> L.	Phanaerophyte	Asia	1
11	Compositae	<i>Erigeron annuus</i> (L.) Pers.	Hemikryptophyte-Therophyte	Northern America	1
12	Compositae	<i>Erigeron canadensis</i> L.	Therophyte	Northern America	1
13	Phytolaccaceae	<i>Phytolacca americana</i> L.	Geophyte-Hemikryptophyte	Northern America	1
14	Polygonaceae	<i>Reynoutria japonica</i> Houtt.	Geophyte	Asia	1
15	Compositae	<i>Solidago canadensis</i> L.	Hemikryptophyte	Northern America	1
16	Compositae	<i>Symphytrichum novi-belgii</i> (L.) G.L.Nesom	Geophyte	Northern America	1
Non-invasive alien species					
17	Fagaceae	<i>Quercus rubra</i> L.	Phanaerophyte	Northern America	3
18	Sapindaceae	<i>Aesculus hippocastanum</i> L.	Phanaerophyte	Southeastern Europe	2
19	Amaranthaceae	<i>Atriplex sagittata</i> Borkh.	Therophyte	Southwestern Asia	2
20	Compositae	<i>Erechtites hieraciifolia</i> (L.) Raf. ex DC.	Therophyte	America	2
21	Amaranthaceae	<i>Atriplex prostrata</i> Boucher ex DC.	Therophyte	Western Europe	1
22	Cucurbitaceae	<i>Echinocystis lobata</i> (Michx.) Torr. & A.Gray	Therophyte	Northern America	1
23	Onagraceae	<i>Epilobium ciliatum</i> Raf.	Hemikryptophyte	Northern America	1
24	Compositae	<i>Galinsoga quadriradiata</i> Ruiz & Pav.	Therophyte	Northern America	1
25	Leguminosae	<i>Lupinus polyphyllus</i> Lindl.	Hemikryptophyte	Northern America	1
26	Moraceae	<i>Morus alba</i> L.	Phanaerophyte	Asia	1
27	Oxalidaceae	<i>Oxalis stricta</i> L.	Geophyte-Therophyte	Northern America	1
28	Pinaceae	<i>Pinus strobus</i> L.	Phanaerophyte	Northern America	1
29	Salicaceae	<i>Populus balsamifera</i> L.	Phanaerophyte	Northern America	1
30	Salicaceae	<i>Populus × canadensis</i> Moench	Phanaerophyte	Northern America	1
31	Rosaceae	<i>Potentilla indica</i> (Jacks.) Th.Wolf	Hemikryptophyte	Asia	1
32	Rosaceae	<i>Rhodotypos scandens</i> (Thunb.) Makino	Phanaerophyte	Asia	1
33	Compositae	<i>Telekia speciosa</i> (Schreb.) Baumg.	Geophyte-Hemikryptophyte	Southeastern Europe	1
34	Ericaceae	<i>Vaccinium macrocarpon</i> Aiton	Chamaephyte	Northern America	1

NFR were aggregated, while 101 NFR remain as individual sites. The 192 NFR were thus reduced to 133 NFR sites. Furthermore, the presence/absence data for each observation were weighted by the number of observations in each NFR site (weights = 1/n).

The relationship between the explanatory variables and the presence of IAS in the NFR was analysed for all 16 IAS together, as well as separately for *Impatiens parviflora*

Table 2. Explanatory variables (alliance, soil type, elevation, exposition, inclination, bedrock class, soil layer depth, and relief) used for the quasi-binomial logistic regression and the Random Forest model of the presence and absence of IAS in 2344 sample plots in 192 NFR.

Variable	Classification	Range/Categories	Description
Alliance	Categorical	N = 21 categories	Root category of phytosociological associations (Willner and Grabherr 2007).
Soil type	Categorical	N = 32 categories	Expert aggregation of soil types determined by Anleitung zur Forstlichen Standortskartierung in Österreich (Englisch and Kilian 1998; Appendix 1)
Elevation (m)	Continuous	120–2080	The elevation was measured with an accuracy of ± 10 m.
Exposition	Categorical	Plain	The aspects of each site was measured in grade and assigned in cardinal directions.
		N-NE	
		E-SE-S	
		SW-S-NW	
Inclination	Continuous	0–170%	The slope inclination of each site in percent (%) was estimated.
Bedrock class	Categorical	Carbonate	Classification into bedrock classes was performed based on the Geological Map of Austria (1: 50,000)
		Flood plain sediments	
		Intermediate	
		Loess soil	
		Silicate	
Soil depth (cm)	Categorical	0	The soil depth describes the thickness of the soil horizons over solid rock. This was determined by way of 3 to 5 samples per site. Classification was performed according to the sample mean values.
		0–15	
		15–30	
		30–60	
		60–120	
		>120	
Relief	Categorical	Deposition	Sedimentation stages were classified according to the description of the macro- and mesoreliefs.
		Erosion	
		Solid	

and *Robinia pseudoacacia*, using generalized linear models (GLM) with a logit link function. This analysis was performed using the freeware *R* (R version 3.4.2 (2017–09–28)) for personal computers (R Core Team 2017). Categorical and continuous data were included in regression models as variables (Table 2), and the most common category was used as the reference category (Press and Wilson 1978). Quasi-binomial logistic regression was applied to investigate which variables were significant for predicting the presence or absence of invasive plants in NFR. The independent candidate variables were alliance, soil type, bedrock class, relief, elevation, soil layer depth, exposition, and inclination. The statistical significance of individual predictors was tested using Pearson's chi-squared test with a significance level of < 0.05 . Several subsequent analyses were run until a minimal final model containing only significant explanatory variables was achieved. After performing the chi-squared test with 95% confidence intervals, the following explanatory variables were used in the final quasi-binomial logistic regression: soil type, alliance, elevation, and inclination. The Akaike information criterion (AIC) was used to determine relative model quality, and variables that

significantly increased the AIC value were excluded (Hosmer Jr et al. 2013). Finally, the deviance was determined using ANOVA.

In addition, the Random Forest (RF) method (Liaw and Wiener 2002) was used to assess the relationship among the explanatory variables (Table 2) and the response variable, i.e. the presence/absence of IAS in NFR. The explanatory variables used were alliance, soil type, bedrock class, relief, elevation, exposition, inclination, and soil layer depth (Table 2). The mean decrease in Gini coefficient was calculated to estimate the importance of each variable (Calle and Urrea 2010).

Results

IAS in NFR and forest alliances

In total, 16 IAS and 18 non-invasive alien species (AS) were recorded (Table 1). The five most frequently occurring IAS were *Impatiens parviflora* (n = 42 NFR) *Robinia pseudoacacia* (n = 16 NFR), *Solidago gigantea* (n=11 NFR), *Impatiens glandulifera* (n = 6 NFR), and *Acer negundo* (n = 4 NFR). The four most frequently occurring AS were *Quercus rubra* (n = 3 NFR), *Aesculus hippocastanum* (n = 2 NFR), *Atriplex sagittata* (n = 2 NFR), and *Erechtites hieraciifolia* (n = 2 NFR). Figure 1 shows the proportion of sites with occurrences of IAS only, IAS and AS, or AS only, ranged from 0 to 100%. The largest proportions of IAS were found in floodplain forest alliances, i.e. *Alnion glutinosae* (Malcuit, 1929) (100%), *Salicion albae* (Soó, 1930) (93%), *Salicion cinereae* (Müller & Görs, 1958) (71%), and *Alnion incanae* (Pawlowski in Pawlowski, Sokolowski and Wallisch 1928) (53%). Furthermore, IAS occurred in relatively large proportions of sites inhabited by the following alliances: slope forests (*Tilio-Acerion* (Klika, 1955): 23%), and oak and oak-hornbeam forests (*Carpinion betuli* (Issler, 1931): 19%).

Analysis of explanatory variables

The final quasi-binomial model showed that soil type, alliance and elevation were the strongest explanatory variables ($p < 0.05$) for the 189 sample plots with recorded IAS presence and 2,151 sample plots with recorded IAS absence. The probability of IAS presence was highest for the following soil types: pseudogley on unconsolidated sediments (130), gley (210), gray-alluvial soils (240), mature brown alluvial soils (250), and half bog (anmoor) (260) (Table 3). The probability of invasive species presence decreased with increasing elevation ($df = 1$, $p < 0.001$) as well as with increasing slope inclination ($df = 1$, $p < 0.001$).

The presence of *Impatiens parviflora* seems to be driving the model, however. We also applied the quasi-binomial model to *I. parviflora* and *Robinia pseudoacacia*, the two

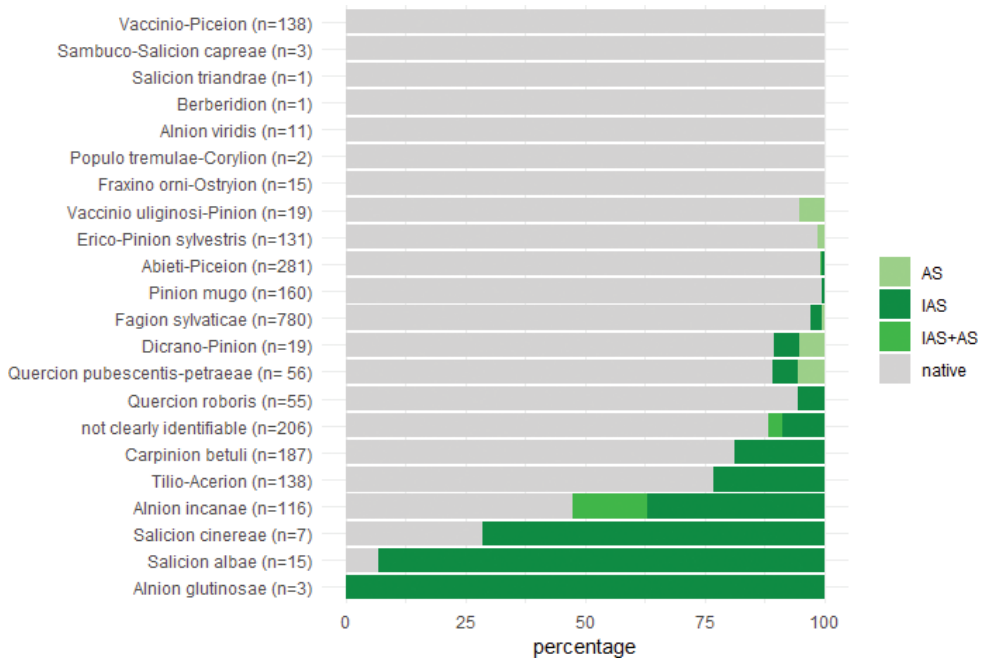


Figure 1. Proportion of sites with occurrence of IAS (dark green), IAS and AS (green), AS (light green) and without IAS (grey) by forest alliances [%] (Willner and Grabherr 2007) in 2,344 vegetation plots in the unmanaged natural forest sites of the NFR programme ($n = 192$). The highest proportions of IAS were found in floodplain forest alliances: *Alnion glutinosae* (Malcuit, 1929) (100%), *Salicion albae* (Soó, 1930) (93%), *Salicion cinerea* (Müller & Görs, 1958) (71%), *Alnion incanae* (Pawłowski in Pawłowski, Sokolowski and Wallisch 1928) (53%).

species with the highest incidence in the vegetation sample set. The strongest explanatory variables for *I. parviflora* are soil type ($df = 32$) and alliance ($df = 21$) (Table 4), while the strongest explanatory variables for *R. pseudoacacia* are bedrock class ($df = 5$), relief ($df = 2$) and elevation ($df = 1$) (Table 5). However, as elevation increases, the probability of *I. parviflora* and *R. pseudoacacia* being present decreases ($df = 1$, $p < 0.001$). The most significant explanatory variable based on mean decrease in Gini was found to be elevation (51.63) followed by soil type (48.76), and alliance (32.10) (Figure 2). Relief (6.98) was the least significant among the test variables.

Tree species composition and development

In total, 11 native tree species and two invasive alien tree species were present in the 64 AC plots of the tree sampling. The native trees species with the highest occurrence by stem number were *Fraxinus angustifolia*, *Acer campestre*, and *Ulmus* spp. (*Ulmus* spp. includes *U. glabra*, *U. minor*, and *U. laevis*). In comparison, the tree species with the

Table 3. Parameter estimates of generalized linear models (error structure = quasi-binomial; link function = logit) explaining the probability of the presence of IAS in NFR sites. Only significant explanatory variables occurring in the minimal adequate GLM were included in the model. Values are on the logit scale. * = factors significant at the $p < 0.05$ level. Data included in the logistic regression model were not transformed.

Variable	Categories	Estimate	Std. error	t value	Pr (> t)
Soil type	130 Pseudogley on unconsolidated sed.	5.77E+03	1.93E+03	2.988	0.00
	250 Mature, brown alluvial soil	4.14E+03	1.50E+03	2.763	0.01
	260 Half-bog	5.70E+03	2.47E+03	2.306	0.02
	210 Gley	3.87E+03	1.82E+03	2.124	0.03
	240 Gray-alluvial soil	3.28E+03	1.64E+03	1.996	0.05
	80 Minor Brown earth	3.20E+03	1.67E+03	1.916	0.06
	150 Gley/Pseudogley on slopes	3.39E+03	1.98E+03	1.712	0.09
	21 Colluvial deposits	4.57E+03	3.94E+03	1.158	0.25
	20 Poor brown earth	1.43E+03	1.31E+03	1.087	0.28
	10 Rankers	1.34E+03	1.32E+03	1.016	0.31
	31 Minor calcaric cambisol	1.30E+03	1.42E+03	0.91	0.36
	30 Eutrophic brown earth	7.43E+02	1.26E+03	0.59	0.56
	180 Rendzinas	-8.79E+02	1.50E+03	-0.59	0.56
	100 Brown earth on loess	1.40E+03	2.66E+03	0.53	0.60
	120 Pseudogley on solid bedrocks	7.21E+02	1.88E+03	0.38	0.70
	200 Terra fusca	-5.87E+02	1.61E+03	-0.37	0.71
	90 Cohesive brown earth	-1.87E+02	1.82E+03	-0.10	0.92
	190 Mixed soil	-1.71E+04	2.73E+06	-0.01	0.99
	40 Semi-Podzols	-1.47E+04	3.86E+06	0.00	1.00
	22 Podzolic brown soil	-1.79E+04	5.35E+06	0.00	1.00
	280 Bog	-1.49E+04	4.74E+06	0.00	1.00
	160 Loamy soil	-1.83E+04	7.09E+06	0.00	1.00
	181 Pararendzina	-1.78E+04	7.46E+06	0.00	1.00
	270 Low peat bog, bog general	-1.43E+04	6.81E+06	0.00	1.00
	220 Alluvial soil, streamside marshes	-1.78E+04	1.09E+07	0.00	1.00
	60 Substrate-induced Podzol	-1.49E+04	9.74E+06	0.00	1.00
	110 Chromic luvisols	-1.77E+04	1.16E+07	0.00	1.00
	131 Pseudogley on loess	-1.76E+04	1.18E+07	0.00	1.00
	50 Climate-induced Podzol	-9.51E+03	7.87E+06	0.00	1.00
	92 Slightly gleyed brown earth	-1.54E+04	1.64E+07	0.00	1.00
	202 Cohesive calcaric cambisol	-1.61E+04	2.27E+07	0.00	1.00
	140 Stagnogley	-1.82E+04	2.61E+07	0.00	1.00
	132 Pseudogley on clay	-1.31E+04	2.09E+07	0.00	1.00
	81 Brown podzolic soil	-1.42E+04	2.70E+07	0.00	1.00
Alliance	Fagion sylvaticae	-2.31E+03	1.07E+03	-2.159	0.03
	Quercion roboris	-2.56E+03	1.24E+03	-2.062	0.04
	Dicrano-Pinion	-2.84E+03	1.58E+03	-1.793	0.07
	Quercion pubescentis-petraeae	-1.97E+03	1.24E+03	-1589.00	0.11
	Alnion incanae	-1.58E+03	1.26E+03	-1.253	0.21
	Alnion glutinosae	-2.62E+03	2.32E+03	-1.129	0.26
	Carpinion betuli	-7.88E+02	1.01E+03	-0.78	0.44
	Salicion cinereae	7.99E+02	1.84E+03	0.43	0.66
	Tilio-Acerion	-2.62E+02	9.54E+02	-0.27	0.78
	Salicion albae	-4.22E+02	1.78E+03	-0.24	0.81
	Pinion mugo	5.85E+02	2.84E+03	0.21	0.84
	Vaccinio-Piceion	-1.92E+04	2.54E+06	-0.01	0.99
	Erico-Pinion sylvestris	-1.75E+04	2.71E+06	-0.01	0.99
	Vaccinio uliginosi-Pinion	-1.95E+04	6.15E+06	0.00	1.00
	Fraxino orn- <i>Ostryion</i>	-1.79E+04	6.62E+06	0.00	1.00
	Alnion viridis	-1.36E+04	7.98E+06	0.00	1.00
	Sambuco-Salicion capreae	-1.80E+04	1.07E+07	0.00	1.00
	Salicion triandrae	-2.47E+04	1.78E+07	0.00	1.00
	Berberidion	-2.14E+04	1.78E+07	0.00	1.00
	Populo tremulae-Corylion	-1.85E+04	1.78E+07	0.00	1.00
Elevation		-6.46E+00	1.33E+00	-4.847	0.00
Atan (inclination/100)		2.60E+03	1.13E+03	2.301	0.02

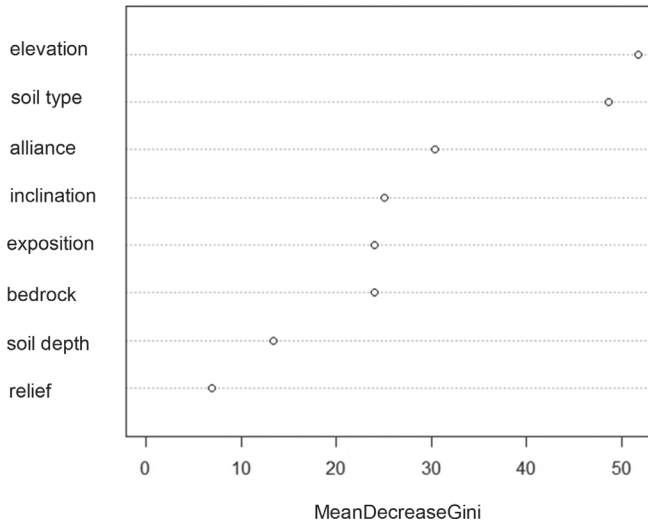


Figure 2. Variable significance plot for IAS presence by mean decrease in Gini values (MeanDecreaseGini) using the Random Forest model, ranked by significance. The points represent the mean decrease in Gini value, indicative of the importance of each variable. A higher value indicates the significance of that variable for predicting IAS occurrence in NFR sites.

highest basal areas were *F. angustifolia*, *Populus* spp. (*Populus* spp. includes *P. alba*, *P. canescens*, *P. tremula*, *P. nigra*, and *P. × canadensis*) and *Quercus* spp. (*Quercus* spp. includes *Q. petraea* and *Q. robur*), owing to a high proportion of large tree dimensions in DBH. During the 15-year monitoring period, the average total stem number increased from 591 to 718 trees per ha and the averaged total basal area increased from 31.1 to 39.3 m² per ha. The invasive tree species recorded were *Fraxinus pennsylvanica* and *Acer negundo*. Invasive tree species occurred in 8% (5 plots) of the total sampled area (64 plots). Figures 3, 4 compare the tree species composition in the AC plots by stem number and basal area between period 1 and period 2. Error bars indicate standard errors. The large error bars in Figure 3 indicate a low number of plots with a strong increase in stem number for *A. negundo*.

The species development data shows an increase in stem number for the native tree species *F. angustifolia* (from 126 to 177 trees per ha) and *Ulmus* spp. (*Ulmus* spp. includes *U. glabra*, *U. minor*, and *U. laevis*) (from 57 to 176 trees per ha), whereas a decrease was recorded for *A. campestre* (from 202 to 174 trees per ha), *Populus* spp. (*Populus* spp. includes *P. alba*, *P. canescens*, *P. tremula*, *P. nigra*, and *P. × canadensis*) (from 61 to 30 trees per ha) and *Quercus* spp. (*Quercus* spp. includes *Q. petraea* and *Q. robur*) (from 37 to 22 trees per ha). In terms of basal area, an increase in the proportion of *F. angustifolia* (from 11.7 to 17.0 m² per ha) and *Ulmus* spp. (from 1.3 to 2.8 m² per ha) was determined during the observation period, while the proportion of *Salix* spp. (*Salix* spp. includes *S. alba*, *S. fragilis*, and *S. × rubens*) was the only one to decrease slightly (from 1.1 to 0.9 m² per ha).

Table 4. Parameter estimates of generalized linear models (error structure = quasi-binomial; link function = logit) explaining the probability of the presence of *Impatiens parviflora* in NFR sites. Only significant explanatory variables occurring in the minimal adequate GLM were included in the model. Values are on the logit scale. * = factors significant at the $p < 0.05$ level. Data included in the logistic regression model were not transformed.

Variable	Categories	Estimate	Std. error	t value	Pr (> t)
Alliance	<i>Abieti-Piceion</i>	-1.39E+00	1.10E+00	-1.26	0.21
	<i>Alnion glutinosae</i>	-1.92E+01	6.83E+03	0.00	1.00
	<i>Alnion incanae</i>	-2.04E+00	9.36E-01	-2.18	0.03
	<i>Alnion viridis</i>	-1.52E+01	5.41E+03	0.00	1.00
	<i>Berberidion</i>	-2.13E+01	1.19E+04	0.00	1.00
	<i>Carpinion betuli</i>	-1.68E+00	6.85E-01	-2.46	0.01
	<i>Dicrano-Pinion</i>	-2.66E+00	1.14E+00	-2.34	0.02
	<i>Erico-Pinion sylvestris</i>	-1.82E+01	1.89E+03	-0.01	0.99
	<i>Fagion sylvaticae</i>	-2.29E+00	7.87E-01	-2.91	0.00
	<i>Fraxino orni-Ostryion</i>	-1.89E+01	4.35E+03	0.00	1.00
	<i>Pinion mugo</i>	-4.49E-01	2.06E+00	-0.22	0.83
	<i>Populo tremulae-Corylion</i>	-1.92E+01	1.19E+04	0.00	1.00
	<i>Quercion pubescentis-petraeae</i>	-2.52E+00	9.16E-01	-2.75	0.01
	<i>Quercion roboris</i>	-2.58E+00	8.88E-01	-2.90	0.00
	<i>Salicion albae</i>	-3.37E+00	1.07E+00	-3.15	0.00
	<i>Salicion cinereae</i>	-2.33E+01	5.73E+03	0.00	1.00
	<i>Salicion triandrae</i>	-2.45E+01	1.19E+04	0.00	1.00
	<i>Sambuco-Salicion capreae</i>	-1.76E+01	7.38E+03	0.00	1.00
	<i>Tilio-Acerion</i>	-4.21E-01	6.69E-01	-0.63	0.53
	<i>Vaccinio-Piceion</i>	-1.83E+01	1.78E+03	-0.01	0.99
	<i>Vaccinio uliginosi-Pinion</i>	-3.12E+00	5.86E+03	0.00	1.00
Soil type	80 Minor Brown earth	2.51E+00	7.54E-01	3.34	0.00
	130 Pseudogley on unconsolidated sediments	2.84E+00	7.55E-01	3.77	0.00
	250 Mature, brown alluvial soil	2.94E+00	9.33E-01	3.16	0.00
	21 Colluvial deposits	4.36E+00	1.76E+00	2.48	0.01
	180 Rendzinas	-1.60E+00	6.78E-01	-2.36	0.02
	150 Hanggley, Hangpseudogley	2.81E+00	1.21E+00	2.32	0.02
	30 Eutrophic brown earth	-1.29E+00	5.82E-01	-2.22	0.03
	200 Terra fusca	-1.95E+00	1.18E+00	-1.66	0.10
	22 Podzolic brown soil	-1.83E+01	3.73E+03	-0.01	0.10
	240 Gray-alluvial soil	1.37E+00	1.10E+00	1.25	0.21
	31 Minor calcaric cambisol	6.83E-01	6.93E-01	0.99	0.32
	120 Pseudogley on solid bedrocks	-2.15E+00	2.90E+00	-0.74	0.46
	20 Poor brown earth	2.88E-01	4.42E-01	0.65	0.52
	210 Gley	6.09E-01	1.50E+00	0.41	0.69
	90 Cohesive brown earth	-4.18E-01	1.11E+00	-0.38	0.71
	190 Mixed soil	-1.79E+01	1.89E+03	-0.01	0.99
	40 Semi-Podzols	-1.60E+01	2.76E+03	-0.01	1.00
	280 Bog	-1.62E+01	3.70E+03	0.00	1.00
	160 Loamy soil	-1.87E+01	5.00E+03	0.00	1.00
	181 Pararendzina	-1.86E+01	5.26E+03	0.00	1.00
	270 Low peat bog, bog general	-1.52E+01	5.02E+03	0.00	1.00
	260 Half-bog	-1.43E+01	5.52E+03	0.00	1.00
	220 Alluvial soil, streamside marshes	-1.82E+01	7.28E+03	0.00	1.00
	60 Substrate-induced Podzol	-1.65E+01	6.66E+03	0.00	1.00
	131 Pseudogley on Loess	-1.83E+01	7.90E+03	0.00	1.00
	110 Chromic luvisols	-1.82E+01	7.95E+03	0.00	1.00
	50 Climate-induced Podzol	-1.23E+01	5.59E+03	0.00	1.00
	140 Stagnogley	-1.88E+01	1.74E+04	0.00	1.00
	100 Brown earth on loess	-2.04E+01	1.98E+04	0.00	1.00
	132 Pseudogley on clay	-1.51E+01	1.49E+04	0.00	1.00
	202 Cohesive calcaric cambisol	-1.72E+01	1.69E+04	0.00	1.00
	81 Brown podzolic soil	-1.56E+01	1.85E+04	0.00	1.00
Relief	Erosion	5.69E-01	4.71E-01	1.21	0.23
	Solid	7.17E-01	3.54E-01	2.03	0.04
Elevation		-4.77E-03	8.92E-04	-5.35	0.00
Atan (inclination/100)		2.14E+00	8.83E-01	2.42	0.02

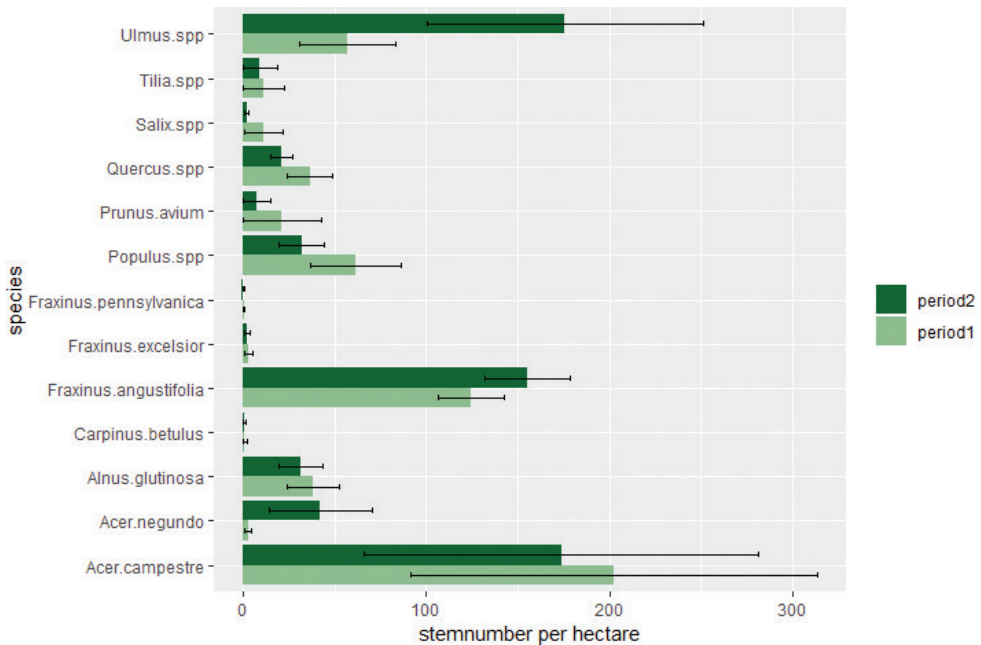


Figure 3. Changes in tree species composition in unmanaged floodplain forests (period 1: 1997 to 1999 – period 2: 2013 to 2014) using the angle count sampling method (Bitterlich, 1984). Average stem number per hectare in floodplain forests alongside the river March on 64 sample plots in 6 NFR in period 1 (light green) and period 2 (dark green); error bars denote standard errors. The large error bars indicate a low number of plots with a high increase in stem number for *A. negundo*. *Ulmus* spp. includes *U. glabra*, *U. minor* und *U. laevis*; *Tilia* spp. includes *T. cordata*, *T. platyphyllos* and *T. × vulgaris*; *Quercus* spp. includes *Q. petraea*, and *Q. robur*; *Populus* spp. includes *P. alba*, *P. canescens*, *P. tremula*, *P. nigra*, and *P. × canadensis*; *Salix* spp. includes *S. alba*, *S. fragilis* and *S. × rubens*.

Focusing on the IAS, the proportion of *F. pennsylvanica* in terms of both stem number and basal area was very low and remained stable during the observation period. The stem number for *A. negundo* increased from 3 to 42 trees per hectare, but its proportion in basal area only increased from 0.2 to 0.7 m² per ha, indicating that the current tree population consists predominantly of small trees ranging from DBH 5 to 30 cm.

Natural tree species regeneration

In total, IAS occurred in 0.4% ($n = 3$) of the investigated regeneration site plots ($n = 784$). The invasive species found were *Robinia pseudoacacia*, *Ailanthus altissima*, and *Acer negundo*, each on one plot. Individuals of *R. pseudoacacia* and *A. altissima* were found in the forest alliance *Galio sylvatici-Carpinetum* (Oberdorfer 1957) at elevations between 250 and 300 m above sea level. *Acer negundo* was found in the regeneration of the *Fraxino pannonicae-Ulmetum* floodplain forest alongside the river March at an

Table 5. Parameter estimates of generalized linear models (error structure = quasi-binomial; link function = logit) explaining the probability of the presence of *Robinia pseudoacacia* in NFR sites. Only significant explanatory variables occurring in the minimal adequate GLM were included in the model. Values are on the logit scale. * = factors significant at the $p < 0.05$ level. Data included in the logistic regression model were not transformed.

Variable	Categories	Estimate	Std. error	t value	Pr (> t)
Bedrock class	Intermediate	3.68E+00	1.82E+00	2.02	0.04
	Carbonate	3.44E+00	1.75E+00	1.97	0.05
	Silicate	1.86E+00	1.80E+00	1.03	0.30
	Flood plain sediments	9.13E-01	1.32E+00	0.69	0.49
	Loess soil	-1.45E+01	6.73E+03	0.00	1.00
Relief	Erosion	-1.68E+01	1.13E+03	-0.02	0,99
	Solid	-1.28E+00	6.85E-01	-1.87	0,06
Elevation		-2,03E-02	5.54E-03	-3.66	0.00

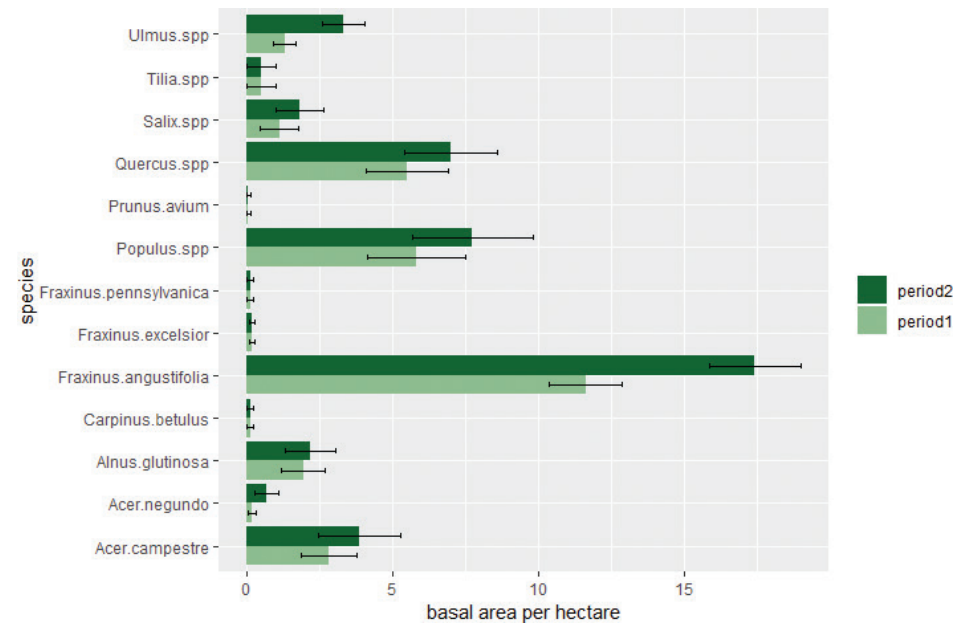


Figure 4. Changes in tree species composition in unmanaged floodplain forests (period 1: 1997–1999; period 2: 2013–2014) using the angle count sampling method (Bitterlich, 1984). Average basal area per hectare in floodplain forests alongside the river March on 64 sample plots in six NFR in period 1 (light green) and period 2 (dark green); error bars denote standard errors. *Ulmus* spp. includes *U. glabra*, *U. minor*, and *U. laevis*; *Tilia* spp. includes *T. cordata*, *T. platyphyllos*, and *T. × vulgaris*; *Quercus* spp. includes *Q. petraea*, and *Q. robur*; *Populus* spp. includes *P. alba*, *P. canadensis*, *P. tremula*, *P. nigra*, and *P. × canadensis*; *Salix* spp. includes *S. alba*, *S. fragilis*, and *S. × rubens*.

elevation of 150 m above sea level. As this data is insufficient for further detailed statistical evaluation, vegetation surveys were used to analyse the spread of alien species in the forest communities of the NFR.

Discussion

The number and distribution of IAS

The IAS and AS identified in both the herbaceous layer and the tree layer are not new to Europe; all of them are commonly known alien species in European temperate forests (Nehring et al. 2013; Braun et al. 2016; Wagner et al. 2017; Campagnaro et al. 2018). Most of the 16 IAS occurring in the NFR have a long history of introduction into Austria for ornamental purposes beginning in the 18th century (Düll and Kutzelnigg 2005; Fischer 2008; Universität Innsbruck 2019). Of the alien plant species found in our study, 64% originate from North America and 21% from Asia. Encountering these species in the NFR plots examined for this study was therefore to be expected. Furthermore, the results show that 36% of the alien plant species recorded were phanerophytes. These findings are in line with Wagner et al. (2017), who found that phanerophytes are the most species-rich life-forms among alien plant species in European woodlands, possibly due to the high introduction pressure of alien trees since the 17th century.

As was likewise to be expected, herbaceous IAS were found more frequently than tree species. Especially common were *Impatiens parviflora* (106 plots in 42 NFR), *Solidago gigantea* (38 plots in 11 NFR), and *Bidens frondosa* (31 plots in 4 NFR). The most common tree species were *Fraxinus pennsylvanica* (17 plots in 4 NFR), *Robinia pseudoacacia* (15 plots in 16 NFR), and *Acer negundo* (9 plots in 4 NFR). Interestingly, one of the most widespread IAS in Europe, *Ailanthus altissima* (the tree of heaven) (Pyšek et al. 2009; Boer 2012), occurred in only one regeneration plot. This may be on the one hand due to the low level of anthropogenic disturbances, e.g. transportation pathways, and on the other hand to closed canopy conditions in the NFR sites. In temperate Europe, the species *A. altissima* can form urban pioneer forests under sufficient light conditions and low competition (Kowarik and Säumel 2007), and its spread within the Danube floodplains is also mostly owed to human disturbances (Drescher and Ließ 2006; Campagnaro et al. 2018).

Drivers influencing the occurrence of IAS in the herbaceous layer

We conclude from the calculated statistical models that the best predictors for the number of IAS in unmanaged forests are alliance, elevation, and soil type (Table 3, Figure 2). Our results show that the probability of IAS occurrence in unmanaged forests decreases as elevation increases. Furthermore, unmanaged forests in lowlands with a low inclination are more likely to be invaded by IAS. These findings are in line with previous investigations showing that IAS preferably invade temperate European forests in warm climates and at lower elevations (Arévalo et al. 2005; Becker et al. 2005; Chytrý et al. 2009; Medvecká et al. 2018).

Besides elevation and alliance, soil type was found to be a highly significant variable. Our observations are similar across European woodlands, where *I. parvi-*

flora has successfully established itself in a wide range of habitat niches with soils of intermediate to high nutrient content (Wagner et al. 2017). Comparison of Table 4 (*Impatiens parviflora*) with Table 3 (all IAS) reveals that *Impatiens parviflora* exhibits a different pattern of occurrence in terms of soil types. It prefers variants of brown earth (21, 30, 80) and pseudogley (130, 150), but in contrast to most other IAS it shows no special affinity for riparian soils (240, 250). While riparian soils occur only in restricted areas, brown earth and pseudogley are very widespread in Austrian lowland forest areas (NFI 2009). Thus, the fact that *I. parviflora* is the most common of the IAS in Austria can be explained by its affinity for the predominant soil types in the area. Based on its high frequency, *I. parviflora* may constitute an example of species where a point of no return has been reached in Austrian forest ecosystems.

The abundance of IAS and AS (in total 34 alien plant species), especially of invasive alien tree species, in the unmanaged forest habitats investigated for this report is lower than in other European forest habitats (Richardson et al. 2007; Chytrý et al. 2009; Vilà et al. 2011; Nehring et al. 2013; Braun et al. 2016). Martin et al. (2009) conclude that unmanaged forests are actually more resistant to biological invasions, but that the speed of invasion by shade-tolerant species is comparatively lower than in grasslands and other habitats and is therefore often underestimated. The timescale of invasions by species with early-successional traits differs from the speed of invasions by shade-tolerant species in forest habitats (Martin and Marks 2006). All of the investigated NFR are closed-canopy forests containing large proportions of shade-tolerant species in the ground vegetation layer. Under the closed canopy of the unmanaged forest sites, the most abundant invasive species in the NFR network is *I. parviflora*, the small balsam, which is one of the most widespread invasive plants occurring in European temperate forests (Jarčuška et al. 2016). *Impatiens parviflora* occurred in a significantly larger number of NFR sites ($n = 42$ NFR) than any of the other less shade-tolerant IAS identified. Given the risk of underestimating the slower invasion mechanisms in forest ecosystems, more emphasis on early detection of alien plant species is required to avoid an increase of propagule pressure in Central European forests (Essl et al. 2011; Nehring et al. 2013).

In many studies, human disturbances, which increase propagule pressure are mentioned as important predictors of the range and abundance of IAS in forest ecosystems (Walter et al. 2005; Pyšek et al. 2009; Berg et al. 2016). The direct anthropogenic influence on NFR sites is kept as low as possible, however, and is thus comparable to core zones of national parks or other strictly protected areas where any form of human disturbance is prohibited (Dudley 2008). Nevertheless, natural disturbances can and do occur, and thus may create gaps facilitating the pathways for invasions by IAS (Walter et al. 2005; Foxcroft et al. 2013). With endogenous (gradual, e.g. aging, decay) and exogenous (episodic, wind, fire, avalanches) disturbances being the main driving forces for development in forest reserves, the potential for invasions depends on the frequency and severity of the disturbances as well as the availability of propagules (Wohlgemuth et al. 2002; Maringer et al. 2012).

Tree species communities in floodplain forests

Riparian areas, defined by Walter et al. (2005) as river banks and the edges of lakes, and floodplain forests are among the most-invaded habitat types in Europe (Planty-Tabacchi et al. 1996; Richardson et al. 2000; Tickner et al. 2001; Berg et al. 2016; Sosa et al. 2018). In floodplain forests, high nutrient levels and frequent disturbances due to flooding facilitate invasions, and rivers additionally serve as very effective propagation corridors for IAS (Kowarik 1992; Pyšek and Prach 1993; Schmiedel et al. 2013). The findings of this study confirm that natural floodplain forests are one of the forest types most vulnerable to biological invasions.

The occurrence of IAS was highest in the natural floodplain forest communities, with IAS were found in the herbaceous layer and the tree layer. Over the past 15 years, *Fraxinus pennsylvanica* and *Acer negundo* (a tree species of North American origin) increased in stem number and DBH in these communities. This increase may signal the beginning of species composition changes in the *Fraxino pannonicae-Ulmetum* community. Over the 15-year period examined in this study (1998/99 to 2013/14), the proportion of invasive tree species increased in the floodplain forest community.

The results of this study do not show any competitive interactions between alien and native floodplain plant species. Rather, they highlight that there has been an increase in total tree diversity. These observations are also reflected when considering the overall species composition of trees in floodplain NFR sites (Figs 3, 4).

The average stem number and basal area increased during the 15-year monitoring period, reflecting the observed high diversity and rapid development of tree species in riparian NFR. The numbers of individual tree species differ considerably between NFR sites, however. High stem numbers combined with low basal areas indicate a large proportion of small trees, whereas high basal areas indicate a large proportion of bigger trees. According to Figures 3, 4, the main tree species are *Fraxinus angustifolia*, *Quercus* spp., and *Populus* spp., trees with smaller DBH are *Acer campestre*, *Acer negundo* and *Ulmus* spp. While the proportion of *F. pennsylvanica* did not increase significantly during the observation period, the stem numbers of *A. negundo* did, although mostly small trees were found.

The most severe changes caused by invasive tree species were detected in NFR Herrschaftsspitz ($n = 9$ AC plots), where the number of *A. negundo* individuals increased from 20 per hectare in period 1 to 117 per hectare in period 2 (results not shown here). *Acer negundo* has spread widely across Europe and Central Asia (DAISIE 2017; GRIS 2018) since being introduced from North America for horticultural purposes in the 17th century (Mędrzycki 2012). *Acer negundo* is commonly planted in parks and gardens in variegated forms (e.g. “*Auratum*”, “*Flamingo*”, “*Aureomarginatum*”, “*Variegatum*”) (van Gelderen and van Gelderen 1999). The impact of *A. negundo* on biodiversity and ecosystem functions of floodplain forests is high; it outcompetes native tree species by forming dense stands and through allelopathic effects on the soil (Mędrzycki 2012; Krevš et al. 2013; Höfle et al. 2014). Management measures for *A. negundo* have been widely applied, but are reported as not effective and too cost-intensive to be sustainable in the long

term (De Poorter and Browne 2005; CABI 2019). Nevertheless, it should be pointed out that invasion by *A. negundo* at this intensity was observed only in one NFR site (NFR Herrschaftsspitz), which is located directly along the shoreline of the river March.

Conclusion

Given the presence of IAS with well-documented negative ecological impacts such as *A. negundo*, *Robinia pseudoacacia*, and *Ailanthus altissima* in comparably local spreads within the NFR sites on the one side and a high frequency of natural disturbances in the NFR sites on the other, the results of this study can be considered under a “no IAS management scenario” in the temperate climate of Central Europe. At high elevations (>800m above sea level) almost no alien plant species were recorded. Nevertheless, the proportion of alien tree species in the sampled plots of the NFR is similar to that in the National Forest Inventory overall (<2% of the total forest cover). The non-intervention management policy in the NFR sites examined in this study offered an opportunity to observe changes in species composition, provide reference data for nature-based silviculture and contribute to management options in unmanaged forests.

In total, 16 IAS were identified in the study; this is in line with many other investigations into the spread of IAS in Europe. Similarities include a common set of IAS led by *Impatiens parviflora*, the small balsam, invading the ground vegetation of temperate forests. The findings of this study show that unmanaged forests at low elevations are not resistant to plant invasions. Instead, the monitoring of invasive plant species in NFR sites shows that biological plant invasions do occur in unmanaged temperate forest ecosystems, albeit at a slower pace than in many other habitat types. The results of the study also show that an absence of human disturbance may lower but not entirely mitigate the propagule pressure in forest ecosystems. Further studies are necessary to investigate the effects on propagule pressure. Nevertheless, it must be taken into consideration that AC sampling may not be an appropriate methodology for evaluating spontaneous regeneration of IAS in NFR and that the observation period was comparatively short in the context of tree species development. Long-term studies with specific IAS monitoring are, therefore, necessary to achieve a better understanding of IAS development in unmanaged forest reserves. The aim of this study was to determine drivers for plant invasions in unmanaged European temperate forests. The explanatory variables alliance, elevation, bedrock class, soil type, and relief were found to be significant predictors for the presence of IAS. Ultimately, the findings of this study show that climatic limitation (elevation) is the main driver for the spread of IAS into unmanaged temperate European forests.

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Appendix I

Legend of soil type classification (Nestroy 1998).

asd

Order	Classification	Soil type	Description
Hydromorphic	Riparian soils	220	Alluvial soil, streamside marshes
		240	Gray-alluvial soil
		250	Mature, braun alluvial soil
	Gley	150	Gley/Pseudogley on slopes
		210	Gley
		260	Half-bog
	Bog and half-bog	270	Low peat bog, bog general
		280	Bog
		120	Pseudogley on solid bedrocks
	Pseudogley	130	Pseudogley on unconsolidated sediments
		131	Pseudogley on Loess
		132	Pseudogley on clay
		140	Stagnogley
		160	Loamy soil
		190	“Mixed soil” (Rendzina/ Terra fusca transition)
Terrestrial	Loamy soil & red clay	200	Terra fusca
		203	Gleyed Terra fusca
		20	Poor brown earth
		22	Podzolic brown soil
		30	Eutrophic brown earth
	Brown elevation earth (Braunerde)	31	Minor calcaric cambisol
		80	Minor Brown earth on unconsolidated sediments
		81	Brown podzolic soil on unconsolidated sediments
		90	Cohesive Brown earth on unconsolidated sediments
		92	Slightly gleyed brown earth on unconsolidated sediments
		100	Brown earth on loess
		110	Chromic luvisols (Para-brown earth)
		202	cohesive calcaric cambisol
		171	Humid black soil
	Humid black soil Podzols	40	Semi-Podzols
		50	Climate-induced Podzol
		60	Substrate-induced Podzol
		10	Rankers
	Rendzinas, Ranker	180	Rendzinas
		181	Pararendzina
		21	Colluvial deposits
	Relocated soils		

Common deficiencies of actions for managing invasive alien species: a decision-support checklist

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Abstract

Despite the increasing number of invasive species, protocols devoted to assess the feasibility (i.e., probability of success or failure) of management actions in the field are scarce, yet success depends on a broad scope of issues beyond the biology of species and the ecosystem to be managed. In this paper we make a retrospective analysis of 90 actions and management proposals developed in Andalusia (southern Spain) in 2004 to 2018. Actions included 59 terrestrial and aquatic taxa. We identified items that in case of deficiency were responsible for either the rejection of action proposals ($n = 44$) or failure of implemented actions for which the goal was not achieved ($n = 22$). The most frequent deficiencies included the absence of funding during the necessary time to achieve the goals, the risk of reinvasion and an insufficient removal rate to achieve the specific objective. Based on the deficiencies found, we built a comprehensive, broad-scope compliance checklist to assist decision-makers to identify deficiencies before action. In addition, implemented actions for which the goal was achieved ($n = 24$) were used for validating the checklist. The checklist contains 40 items related to IAS features, administrative features, methodology effectiveness, efficiency and impacts of the action, and invaded ecosystem features. The checklist is valid across all taxa and habitats. The use of this checklist will help reduce the degree of arbitrariness and subjectivity of actions aimed at managing IAS, and a more efficient use of resources.

Keywords

control, decision-making, eradication, failure, feasibility, invasion, management, success

Introduction

The large number of invasive alien species (IAS) in natural areas contrasts with the scarce resources available for their management (Andreu et al. 2009). The increasing number of problems related to biological invasions has led to a growing need to of evidence-based support to policy-makers in order to enhance their decisions about IAS management (Andersen et al. 2004). However, actions may hide mistakes, weak points, inadequacies, gaps of knowledge, or methodological limitations (hereinafter referred to as ‘deficiencies’) that go unnoticed during their preparation (Maguire 2004; Campbell et al. 2018). These planning deficiencies may include inadequate budget (e.g., underestimation of operational costs), insufficient duration of the financing, or removal methods that are not adapted to the IAS biology and life cycle (i.e., methods that do not consider the ‘weak points’ of the IAS; Bohren 2017). These deficiencies may compromise the achievement of the main goal or the specific objectives. Besides, when no evidence-based and standardised protocol is used to guide decision-making, decisions may be taken on arbitrary or biased judgements or guess-timates of stakeholders, planners or the general public rather than on comprehensive scientific and technical evidence (Bardsley and Edwards-Jones 2006; Sharp et al. 2011). These deficiencies may cause a series of ‘cascade effects’ resulting in: (i) a poor definition of main objectives, actions and resource constraints (Game et al. 2013), (ii) the application of different and erratic strategies between neighbour countries, regions and even municipalities (Keller et al. 2011; Monceau et al. 2014); (iii) short-lasting actions that have a high probability of failure (Blossey 1999); (iv) an inefficient use of resources, both monetary and non-monetary, something that is especially relevant given the paucity of available funds (Pluess et al. 2012); (v) overlooking certain introduction pathways and the dynamics of propagule pressure (Simberloff 2006; Brasier 2008); (vi) disregarding action side effects such as the enhancement of other potentially invasive species or major ecosystem disturbances (Águas et al. 2014; Buckley and Han 2014).

The importance of analysing the feasibility of management actions has been recognised in international policy frameworks such as the Biological Convention on Biological Diversity (COP 6 Decision VI/23 on Alien species that threaten ecosystems, habitats or species: guiding principles for the prevention, introduction and mitigation of impacts of alien species that threaten ecosystems, habitats or species) and the Regulation (EU) 1143/2014 of the European Parliament and of the Council of 22 October 2014. This recognition has led to the formulation of general recommendations to evaluate global feasibility of a given action. Most published criteria to affect the feasibility of actions focus on particular eradication experiences (Simberloff 2003; Pacific Invasives Initiative 2011) or analyse the effect of a few variables such as detectability, search effort and duration of the eradication program (Cacho et al. 2006). However, to our knowledge, no comprehensive checklist applicable across taxonomic groups, habitat types, or specific management aims (prevention, eradication, containment, or control) is available.

In this paper, we list general items related to the feasibility of actions based on a retrospective analysis of 90 real IAS management cases applied to 59 species that were proposed or implemented by the Regional Environmental administration in Andalusia (southern Spain) during 14 years (2004–2018). Specifically, (1) we gathered items responsible for action failure (in unsuccessful actions) and for rejection of action proposals; (2) we assessed the most frequent items related to action failure; and (3) we compared the number of items with deficiency among successful and unsuccessful actions and not-implemented proposals as a basis to validate the usefulness of these items to distinguish between feasible and unfeasible actions. As a result, (4) we built a comprehensive and easy-to-use general checklist (Table 1) to assist decision makers to detect deficiencies that might lead to action failure.

Methods

Description of actions on IAS management

We analysed 90 field management actions and proposals of IAS received or implemented by the Regional Environmental Administration of Andalusia in 2004 to 2018 (Suppl. material 1: Table S1). Andalusia (87,268 km²) is the southernmost administrative region in Spain. The region has a population of ca 8.4 million inhabitants (Instituto Nacional de Estadística 2018) and harbours a wide variety of inland, coastal and marine habitats including 340 protected areas accounting for 49% of the total administrative area (CMAOT 2017). From east to west, Andalusia is characterised by an extensive coast (945 km, along both the Mediterranean Sea and the Atlantic Ocean) and several mountainous ranges with a maximum altitude in Sierra Nevada National Park (Mulhacén Peak: 3,481 m a.s.l.). The dominant climate is Mediterranean, with dry, hot summers, but arid, cold steppe conditions occur in the south-east (Kottek et al. 2006).

The actions encompassed a variety of taxonomic groups, life forms, and habitats (Fig. 1). Plant taxa represented 50% of the action plans analysed (45 out of 90), most of them (37) were terrestrial plants, whereas animals included 24 vertebrate and 21 invertebrate taxa. Regarding the habitat type, action plans included both aquatic and terrestrial habitats with dominance of inland waters and coastal habitats (Fig. 1). Some of the actions involved the same species in different localities with varying characteristics or different elimination methods. Therefore, the total number of actions analysed ($N = 90$) was higher than the total number of taxa managed (59 taxa: 28 plants and 31 animals).

Action proposals and implemented actions aimed at eradication, control or containment of IAS in the field were made by collectives (NGO, professional associations), managers, scientists, or public institutions. Part of the proposals were selected and implemented as the result of coordinated decisions made by regional decision-makers, local authorities, specialised technicians, and rangers and based on documented and expert knowledge.

Table 1. Checklist for identifying deficiencies of actions for management of invasive alien species (IAS) in the field aimed to biodiversity conservation. The items must be answered in the framework of the action plan area. For assessments, the proposed methodology is defined by the elimination technique (biological, mechanical, chemical), the time or season of application, the number of applications, the final concentration (in case of a biocide), the frequency of monitoring and rounds of control, and methodological adaptations to minimise the impact and to promote ecosystem recovery.

Block 1: Basic prerequisites and definition of the main conservation goal and specific objective
1. The target species is alien
2. The alien species causes (or will cause) significant negative impacts (damage) on biodiversity
3. The main conservation goal of the action plan is [select one option]: a) Ecological restoration: to return the ecosystem to a 'reference' state b) Ecological enhancement or rehabilitation: to increase the quality or quantity of some characteristic or functions of the action plan area c) Ecological reallocation, reassignment or replacement: to replace the ecosystem by a different one d) Protection: to preserve (maintain or recover) the abundance of certain native species or habitats e) Mitigation: to compensate the permitted loss of species or ecosystems f) Others not related with biodiversity conservation (e.g., to keep or recover uses or to protect human health); or the goal is unknown/uncertain
4. The specific objective against the IAS is [select one option]: a) Prevention: to avoid or minimise the risk of introduction b) Eradication: all individuals and propagules must be permanently removed c) Containment: to minimise the risk of spread d) Population control: to maintain population size below a desired threshold e) Other management or conservation actions not involving the IAS but other elements of the ecosystem, or the goal is unknown
5. The size of invasion impedes the application of any effective method nowadays
6. The removal rate and the frequency of post-treatment reviews and rounds of control are coherent to the specific objective (item #4): (a) eradication: removal rate exceeds recruitment and dispersal rate and all individuals can be removed; (b) containment: removal rate stops colonization rate; (c) control: removal rate allows reducing the population size below the desired threshold
7. The action plan is legal and meets all administrative requirements (permits of landowner, authorisations of responsible institutions, authorization to use chemical compound, etc.)
8. The methodology proposed is selective against the target IAS and does not provoke irreversible or long-lasting impacts in the ecosystem, site characteristics, economic activities and values (e.g., religious, cultural, recreational, etc.)
9. The methodology proposed can have an impact on human health
10. The expected environmental impacts provoked by the methodology exceed those caused by the IAS
11. There are other processes (e.g., habitat loss, pollution, resources overexploitation, etc.) not included in the action plan that are responsible for a greater negative impact than the target IAS
12. Hazards for workers can be avoided or minimised with personal protective equipment. In case of a possible accident, potential risks for workers are acceptable
Block 2: Ias and invasive population features
13. The possible benefits and functions of the IAS (refuge, feeding, nesting sites, dispersal, uses, etc.) have been assessed
14. In the case that more than one IAS is present in the action plan area, the target IAS is the main threat for biodiversity conservation
15. Indicators related to the IAS will be measured and are coherent to the specific objective (item #4): (a) prevention and eradication: the absence of the IAS can be confirmed; (b) containment: the absence of the IAS can be confirmed in the preserved area; (c) control: a population threshold has been selected
16. The IAS spatial distribution is known
17. The IAS reproductive cycle is known

18. The IAS regeneration rate (expressed as year recruitment, growth rate, biomass production, etc.) has been or will be gathered at the action plan area or in comparable areas
19. IAS abundance and demography (e.g. estimate or census of the size of the population, cohorts/size classes, sex ratio, etc.) has been or will be gathered
20. The ecological niche of the IAS (biotic, abiotic and movement requirements) is known at the action plan area or in comparable areas

Block 3: Administrative features

21. The institution (agency, ministry, section, or department) that will conduct the action plan has the necessary competences
22. The budget includes all the tasks necessary to undertake the action (staff, machinery, materials, transports, fuel, external analyses, contracts, characterization of ecosystem, etc.)
23. Availability of funds is guaranteed during the necessary time frame to achieve the specific IAS management objective
24. Availability of specialized staff is guaranteed during the time frame needed to achieve the specific IAS management objective
25. There is a lack of consensus of involved administrations/departments on the decision to execute the action plan or the methodology to be used
26. All or part of the invading population is on private property and: (i) there is no will or permission from the owner to work on their property; (ii) there is no legislation that obliges the owner to facilitate access to undertake the removal of the target IAS

Block 4: Methodology effectiveness, efficiency and impacts

27. In the short or the medium term, the area will surely be re-invaded from connected areas/ vectors and the positive effects of the action plan will disappear. Consider the possibility of (i) accidental introductions by not managed pathways (e.g., ballast water), (ii) recolonisation from non-treated areas that could act as propagule sources; or (iii) deliberate introduction. Answer 'unknown/uncertain' in case the IAS distribution is unknown (item #16)
28. The action plan area is entirely accessible for workers. No refuges or IAS individuals remain inaccessible
29. Field and environmental conditions are adequate for the treatment to reach the entire target IAS population (e.g., proper diffusion of a biocide)
30. The best time (season, moment of the day) to act has been chosen in order to maximize efficiency (total catch, yield, biomass per unit effort)
31. Previously published reports or experimental evidence (including previous experience by planners and field workers) show that the methodology proposed is effective in similar cases
32. Previously published or experimental evidence shows that the methodology proposed is not effective in similar cases
33. The methodology is adapted to the expected population changes (e.g., size classes, sex ratio, abundance, changes in spatial distribution, etc.) and to the presence of resistance structures (e.g. seed bank, spores, cysts), hidden or hibernating individuals
34. The plan includes field supervision to ensure that people involved in the action plan will strictly adhere to methodological instructions and will not change them without previous notice

Block 5: Native ecosystem features and social perception

35. The presence and abundance of native species with conservation value (e.g., endangered, protected, or locally rare species) is known and will not be negatively influenced by the action plan
 36. The presence of habitats of special conservation value has been or will be gathered
 37. Ecological processes of special importance in the action plan area has been or will be gathered
 38. Results of the action plan will be monitored using indicators. Indicators design and sampling frequency will be adapted to the conservation goal and the ecosystem treated
 39. Indicators will be compared between invaded, non-invaded, treated, and reference areas
 40. Social opposition is expected. Take special care if opposition may involve physical/verbal violence, complaints, or smear campaigns (e.g., against the staff or the leading institution)
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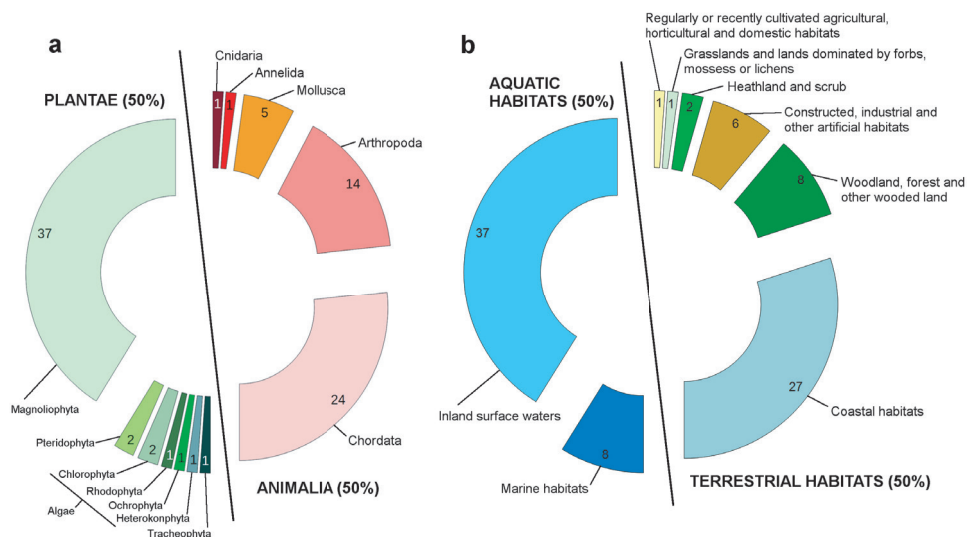


Figure 1. a Taxonomic groups represented in 90 action plans evaluated in this study. The taxonomic classification is based on BOLD (Barcode of Life Data system), a cloud-based data storage and analysis platform developed at the Centre for Biodiversity Genomics in Canada (<http://www.boldsystems.org>) **b** major habitat types represented in these action plans, following the EUNIS classification. Numbers inside the pie chart indicate the number of actions for each.

Monitoring of goal achievement

We visited managed localities annually to check if initially defined goals were accomplished. Eradication was considered achieved when no new individual was detected for five years. Control was considered achieved when the IAS abundance (e.g. plant mean coverage or captures per unit effort) decreased at least 90% after the action and maintained at least at 75% of the initial abundance for a minimum of 3 years. Containment was reached when the treated area was not reinvaded after the action. Accordingly, each action was classified into the following categories: (i) implemented actions that did not achieve the goals or specific objectives initially defined ($n = 22$) (hereinafter ‘unsuccessful actions’), (ii) implemented actions that achieved the goals or specific objectives initially defined ($n = 24$) (hereinafter ‘successful actions’), or (iii) proposals for management actions that were not implemented ($n = 45$) (hereinafter, ‘not-implemented proposals’).

Items related to feasibility and checklist design

After the execution of the action, we gathered information on the causes responsible for not-implemented proposals and for unsuccessful actions based on discussions with the different participants responsible for the execution of the action. With all the information, we generated a raw list of items associated with rejection or failure of each action.

Then, the raw list of items was refined (e.g., redundancies removed) and transformed into an easy-to-understand checklist of 40 items organised in five blocks, namely 'basic prerequisites' (items #1–12), 'IAS and invasive population features' (items #13–20), 'administrative features' (#21–26), 'methodology effectiveness, efficiency and impacts' (#27–34), and 'native ecosystem features and social perception' (items #35–40) (Table 1). This checklist was applicable to any action or proposal independent of its specific objective (prevention, eradication, containment, or control), the taxonomic group or the habitat type. To validate the extent to which the checklist serves to discern between feasible and unfeasible actions, the checklist was systematically used to assess all the not-implemented proposals ($n = 44$) and unsuccessful actions ($n = 22$) previously used for the raw list preparation and also successful actions ($n = 24$). For assessments, the proposed methodology was defined by the elimination technique (biological, mechanical, chemical), the time or season of application, the number of applications, the final concentration (in case of a biocide), the frequency of monitoring and rounds of control, and methodological adaptations to minimise the impact and to promote ecosystem recovery. In the case of not-implemented proposals, we only evaluated the prerequisites (first 12 items in Table 1) except for one case that did not show any deficiency in these prerequisites. Finally, we built up a database including the action, whether the goal was achieved or not and deficient items for each action.

Statistical analysis

First, we assessed the relative importance of each checklist item for determining the failure of unsuccessful actions or rejection of not-implemented proposals by calculating the frequency of deficiency of each item (number of times that item i showed a deficiency $\times 100$ / total number of actions of category j), being j either not-implemented proposals ($j = 44$) or unsuccessful actions ($j = 22$). Second, to evaluate to what extent the checklist discerns between feasible (successful, $j = 24$ in the previous equation) and unfeasible (unsuccessful) actions, both the frequency of deficiency of each item and the amount of items with deficiency were compared between successful and unsuccessful actions. We compared the total number of items with deficiency, considering both the number of prerequisites (items #1–12) and the rest of items (items #13–40) separately and all together. Since the data did not follow a normal distribution, pairwise Mann-Whitney U tests (Zar 1996) were used. Significant differences were considered when $p < 0.05$. The software Past® version 3.15 (Hammer 2001) was used.

Results

Forty items were found to induce rejection or failure of actions (Table 1). All the non-implemented proposals shared deficiencies in 12 items which were nearly absent in implemented successful and unsuccessful actions (Fig. 2). These 12 deficiencies were

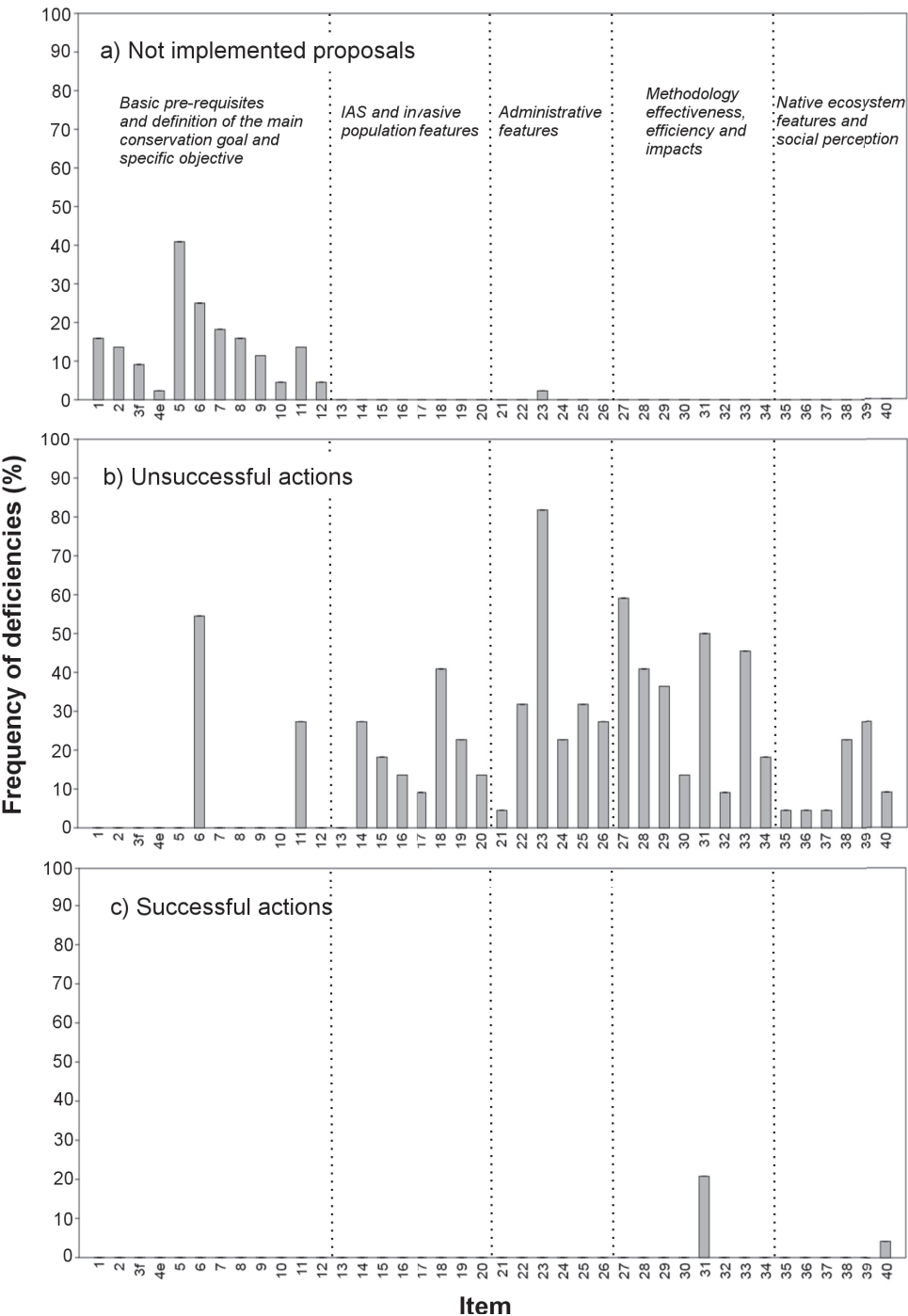


Figure 2. Percentage of deficiencies for the different checklist items (see Suppl. material 1: Table S1) in **a** not-implemented ($n = 44$) **b** unsuccessful ($n = 22$), and **c** successful ($n = 24$) actions aimed at managing IAS in Andalusia in 2004–2018. See Table 1 for a description of each item.

related to basic aspects of the action and therefore, were considered as pre-requisites (items #1–12, Table 1). These prerequisites include whether the target species is alien and invasive (i.e. causes a significant negative damage on biodiversity; Bartz and Kowarik 2019), the type of main conservation goal and IAS management specific objective (eradication, containment, or control), the absence of any effective methodology (usually in large scale invasions), legality, impacts on native ecosystem caused by the action implementation, incoherence between the methodology application, and the specific objective, risks for humans or workers.

The most common deficient prerequisite in not-implemented proposals was the absence of an effective methodology to be applied at the full scale, because the invaded area was very large (over 100 ha, data not shown) (item #5, 41% of cases analysed). Examples of such proposals are the control of the brown algae *Rugulopteryx okamurae* in the Strait of Gibraltar (area invaded >1000 ha), the eradication of the zebra mussel (*Dreissena polymorpha*) and European catfish (*Silurus glanis*) in a reservoir of 2,500 ha, the eradication of *Caulerpa cylindracea* in the sea bed of Almería (area invaded >100 ha, including depths > 30 m), and the control of the cord grass (*Spartina densiflora*) in Huelva salt marshes (area invaded of ca 1000 ha) (Suppl. material 1: Table S1).

In unsuccessful actions, the most items with deficiency belonged to the blocks 'Methodology effectiveness, efficiency and impacts' (median frequency of items with deficiency = 38.6%) and 'Administrative features' (median frequency = 29.5%) (Fig. 2).

Not-implemented proposals showed a higher number of prerequisites with deficiency ($p = 0.0010$, $DF = 65$, 1, Mann-Whitney U test) than unsuccessful actions (Figs 2, 3). The number of items with deficiency was significantly higher ($p < 0.001$, $DF = 45$, 1, Mann-Whitney U test) in unsuccessful actions than in successful actions within a block and across the overall checklist (Fig. 3). Unexpectedly, unsuccessful actions showed deficiency in two prerequisites related to an inconsistency between removal rate and objective needs (item #6, 54.5%) (e.g., eradication of *Arundo donax* on a river bank; eradication of *Eriocheir sinensis* in the Guadalquivir estuary) and the existence of other processes responsible for a greater negative impact than the target IAS whose management was not included in the action (item #11, 25%) (e.g., Eradication of *Pelodiscus sinensis* in the Guadalquivir estuary; control of *Galenia pubescens* in coastal areas from Málaga).

In sum, up to 29 items (out of 40) showed deficiency in unsuccessful actions (76% of items, median frequency = 7.5%), whereas only two items (5.1%, median frequency = 0.0%) showed deficiency in successful actions (Fig. 2).

The top 5 items that showed the highest frequency of occurrence in unsuccessful actions (Fig. 2) were: (1) the absence of funding during the necessary time to achieve the goals (item # 23, 82% of cases analysed); (2) the risk of reinvasion (item #27, 59% of cases analysed); (3) an insufficient removal rate to achieve the specific objective (item #6, 54% of cases analysed); (4) the absence of evidence reporting that the methodology applied is effective (item #31, 50% of cases analysed); and (5) the lack of adaptation of methodology to the expected population changes (item #33, 45% of cases analysed).

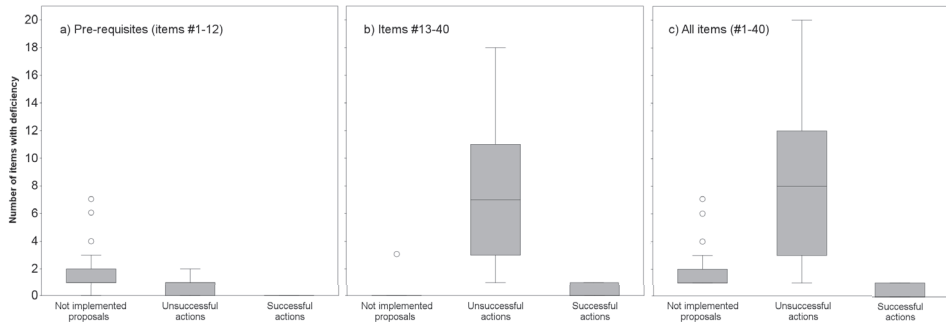


Figure 3. Number of items with deficiency in each action type. The block of prerequisites (**a**) was analysed separately from the rest of checklist items (**b**). In **c** the number of deficiencies is shown for all checklist items.

Discussion

Importance of unsuccessful actions for improving IAS management practices

Mistakes or unexpected outcomes constitute the basis for individual, professional, and organisational learning (Clark 2002), and their analysis may provide useful information to improve management practice. Management failures may be considered fiascos prone to be swept under the carpet. However, excepting for negligence or wilful ineptitude, failures may be simply mismatches between expectations and outcomes or the result of contingencies, uncertainties, or limitations of existing knowledge (Argyris and Schön 1978; Simberloff 2003). In this study, the analysis of not-implemented proposals and unsuccessful actions served as the basis for defining what items were related to feasibility of IAS management actions. These items included basic prerequisites and different topics related to the IAS biology, the administrative requirements, the methodology used to remove the IAS and the characteristics of the native ecosystem. This checklist is the basis to avoid the same mistakes in future actions.

Feasibility analysis as a prior step to prioritization

The feasibility analysis of IAS management actions has received little attention compared to risk (Dana et al. 2014) and priority analysis (Nielsen and Fei 2015; Kerr et al. 2016; Courtois et al. 2018). While feasibility analysis is based on criteria related to the outcome of management actions, priorities setting seeks to identify where, how, on what, and when we should act first (Wilson et al. 2009). A step-by-step assessment of feasibility and priority-setting as the one we present in this paper can help to differentiate those unfeasible actions from those that, being feasible, are not prioritized, for example, due to a transitory lack of resources (Simberloff 2003). Accordingly, decision-making in biological invasion management should be considered as a three-step process: invasion risk analysis (e.g., Vilà et al. 2018; Copp et al. 2005; D'hondt et al. 2015), feasibility analysis, and, finally, priority-setting (Fig. 4).

Basic steps in decision-making for managing biological invasions

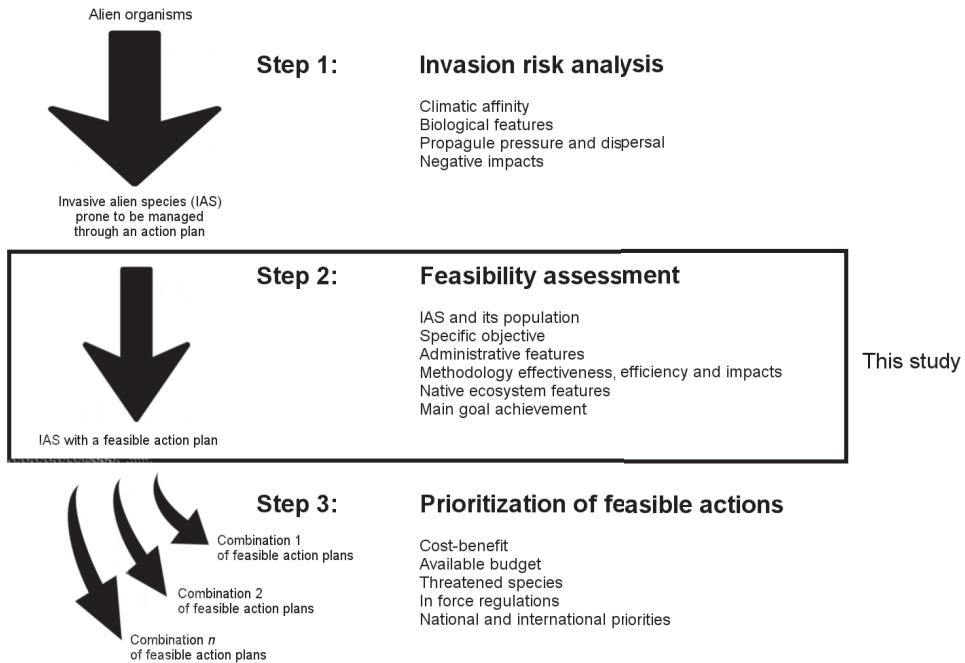


Figure 4. Basic steps in decision-making for managing biological invasions. The checklist proposed in this study focuses on step 2.

Common deficiencies of IAS management actions

The consideration of up to 40 sources of deficiencies highlights the underlying complexity associated with the decision making for IAS management. The relatively high number of items may be the consequence of the number and heterogeneity of actions and proposals assessed but also of specific circumstances of management at the regional scale (e.g., administrative features).

The application of methodologies that are not consistent with the IAS management objective is a prerequisite that was commonly overlooked in unsuccessful actions (up to 54.5% of cases analysed), probably because the initial objective was too ambitious (e.g., eradication of invasive crayfish in rivers; Dana et al. 2010) or simply because the impact thresholds was rarely defined in control actions (Panetta and Gooden 2017). Consequently, it is difficult to establish the necessary removal rate or even to conclude whether the action was a success or a failure.

The absence of funding during the time frame to accomplish the management goals showed the highest occurrence in unsuccessful actions. This is a consequence of the current approach of conservation in the area of study, where IAS conservation actions are financed by biennial programmes whose long term durability is not guaran-

teed. Funding is a critical factor (Simberloff 2003) but may be a temporary obstacle as the planner or decision-maker can often search for different funding sources to implement feasible actions. Therefore, we decided not to include this item as a prerequisite to avoid stopping the feasibility assessment of an action at early stages.

Technical viability, social acceptance, legality, assumable impact, the possibility of restoration or the availability of specialised personnel have been considered as key factors related to feasibility of actions in several reports (Simberloff 2003; Pacific Invasives Initiative 2011; Dana et al. 2016), but the relative importance of each factor has not been previously assessed. IAS biology and life cycle are crucial aspects to define effective removal methods. For instance, annual dicotyledons and grasses may request very different biocides. The relevance of these aspects was considered in items #17, 18, 30, and 33 (Table 1). Besides, our analysis demonstrated that also non-biological aspects such as administrative features linked to the management action have often determined the likelihood of goal achievement. For example, management of IAS populations that are located inside private properties can involve additional difficulties when implementing an action plan. This was the case of *Aedes albopictus* in Málaga (Suppl. material 1: Table S1), which currently colonises a high number of private properties (e.g., saucers under flowerpots, and other small containers). In such cases, it is unfeasible to enter house by house to control potential breeding sites or colonies. Very often, part of the invasive population traverses private properties (e.g., *Colocasia esculenta* in Dos Hermanas, Seville or *Ailanthus altissima* in Aracena, Huelva) (Suppl. material 1: Table S1). In Andalusia, management of IAS in private properties requires of signed agreements between the public administration and landowners are necessary. Thus, the absence of will by any of the parties prevents a feasible, effective management of the invading population. Our work also revealed limitations in the efficacy of the existing approved methodologies, which often may lead to inadmissible impacts or to social rejection. This was the case of chemical control of *Oenothera drummondii* in coastal dunes of Huelva (García-de-Lomas et al. 2016). The analysis supports the need of investing in adequate (in terms of ecological indicators selected and design), adaptive, long-term monitoring (Lindenmayer and Likens 2009). Although directly related to goal achievements, the incorporation of long-term monitoring may involve an added challenge, as it requires extending the duration of the projects beyond possible changes of government. Again, long-term IAS management actions do not fit well with current short-term funding sources (Blossey 1999). The use of the proposed checklist prior to the implementation of IAS management proposals will encourage the definition of a monitoring programme in advance with an array of indicators consistent with a previously defined conservation goal and specific objectives (Lovett et al. 2007).

Validation of the checklist to assess the feasibility of actions

The significant differences found in the number, frequency, and identity of deficient items between successful and unsuccessful actions suggest that the present checklist discerns reasonably well between feasible and unfeasible actions. The use of a checklist prior to implementation of management proposals is of high interest to decrease the number

of unsuccessful actions worldwide. The presence of basic prerequisites in some unsuccessful actions supports a systematic assessment of feasibility before action. The basic prerequisites (i.e., 12 simple items) we listed may seem obvious, however, we decided to include such items in the checklist for three different reasons: (i) the analysis of feasibility starts at the planning stage and pre-requisites are essential to decide whether or not to implement an action proposal; (ii) planning may be done by people from different disciplines or different level of expertise on IAS, therefore, items that may seem obvious for some decision-makers may be overlooked by others; and (iii) the assessment of pre-requisites is a quick step in decision-making in comparison with the major implications that the implementation of actions can have. For example, in the present study area up to four native species were confused with IAS, something that it is not rare among practitioners (Bardsley and Edwards-Jones 2006). Other rejected proposals included species whose origins of introduction remain uncertain. Such cases (e.g., *Alopochen aegyptiacus*, *Alpheus ponteridae*) may represent expansions at range edges without an apparent human intervention or in response to climate change (Gutiérrez 2003; Lindström et al. 2013).

In successful actions, the occurrence of deficiencies in two items suggests that certain items may or may not provoke failure depending on different circumstances. The valuation of a greater number of cases from different regions could help to distinguish items that are unambiguously related to non-feasibility (as the basic prerequisites seem to be) from others that may or may not motivate the action failure depending on additional factors (e.g., the planner experience). In this sense, conducting pilot tests or research projects on the use of novel methodologies are needed as a basis for improving the management of IAS.

To our knowledge, the present checklist is the most comprehensive ever done to date, as it includes a broad range of items integrating an interdisciplinary scope, useful to evaluate management of biological invasions in different habitats, involving taxonomic groups, and specific objectives. Therefore, the present checklist could be potentially used to detect weak points of IAS management actions before implementation in different parts of the world.

Acknowledgements

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Supplementary material I

Table S1

Authors: Elías D. Dana, Juan García-de-Lomas, Filip Verloove, Montserrat Vilà

Data type: Description of actions aimed at managing IAS that were analysed in this study

Explanation note: For each action, the name of the target IAS, the specific objective, the locality, year of implementation and deficiencies found (according to Table 1) are indicated.

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Scientific literature on invasive alien species in a megadiverse country: advances and challenges in Mexico

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Abstract

Interest in invasive species has increased around the world over the last several decades. In Mexico, studies on invasive species date as early as 1939 and the number of publications has increased considerably in recent decades. However, to our knowledge, the analysis of information gaps and research priorities is lacking. Therefore, it is necessary to identify gaps in the knowledge of invasive species in order to define future research priorities and focus conservation efforts. We assessed the current state of knowledge of biological invasions in Mexico based on the existing literature. Our aim was to identify in which areas information is absent or insufficient and which areas should be prioritised. We identified a total of 869 references. The number of references increased over time and the topics were strongly biased towards two areas: 1) natural history and geographical distribution patterns and 2) effects on native biota and ecosystems. The remaining topics were only moderately or poorly studied. Most studies focused on vascular plants (n = 280) and fishes (n = 174). Notably, a large portion of the references (n = 215) focused on only eight invasive alien species, including their ecological and socioeconomic impacts. Only 95 references examined the effects of alien species on biodiversity; these studies were mainly carried out on islands (n = 41) or in terrestrial or freshwater ecosystems in protected natural areas (n = 165). The findings of the

present review can guide future studies in filling in the existing research gaps on biological invasions. Additionally, future studies should aim to define national priorities of the impacts of biological invasions and to promote the prevention and control of alien species by considering the distinct vectors and pathways of introduction and movement.

Keywords

Alien species, invasive species, megadiverse, scientific references

Introduction

The movement of species by humans has been a common practice since the origins of agriculture and cattle raising. Since the European colonisation in the 16th century, this practice has intensified as a result of increased commercial exchange across different regions of the world (MacIsaac et al. 2011). In this regard, alien species are defined as those moved by human activities beyond the limits of their native geographic ranges to areas where they do not naturally occur. Movement by humans allows species to overcome fundamental biogeographic barriers to their natural dispersal (Richardson et al. 2011). However, invasive species are one of the major environmental concerns of the globalisation era because of their detrimental effects on native biodiversity and economic activities (D’Antonio and Vitousek 1992; Wilcove et al. 1998; Charles and Dukes 2007).

The publication of Charles Elton’s book *The Ecology of Invasions by Animals and Plants* (Elton 1958) sparked greater interest in invasive species in the ecological sciences, as researchers aimed to determine which characteristics make certain species better invaders than others (Rejmánek and Richardson 1996; Heenan et al. 1998; Pyšek and Richardson 2006). In this regard, the population dynamics of invasive species that aggressively colonise new sites can provide valuable information on how to counter the potentially detrimental effects on biodiversity and economic activities. However, one current challenge facing many countries is simply the assessment of the number of alien species within their borders, including which species have become naturalised and which have the potential to become invasive. This is a particularly key issue for megadiverse countries that cover less than 10% of the Earth’s surface yet contain up to 70% of the Earth’s biota (Mittermeier et al. 1997; Challenger and Caballero 1998). In these regions, biological invasions can strongly threaten the environmental goods and services provided by biodiversity (Vitousek 1990; Charles and Dukes 2007). In developed megadiverse countries, such as the United States, biological invasions currently constitute one of the largest threats to biodiversity after land use change (Wilcove et al. 1998). Nevertheless, little is yet known about the impacts of biological invasions in countries with emerging economies (Nuñez and Pauchard 2010), including the megadiverse countries of Latin America: Mexico, Brazil, Colombia, Ecuador and Venezuela (Challenger and Caballero 1998). Definitively, the introduction of alien species in the Americas has gradually occurred since the arrival of the European colonisers. In the recent era of globalisation, international trade and exchange have intensified the introduction of alien species (Meyerson and Mooney 2007).

Mexico contains 10% of the Earth's species diversity and harbours the largest diversity of ecosystems in the world (Challenger and Caballero 1998). However, the progressive economic development of Mexico is expected to increase the rate of introduction of alien species, which may threaten the stability and integrity of ecosystems in the short term, as has occurred in other countries (Lin et al. 2007; Meyerson and Mooney 2007). In 2018, the National Commission for the Knowledge and Use of Biodiversity of Mexico (CONABIO) indicated that > 300 alien species are present in the country, threatening both the economy and biodiversity. Nevertheless, these estimations may be inaccurate because scientific studies assessing the spreading of alien species in Mexico are scarce (Espinosa-García 2008), even though more information exists for Mexico than most Latin American countries (e.g. CONABIO). This is likely due to the priorities of developing nations, which are generally focused on governance issues (e.g. social development and industrialisation) rather than biodiversity conservation.

Therefore, the aims of the present article were to compile the first comprehensive list of references on biological invasions in a megadiverse country as Mexico, to provide an analysis of the encountered trends and to identify advances in the scientific knowledge of invasive species. We performed an extensive review of references relating to biological invasions in Mexico from 1910 to 2018. We additionally sought to answer the following questions: Is biological invasion research in Mexico following worldwide trends regarding the number of publications over time; which species group has been most studied; what types of references are most frequent; which topics are studied most intensively; what is the scope of existing studies; and finally, which Mexican regions are studied more intensively? This information will enable researchers to understand the current state of knowledge of biological invasions in Mexico and prioritise future research on the subject. Furthermore, it can help guide public policies regarding biological invasions in Mexico in order to prevent, or at least mitigate, the impacts of invasive species on native biota, natural ecosystems and productive human activities.

Methods

An extensive search was conducted of literature published on biological invasions in Mexico. Several academic databases were searched to gather the most information possible, considering both indexed and non-indexed publications in both English and Spanish. The searched databases included the following: Web of Knowledge (Thomson Reuters), Scopus (Elsevier), Current Contents Connect (Thomson Reuters), Biological Abstracts (Thomson Reuters), Zoological Record (Thomson Reuters), the Journal Storage Project-JSTOR (ITHAKA), Google Scholar (Google), the Scientific Electronic Library Online (BIREME-OPS-OMS) and the Network of Scientific Journals from Latin America and the Caribbean and from Spain and Portugal (Redalyc-Universidad Autónoma del Estado de México). In each database, an extensive search of bibliographic references was performed using combinations of the following keywords: biological invasion OR invasion OR invasive OR invasiveness OR invader OR naturalised OR

introduced OR alien OR exotic OR non-native OR feral OR non-indigenous OR pest OR ruderal OR weed in addition to AND Mexico or AND Mexican.

Several filters were applied: (i) Only publications (based on the title) in the research areas of agronomy, biology, biodiversity conservation, ecology, entomology, environmental sciences, fisheries, forestry, marine freshwater sciences, plant sciences and zoology were included in the present review. (ii) Numerous types of documents were considered, including scientific articles, reviews, books, book chapters, theses, technical brochures, conference proceedings and divulgation articles. We searched for theses, technical reports and conference proceedings in the bibliographic repositories or electronic databases of different universities and research centres in Mexico. (iii) All searches were conducted, based on the content of the titles and abstracts. The keywords in English, as well as their translations into Spanish, were searched in the databases. (iv) Only documents focusing in their entirety on the topics of biological invasion, invasion, invader, invasive species and invasiveness were considered, excluding misquoted or incomplete references. (v) Additionally, literature that addressed biological invasions or projections at a regional or global level that included Mexico were considered, i.e. studies by researchers from other countries addressing global patterns of invasion. (vi) Finally, we excluded literature under review and reports on informal websites, such as personal blogs and webpages without affiliations to academic or government institutions. Repeated titles were discarded, as some references, for example, were presented in more than one congress or were published as both a thesis and a scientific article. A total of 869 documents were returned in the search and were carefully reviewed and included in the present study, based on the above-described criteria. To identify the scientific trends in the compiled references, we classified them according to the criteria listed in Table 1. Finally, in order to determine significant heterogeneity between publication type and species group, main topic and scope of the study (see Table 1), a chi-square test for “goodness of fit” was made (Zar 1999).

Results

The literature search generated 869 references from the year 1910 to 2018 that complied with the established criteria (Table 1, Suppl material 1: Appendix S1). Most references were scientific articles ($n = 324$) followed by conference proceedings ($n = 261$) and scientific books and book chapters ($n = 139$). Although most references were scientific publications (i.e. scientific articles), only 244 were published in journals catalogued in the 2018 Journal Citation Reports (i.e. Journal Citation Reports provides information about the academic journals with the highest impact, value and scientific contribution). Regarding temporal trends, exponential growth occurred in the number of scientific references over time, especially scientific articles and conference proceedings (Fig. 1). Of these references, 280 were studies on vascular plants and 174 on fishes; the remainder were on other species groups (Table 2). The relative importance of species groups varied significantly amongst reference types, with significant heterogeneity

Table 1. Criteria for classifying references on biological invasions in Mexico and identifying scientific trends.

Criteria	Details
Publication year	Year in which the publication was released
Species group	<ul style="list-style-type: none"> a) algae, including microalgae and macroalgae; b) vascular plants, including angiosperms, gymnosperms and ferns; c) amphibians; d) reptiles; e) fishes (freshwater and saltwater); f) mammals; g) birds; h) molluscs; i) crustaceans; j) polychaetes; k) poriferans; l) insects and arachnids; m) vectors and parasites, which were considered because of their threats to human health, agriculture and/or cattle, including virus, bacteria and helminths; n) other invertebrates, including cnidarians, echinoderms, rotifers and tunicates; o) and "all groups" to denote references dealing with several species' groups.
Main topic	<ul style="list-style-type: none"> a) effects on native biota and ecosystems; b) impacts on human and socioeconomic activities; c) traditional uses in current Mexican culture, including cultural uses and ethnobotanical uses; d) control, eradication and restoration; e) natural history and geographical distribution patterns, including autecology, geographical distribution (including ecological niche), species descriptions and species checklist; f) and risk analysis.
Information provided by the reference according to Quiroz et al. (2009) and Richardson and Rejmánek (2011)	<ul style="list-style-type: none"> a) actors' organisation and perception, b) adaptative evolution, c) allelopathy, d) biocontrol techniques, e) biological data, f) biotic homogenisation, g) checklist, h) current status, i) ecological and socioeconomic knowledge, j) ecological and socioeconomic impacts, k) habitat use, l) human use, m) interspecific interactions, n) invasion process, o) new record of geographical distribution, p) ecological niche (ecological niche models, species distribution models, niche conservatism, niche shift), q) geographical distribution patterns, r) phylogeny, s) population dynamics, t) population genetics, u) reproductive success, v) restoration, w) and risk analysis.
Reference type	<ul style="list-style-type: none"> a) thesis, including dissertations; b) scientific article; c) divulgation article in popular science magazine; d) scientific book or book chapter; e) technical brochure published by a government agency or academic institution; f) and conference proceedings, including abstracts from meetings in biology, ecology and related fields.
Scope of the study	<ul style="list-style-type: none"> a) Local scope: references whose area of study was smaller than the entire area of Mexico (e.g. state, natural protected area) and were further classified as belonging to the Northwest (Baja California, Baja California Sur, Chihuahua, Durango, Sinaloa and Sonora), Northeast (Coahuila, Tamaulipas and Nuevo León), West (Jalisco, Colima, Michoacán and Nayarit), East (Hidalgo, Puebla, Tlaxcala and Veracruz), North-Central (Aguascalientes, Guanajuato, Querétaro, San Luis Potosi and Zacatecas), South-Central (Mexico City, State of Mexico and Morelos), Southwest (Chiapas, Guerrero and Oaxaca) and Southeast (Campeche, Yucatán, Tabasco and Quintana Roo), as these areas share distinct physical-natural and historical-cultural characteristics. b) Regional scope: references that considered the entire area of Mexico were considered. c) Global scope: references that considered two or more countries.

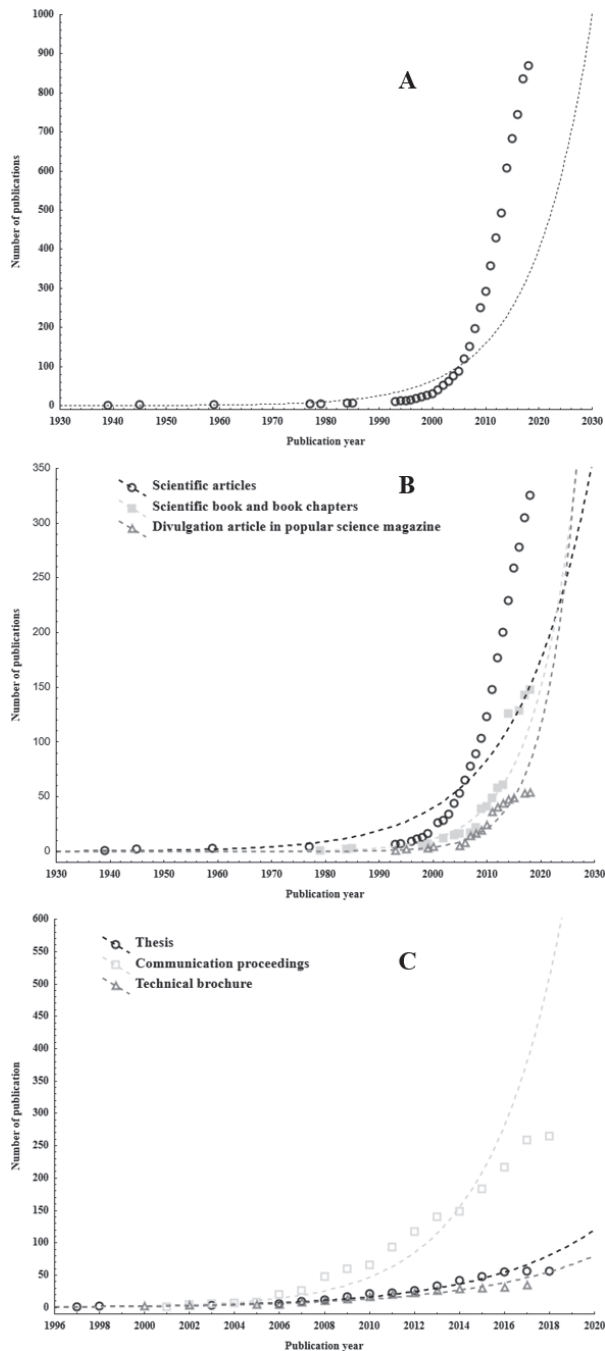


Figure I. References on biological invasions in Mexico during the 1910–2018 period. The curves show exponential growth (dotted line): **A** total references ($r^2_{adj} = 0.34$, $p < 0.001$) **B** scientific articles ($r^2_{adj} = 0.37$, $p < 0.001$), scientific books and book chapters ($r^2_{adj} = 0.46$, $p < 0.001$) and divulgation articles in popular science magazines ($r^2_{adj} = 0.79$, $p < 0.001$) **C** technical brochures ($r^2_{adj} = 0.99$, $p < 0.001$), conference proceedings ($r^2_{adj} = 0.86$, $p < 0.001$) and theses ($r^2_{adj} = 0.80$, $p < 0.001$).

Table 2. Distribution of references on biological invasions in Mexico per species group.

	Scientific article	Scientific book and book chapter	Divulgate article in popular science magazine	Thesis	Conference proceedings	Technical brochure
Algae	16	3	1	1		1
Amphibians	7	1	1		3	
Birds	38	1	3	3	31	
Crustaceans	8	3		2	1	1
Fishes	58	28	10	11	62	5
Insects and arachnids	47	3	5	5	13	1
Mammals	12	9	3	6	15	2
Molluscs	14	2	2		4	
Other invertebrates	4	2		1	2	
Polychaetas	1	4	1		1	1
Reptiles	7	1		1	5	1
Vascular plants	100	22	14	22	101	14
Vectors and parasites		1		1		
All groups	2	37	12	1	15	5

(chi-square = 107.16, $df = 11$, $p < 0.001$), due to over-representation references on vascular plant and fishes while amphibians, reptiles, crustaceans, polychaetas, molluscs and other invertebrates were under-represented.

Of the compiled references, 377 focused on the natural history and geographic distribution patterns of invasive species and 203 on risk analysis. The remainder corresponded with other topics (Fig. 2A). The relative importance of these topics varied significantly amongst reference types, with significant heterogeneity amongst reference types in the focus of study (chi-square = 192.26, $df = 3$, $p < 0.001$), largely as a result of scarce studies on the control, eradication and restoration and effects on native biota and ecosystems. The most studied topic were: actors' organisation and perception, bio-control techniques, current status, ecological and socioeconomic impacts, geographical distribution patterns, interspecific interactions, new records of geographical distribution and risk analysis (Table 3); the least studied topics were the phylogeny, habitat use, biotic homogenisation and allelopathy of invasive species (Table 3).

Only 94 references addressed the effects of alien species on biodiversity; nearly half of these studies ($n = 41$) were carried out on islands (e.g. Socorro Island, Cozumel Island, Guadalupe Island and Santa Catalina Island, amongst others). These latter studies on islands mostly focused on the introduction, control and eradication of invasive species, including reptiles and feral mammals (cats, mice, goats, sheep, rats and dogs) that had led to the near extinction of different native species of birds, mammals and reptiles. Few studies focused on terrestrial or freshwater ecosystems, particularly in protected natural areas ($n = 164$).

Regarding damage to socioeconomic activities, the Cactus moth (*Cactoblastis cactorum*) was identified as one of the most dangerous agricultural pests in Mexico with disastrous effects. Additional invasive species with documented harmful effects include Buffelgrass (*Pennisetum ciliare*) and the Red-bay ambrosia beetle (*Xyleborus glabratus*), which

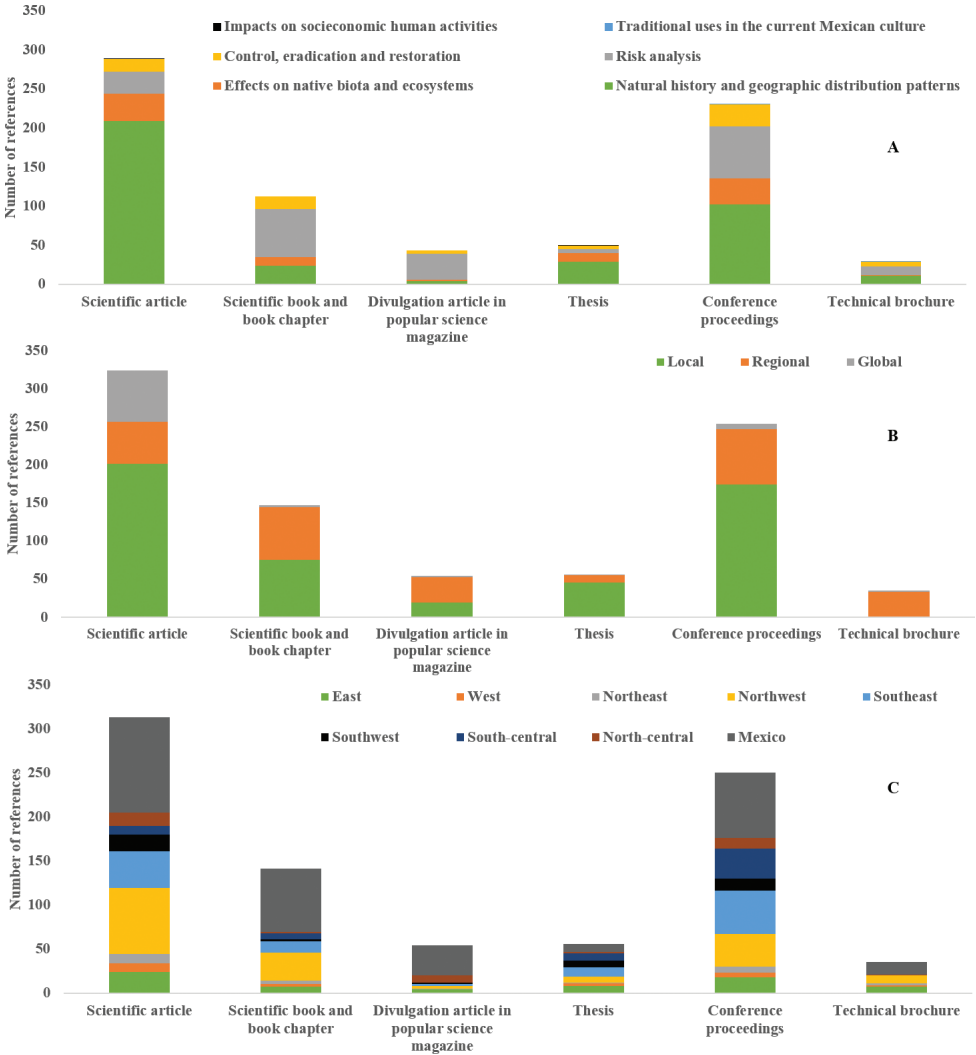


Figure 2. Distribution of references on biological invasions in Mexico per publication type and **A** main topic **B** scope study and **C** study region in Mexico.

threaten farmland and the Armored catfish (*Pterygoplichthys* spp.), which affects aquaculture operations. Other studies focused on the control and eradication of alien species such as insects and arachnids that act as pests and damage crops of economic importance, such as corn, citrus, bean, coffee, avocado, cotton and mango crops, amongst others, as well as forest plantations. Studies on the control and eradication of invasive species were mainly carried out in natural protected areas or wetlands, including the eradication of rodents on islands. Additional studies assessed the use of bio-insecticides or bio-pesticides for controlling agricultural pests. However, as mentioned, the largest number of references focused on the natural history and geographic distribution patterns of alien species, mainly based

Table 3. Information provided by the reference according to Quiroz et al. (2009) and Richardson and Rejmánek (2011).

	Scientific article	Scientific book and book chapter	Divulcation article in popular science magazine	Thesis	Conference proceedings	Technical brochure
Actors' organisation and perception	4	19	6	2	18	5
Adaptative evolution	3			3	4	2
Allelopathy	1			1	2	
Biocontrol techniques	11	7	1	1	18	2
Biological data	6	1		4	7	
Biotic homogenisation	2	1		1	1	
Checklist	5	12	3		9	5
Current status	27	13	3	2	10	3
Ecological and socioeconomic impacts	15	15	5	2	22	2
Ecological and socioeconomic knowledge	1	5			4	1
Ecological niche	14			1		
Geographical distribution patterns	46	1			11	5
Habitat use					6	
Human use	1	2	2		4	
Interspecific interactions	22	3			20	9
Invasive process	16	7	3	1	8	1
New record of geographical distribution	38	2			9	
Novel monitoring techniques	4	3	2		6	2
Phylogeny		1			1	
Population dynamics	15	2		5	18	
Population genetics	4			1	3	
Reproductive success	15		1	5	13	
Restoration	5	6	1		5	1
Risk analysis	10	9	15	2	18	3

on presence records. Several additional studies focused on autecology, interactions with native species and geographic patterns and ranges. Numerous studies addressed biological invasion from different perspectives or performed risk analysis to determine the possible impacts of invasive species, identify potential risk areas or outline the prospects for the management of invasive species, as well as policies and strategies for their control. Finally, most studies had a local scope ($n = 533$) followed by a regional ($n = 251$) and global scope ($n = 82$, Fig. 2B). Of the local studies, most were carried out in the north-western region of Mexico ($n = 162$) followed by the south-eastern ($n = 116$) and eastern regions ($n = 68$)

(Fig. 2C). The scope of the study varied significantly amongst reference types, with significant heterogeneity in terms of their scope study (chi-square = 203.72, $df = 2$, $p < 0.001$) and study region (chi-square = 136.82, $df = 8$, $p < 0.001$). In both cases, most references were of local and regional scope, in specific north-western and south-western Mexican regions, while western and north-eastern Mexican region had few references.

Moreover, a total of 510 references focused on one or two species; of these, 164 corresponded with vascular plants, 66 with insects and arachnids, 60 with birds and 118 with fishes. Notably, 213 references focused on the ecological and socio-economic aspects of only eight notorious invasive alien species in Mexico: the Indo-Pacific lionfish (*Pterois volitans*), the Monk parakeet (*Myiopsitta monachus*), the Armored catfish (*Pterygoplichthys* spp.), Buffelgrass (*Pennisetum ciliare*), Kalanchoes (*Kalanchoe* spp.), Antelope grass (*Echinochloa pyramidalis*), Eurasian collared dove (*Streptopelia decaocto*) and the Cactus moth (*Cactoblastis cactorum*). On the other hand, there were few studies on feral cats, feral dogs, rodents (*Rattus rattus*, *R. norvegicus* and *Mus musculus*) and the Common carp (*Cyprinus carpio*), as well as other widely distributed invasive species such as Eucalypti (*Eucalyptus* spp.), Pampas grass (*Cortaderia selloana*) and the Red-bay ambrosia beetle (*Xyleborus glabratus*), which pose a high risk to native biota, socio-economic activities and human health (e.g. Zambrano et al. 2010; Lira-Noriega et al. 2018).

Discussion and conclusions

The present review is the first comprehensive compilation of studies on biological invasion in Mexico (see Suppl material 1: Appendix S1) and presents the first overall assessment of the knowledge of biological invasions according to the area of study and main research topics and regions. Only one previous review, focusing on the biological invasion of non-native weeds in Mexico, identified 229 publications (scientific articles and books) (Espinosa-García and Villaseñor 2017). Ten notable findings can be highlighted: (i) One of the earlier scientific studies on biological invasion was performed by Itie (1939, 1945) on California grass [*Brachiaria mutica* (Forssk.) Stapf.] and Natal grass [*Rhynchelytrum repens* (Willd.) Zizka], which were introduced as forage in Mexico. (ii) Several years later, Rzedowski (1959) described the presence of Russian thistle (*Salsola kali* var. *tenuifolia*) in central Mexico. (iii) Several decades later, Rzedowski and Calderón-de Rzedowski (1979, 1985) published the Flora Fanerogámica del Valle de México (The Phanerogamic Flora of the Valley of Mexico in English) and Flora del Bajío (The Flora of the Lowlands in English), in which the presence of several invasive species was recognised. (iv) More recently, Villaseñor and Espinosa-García (2004) made an important contribution to the knowledge of alien plant richness in Mexico. (v) Álvarez-Romero et al. (2008) presented a review of the ecology, distribution, impacts and control of exotic vertebrates in Mexico. (vi) In addition, Aguirre-Muñoz et al. (2009) conducted a review of alien species and their impacts on native biota and human activities. (vii) Most recently, the National Strategy for the Prevention, Control and Eradication of Invasive Species was established to monitor and control

invasive species in Mexico (Comité Asesor Nacional sobre Especies Invasoras 2010). (viii) Haemig (2012, 2014) described perhaps the first documented case of an invasive species in Mexico wherein the Great-tailed grackle (*Quiscalus mexicanus*), originally from the coastal plain of the Gulf of Mexico, was introduced to the Valley of Mexico by the Aztec emperor Auitzotl (1486–1502). (ix) Espinosa-García and Villaseñor (2017) then briefly reviewed current knowledge of the richness, ecology, distribution and management of non-native weeds in Mexico and provided some data on their possible environmental and economic impacts, identifying approximately 700 wild alien species and 229 related references in Mexico. Lastly, (x) Born-Schmidt et al. (2017) summarised the main challenges facing Mexico in combating invasive alien species.

Generally, research on biological invasions in Mexico was scarce during the last two decades of the latter century. However, research substantially increased during the first decade of the 21st century and this trend continues today (Figure 1). Therefore, the study of biological invasions may be considered an emerging discipline in Mexico that has grown in recent years. Mexico is one of the four Latin American countries with the greatest scientific productivity with regard to biological invasions yet, comparatively, the number of references for Mexico is relatively low if we take into account the scientific references indexed in the Web of Knowledge: 105 references were found for Argentina from 1988 to 2008 (Pauchard et al. 2011), 354 for Brazil from 1991 to 2013 (Frehse et al. 2016) and 92 for Chile from 1991 to 2008 (Quiroz et al. 2009; Pauchard et al. 2011). The number of studies is also particularly low compared to that generated in countries like the United States, Australia and New Zealand (Nuñez and Pauchard 2010).

When we compared studies in Mexico with those in other regions of the world, we identified several topics that should be more thoroughly addressed by Mexican ecologists: demographic patterns, behavioural ecology, interactions with native species, population genetics and adaptive processes. The scarcity of historical references is likely since the study of biological invasions in Mexico did not attract the interest of ecologists until the late 1990s. During this period, biological invasions began to be recognised by the scientific community and society in general given the increasing rate, scale and magnitude of anthropogenic activities and their effects on ecosystems (Vitousek et al. 1997a, 1997b). The ecology of invasive species was consolidated in the late 1990s as a sub-discipline of ecology and an increasing number of studies on biological invasions were performed during that decade. So finally, from the year 2000, the concept of biological invasions was introduced into environmental decision-making.

Despite the increasing number of studies on invasive species in Mexico over the last two decades, there are several pending challenges. A significant number of studies solely focus on the natural history and geographical distribution patterns of invasive species or distinct perspectives and risk analysis. However, to improve the understanding of biological invasions and their impacts, it is necessary to examine in greater depth the effects of invasive species on native biota and ecosystems, including the effects in terms of restoration and socioeconomic costs (Quiroz et al. 2009). Such research could potentially identify new possibilities for the management and control of invasive species based on their behaviour and the mechanisms related to their invasion. In this

regard, further experimental studies are necessary in addition to early research studies to anticipate potential invasions that could be harmful to biodiversity and human productive activities. It is also important to carry out further research geared towards implementing measures or programmes to control or eradicate alien species (Temple 1990). In addition, there is a lack of studies on the potential hazards that cause alien species to “drive” other alien species and the potential uses (ornamental, forestry, recreational or food) of invasive species.

According to Espinosa-García and Villaseñor (2017), research on biological invasions in Mexico follows a prevalent pattern in which research is produced by only a few academic groups and is mostly disarticulated. Only on a few occasions have the results of such research studies been communicated with decision-makers in governmental agencies such as CONABIO, one of the world’s most recognised sources for information on biodiversity, which also created the Information System on Invasive Species in Mexico (CONABIO 2018) and the National Strategy for Biological Invasions (Comité Asesor Nacional sobre Especies Invasoras 2010). In this regard, the knowledge generated by national scientific institutions should relate to national and global initiatives (e.g. GloNAF, GBIF, GISP and GRIIS) in order to coordinate efforts on the different topics identified in the National Strategy for Biological Invasions (Comité Asesor Nacional sobre Especies Invasoras 2010). It would be important for such efforts to consider available information on alien or invasive species in different scientific publications (e.g. scientific articles, theses etc.). One final task is the standardisation of the criteria for determining the current status and categorisation of invasive or naturalised species.

Currently, biological invasions are altering the functioning of natural ecosystems in a way that is unprecedented in the history of our planet, leading to substantial economic losses in many countries (Hulme 2009). Mexico is not immune to this problem. However, the scarcity of scientific information on some topics in Mexico regarding biological invasions, including the number of invasive species and the status of alien species, makes it difficult to predict the magnitude of their impacts on native biota and ecosystems. Furthermore, this lack of information prevents the development of efficient management, control and eradication plans. Therefore, the current gaps in the knowledge of biological invasions in Mexico outlined in the present review can help to prioritise future research studies. In particular, the challenges of future research studies include defining national priorities for controlling invasive alien species and examining previously unexplored topics, such as interspecific interactions with native biota, food habits, habitat use, adaptative evolution and geographical distribution under climate change.

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Supplementary material I

Appendix S1. Reference database on biological invasions in Mexico (N = 869).

Authors: Jorge E. Ramírez-Albores, Ernesto I. Badano, Joel Flores, José Luis Flores-Flores, Laura Yáñez-Espinosa

Data type: species data

Explanation note: This database included all the bibliographic references with main topic, information provided by the reference, species group, publication type, scope study, study region and language. (*) The study was realised in natural protected areas and (§) the study was realised on an island.

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