NeoBiota 45: 1–17 (2019)
doi: 10.3897/neobiota.45.33366
http://neobiota.pensoft.net

NEW DEVELOPMENT

A peer-reviewed open-access journal
NeoBiota
Advancing research on alien species and biological invasions

Introducing AlienScenarios: a project to develop scenarios and models of biological invasions for the 21st century

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Academic editor: *Petr Pyšek* | Received 25 January 2019 | Accepted 19 March 2019 | Published 15 April 2019

Citation: Essl F, Lenzner B, Courchamp F, Dullinger S, Jeschke JM, Kühn I, Leung B, Moser D, Roura-Pascual N, Seebens H (2019) Introducing AlienScenarios: a project to develop scenarios and models of biological invasions for the 21st century. NeoBiota 45: 1–17. https://doi.org/10.3897/neobiota.45.33366

Abstract

AlienScenarios, a three-year project starting in March 2019, will evaluate for the first time the range of plausible futures of biological invasions for the 21st century. AlienScenarios consists of seven project partners and seven integrated complementary subprojects. We will develop the qualitative narratives for plausible futures of global alien species richness and impacts in the 21st century – the Alien Species Narratives

(ASNs). The ASNs further serve as overarching concept to parameterize quantitative models of global, continental and regional futures of biological invasions. We will also establish the first global mechanistic invasion model considering major processes of biological invasions such as source pools, driver dynamics and establishment rates. Further, we will assess the impacts of invasive alien species (IAS) in terms of economic costs according to the different ASNs. In addition, we will assess the consequences of different levels of implementation of the European Union Regulation on IAS. Providing some more detailed regional information, we will analyse changes of the functional composition of communities in mountain regions under different scenario storylines and will extend the analyses to the Global South using Panama as a country-level case study. Finally, the results of the other WPs will be synthesized, and the approach and results of AlienScenarios will be discussed with and communicated to stakeholders and the wider community. AlienScenarios will provide crucially needed insights for pro-active alien species management and policy. It will thus make an important contribution to global assessments and projections of biodiversity and ecosystem services, as well as regional policies (e.g. EU regulation on IAS).

Keywords
Biological invasions, global change, impacts, models, policy advice, projections, scenarios

Introduction

Human agency has modified virtually every facet of the biophysical environment (Lewis and Maslin 2015) with profound implications for the status, distribution and resilience of biodiversity worldwide (Leadley et al. 2010). Several major drivers of biodiversity loss have been identified with climate change, land-use change and invasive alien species (IAS) being among the most important ones (Secretariat of the Convention on Biological Diversity 2014). Changes in climate and land use have received much attention during the last decades, which resulted in readily available scenarios (Lamarque et al. 2005; Moss et al. 2010; Hurtt et al. 2011; IPCC 2014; Popp et al. 2016). In contrast, comparable approaches are completely missing for biological invasions despite their importance in driving biodiversity losses (Simberloff et al. 2013; Blackburn et al. 2014), and causing substantial negative impacts on human livelihoods (Pejchar and Mooney 2009). Worryingly, recent research has shown that numbers of alien species are rising unabatedly in most taxonomic groups (Seebens et al. 2017, 2018). Therefore, a thorough evaluation of plausible future trajectories of biological invasions is urgently needed to (i) enable comprehensive assessments of biodiversity changes for the decades to come, (ii) allow better-informed decisions of policy makers and stakeholders (Ferrier et al. 2016) and (iii) examine the future implications of different societal responses for biological invasions.

Objectives and approach

In AlienScenarios, we will close the knowledge gap outlined above by evaluating the range of plausible futures of biological invasions for the 21st century at different spatial scales and for a range of taxonomic groups. We will use complementary data and approaches, and examine multiple measures of impacts. We will combine the strategic forward-looking methodology of scenario planning with advanced modelling approaches to construct plausible global mid-term (2050) and long-term (2100) futures of biological invasions and their impacts taking into account uncertainties. In this context, we will take advantage of several recently compiled large data sets of global alien species distributions, which have partly been compiled by members of the project team: vascular plants (GloNAF, (van Kleunen et al. 2015, 2018; Pyšek et al. 2017), amphibians and reptiles (Capinha et al. 2017), mammals (Dawson et al. 2017), birds (GAVIA, (Dyer et al. 2017), freshwater fish (Dawson et al. 2017) and selected invertebrates (ants, spiders, Bertelsmeier et al. 2013; Roura-Pascual et al. 2016; Dawson et al. 2017). In addition, we will use the Alien Species First Record Database (Seebens et al. 2017, 2018), an exhaustive database of global historic alien species accumulation rates. Finally, for regional analyses AlienScenarios will make use of complementary alien species data for in depth-analyses.

Overview of the AlienScenarios project structure

AlienScenarios consists of seven work packages (WPs) (Figure 1) that are briefly described below.

WP I: Developing global storylines and scenarios of biological invasions in the 21st century (Lead: University Vienna, Bernd Lenzner, Franz Essl)

Alien species displacement and establishment are affected by a range of drivers. These drivers have been comprehensively assessed in a workshop on alien species scenarios co-organized by three partners of AlienScenarios (F. Essl, B. Leung, N. Roura-Pascual) in Vienna in October 2016. In this workshop, an interdisciplinary panel of c. 30 experts performed an elicitation of the existing literature, and assessed relevant mechanisms and pathways. The assessment identified the seven most relevant drivers for biological invasions in the 21st century: land-use and land cover change, biodiversity change, climate change, human population development, international trade and transport, legislation, and agreements as well as scientific, technological and societal development (Roura-Pascual in prep.).

WP I builds on this preparatory work and transforms it into a conceptual framework for the development of scenarios on how alien species richness and impacts might change throughout the 21st century. Based on the subset of the seven most relevant drivers of biological invasions, we will develop internally consistent storylines – the Alien Species Narratives (ASNs) (Figure 2) – that form the core elements of our scenario framework (Rounsevell and Metzger 2010). Given that we are developing biological invasion scenarios for the first time, and thus want to explore the full range of potential future alien species trajectories, we choose a descriptive approach (Priess and Hauck 2014; IPBES 2016) to come up with four to five ASNs.

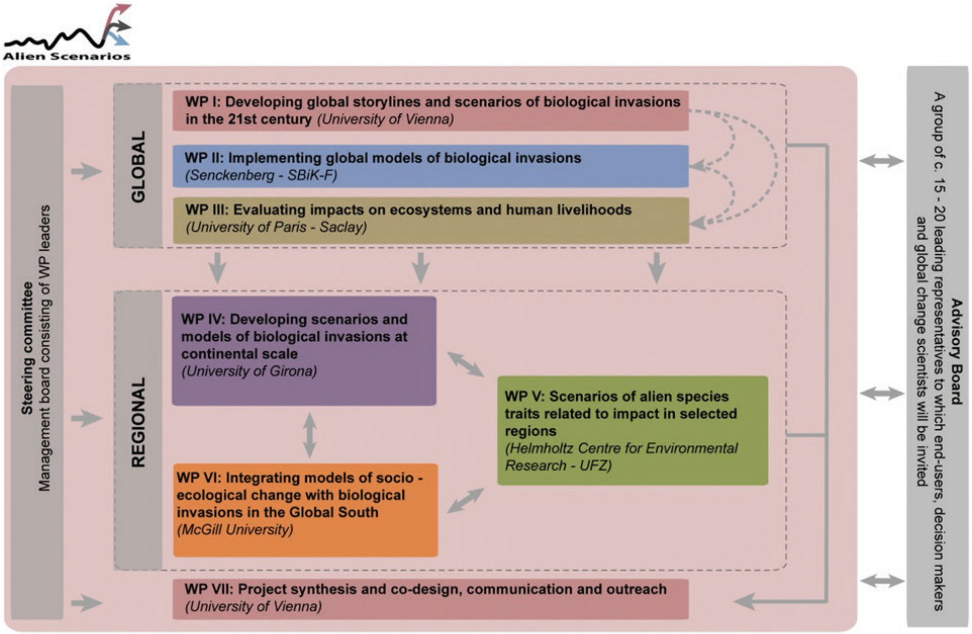

Figure 1. Project management structure and the interactions between the work packages of AlienScenarios. Shown are the seven work packages (WPs), the institution of the WP lead, the integration of the WPs within the project, the external Advisory Board, and the Steering Committee consisting of the WP leaders that is responsible for internal decision making. The arrows indicate the interconnectedness of the WPs in terms of data, idea and material exchange.

Further, we are going to construct the ASNs independent of other frameworks to ensure the greatest freedom in exploring different facets of the system more rigorously. This way we will avoid constraints held by pre-existing storylines that are likely too general for the specific needs in invasion science (Chytrý et al. 2012). The ASNs will then a posteriori be set into a broader context (see Spangenberg et al. 2012) and for example linked to the widely used Shared Socio-economic Pathways (SSPs, O'Neill et al. 2014) and Representative Concentration Pathways (RCPs, van Vuuren et al. 2011) developed for climate change research. We will follow a matrix architecture approach (van Vuuren et al. 2014) combined with a "one-on-one" mapping of the scenario narratives (Zurek and Henrichs 2007) to assess the congruence between the RCP x SSP and the ASN frameworks. This way, we will identify the relationships of biological invasions to global socio-economic and environmental change scenarios.

The ASN framework developed here will serve as the overarching concept for the simulations of the global (WP II) models of biological invasions, for assessing the global impacts that future invasions may cause (WP III), and for developing continental (WP IV) and regional alien species scenarios and models (WPs V, VI).

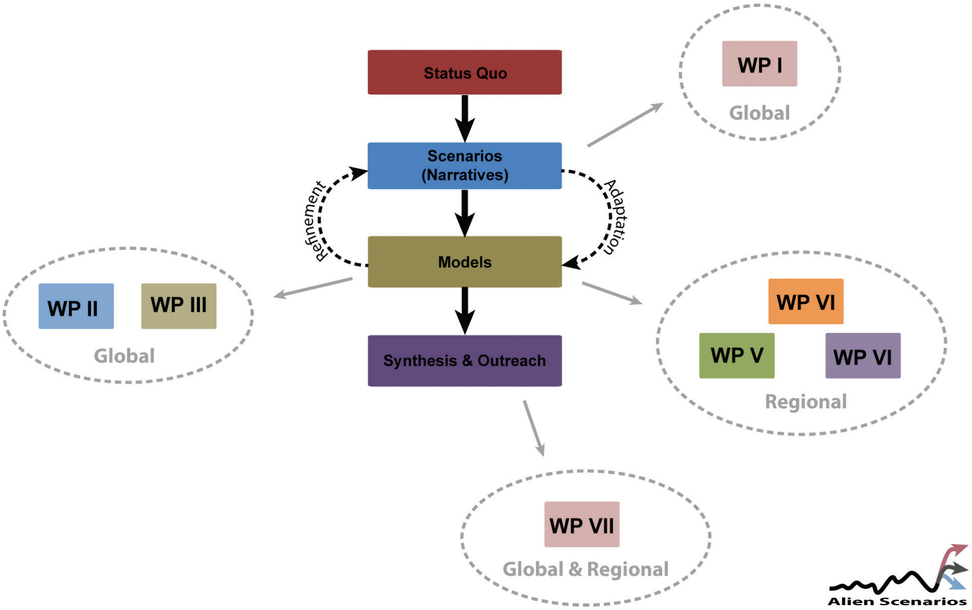

Figure 2. Conceptual figure showing the key elements and key steps for developing a framework for global scenarios (WP I) and models (WPs II, III) of biological invasions, from which continental and regional scenarios and models will be derived (WPs IV, V, VI). The figure is composed of a conceptual layer (boxes) that describes the stepwise scenario- and model-development process from initial data assessment and mobilisation to storyline construction, model quantification and, finally, to the synthesis of the full biological invasion scenarios and their communication. The position of the seven WPs of AlienScenarios along this scenario- and model-development axis is shown separately for global and regional scenarios.

WP II: Implementing global models of biological invasions (Lead: Senckenberg BiK-F, Hanno Seebens)

In this WP, a model of alien species accumulations on large spatial (global, continental) and temporal scales (centuries) will be developed and explored for various scenarios obtained from WP I. A common feature of existing invasion models (e.g. Leung et al. 2004; Costello et al. 2007; Brockerhoff et al. 2014) is that invasion dynamics were calculated based on trends of drivers such as import volumes of a country. While driver dynamics have been proven to be valuable predictors of invasion dynamics (Levine and D'Antonio 2003; Pyšek et al. 2010), it is essential to additionally consider potential constraints on the number of establishing species by the size of source pools (Liebhold et al. 2017; Seebens et al. 2018).

Here, we will combine the process-based extension of the statistical invasion model developed by Liebhold et al. (2017) with the modelling approach of Seebens et al. (2018) to estimate candidate species pools and to simulate the spread from these pools to alien ranges. The model will simulate the rate of invasion based on various drivers of invasion, while the total number of establishments will be constrained by the size of the source pools. The implementation of ASNs into the newly developed model will require adaptations of the model structure as well as refinements of the scenarios.

The model will be evaluated against long-term trends of alien species accumulations obtained from the recently established Alien Species First Record Database, which provides regional time series (1500–2005) of invasions for >17,000 established alien species from various taxonomic groups (Seebens et al. 2017, 2018).

An invasion model as proposed here will provide the ideal tool to reach our objectives of developing future projections, as it integrates the most important mechanisms of invasion dynamics and at the same time provides a simple framework to simulate alien species accumulations for the drivers for which data are available in future scenarios. At the end of the project, we will have a set of invasion trajectories for each taxonomic group considered here, spanning the full range of potential developments for the 21st century. These results will also be used as baseline input for assessing future impacts (WPs III, V) and for discussing future pro-active policies and management options (WP VII).

WP III: Evaluating impacts on ecosystem services and human livelihoods (Lead: University of Paris Saclay, Franck Courchamp)

This WP focuses on evaluating impacts of the different global scenarios. Because the currency metrics is one that allows impact comparisons across different scales (time, space, taxonomy, category of impact, etc.), we will focus on economic costs as an output of most facets of this WP.

The WP will proceed with different, complementary approaches. The first one will use a meta-analysis of the state-of-the-art of current economic costs of IAS worldwide (in collaboration with environmental economists). This analysis will provide us with the first high-quality global map of costs, but also with a detailed description of current knowledge gaps, be they taxonomic, geographic or economic markets. These comprehensive current costs will then use the ASNs and results obtained by other WPs to assess (i) which species are likely to become (or remain) invasive in areas of interest and (ii) which areas on the globe are likely to become invaded by focal species, both for mid-term (2050) and long-term (2100) futures. The WP will focus on alien vertebrates, vascular plants and selected groups of insects (such as ants) for which the necessary global distribution data are available (e.g. van Kleunen et al. 2015, 2018; Capinha et al. 2017; Dawson et al. 2017; Dyer et al. 2017). We will then use local, current costs of selected alien species and project them to spatially explicit maps in order to obtain more quantitative estimates for different areas.

These invasion costs will be put in regards with costs of policies and biosecurity measures to provide an integrated scheme of prioritization according to the different ASNs developed in WP I. The approach will allow for evaluating and ranking different political and management options of biological invasions for the 21st century according to climatic and socio-economic scenarios, regions and possibly economic markets.

WP IV: Developing scenarios and models of biological invasions at continental scale (Lead: University of Girona, Nuria Roura-Pascual)

Based on the global ASN framework developed in WP I, we will zoom in on a continental (Europe) scale and construct scenarios nested within the global ones.

The main objective is to assess the consequences of different levels of implementation of the European Union Regulation on IAS (Regulation No. 1143/2014, EU 2014). This regulation has become the key policy tool in coordinating and improving the efforts of EU member states to combat IAS. EU member states differ in policies and regulatory histories, risk assessment tools and data availability (Sonigo et al. 2011), but the ramification this heterogeneity has on IAS is unknown (Tollington et al. 2017). We will examine regulations, management capacities and other socio-ecological factors (e.g. environmental heterogeneity, length of common borders) across EU member states, integrate these into a spatially-explicit model along with human vector movement (i.e. the primary mechanism of alien species transport and dispersion; Leung et al. 2004; Della Venezia et al. 2018).

We will statistically relate these socio-ecological constraints and human-mediated pathways of spread to the patterns of alien species establishment and impact across the EU (in collaboration with WPs II and III). We will focus on the IAS of EU concern (currently 49 species) as listed in the EU regulation on IAS (EU 2014). Our analyses will allow us to unravel the effect that differing policy implementation and capacities may have on the studied IAS in each member state. Further, since member states are interconnected by transportation and trade in goods, we will also parse out their ramifications for other member states (i.e. what is the effect of a "weak link"). We will also use this model to simulate the effect of alternative policies and capacities, based on a series of qualitative scenarios for managing IAS in Europe constructed by applying the methodology of scenario-planning following the premises of the conceptual framework. Such an integrated approach will give a scientific basis to quantitatively examine the consequences of the differing degrees of policy implementation across the EU.

WP V: Scenarios of alien species traits related to impact in selected regions (Lead: Helmholtz Centre for Environmental Research – UFZ, Ingolf Kühn)

There is a long history of analysing species traits that are related to the success of alien species (e.g. Pyšek and Richardson 2007; Küster et al. 2008). The impacts of alien species on ecosystem functions and services, though, are mediated through effect traits (Pyšek et al. 2012). Here, we will use the downscaled scenarios and model projections of the WPs I, II and IV to apply case studies on selected taxonomic groups (such as plants, birds, mammals) and regions (mountain regions).

In particular, we will extend the results from scenario development (WPs I, II, IV) to species traits, i.e. to the increase or decrease in specific traits. This means that we will not only consider the magnitude of change in terms of species richness (WPs II, IV), but will also consider which traits will benefit or suffer under the respective scenarios. We will applying both network analyses as well as already existing trait distribution models (e.g. Kühn et al. 2006, 2009), by combining the same environmental drivers as in WP III on land use, climate (and preferably traffic/trade routes) with traits and propagule pressure to project which trait compositions to expect under different ASN assumptions (from WP II). This will allow us to analyse alien species impacts under scenario conditions by regionalization and to recognize specific context sensitivity (Kueffer et al. 2013), but also quantify uncertainties.

Because trait information is not equally available throughout Europe, we will focus with the previous analysis on ecosystems in Europe that are highly sensitive to invasions, but not yet too heavily invaded, such as mountains (Pyšek et al. 2009). Further, these systems will have strong anticipated changes in climate and land use and an increase in trade and traffic, so that a massive transformation by alien species is likely (Alexander et al. 2016). This also means that the storylines and scenarios developed in WPs I and IV need to be extended regionally. The choice of analysed systems follows a hierarchical selection strategy, especially based on good data availability in Central Europe. By acquiring more data, this can be extended to other regions. Mountain ecosystems fulfil all requirements mentioned above and will serve as a model system to start with.

To this end, we will prioritize (i) regions and, within regions, ecosystems that are more sensitive than others, and (ii) traits that are more effective than others in causing an impact onto these systems.

WP VI: Integrating models of socio-ecological change with biological invasions in the Global South: Panama as a model system (Lead: McGill University, Brian Leung)

This WP focuses on a tropical region of particular importance for biological invasions, i.e. Panama. Panama is a tropical biodiversity hotspot (Ibáñez et al. 2002) and home to the Panama Canal, one of the major gateways of inter-oceanic marine alien species exchanges (Muirhead et al. 2015). Simultaneously, Panama faces rapid economic growth (10.6% in 2011) and population growth (>40% by 2050), and highly skewed wealth distribution (17/136 in the world). These factors influence the movement of goods and people, as well as societal values and choices (e.g. land use), which in turn, can affect biological invasions. Thus, Panama is an excellent model system of developing, tropical nations. In pursuing WP VI, we complement the global (WP II) and continental analyses (WP IV) by (1) scale: analyzing an indepth country-level analysis, (2) region: focusing on a tropical region in the Global South, which are under-represented in invasion biology studies, and (3) drivers: focusing on detailed socio-ecological models.

We will connect to an ongoing initiative, the Panama Research and Integrated Sustainability Model (PRISM, see http://prism.research.mcgill.ca), which is a first-generation nationwide spatially-explicit computational model of ecological and social components of sustainability. PRISM currently incorporates sub-models for physical processes linked to water availability and land use, and biological patterns for the bias-corrected distributions of >6000 plant species across Panama. Further, socio-economic layers are currently being developed, including urban growth of Panama City, changes in shipping through the Panama Canal over the coming decades, and connectivity, which will influence the movement of alien species. PRISM will act as a foundation on which to explore the introduction, establishment, spread and impact of alien species. In turn, WP VI will contribute a biological invasions layer to PRISM.

In particular, WP VI will integrate quantitative socio-ecological models with the drivers of invasions identified in the ASN framework of WP I. In close collaboration with WPs IV and V, we will develop national alien species storylines nested in the global ASN framework. We will apply the general scenarios of driver changes from WP I to the context-rich knowledge of Panama, and use PRISM to actually quantify the interactions between those drivers (e.g. urban growth increases by x%, resulting in y% increase of material flow and human migration, which then results in z% land-use and biodiversity change). We will use the models from WP II as the global context, within which Panama exists (e.g. how will the invasions of trading partners change introduction pressure to Panama?). We will then model how future biological invasions in Panama quantitatively flow through the country to 2050, by combining PRISM's socio-ecological outputs with invasion models.

WP VII: Project synthesis and co-design, communication and outreach (Lead: University of Vienna, Franz Essl)

This integrative WP has three closely related goals: (i) it will use a participatory approach involving the AlienScenarios project team and an external Advisory Board for ensuring strong integration and co-design of the sub-projects and for monitoring project progress; (ii) building on the results of the other WPs, it develops a synthesis of the project results which will be discussed with the Advisory Board; and (iii) it ensures that the project and its results are communicated to stakeholders and the wider community using a range of different tools and formats.

AlienScenarios has an interdisciplinary Advisory Board of ca. 20 leading representatives to end-users, decision makers and global change scientists. The Advisory Board serves several purposes: (i) to co-develop and discuss the planned implementation of project approaches and goals to maximize applicability and transferability to other relevant initiatives (e.g. IPBES, Future Earth, CBD, GEOBON), (ii) to discuss project results and their implications for alien species policies and management, (iii) to ensure that inputs and views of the wider community will fertilize the implementation of the project and (iv) to provide advice to the WPs on specific questions and problems.

The second goal of this WP is to provide a synthesis of developed methodological approaches and obtained results for different audiences. This will be done by producing (i) a leaflet (policy brief) introducing the global ASNs, (ii) a scientific project synthesis on the implications of the project results for policy making, alien species management and science, and (iii) a short version aimed at a more general audience as a policy brief. For the scientific project synthesis, we plan to write this either as a dedicated book with an international publisher, or as a comprehensive review publication. This will also include an in-depth analysis of the advantages and weaknesses of the different model approaches in predicting biological invasions. We will also synthesise the results obtained for the different spatial scales, regions and taxa in an integrative analysis and assessment. Finally, we will apply network analysis tools developed by J. Jeschke's team to connect concepts and hypotheses that have been proposed to explain biological invasions with the scenarios (e.g. Enders et al. 2018). This will be done in a dedicated workshop hosted in Berlin in the final project year.

Outlook

The importance of scenarios on biological invasions for science, policy and biodiversity conservation

While there has recently been substantial progress in many fields in invasion science, and while in particular modelling approaches that include projections into the future (e.g. Bradley et al. 2012; Seebens et al. 2015; Early et al. 2016), the long-term dynamics of biological invasions and the impacts they cause is still understudied. In particular, there a lack of understanding the interactions of biological invasions with other drivers of environmental change, and how different policies and trajectories of drivers may modify the future impacts of invasions.

The unabated rise in alien species numbers and their impacts on nature and human livelihood have been a growing global concern, which resulted in new regulations and initiatives attempting to tackle the alien species challenge (e.g. the new EU regulation or the likely forthcoming IPBES thematic assessment of IAS, IPBES 2016). Given the substantial impacts of biological invasions (e.g. Vilà et al. 2011; Bradshaw et al. 2016), this lack of long-term projections of biological invasions and their impacts is considered an important knowledge gap (Ferrier et al. 2016). AlienScenarios will address these questions and will thus provide results of high importance for environmental planning and policy advice (e.g. IPBES, Ferrier et al. 2016; Essential Biodiversity Variables in GEOBON, Latombe et al. 2017).

The contribution of AlienScenarios to synthesis initiatives and conservation agreements

AlienScenarios aims to deliver important contributions to several high-profile initiatives on biodiversity conservation, sustainable development and knowledge synthesis. The Convention on Biological Diversity CBD (https://www.cbd.int/) and the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services IPBES (https://www.ipbes.net/) are the two most prominent ones; both are crucial for formulating and advising global IAS policy, and improved information on potential long-term dynamics of alien species is highly relevant for this purpose.

On a continental level, the EU legislation on IAS (http://ec.europa.eu/environment/nature/invasivealien/index._en.htm) is one of the most ambitious laws for managing IAS worldwide. In particular, WP IV of AlienScenarios will deliver important insights on the potential impact of implementing this regulation on future alien species dynamics in Europe.

The Invasion Dynamics Network (InDyNet) (https://indynet.de) was launched 2015 and studies temporal changes in biological invasions and their impacts. It will highly benefit from the results of the AlienScenarios project. Further, a working group on "Theory and Workflows for Alien and Invasive Species Tracking (sTwist)" (https://www.idiv.de/sdiv/working_groups/wg_pool/stwist.html) has been funded by the German Biodiversity Synthesis Centre iDiv in 2018. sTwist brings together the knowledge, methods and data needed to track alien species globally and develops robust indicators for biological invasions. For elucidating the potential future trajectories of such indicators on biological invasions, AlienScenarios will deliver crucial insights.

Finally, AlienScenarios will provide results that will be useful for elucidating potential trajectories of invasions at different scales (from national to global), and for different purposes (e.g. impacts on the environment, human livelihood).

Conclusions

Formulating and applying scenarios and models of how biological invasions may unfold in the coming decades is a daunting task. AlienScenarios will be a crucial step towards this goal, but clearly, it will only be a first step on a long road to travel. Thus, future collaborative work will be needed to advance the understanding on future invasion dynamics refining and expanding the results of this project. This will need the expertise and commitment of different stakeholders ranging from scientists of different disciplines, biodiversity managers, politicians and funding institutions.

By providing the first coherent set of projections of how biological invasions may unfold in the 21st century under different storylines of human behavior, we hope that AlienScenarios will initiate a process similar to work done in the climate change research community (IPCC 2014) and that has become hugely influential.

Acknowledgements

We acknowledge funding by the BiodivERsA and Belmont-Forum call 218 on biodiversity scenarios (https://www.biodiversa.org/1360). FE, SD, DM, and BL appreciate funding by the FWF (project no I 4011-B32).

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NeoBiota 45: 19–37 (2019)
doi: 10.3897/neobiota.45.33116
http://neobiota.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
NeoBiota
Advancing research on alien species and biological invasions

Relative impacts of the invasive Pacific oyster, *Crassostrea gigas*, over the native blue mussel, *Mytilus edulis*, are mediated by flow velocity and food concentration

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Academic editor: *A. Ricciardi* | Received 15 January 2019 | Accepted 27 March 2019 | Published 15 April 2019

Citation: Joyce PWS, Kregting LT, Dick JTA (2019) Relative impacts of the invasive Pacific oyster, *Crassostrea gigas*, over the native blue mussel, *Mytilus edulis*, are mediated by flow velocity and food concentration. NeoBiota 45: 19–37. https://doi.org/10.3897/neobiota.45.33116

Abstract

The ecological impacts of invasive species can be severe, but are generally viewed as highly unpredictable. Recent methods combining *per capita* feeding rates, population abundances and environmental contexts have shown great utility in predicting invader impacts. Here, clearance rates of the invasive Pacific oyster, *Crassostrea gigas*, and native mussel, *Mytilus edulis*, were investigated in a laboratory experiment where oscillatory water flow and algal food concentrations were manipulated. Invasive oysters had lower clearance rates than native mussels in all experimental groups and did not differ among flow velocities or food concentrations. Native mussel clearance rates were higher at 5 cm s^{-1} compared to 0 and 15 cm s^{-1} flow velocities and increased with increasing food concentration. The Relative Impact Potential (RIP) metric was used to assess (i) the influence of flow velocity and food concentration on potential impacts of *C. gigas* on plankton resources and, (ii) the impacts of coexisting reefs, containing both species, on resources compared to monospecific native mussel beds. Greatest Relative Impact Potential of invasive oysters was seen at the lowest flow velocity, but became reduced with increasing flow velocity and food concentration. Relative Impact Potentials of coexisting reefs were generally greater than monospecific native mussel beds, with greatest impacts predicted at lowest flow velocity. We suggest that the greatest ecological impacts and competition potential of *C. gigas* will occur in areas with low flow velocity, but that increased flow will mediate co-existence between the two species.

Keywords
Bivalves; Clearance rate; Ecological impacts; Filter feeding; Hydrodynamics; Invasive species; *Per capita* resource use; Relative Impact Potential

Introduction

The ecological impacts of invasive species can be severe (Simberloff et al. 2013, Dick et al. 2017b) and the rate of invasive species introductions shows no sign of decline (Seebens et al. 2017, 2018). It is therefore necessary to improve our abilities to predict the ecological impacts of current, emerging and future invasive species (Dick et al. 2013, 2017b, Alexander et al. 2014). Recently, the quantification and comparison of *per capita* effects of invasive species, through for example comparative functional responses (inter- and intraspecific comparisons of consumption in relation to resource densities), have been revealed as a strong predictor of invasive species impacts (Dick et al. 2014, 2017b). Invasive species are often associated with higher consumption rates than comparative native species, with these higher *per capita* metrics predicting ecological impact (Dick et al. 2013). Further, the recent incorporation of contexts such as temperature (South and Dick 2017; South et al. 2017) or habitat complexity (Alexander et al. 2012; Wasserman et al. 2016) allow such experiments to increase our understanding and prediction of impacts under various environmental contexts (Dick et al. 2014, Paterson et al. 2015).

Recently, the Relative Impact Potential (RIP), a metric proposed by Dick et al. (2017b), has combined *per capita* resource use with population abundances to better predict the ecological impacts of invasive species. Although Dick et al. (2017b) primarily use functional responses combined with abundance data to produce RIP scores, they suggest that suitable, relevant proxies for such measures can be used in their place. For example, in the case of filter feeders, algal uptake or clearance rates as a measure of *per capita* resource use are more common than functional responses (e.g. Alexander et al. 2015). Similarly, biomass may be an equally relevant metric as a proxy for population abundance depending upon the species in question (Dick et al. 2017b). The RIP combines facets of the 'Total Response' and the 'Parker-Lonsdale' equations (see Dick et al. 2017b and Parker et al. 1999, respectively) into one metric that produces absolute values of species impact on a resource. These absolute values can then be used to compare impact, for example, the baseline impacts of native consumers in relation to invasive species. This approach was highly successful in identifying high impact invaders and indeed RIP scores are correlated tightly with independent measures of the degree of ecological impact of such invaders (Dick et al. 2017b). Here, "impact" is defined as a documented effect on a native population, whereas invasion "success" is best defined as the rate of establishment or spread of a species. The semantic distinction between the two terms should be clarified as no link between the two has been found (Ricciardi and Cohen 2007).

Per capita resource use has traditionally been used in animal ecology to investigate impacts on resources (Holling 1959, 1966, Dick et al. 2017b), whereas plant ecologists use the same method to explicitly study interspecific resource competition (Tilman 1977, Dick et al. 2017a). In ecosystems containing sessile animals that cannot move and search for different resources, such comparative resource use may reveal patterns of interspecific competition as well as impacts on resources. Investigations of interactions between sessile organisms often consider space as the only limiting resource worth studying (Connell 1961). However, local seston depletion can occur above bivalves beds (Wildish and Kristmanson 1984, Dolmer 2000a, b) leading to resource limitation (e.g. Vismann et al. 2016), and hence potential competition between filter feeding species due to their limited ability to actively search for new resources.

While comparative *per capita* resource use has been applied to a range of taxonomic groups, the method has only recently been applied to filter feeders (Alexander et al. 2015, Kemp and Aldridge 2018). However, the incorporation of environmental parameters such as water motion, a fundamental process for filter feeders, have not been included. Sessile suspension feeders rely greatly upon water motion as it is the bulk water column flow that supplies them with fresh food (Genin et al. 1986). Although water motion is necessary for replenishing plankton resources, hydrodynamic forces exerted by the movement of water can also exert destructive forces on organisms, therefore trade-offs between food provision and dislodgement pressures occur (Denny 2006).

The clear majority of work and our understanding of bivalve feeding with regards to water motion has been conducted in uni-directional currents characteristic of estuaries, inland bays and harbours. It is unknown if these studies provide a reasonable basis for the prediction of responses of bivalves to oscillatory water motion characteristic of wind and swell-driven open coasts (Denny and Gaylord 2002). Continuous reversals in flow direction increase turbulence within the water column (Denny et al. 1998), thus it is less likely that seston depletion above bivalve beds would occur. Several studies into the effects of flow velocity on clearance rates of bivalves have been conducted using mussels (*Mytilus* spp.) but with conflicting results. Some studies have found clearance rates to be unaffected by increasing flow velocity while others show significant reductions in clearance rates with increases in flow (Denis 1999; Newell et al. 2001; Widdows et al. 2002; Ackerman and Nishizaki 2004; Nielsen and Vismann 2014). To date, there have been no studies on the influence of water motion on clearance rates of the invasive Pacific oyster, *Crassostrea gigas*.

The Pacific oyster, *C. gigas*, is one of the most ‘globalised’ marine invertebrates, dominating shellfish production in many regions (Ruesink 2007, Herbert et al. 2016), and is considered invasive in several countries. For example, the Wadden Sea has seen *C. gigas* settle onto beds of the native blue mussel, *Mytilus edulis*, on such a scale that there has been a shift in dominance from native mussels to non-native oysters (Kochmann et al. 2008), suggesting that *C. gigas* can compete with native *M. edulis* for resources and potentially impact those resources to the detriment of the wider community.

The present study thus examined the Relative Impact Potentials of the invasive Pacific oyster, *C. gigas*, and the native blue mussel, *M. edulis*, in relation to effects of oscillatory flow velocity and algal food concentration on their clearance rates. The experimental treatments simulated environmental conditions experienced on inshore coasts. The main objectives were to: (i) assess the influence of oscillatory flow velocity and food concentration on the clearance rates of the two species; (ii) combine *per capita* resource use with field biomass, using the RIP metric to identify conditions that may lead to impacts on plankton resources; and (iii) use the RIP metric to compare the impacts on plankton resources of co-existing bivalve beds with those of monospecific native mussel beds on plankton resources.

Methods

Bivalve collection

In August 2016, adult Pacific oysters, *Crassostrea gigas*, with a shell length 65–105 mm, were obtained from a local commercial oyster farm, Killough Oysters Ltd. Adult native mussels, *Mytilus edulis*, with a shell length of 45–50 mm, were collected from an intertidal rocky shore in Strangford Lough, County Down, Northern Ireland (54°28'11.2"N, 5°32'25.4"W). Animals of these sizes were used as they are representative of adult organisms, thus results from the experiments would provide data for mature populations. Animals were housed at Queen's University Marine Laboratory, Portaferry in large holding tanks (~500L) with through-flowing, sand filtered seawater pumped directly from the adjacent Strangford Lough. Prior to experimental testing, shells were cleaned of any mud and epibionts and returned to the holding tanks for at least 48 hours prior to testing.

Experimental tank system

Clearance rates of the bivalves were determined in an aerated experimental tank system designed to simulate oscillatory water motion (full details of the design can be found in Kregting et al. 2015). The tank system consisted of four tanks where the bivalves were moved back and forth through a stationary body of aerated water to simulate water motion representative of the horizontal oscillatory water motion benthic animals experience at the seabed on shallow inshore coasts. The horizontal oscillatory water motion was simulated in the four laboratory experimental tanks by two horizontal rods mounted above the tanks on a steel frame allowing free oscillatory movement of the rods. The rods were attached to a rotating arm driven by a 12 V car windscreen wiper motor. Two detachable, vertical polypropylene arms with perpendicular base plates were fixed to each rod (arms = 4). Each arm was suspended over a 65 L polypropylene container (60 × 40 × 32 cm). The driving motor was powered using a regulated power supply (Skytronic 0–30 V) which could be altered to control the horizontal velocity of the arms. Three flow scenarios were selected; static (0 cm s^{-1}) and two which oscillated over a distance of 21 cm with amplitudes of 5 and 15 cm s^{-1}.

Either 4 oysters or 10 mussels were attached to the experimental base plates. Different numbers of each species were used in the experiment to keep the area covered by the animals the same, with clearance rates then corrected by biomass (see below). Oysters were attached to the baseplates using cyanoacrylate glue. Mussels were placed onto baseplates and covered with plastic mesh netting to hold them in place allowing natural byssus attachment. Plates with animals attached were placed into 1 μm filtered, UV sterilised seawater for 22 hours to standardise starvation. After the starvation period which allowed sufficient byssus attachment from mussels, the mesh netting was removed from the mussels prior to testing.

Microalgal culture

The microalga *Tetraselmis suecica* was chosen for the experiment, as plankton of this size (~6–10 μm) (Chrétiennot-Dinet et al. 1986, Hansen et al. 1996) are retained with high efficiency by both species (Bougrier et al. 1997; Ward and Shumway 2004). Algae were cultured in 1 μm filtered, UV sterilised seawater using f/2 media and were on-grown until sufficient stock could be maintained in a 150L bag culture.

Clearance rate experiment

Experimental tanks were filled with 30 L of 1 μm filtered, UV sterilised seawater and aerated at one end to ensure the water was well mixed, but not interfering with the oscillatory movement, allowing use of the clearance equation (see below). The selected animals were subjected to a randomly selected flow velocity for 30 minutes before the addition and mixing of a randomly selected, pre-defined volume of algal monoculture (Table 1). To measure algal depletion in the tanks, two 3 ml water samples were taken immediately after the algal monoculture was sufficiently mixed within the experimental tanks and again after 1 hour. Cell concentration of the water samples were analysed using an electronic particle counter (Coulter Z1). Experimental tanks were emptied, cleaned with freshwater, and rinsed with 1 μm filtered, UV sterilised seawater after each trial. This process was carried out for both species at the three flow velocities (0, 5, 15 cm s^{-1}) and five algal culture volumes (4, 8, 16, 32, 64 ml; corresponding cell

Table 1. Volumes of *Tetraselmis suecica* added to experimental tanks with corresponding initial cell concentrations within experimental tanks for clearance trials (mean ± S.E.).

ml of *T. suecica*	Cell concentration (cells ml^{-1}) ± S.E.
4	5954 ± 188
8	8198 ± 265
16	13567 ± 342
32	22221 ± 381
64	42003 ± 664

concentrations in Table 1) with four replicates per experimental group. Due to the experimental setup, accurate measurement of animal valve gape was not achievable however, all animals were visually inspected during feeding trials. After experimentation, the soft tissue of each animal was removed from the shell and dried at 70 °C for 24 hours to determine the shell-free dry weight (SFDW) of each replicate. Control trials without animals in the experimental tanks (n = 2) were conducted to identify any natural reductions in algal concentration over the feeding period due to sinking.

Clearance rate calculations

Due to adequate water mixing within experimental tanks, the 'clearance method' (Riisgård et al. 2013) was used to measure the rates of algal consumption of the bivalves. Clearance rates (CR), measured as the volume of water cleared of particles per hour (*h*) per gram of SFDW (*g*), were calculated as:

$$CR\ (L\ h^{-1}\ g\ SFDW^{-1}) = \frac{V\ (\ln C_0 - \ln C_t)}{t * SFDW}$$

where V is the volume of water in the experimental tank, C_0 and C_t are algal concentrations at time 0 and time t, *SFDW* is the shell-free dry weight of animal flesh in each replicate. SFDW was used to standardise clearance rates between species as, although the area occupied by both species was kept constant, differences in biomass occurred between the two species.

Data analyses

All analyses were performed in R 3.3.1 (R Core Team 2012). One replicate from two separate experimental groups were removed from the analysis due to mussel detachment during the feeding period. A three-factor analysis of variance (ANOVA) compared clearance rates between species (2 levels; *C. gigas* and *M. edulis*), among flow velocities (3 levels; 0, 5, 15 cm s^{-1}), and among food concentrations (5 levels; 4, 8, 16, 32, 64 ml of *Tetraselmis suecica*). Levene's test for homogeneity of variance ($F_{29,88} = 0.9$, $p > 0.05$) and Shapiro-Wilk's test for normality ($p > 0.05$) ensured ANOVA assumptions were met. Significant differences between treatments were compared with Tukey's honest significant difference post hoc test.

Species biomass and the Relative Impact Potential (RIP) metric

A systematic search of the on-line scientific databases *Scopus*, *Web of Science* and *Google Scholar* was used to collect field biomass data for both *Crassostrea gigas* and *Mytilus edulis*. All searches were performed in October 2017 using the search terms (*Crassostrea gigas*

OR *Magallana gigas* OR *Mytilus edulis*) AND (biomass OR abundance OR density) AND (invasive OR non-native OR native). References from retrieved articles were screened for other relevant publications. Literature was selected (Table 2) if biomass estimates were given as total wet weight (WW), shell-free dry weight (SFDW) or ash-free dry weight (AFDW). Data given as WW or AFDW were converted to SFDW using published weight conversion factors for bivalves (Ricciardi and Bourget 1998), as SFDW was used in the clearance rate calculations. Clearance rates averaged across food concentrations, as well as those at the lowest and highest food concentrations for each species from this study, were combined with biomasses for each species to create RIP biplots (Laverty et al. 2017). Biplots represent the Relative Impact Potential of *C. gigas* compared to *M. edulis* to under the contexts of 'flow velocity' and 'food concentration'. Biomass data from the Wadden Sea were also available for reefs where the two species are coexisting, dubbed 'oyssel reefs' (Reise et al. 2017). In these cases, clearance rates averaged across food concentrations, as well as at the lowest and highest food concentrations of each species, were multiplied by their proportional contribution to the overall reef biomass. The proportionally adjusted clearance rates were then combined to give an overall clearance rate for the mixed species reef. Clearance rates combined with biomass data were used to create RIP biplots to represent Relative Impact Potentials of coexisting 'oyssel reefs' compared to monospecific *M. edulis* beds. RIP biplots combine biomass and clearance rate data to give a visualisation of ecological impact with greater impacts being shifted towards the top and right of the plot, and lesser impacts being shifted towards the bottom and left of the plot (Laverty et al. 2017).

Results

Clearance rate experiment

Visual inspection found that all animals were open and appeared to be feeding during experimental trials. Control groups saw changes in algal concentrations < 2% of the changes that occurred in treatments with animals, thus any changes in algal concentration over the feeding period with animals present were attributed to intake by the animals and not sinking.

Overall, clearance rates of *Crassostrea gigas* were significantly lower than those of *Mytilus edulis* (Table 3; Figure 1). There was a significant main effect of flow velocity on clearance rate (Table 3), with clearance rates at 5 cm s^{-1} significantly higher than both other velocities tested (Tukey's HSD, $p < 0.05$). However, the significant 'species' × 'flow' interaction (Table 3) reflects the lack of change in the *C. gigas* clearance rate but increase in *M. edulis* clearance rate at 5 cm s^{-1}.

Overall, clearance rate increased with food concentration (Table 3). The significant 'species' × 'food concentration' interaction (Table 3) reflects that increasing clearance rates over increasing algal food concentrations occurred only for the native *M. edulis* (Tukey's HSD, $p < 0.05$; Fig. 1).

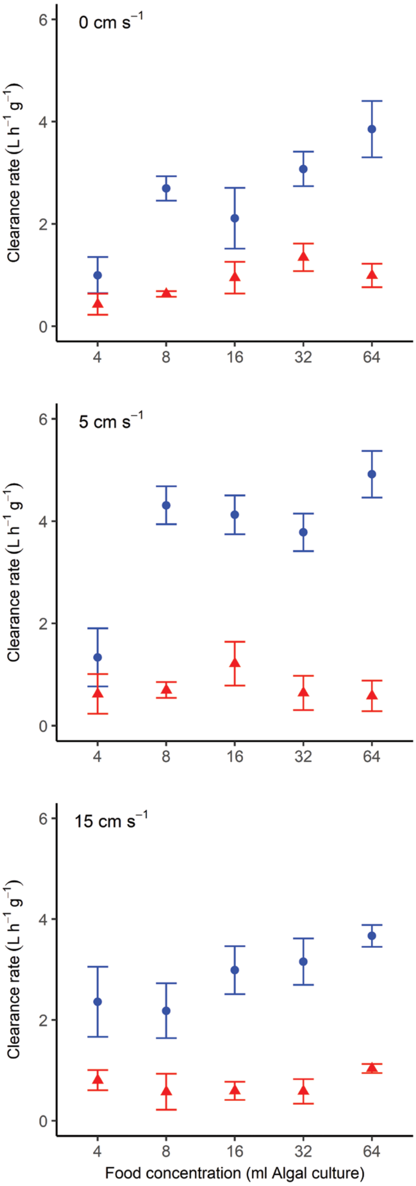

Figure 1. Clearance rates of the native mussel, *Mytilus edulis* (blue circles), and invasive Pacific oyster, *Crassostrea gigas* (red triangles), as a function of algal food concentration at flow velocities of 0, 5 and 15 cm s^{-1}.

Relative impact potentials

Biomass data from the Wadden Sea show that *C. gigas* generally has a higher biomass than *M. edulis*. Combined with average clearance rates from this study, *C. gigas* is shown to have similar Relative Impact Potential to *M. edulis* at 0 and 15 cm s^{-1} flow

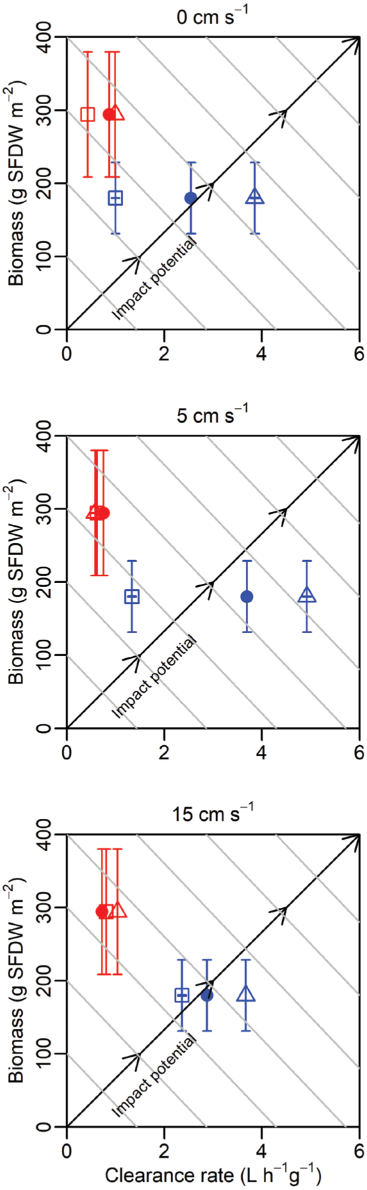

Figure 2. RIP biplots of the native mussel, *Mytilus edulis* (blue), and invasive Pacific oyster, *Crassostrea gigas* (red), using biomass data from the Wadden Sea (mean ± S.E.). Squares indicate clearance rate (CR; L h^{-1} g^{-1}) at minimum food level, circles indicate average CR over all food levels, triangles indicate CR at maximum food level (mean ± S.E.). Impact increases from bottom left to top right.

velocities (Fig. 2). The increased average clearance rate of *M. edulis* at 5 cm s^{-1} reveals that impacts of *M. edulis* at this flow velocity are higher than *C. gigas* (i.e. shifted further to the right, Fig. 2). At low food concentrations, the RIP of *C. gigas* is higher than that of *M. edulis* at both 0 and 5 cm s^{-1} due to reduced *M. edulis* clearance rates

Table 2. Biomass data for *Crassostrea gigas*, *Mytilus edulis*, and coexisting 'oyssel' reefs from the Wadden Sea with corresponding references. Symbols denote separate species biomass contributions to coexisting 'oyssel' reefs.

Species	Biomass (g SFDW m^{-2})	Reference
C. gigas	508†	(Markert et al. 2010)
	348‡	(Markert et al. 2013)
	201*	(Markert et al. 2013)
	118	(Fey et al. 2010)
M. edulis	328	(Markert et al. 2010)
	247†	(Markert et al. 2010)
	85‡	(Markert et al. 2013)
	71*	(Markert et al. 2013)
	166	(Munch-Petersen and Kristensen 2001)
Coexisting reef	755†	(Markert et al. 2010)
	433‡	(Markert et al. 2013)
	273*	(Markert et al. 2013)

Table 3. Three-way ANOVA of the effects of species (2 levels; *Crassostrea gigas* and *Mytilus edulis*), flow velocity (3 levels; 0, 5, 15 cm s^{-1}), and food concentration (5 levels; 4, 8, 16, 32, 64 ml of algal monoculture) on clearance rates.

	Df	Mean Sq	F value	Pr(>F)
Species	1	151.24	275.725	< 0.001
Flow	2	3.28	5.985	<0.01
Food	4	5.83	10.636	< 0.001
Species × flow	2	4.3	7.836	< 0.001
Species × food	4	3.83	6.989	< 0.001
Flow × food	8	1.09	1.985	0.0575
Species × flow × food	8	0.71	1.303	0.2523
Residuals	88	0.55		

(i.e. *M. edulis* toward bottom and shifted left, Fig. 2). At 15 cm s^{-1}, impacts of the two species under low food conditions are similar. High food concentrations indicate greater impacts of *M. edulis* under all flow scenarios due to increased clearance rates.

The total biomass of coexisting reefs was higher than monospecific *M. edulis* beds (Table 2). The elevated average clearance rate of *M. edulis* at 5 cm s^{-1} leads to the impacts of coexisting reefs and monospecific *M. edulis* beds to be similar. At 0 and 15 cm s^{-1}, however, the impacts of coexisting reefs are higher than those of monospecific *M. edulis* beds (Fig. 3). At low food concentrations, impacts of coexisting reefs are shown to be higher than monospecific *M. edulis* beds at all flow velocities (Fig. 3). High food concentrations lead to similar impacts of coexisting reefs and monospecific *M. edulis* beds at 0 and 15 cm s^{-1} but greater impacts of monospecific *M. edulis* beds at 5 cm s^{-1} (Fig. 3).

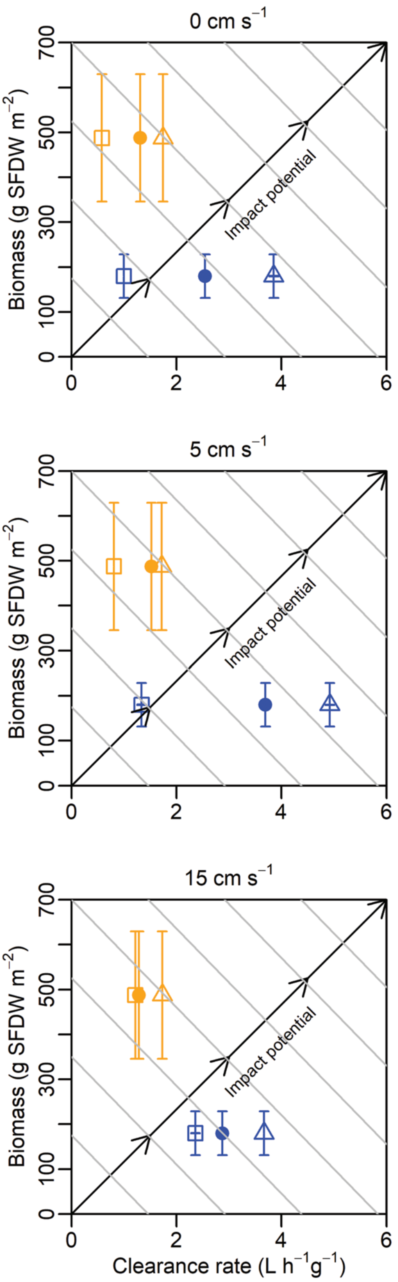

Figure 3. RIP biplots of the native mussel, *Mytilus edulis* (blue), and coexisting 'oyssel' reefs (orange) using biomass data from the Wadden Sea (mean ± S.E.). Squares indicate clearance rate (CR; L h^{-1} g^{-1}) at minimum food level, circles indicate average CR over all food levels, triangles indicate CR at maximum food level (mean ± S.E.). Impact increases from bottom left to top right.

Discussion

Comparative resource use and Relative Impact Potential studies involving native and invasive bivalves to investigate species interactions have not been explored in depth (Alexander et al. 2015, Kemp and Aldridge 2018). This study has thus coupled a comparative resource use concept, with population abundance and the environmental context of oscillatory flow, to examine whether invasion impact on resources and competitive effects by the invasive Pacific oyster, *Crassostrea gigas*, could be predicted based on algal uptake in the different hydrodynamic conditions tested. We found that *per capita* resource use of the invasive Pacific oyster, *C. gigas* was lower than that of native *Mytilus edulis*. However, when accounting for field densities, sites that have seen large invasions of *C. gigas* may experience ecological impacts on resource communities, especially in areas with little water motion.

The flow velocities chosen in this study are within the range that mussels and oysters are likely to experience regularly in open coastal areas, for example, the Wadden Sea (Janssen-Stelder 2000). Changes in flow velocity and food concentration had no effect on invasive *C. gigas* but significantly altered native *M. edulis* clearance rates. Flow velocity and food concentration mediated the Relative Impact Potential of the invasive *C. gigas* over the native *M. edulis*. Low flow velocities and food concentrations led to the RIP of *C. gigas* being higher than that of *M. edulis*, suggesting a greater impact on resources (i.e. plankton) by *C. gigas* under such conditions. Increases in flow and food however, increased the RIP of *M. edulis* due to the increases in clearance rate, thus suggesting a lower comparative impact of *C. gigas* when flow velocity and food concentrations increase. The RIP biplots also show that in reefs where coexistence between the two species occurs, impacts on plankton resources are likely to be greater than monospecific *M. edulis* beds in the majority of flow velocity and food concentration contexts tested.

This is the first study investigating the effects of oscillatory water flow on bivalve clearance rates thus we cannot compare the results found to other studies. Previous investigation into *M. edulis* clearance rates in uni-directional currents have provided mixed results (Ackerman 1999, Denis 1999, Widdows et al. 2002, Ackerman and Nishizaki 2004). Here, we found a uni-modal response of *M. edulis* clearance rates with increasing water velocity. Although unclear, it may be predicted that clearance rates may decrease at lower oscillatory flow velocities compared to uni-directional current velocities due to increased turbulence created by oscillating motion. Such turbulence may inhibit feeding as well as the fact that in oscillatory flows, inhalant siphons would face into the flow 50% of the time, which has been linked with decreased clearance rates (Newell et al. 2001). The lack of influence of flow velocity on the clearance rate of *C. gigas* differed from responses shown by *M. edulis*. No previous studies have investigated the influence of flow velocity on *C. gigas* clearance rates although this species can be found in environments with a wide range of hydrodynamic conditions from high energy to sheltered environments (Wrange et al. 2010, Strand et al. 2012, Dolmer et al. 2014).

Food concentration only significantly increased *M. edulis* clearance rate. This is consistent with patterns observed whereby, at a lower threshold, bivalves can cease filtering (Denis 1999, Riisgård et al. 2013, Sarnelle et al. 2015). This is not shown by *C. gigas* which, although it has a lower clearance rate, appears to maximise its feeding capability even at low food levels.

Here, our measured clearance rates for *C. gigas* were <1 L h^{-1} g^{-1}, which is lower than other studies ranging from 2–11.8 L h^{-1} g^{-1} (Walne et al. 1972, Gerdes et al. 1983, Bougrier et al. 1995, Dupuy et al. 2000). These studies, however, used a range of oyster sizes generally smaller than those used here, which may lead to higher body weight specific clearance rates. Previous studies also measured clearance rates in static systems which provide unrealistic, idealised conditions for filtration. Although our measured clearance rates are lower than other laboratory studies, they are similar to field observations of < 1 L h^{-1} g^{-1} (Wheat and Ruesink 2013). Our measured clearance rates for *M. edulis* are comparable to those of other laboratory studies (examples in Troost et al. 2010).

Although *C. gigas* is a successful invader, it produces varied ecological impacts, both positive and negative depending on context (Padilla 2010, Herbert et al. 2012, 2016). Invasion "success" and "impact" should be distinguished as the two are not necessarily correlated (Ricciardi and Cohen 2007). Common misinterpretation leads to the incorrect use of the terms whereby success should be defined as the rate of establishment and spread whereas impact is a documented effect on native populations. Here, we show that the relatively low *per capita* clearance rates of *C. gigas* found are in line with theory that high relative *per capita* rates are associated with high impact, with the corollary being that low impact should be associated with low *per capita* rates (Dick et al. 2013, 2014, 2017b). By combing *per capita* clearance rates with field biomass data into the RIP metric, we show again that, even with the higher biomass of *C. gigas*, because this is mitigated by lower *per capita* feeding rates, the invader is predicted to have relatively low impact on native resources.

Further, although the RIP would usually be used to assess or predict species impacts on a resource, we contend that it may also be useful in understanding interspecific competition (Dick et al. 2017a), due to the inability of bivalves to move and search for new food resources. Although plankton resources are not thought of to be limiting, it has been shown that seston depletion can occur above bivalve beds (Wildish and Kristmanson 1984, Dolmer 2000a), and that bivalve beds can become food limited (Vismann et al. 2016), which may result in interspecific competition for limited resources. The RIPs shown here suggest that only under low flow and low food conditions may the invader, *C. gigas*, exhibit ecological impacts over, and compete effectively with the native, *M. edulis*. Such areas are therefore most likely to see resource based ecological impacts from *C. gigas*. However, due to daily fluctuations in wind/storm driven changes in flow velocity as well as seasonal variations in plankton abundance, *M. edulis* will not always be outcompeted for resources which is reflected by the regular coexistence found between the two species (Holm et al. 2016; Reise et al. 2017). Although these species may compete for other resources (i.e. space), our data, using measured clearance rates, are fully in line with field patterns of invasive impacts and coexistence, and indeed, the *per capita*, RIP and context-dependency approach could be used more predictively for emerging and potential invasive species impacts (Dick et al. 2017b).

The RIP metric also revealed that the impacts of mixed species 'oyssel reefs' (Reise et al. 2017) on resources are predicted to be greater than baseline impacts of monospecific *M. edulis* beds. The magnitude of these impacts is shown to be greatest in areas with low flow velocities and food concentrations. A lack of investigation into differences in plankton resources over native monospecific *M. edulis* beds compared to those that have been invaded by *C. gigas* cannot allow statements of whether such field impacts have occurred. However, with the RIP clearly a successful predictive tool for invasive species impacts on resources, studies into plankton abundances above native and non-native bivalve beds clearly need further investigation.

Conclusion

Due to the differential effects of flow velocity on *C. gigas* and *M. edulis*, additional investigations into the effects of flow type (i.e. currents vs. waves) may be required to further understand differences in feeding and growth *in situ*, especially as these species are sensitive to interspecific competition. As growth is directly related to feeding, investigation into growth rates in different hydrodynamic conditions, which vary both naturally and due to anthropogenic influences, should be conducted to validate the results of this study. Based on our results, we suggest that areas with little water motion and those where local food limitation may occur are likely to be most at risk of impacts from *C. gigas*. Areas with increased water motion are unlikely to be resource limited due to increased food replenishment however, destructive forces exerted by the water itself may affect species growth and success. The field patterns of low invasion impact and coexistence with the native analogue, *M. edulis*, further highlight the excellent explanatory and predictive power of coupling *per capita* resource use with field abundances for invasion ecology, however, investigation into growth rates under these environmental contexts would achieve an even better understanding of competition between the two species.

Acknowledgements

All authors conceived the work and designed the experiment. PWSJ carried out data collection and analysis. All authors contributed to writing the final manuscript and gave approval for publication. The authors thank Aidan Flaherty for assistance in adapting the experimental setup, Emma Gorman for providing the algal culture and Daniel Barrios-O'Neill for advice regarding statistical analyses. JTAD also thanks the Natural Environment Research Council (NERC). This work was funded by the Department for the Economy (DfE) N. Ireland and part of SuperGen Marine Energy Research Consortium II, which was funded by the UK Engineering and Physical Science Research Council. The authors extend their gratitude to Andrea Anton Gamazo and an anonymous reviewer for their helpful comments which have improved the manuscript.

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NeoBiota 45: 39–54 (2019)
doi: 10.3897/neobiota.45.33515
http://neobiota.pensoft.net

SHORT COMMUNICATION

A peer-reviewed open-access journal
NeoBiota
Advancing research on alien species and biological invasions

Whistling invaders: Status and distribution of Johnstone's Whistling frog (*Eleutherodactylus johnstonei* Barbour, 1914), 25 years after its introduction to Colombia

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Academic editor: *R. Colautti* | Received 30 January 2019 | Accepted 1 April 2019 | Published 18 April 2019

Citation: Leonhardt F, Jimenez-Bolaño JD, Ernst R (2019) Whistling invaders: Status and distribution of Johnstone's Whistling frog (*Eleutherodactylus johnstonei* Barbour, 1914), 25 years after its introduction to Colombia. NeoBiota 45: 39–54. https://doi.org/10.3897/neobiota.45.33515

Abstract

Despite increased attention to the problem of alien amphibian invasions, systematic assessments of the actual invasion status and potential, required to estimate possible environmental and economic impacts of introduced species, are often missing. A prime example is Johnstone's Whistling Frog (*Eleutherodactylus johnstonei*), a Caribbean native that now occurs widely throughout the South American mainland, including Colombia. We conducted the first systematic and comprehensive countrywide assessment of the introduction status of the species in Colombia, combining both intensive field surveys, as well as a first population genetic analysis. The species was strictly confined to urban habitats with specific environmental conditions (plant nurseries and private gardens) and did not show any signs of dispersal into the extra-urban matrix. Genetic data support previously hypothesised independent introduction events in the Andes and along the Caribbean Coast and shed light on potential dispersal pathways. The results of this study challenge both the active spread, as well as the broad environmental tolerance hypothesis previously suggested, to explain the observed range extension. A critical reassessment of the categorisation of the species as highly invasive under IUCN-ISSG standards is required.

Keywords

Anura, alien amphibians; Colombia; distribution; disturbed areas; invasion status; new records; population genetics

Introduction

Johnstone's Whistling Frog, *Eleutherodactylus johnstonei* Barbour, 1914, a native of the Lesser Antilles, presumably St. Lucia or the northern Lesser Antilles (Kaiser 1997), has a long history of human mediated range expansion, dating back to at least 1880 when it was first discovered on Bermuda (reviewed in Kaiser 1997; Kraus 2008). Subsequently the species became established on other Caribbean Islands and on the Middle and South American mainland, with Sao Paolo, Brazil being the southernmost confirmed record to date (Melo et al. 2014). It is one of the few tropical species that even managed to establish populations in the temperate zones of the palearctic of Europe. However, this introduction occurred under very peculiar circumstances and here, the species is restricted to non-natural environments, namely botanical gardens and greenhouses. In Europe, the species was first recorded in the botanical garden of the University of Basel and its introduction was traced back to a plant shipment from Guadeloupe received in 1993 (H. Schneider pers. comm.). Today, at least 10 different greenhouse populations are known from zoological and botanical institutions in Germany and the Netherlands (this study).

Given this broad distribution (Fig.1), *E. johnstonei* can be considered one of the most widely and successfully expanding invasive amphibian species, outperformed probably only by the cane toad *Rhinella marina* (Kaiser 2002, IUCN-GISD 2018) and the American bullfrog *Lithobates catesbeianus* (Escoriza and Ruhí 2016). Earlier studies suggested that *E. johnstonei* actively disperses in a process of slow and steady migration events (e.g. Schwartz and Fowler 1973; for introduced populations on Jamaica). It was therefore expected to spread into natural habitats on several Lesser Antillean islands, where it was assumed to compete with endemic species (Hedges et al. 2010). Macroecological models, mainly based on coarse-grained climate data, even predict a very high invasion potential far beyond its natural Caribbean range (Rödder 2010) and the current distribution on the South American mainland seems to corroborate this notion. Despite this wide distribution, active dispersal beyond non-natural, human modified habitats could not convincingly be shown to be a realistic scenario (Kaiser 1997, 2002; Ernst et al. 2011). Yet, the majority of studies consider the invasion potential to be high and thus propose proactive eradication measures (Melo et al. 2014)

Amongst all countries, to which *E. johnstonei* has been introduced successfully, Colombia deserves special attention because of the comparatively long introduction history and the large number of populations reported to have established in different parts of the country. In the present study, we provide the first systematic and comprehensive countrywide assessment of the introduction status of *E. johnstonei* in Colombia. Known populations are reassessed and additional localities are investigated for the occurrence of the target species. For the first time, we assessed the species' population genetic structure in Colombia. We subsequently discuss the geographic distribution pattern in the light of the controversy surrounding the actual invasion potential of the species in Colombia and finally provide an outlook for future research directions.

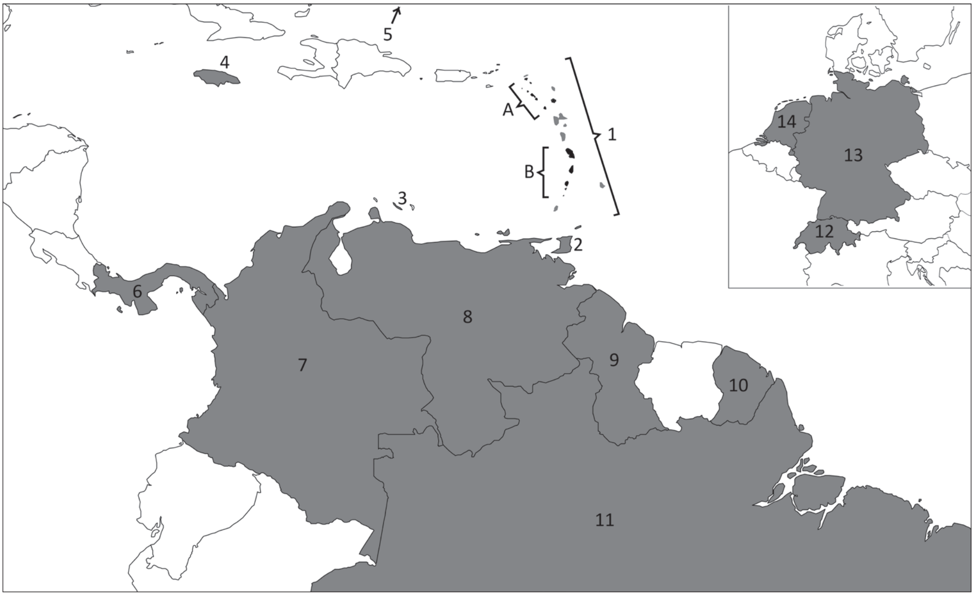

Figure 1. Global (country-level) distribution of *Eleutherodactylus johnstonei*. Black, Presumed native range (**A** or **B**); grey, introduced range (**1–13**). **A** St Maarten/St Martin, Saba, St Eustatius, St Kitts and Nevis, Antigua (Kaiser 1997) **B** Montserrat, Martinique, St Lucia, St Vincent (Kaiser 1997); **1:** Anguilla, Barbuda, Guadeloupe, Dominica, Barbados, Grenadines, Grenada (Kaiser 1997); **2:** Trinidad (Hardy and Harris 1979); **3:** Curaçao (Hardy and Harris 1979); **4:** Jamaica (Barbour 1910); **5:** Bermuda (Pope 1917); **6:** Panama (Ibáñez and Rand 1990); **7:** Colombia (Ruiz-Carranza et al. 1996); **8:** Venezuela (Hardy and Harris 1979); **9:** Guyana (Hardy and Harris 1979); **10:** French-Guiana (Lescure and Marty 1996); **11:** Brazil (Melo et al. 2014); Inset top right: Greenhouse populations in Europe: **12:** Switzerland (this study); **13:** Germany (this study); **14:** Netherlands (this study).

Methods

Study area

To assess the countrywide distribution of *E. johnstonei*, we conducted opportunistic surveys, covering natural urban peripheral and urban areas, in all major biogeographic regions (Caribbean, Andean, Pacific, Orinoco and Amazonas region; Fig 2, Suppl. material 1: Table S1) of Colombia. In addition, we selected nine focus areas for systematic surveys (see below and Fig 2). These were located in the following regions: 1. Santa Marta (12 m a.s.l.), 2. Barranquilla (24 m a.s.l.) and 3. Cartagena (34 m a.s.l.) in the Caribbean coastal lowlands; 4. Bucaramanga (993 m a.s.l.) and 5. Fusagasugá (1,717 m a.s.l.) in the Eastern Andean Cordillera; 6. Ibagué (1,229 m a.s.l.) and 7. Mariquita (485 m a.s.l.) in the Central Andean Cordillera; 8. Medellín (1,500 m a.s.l.) and 9. Cali (967 m a.s.l.) in the western Andean Cordillera. The population size varies between localities, ranging from 500,000 inhabitants (Santa Marta, Bucaramanga and Ibagué) to 1 Mio (Cartagena, Barranquilla, Cali), and even up to 2.5 Mio (Medellin) in major urban centres to only approximately100,000 (Fusagasugá) and 33,000 (Mariquita), respectively. Given the broad altitudinal and geographic range covered, climate conditions vary significantly amongst the nine locations: Hot semi-arid climate (Bsh) in Santa Marta (> 27 °C, dry season [arid] Dec.-April); Tropical wet and dry climate (Aw) in Cartagena and Barranquilla (> 27 °C, dry season [arid] Dec.-April), Fusagasugá and Cali (> 19 °C, two dry and wet seasons [no arid month]) ; Tropical monsoon climate (Am) in Medellín (average 21.6 °C, less pronounced dry season); Tropical rainforest climate (Af) in Bucaramanga, Ibagué, Mariquita (> 21 °C, no dry season) (climate-data.org, categories according to Köppen 1936; Geiger 1961).

Sampling strategy and data acquisition

Occurrence data (presence-absence) in both urban and pristine areas were acquired through opportunistic visual and acoustic encounter surveys (VES and AES, following Rödel and Ernst 2004) conducted between 2016 and 2018, covering both rainy and dry season. Localities for systematic surveys in focus areas were chosen based on occurrence evidence derived from (1) literature, (2) museum vouchers listed in the online databases www.gbif.org and www.vertnet.org, (3) unpublished museum vouchers deposited in visited collections, (4) expert knowledge (personal communication) and (5) interviews with local stakeholders (For a full list of sample areas, including focus areas and sampled localities therein, consult the gazetteer in Suppl. material 1: Table S1). Institutional abbreviations used throughout the text are as follows: ICN, Museo de Historia Natural, Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá; MTD, Museum für Tierkunde, Senckenberg Naturhistorische Sammlungen Dresden; UIS, Colección Herpetologia, Museo de Historia Natural, Universidad Industrial de Santander, Bucaramanga, Colombia; UVC, Museo de Vertebrados, Universidad del Valle, Cali, Colombia; CZA-UT, Colección Zoológica (Anfibios), Facultad de Ciencias, Universidad del Tolima, Ibagué, Tolima; MHUA-A, Museo de Herpetología (Anfibios), Universidad de Antioquia, Medellín, Colombia.

Systematic surveys in the nine urban focus areas were undertaken between June and August 2017 and in March 2018, thus covering both wet and dry season periods. We pre-selected at least two urban districts per focus area, in which two of us (FL and JDJB) conducted standardised VES and AES (following Rödel and Ernst 2004).The number of sampled localities varied for respective districts, due to differences in geographic extent and logistic restrictions (Suppl. material 1: Table S1). Each survey lasted from 6:00 pm – 10:00 pm in respective localities. Presence-absence data include audiovisual records and collected vouchers. Specimens designated as collection vouchers were euthanised using commercially available toothache pain relief gel containing 20% Benzocaine and subsequently preserved in 70% ethanol. Specimens are deposited in the collection of the ICN under collection numbers ICN 57694–57763 and ICN 57960–57962. Additional genetic samples were obtained by taking independent toe clips of uncollected individuals. We aimed at obtaining at least ten genetic samples per focus area for subsequent population genetic analysis (Suppl. material 1: Table S1). All genetic samples were stored in 95% ethanol. Clipped toes were subsequently disinfected using cotton pads soaked in 70% ethanol to prevent infections and individuals were immediately released on the spot. Genetic samples are deposited in the tissue collection at MTD.

Population genetic analyses

A total of 69 tissue samples from all sampled localities were used to generate mitochondrial (mt) haplotypes from partial sequences of 12S rRNA and D-loop regions, two established mt-markers previously used for population genetic and phylogeographic analyses in congeneric species (Barker and Rodríguez-Robles 2017; Rodríguez et al. 2010). DNA was isolated from tissue samples using the innuPREP DNA Mini Kit (Analytik Jena AG, Jena, Germany), protocol 1: DNA extraction from tissue samples. For PCR amplification of the 12S rRNA sequences primers L25195 (forward, 5'-AAA CTG GGA TTA GAT ACC CCA CTA T-3') and H2916 (reverse, 5'-GAG GGT GAC GGG CGG TGT GT-3') from Palumbi et al. (1991) following Vences et al. (2000) were used with the following conditions on an Eppendorf Mastercycler: initial denaturation at 94 °C for 5 min, 35 cycles with denaturation at 94 °C for 45 s, annealing at 55 °C for 45 s and extension at 72 °C for 1 min, with a final extension at 72 °C for 10 min. For amplification of a D-loop fragment, primers Eleu-CR-1-For (5′-TCCWGTTGWCWRGGATAGAGAAGG-3′) and Eleu-CR-2-Rev (5′-GAAYATATRTTCTCCTATGATGG-3′) were designed, based on an alignment of existing D-loop sequences for the genus *Eleutherodactylus* available on NCBI GenBank. The following PCR conditions were used: initial denaturation at 94 °C for 5 min, 40 cycles with denaturation at 94 °C for 20 s, annealing at 45 °C for 30 s and extension at 72 °C for 2 min 30 s, with a final extension at 72 °C for 10 min. The total reaction volume of 20 µl contained 1 µl template DNA, 0.2 µl Taq Polymerase (Roth), 2 µl reaction buffer, 0.5 µl dNTPs, 1 µl of each forward and reverse primer and 14.3 µl ddH_2O. PCR products were purified using the ExoSAP-IT PCR Product Cleanup Reagent (Applied Biosystems; 1:20 dilution; modified protocol: 30 min at 37 °C, 15 min at 80 °C). For sequencing, BigDye Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems) with the respective forward primers (as used for PCR amplification) was used with the following conditions: initial denaturation at 96 °C for 1 min, 25 cycles with denaturation at 96 °C for 10 s, annealing at 50 °C for 5 s, elongation at 60 °C for 1 min 15 s. Cycle sequencing reaction products were purified using the Performa DTR V3 96-Well Short Plate (Edge Biosystems, Gaithersburg, MD, USA), with each well filled with 400 µl Sephadex™ (GE Healthcare, 1:20 solution). In total, we successfully generated 69 partial 12S rRNA sequences (360 bp) and 48 partial sequences of the D-loop region (249 bp). All D-loop sequences and a single 12S rRNA sequence (identical for all analysed samples) are deposited in NCBI GenBank under accession numbers LR215271-LR215318 (D-Loop) and LR215270 (12S rRNA). After manually aligning sequences using BIOEDIT Sequence Alignment Editor 7.2.5 (Hall 1999), a haplotype network was generated with POPART (Leigh and Bryant 2015). All available network inference methods (Minimum Spanning Network, Median Joining Network, Integer Neighbour-Joining, Tight Span Walker, TCS network) yielded identical results; the Integer Neighbour-Joining Network was used to represent the haplotype network.

History of introduction to Colombia

The first published record of *E. johnstonei* for Colombia dates back to 1992. The species was reported for Barranquilla (Ruiz-Carranza et al. 1996) and the record is likely based on the first collected specimen (ICN 40380, collected 1992 by J.V. Rueda A.). Ruiz-Carranza et al. (1996) do not provide any information on potential introduction pathways, but it is likely that the species was unintentionally introduced via the ornamental plant trade (Kaiser 1997). A possible second, independent introduction was reported for Bucaramanga, where the species was sold and intentionally released to enrich gardens and yards of private properties (Ortega et al. 2001; UIS A346-350 collected 1996). In both cases, neither the origin of the frogs is clear, nor whether these introductions can actually be considered to represent two independent events, as individuals sold in Bucaramanga may have been transferred from Barranquilla. Although several single locality records have previously been published, no comprehensive assessment of the distribution and potential dispersal pathways of *E. johnstonei* throughout Colombia is available to date. The most recent status report for the country is included in a broader continental assessment compiled by Kaiser (2002). At the time of publication, only three confirmed locality records were available. These include the above-mentioned records for Barranquilla and Bucaramanga, as well as specimens collected in Cali (UVC 13885–13904, collected by W. Bolívar in 1998). In addition, an unconfirmed record based on a personal communication by J.D. Lynch was given for Cartagena. More recently, the species has been reported for Mariquita (Montes and Bernal 2012; confirmed by vouchers CZA-UT 1259, 1260), Ibagué (Llano-Mejía et al. 2014; Gómez-Martínez et al. 2016; not confirmed by vouchers) and Fusgasugá (Gómez-Martínez et al. 2016, not confirmed by vouchers). Without exception, all previous records of *E. johnstonei* in Colombia came from urban areas where individuals mostly occupy private gardens or nurseries. However, Córdoba Hernández (2014) reports *E. johnstonei* from an urban riverside, namely the Meléndez river in Cali, which is dominated by pasture and shrubs.

Results

Distribution and status of introduction in Colombia

The presence of *E. johnstonei* was confirmed for three out of the five major geographic areas in Columbia. These include the costal lowlands of the Caribbean region and the

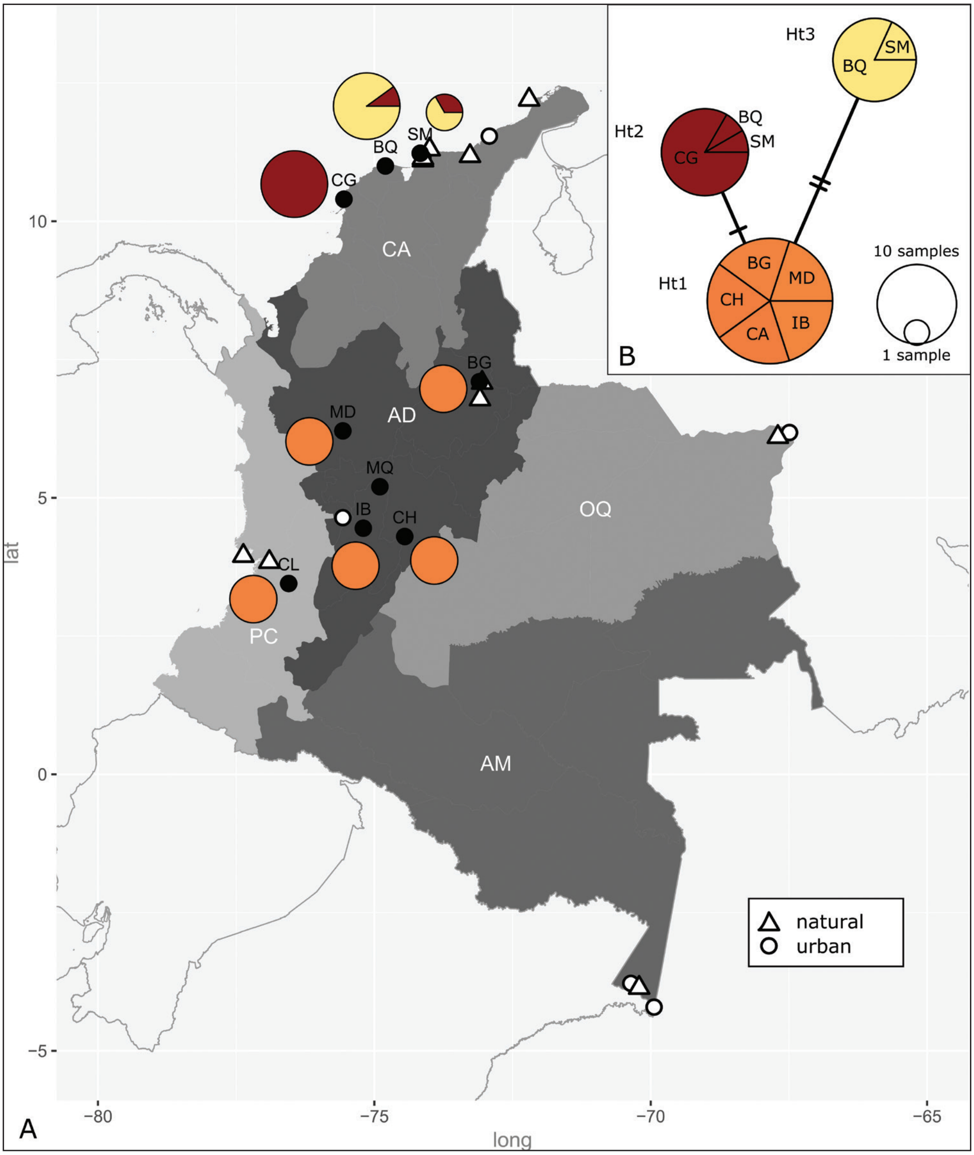

Figure 2. Presence-absence and haplotype distribution (**A**) and network (**B**) for *Eleutherodactylus johnstonei* in Colombia. **A** Small symbols: circles = urban areas; triangles = natural areas; filled symbols = presence, blank symbols = absence. White labels encode major geographic regions based on affiliation of administrative regions (www.colombia.com/colombia-info/informacion-general/geografia/regiones/): CA, Caribbean region; AD, Andean region; PC, Pacific region; OQ, Orinoco region; AM, Amazonas region. Black labels encode cities with presence of *E. johnstonei*: SM, Santa Marta; BQ, Barranquilla; CG, Cartagena; BG, Bucaramanga; MD, Medellín; MQ, Mariquita; IB, Ibague; CH, Fusagasuga-Chinauta; CL, Cali. Large coloured circles present haplotype frequencies at sampled localities. Orange: Ht1, red: Ht2, yellow: Ht3; circle sizes refer to numbers of samples at each locality as illustrated in inlet **B** Haplotype network based on the Integer-Neighbour-Joining Network implemented in POPART (Leigh and Bryant 2015). Mutations segregating haplotypes are depicted as hatch marks; partitions illustrate localities (abbreviations as in **A**) featuring the respective haplotype; circle and partition sizes represent numbers of samples.

Eastern, Central and Western Andes within the Andean and the Pacific Region. Unlike previous reports, these records are based on multiple evidence (visual, acoustic and voucher records). We could not find any evidence for the presence of the target species along the Pacific coast and in the Amazon and Orinoco region. Moreover, opportunistic VES and AES did not yield records outside of urban areas in any of the investigated regions throughout Colombia (see Fig. 2). Voucher specimens and audio-visual evidence confirm previously published records for Barranquilla (ICN 57694–57710), Bucaramanga (ICN 57732–57736), Cali (ICN 57756, 57757) and Mariquita (audio-visual evidence). For the first time, voucher specimens and tissue samples were collected for previously reported localities at Fusagasugá (ICN 57758–57763), Cartagena (ICN 57711–57731) and Ibagué (ICN 57744–57755), thus confirming previous reports based on visual and acoustic evidence (Gómez-Martínez et al. 2016; Kaiser 2002). The proposed occurrence at Medellin, based on unpublished museum vouchers (J.M. Daza pers. comm.; MHUA-A 10333, 10334), was confirmed and additional vouchers were added to these records (ICN 57737–57743). Finally, our surveys resulted in the discovery of a previously unreported population at the Caribbean coast of Santa Marta (ICN 57960–57962). In total, we were able to confirm and/or establish the occurrence of *E. johnstonei* for nine localities. Three are located in the Caribbean and two each in the Eastern, Western and Central Andean Cordillera, respectively (see Fig. 2). At all sampled localities, *E. johnstonei* exclusively occupied nurseries and urban private gardens in front of private houses, apartment complexes or hotels, while we never found populations in other urban areas such as public parks or gardens, even if these were located in the immediate vicinity of occupied sites. The observed general occurrence pattern was thus scattered within particular city districts, rather than continuous across the entire urban matrix. In total, we intensively surveyed 52 independent sites within and across our nine urban focus areas (see Suppl. material 1: Table S1). The majority of surveyed sites (67%) exhibited low abundances (≤ 5 calling males per site/survey), while we recorded intermediate abundances (6–15 calling males) for 21% and high abundances (> 15 calling males) for only 14% of all surveyed sites. All sites (9 total), located in the cities of Fusagasugá, Mariquita, Medellín and Santa Marta, exhibited lowest abundances, whereas sites with highest abundance levels were exclusively found in Barranquilla, Bucaramanga and Cartagena.

Population genetic patterns

12S rRNA mitochondrial marker sequences (360 bp, partial sequence) did not show any variation amongst the 69 samples collected across the entire Colombian distributional range. However, a clear differentiation existed in respective D-loop sequences (249 bp, partial sequence). Nucleotide diversity amongst the 48 individuals, for which sequences could be generated, amounted to 0.46% with a maximum of three variable sites, revealing three distinct haplotypes (Ht, see Table 1). Ht1, the most common haplotype (52% of all samples) was detected in all populations except those from the Caribbean coast.

Table 1. Haplotype distribution at sampled localities. N, number of individuals sampled per locality, haplotype (Ht) diversity and haplotype frequencies at each locality.

Locality	N	Haplotype diversity	Haplotype frequency		
			GGT (Ht1)	GGC (Ht2)	AAT (Ht3)
Barranquilla	10	0.18		0.1	0.9
Cartagena	10	0		1.0	
Santa Marta	3	0.67		0.33	0.67
Bucaramanga	5	0	1.0		
Medellin	5	0	1.0		
Ibagué	5	0	1.0		
Cali	5	0	1.0		
Fusgasugá	5	0	1.0		
Total	48	0.61	0.52	0.25	0.23

On the other hand, Ht2 and Ht3, both diverging from Ht1 by one and two mutations, respectively, were exclusively present in populations of the Caribbean coast. Here, tested individuals from populations in Cartagena exclusively belong to Ht2, while populations from Barranquilla and Santa Marta both share Ht2 as well as Ht3 (see Fig. 2).

Discussion

Status of introduction and invasion potential

Roughly 25 years after its introduction to Colombia, *E. johnstonei* has managed to establish populations in nine different urban areas, ranging from the Caribbean Coast at almost sea level to the Andes at altitudes of more than 1,700 m a.s.l. Climatic conditions in these newly colonised localities vary significantly and comprise arid to semiarid as well as tropical wet environments. Mean annual temperatures range from as low as 19.4 °C (Fusagasugá, 1,717 m a.s.l.) to as high as 28.3 °C (Santa Marta, 12 m a.s.l.).

This broad environmental gradient implies a significant environmental tolerance and, in combination with the comparatively wide geographic distribution across the country, it appears to corroborate results from macroecological models predicting significant future range extensions (Rödder 2010). This notion receives further support when considering the apparent speed of the range expansions from a single known introduction locality in 1992 (Ruiz-Carranza et al. 1996) to four known localities in 2002 (Kaiser 2002) and already nine confirmed localities to date (this study), reflecting the overall global expansion trend of the species within the last two decades.

However, this macro-perspective is misleading. A rather different interpretation suggests itself, when considering small-scale spatial patterns and local environmental features obtained from field surveys. A look at the spatial pattern of distribution reveals markedly disjunct distributions at larger geographic scales (countrywide distribution) that are recursively replicated at smaller geographic scales (within cities). This pattern confirms earlier findings suggesting human facilitated jump dispersal (Ernst et al. 2011; Kaiser 2002), rather than active spread leading to continuous distributions along an “invasion front” (e.g. Phillips et al. 2007).

A prevalence for site tenacity and very small home ranges d (≤ 2 m in diameter) has previously been shown in a study on long-term and nightly movement patterns in *E. johnstonei* in Barbados (Ovaska 1992). This is reflected in our observations from urban populations in Colombia. Here, we found the species in small private front yards in direct vicinity to public recreational parks, without ever recording individuals from within the parks’ boundaries, even when these contained large numbers of ornamental plants that otherwise represent favourable reproductive habitats and provide male calling perches. A consistent absence of *E. johnstonei* in vegetation patches, neighbouring ornamental plants in Bucaramanga, was previously reported by Ortega et al. (2001). This pattern was confirmed in the present study, indicating that no significant migration into the surrounding matrix took place within the past 16 years. A low capacity for active dispersal was previously also reported for non-native populations in French Guiana (Ernst et al. 2011). It is well known that significant lag phases can exist between particular invasion phases (Kowarik 1995) and land use changes, including growth and expansion of urban centres may enhance further spread of the species by counteracting present day dispersal limitations. However, there is no evidence that this will alter the species’ ecological response capacity in the short term, thus allowing for active dispersal into pristine habitats.

We therefore conclude that the active invasion potential seems to be very limited and distributional extensions are rather determined by the availability and frequency of passive transportation mediated by human transport.

When considering site-specific attributes, a second non-random pattern emerges that challenges both the active spread as well as the broad environmental tolerance hypothesis. Again this pattern is somewhat recursive as it can be observed at two spatial scales. At the country level, *E. johnstonei* is restricted to urban or disturbed urban peripheral areas as previously reported from countries outside the native range (e.g. Ernst et al. 2011; Kaiser 2002; Montes and Bernal 2012). Moreover, the distribution within the respective urban matrix is not random but habitat specific. In Colombia, the species was exclusively found in plant nurseries and private gardens that provide very specific microclimatic conditions, somewhat independent from overall climatic conditions in the surrounding landscape matrix. Regular watering and artificial provisioning of structural habitat elements that are exploited for reproduction (plants and moist substrate) may create more favourable and stable conditions than in comparative unattended, (semi-) natural habitats and thus allow for continuous rather than seasonally limited reproduction (Bourne 1998; Ortega et al. 2005). This, in turn, facilitates the establishment of stable populations by increasing propagule pressure (*sensu* Lockwood et al. 2005).The above-described localities can therefore be considered as artificial, semi-natural outdoor enclosures, rather comparable to greenhouse environments, from which the species is reported in Europe. This casts serious doubt on the definition of “invasive“ itself, as the establishment criterion *sensu* Blackburn et al. (2011), which requires self-sustaining populations in the wild, may not be fulfilled. If habitat suitability models, designed to predict future range expansions, are exclusively based on coarse-grained occurrence data in combination with macroecological predictors and include occurrences from within the exotic range of the species, this would have severe consequences for the model outcome. Under the described scenario, standard modelling schemes would be similar to using occurrence data from zoological and botanical gardens in Europe to predict potential range extensions in continental South America and beyond. The distinction between using exotic range data from continental South America and greenhouse data from European distributions may thus simply be a matter of degree of difference. However, it is far from being merely a semantic question, as ignoring the above-mentioned small-scale factors will certainly lead to flawed and imprecise (most likely exaggerated) model predictions.

Overall, our results are in line with studies that report *E. johnstonei* exclusively from non-natural, urban areas in Colombia (e.g. Córdoba Hernández 2014; Gómez-Martínez et al. 2016; Montes and Bernal 2012). However, in contrast to these, we consider the potential to actively spread and become established in natural areas, thereby negatively impacting native species, as comparatively low. Despite reported negative economic impacts imposed by *E. johnstonei*, there are currently no studies that convincingly show negative environmental impacts (Measey et al. 2016), probably also because interactions with native fauna are limited due to the strict confinement of the species to urban areas. A critical reassessment of the categorisation of the species under IUCN-ISSG standards (compare Global Invasive Species Database www.issg.org) is thus required.

Origins and history of introduction

Despite obvious limitations with respect to genetic sample sizes (N = 69/48), as well as limited choice of molecular markers (two different markers covering a total of 609 bp) that prove to be applicable in the current analytical framework, we were able to retrieve first informative patterns describing the population genetic setup of the Colombian populations under investigation. The macro-scale pattern (coastal vs. hinterland populations) is likely to prove robust and should be confirmed in future studies. With only 0.46% nucleotide divergence and only three variable sites recovered, the overall genetic diversity amongst the Colombian populations is much lower than expected, based on the limited data available from studies on congeneric frog species from the Caribbean that used similar markers (Barker et al. 2012; Barker and Rodríguez-Robles 2017). However, since we were not able to include samples from native range populations in our analyses, the crucial question of how genetically diverse these island populations are to begin with, remains to be answered in a more comprehensive future study. Studies on genetic diversity within and amongst introduced and native *E. johnstonei* populations are so far completely lacking. Our study thus provides first data on any of the known populations. It thus represents a necessary first step in addressing these questions.

The observed geographic distribution of D-loop haplotypes (see Figure 2) supports the assumption of at least two independent introductions. Haplotype Ht1 is not present along the Caribbean coast. Instead it is the single haplotype observed in all Colombian hinterland populations. A second independent introduction to Bucaramanga and subsequent translocations to other interior localities, previously hypothesised by Ortega et al. (2001), thus becomes likely. The distribution of the haplotypes Ht2 and Ht3 along the Caribbean Coast is consistent with an introduction scenario, previously outlined by Ruiz-Carranza et al. (1996) and receives additional support from plant trade information provided by local nursery owners. In this scenario, individuals carrying Ht3 were originally introduced to Barranquilla, from where they were transferred to Santa Marta. However, this haplotype is missing from Cartagena. The distribution of the second haplotype, Ht2, which is found in all three Caribbean localities, including Cartagena, where it represents the only haplotype detected, hints at a possible third independent introduction. Evidence for this scenario comes from anecdotal reports of a deliberate introduction of frogs of unknown origin in private gardens in Cartagena. Local nursery owners report frequent transports of plant material to Barranquilla and Santa Marta, opening possible pathways for the introduction of Ht2 to these cities. Since genetic differentiation between Ht1, Ht2 and Ht3 is relatively weak, with only one mutation between Ht1 and Ht2 and two mutations, between Ht1 and Ht3, respectively, we cannot completely rule out the possibility that both Ht2 and Ht3 derived from Ht1 by mutational steps. However, this seems very unlikely, as these haplotypes are geographically strictly separated by large distances and have not been found to co-occur in any of the investigated sites. A robust test of the outlined scenarios certainly requires additional genetic sampling and, ideally, the application of higher resolution markers.

Conclusion

The results of our study underscore the need to critically reassess the actual distribution status and dispersal potential of Johnstone's Whistling Frog in its non-native range and re-evaluate the current classification as an extensively spreading invasive amphibian species. Both the observed historic dispersal patterns revealed through a first population genetic assessment of the Colombian populations, as well as the actual present distributional patterns retrieved through intense field surveys, challenge available model predictions that are based on macro-ecological descriptors and coarse-scale climatic variables. Based on the two lines of evidence (molecular and field-data) provided in this study, we consider the current risk of further range extensions into natural or even ex-urban areas as very low but recommend intensified surveys in non-urban areas. In keeping with Mecke (2014), we caution against disproportionate and premature countermeasures including eradication programmes (compare Melo et al. 2014). We rather advocate intensified systematic monitoring of the species. Moreover, increased genetic sampling is required to verify or revise the uncovered population genetic pattern and shed light on potential dispersal pathways that may have remained undetected. Despite the fact that threats to native biota imposed by direct interactions with *E .johnstonei* appear to be limited, we cannot rule out indirect negative effects mediated through the co-introduction of pathogenic microbiota associated with *E. johnstonei* (nested invasions, see current debate related to BSal, Martel et al. 2014). These factors should be addressed in an extended analytical framework and ideally applied to non-native populations in Colombia and across the entire native and introduced range of the species.

Acknowledgements

Permission for fieldwork was given by the government of Colombia, Ministry of Environment and Sustainable Development, through resolution no. 0255 (permiso marco otorgado a la UNC de recolección de especímenes de especies silvestres de la diversidad biológica con fines de investigación científica no comercial para la asignatura 'Conservación genética'). Export of genetic samples was authorised by the Colombian "Autoridad Nacional de Licancias Ambientales" under reference number 2018060578-2-000. We are particularly indebted to M. Vargas-Ramírez for his help in obtaining permission, as well as for providing logistic support during fieldwork. We especially like to thank all local partners who granted access to their private properties. Without this support, fieldwork would not have been possible. C. Kehlmaier, A. Müller and H. Stuckas significantly supported the lab work and helped with primer design. We thank D. Escoriza and W. Dawson for their valuable comments on our manuscript.

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Supplementary material 1

Table S1

Authors: Franziska Leonhardt, Juan David Jimenez-Bolaño, Raffael Ernst

Data type: occurence

Explanation note: Presence-absence data for *Eleutherodactylus johnstonei* in Colombia.

Link: https://doi.org/10.3897/neobiota.45.33515.suppl1

NeoBiota 45: 55–74 (2019)
doi: 10.3897/neobiota.45.30645
http://neobiota.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
NeoBiota
Advancing research on alien species and biological invasions

Temporal activity of rural free-ranging dogs: implications for the predator and prey species in the Brazilian Atlantic Forest

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Academic editor: *Jonathan Jeschke* | Received 17 October 2018 | Accepted 27 March 2019 | Published 22 April 2019

Citation: Carvalho WD, Rosalino LM, Godoy MSAM, Giorgete MF, Adania CH, Esbérard CEL (2019)Temporal activity of rural free-ranging dogs: implications for the predator and prey species in the Brazilian Atlantic Forest. NeoBiota 45: 55–74. https://doi.org/10.3897/neobiota.45.30645

Abstract

Domestic or free-ranging dogs (*Canis lupus familiaris*) can have deleterious effects on wildlife, acting as predators or competitors to native species. These impacts can be highly important in fragmented pristine habitats or well-preserved areas located in human dominated landscapes and where biodiversity values are usually high, such as those in southeastern Brazil. Here we explored the level of overlap or mismatch in the distributions of activity patterns of rural free-ranging dogs and potential wild prey (*Didelphis aurita*, *Cuniculus paca*; *Sylvilagus brasiliensis*) and a wild predator (*Leopardus pardalis*) in areas of Atlantic Forest in southeastern Brazil. We further explored the possible influence of the wild predator on the dog presence pattern detected in the territory analyzed. Our camera-trap data (714 camera-trap days) showed that while rural free-ranging dogs display a cathemeral activity pattern, with activity peaks at dusk and dawn, ocelot and prey species are mainly nocturnal. Moreover, we found no evidence of an effect of ocelot presence, the distance to human houses and the presence of native forests on site occupancy by dogs. The ocelot activity patterns in this study were similar to those already reported in previous studies. On the other hand, previous studies have indicated that that free-ranging dogs are often reported to be more diurnal, and it seems that the rural free-ranging dogs in our study area may have adjusted their behaviour to be more active at dawn and dusk periods. This might be to both maintain some overlap with potential prey, e.g. *Sylvilagus brasiliensis*, and also to avoid ocelots by being less active in periods when this predator is more active (which also coincides with peaks in activity for potential prey species). We hypothesize that the presence of ocelots might be influencing the temporal niche dimension of rural free-ranging dogs. As a sustainable management strategy, we propose conserving territories to promote the presence of medium to large predators in natural areas, in order to control free-ranging dogs and protect their vertebrate prey species.

Keywords

Canis lupus familiaris, carnivores, competitive exclusion, *Leopardus pardalis*, mesopredators, prey, temporal segregation

Introduction

Dogs (*Canis lupus familiaris*) were the first mammals to be domesticated by humans (Morey 1994), and now occur on every continent (with the exception of Antarctica), with an estimated global population of more than 500 million (Vanak and Gompper 2009). Dogs owned by humans or associated with human houses but that use outdoor areas are not restricted to house limits (hereafter referred to as rural free-ranging dogs; Vanak and Gompper 2009). They occur on the outskirts of natural forested areas, as well as enter into those natural environments, where they may threaten wildlife due to predation (Galetti and Sazima 2006; Silva-Rodríguez et al. 2010; Doherty et al. 2017) and disease transmission (see Young et al. 2011; Doherty et al. 2017). Globally, domestic dogs have already contributed to the extinction of 11 vertebrate species and are listed as a potential threat to at least 188 threatened extant species (Doherty et al. 2017). Mammals, birds, reptiles, and amphibians all suffer negative impacts (Doherty et al. 2017). In tropical regions, studies have documented the impact of dogs on forest wildlife (Galetti and Sazima 2006; Lenth et al. 2008; Srbek-Araujo and Chiarello 2008; Lacerda et al. 2009; Paschoal et al. 2012; Carvalho et al. 2013; Lessa et al. 2016; Zapata-Ríos and Branch 2016) and have shown that dogs may have a negative effect on wild animals that move along trails and roads between forest fragments and in forest patches (Galetti and Sazima 2006; Lacerda et al. 2009; Silva-Rodríguez and Sieving 2012).

The negative impacts of domestic dogs can be a major problem for conservation units located near major urban centers, with the number and frequency of dog incursions increasing with proximity to urban areas (Lacerda et al. 2009; Paschoal et al. 2012; Carvalho et al. 2013; Lessa et al 2016). Dog-related predation in these areas often results in a decline of the relative abundance and occurrence of wild species (Galetti and Sazima 2006; Carvalho et al. 2013; Zapata-Ríos and Branch 2016; Farris et al. 2017). For example, Galetti and Sazima (2006) found 46 carcasses of 12 different wild species resulting from predation by domestic dogs in an Atlantic Forest reserve in Brazil. Moreover, during their 44-month study, they did not find any evidence of selective predation, with dogs preying upon a wide range of vertebrates, from small amphibians to deer. Thus, the presence of dogs in protected areas, especially those that harbor endangered species, should motivate a proactive management plan focused on this domestic predator and aimed at reducing wildlife predation events (Lenth et al. 2008; Paschoal et al. 2012).

The impacts of competition for resources (e.g. prey) between dogs and wild carnivores are less well documented (Vanak and Gompper 2009; Paschoal et al. 2012; and Young et al. 2011 for a review), although some studies have shown that some wild species avoid areas frequented by dogs (Lacerda et al. 2009; Silva-Rodríguez and Sieving 2012). Prey may also avoid time periods where this predator is more active (Zapata-Ríos and Branch 2016), resulting in a temporal mismatch in activity between species. Dogs may themselves be preyed upon by larger carnivores, occasionally forming part of the diet of medium-sized to large felids, such as pumas (*Puma concolor* – Farrell et al. 2000), jaguars (*Panthera onca* – Whiteman et al. 2007; Foster et al. 2010), leopards (*Panthera pardus*) and lions (*Panthera leo* – Butler et al. 2004), or hyenids and canids, such as spotted hyaenas (*Crocuta crocuta* – Butler et al. 2004) and coyotes (*Canis latrans* – Grinder and Krausman, 1998). Large-bodied wild carnivores may kill dogs (Vos 2000; Butler et al. 2014), and thus, dogs may use different areas than larger carnivores, or the same area but avoid being active when a potential wild predator has an activity peak. For example, in southern Chile, most of the foraging excursions of the free-ranging dog take place during the day, while the activity of carnivores is mostly concentrated at night (Sepúlveda et al. 2015). Whatever the functional role played by free-ranging dogs in wild communities (e.g. as predator, competitor, or prey), their presence influences the activity of wild species and their use of the landscape (Lacerda et al. 2009; Silva-Rodríguez et al. 2010; Silva-Rodríguez and Sieving 2012); in turn, their spatial and temporal behavior when invading natural areas is influenced by potential predators, competitors or prey (Silva-Rodríguez and Sieving 2012). Understanding the dynamics of wild vertebrate communities inhabiting protected areas invaded by free-ranging dogs and the impact of this domestic predator is crucial for efficiently managing different forms of population control in order to reduce the impacts of free-ranging dogs. Nevertheless, in many tropical regions this important information is lacking. For example, the activity patterns of dogs and sympatric wild predators, competitors and prey is almost unknown in Brazil (Silva et al. 2018), and the influence of potential predators or competitors on the occupancy patterns of dogs, and vice versa, is still insufficiently studied in the country (but see Massara et al. 2018). Occupancy, which is the proportion of sites occupied by a species or population, is often used as a surrogate for the species habitat relationship (Guillera-Arroita et al. 2010). This metric can be influenced by imperfect detection, which can determine that an occupied site be classified as unoccupied. Thus, occupancy modeling approaches currently account for this bias and estimate simultaneously occupancy and detectability, leading to a more realistic perception of spatial use patterns (MacKenzie et al. 2006).

In this study, we used camera-trapping data from an Atlantic Forest area to: (1) compare the activity patterns of *Canis lupus familiaris* (rural free-ranging dogs) and *Leopardus pardalis* (ocelot); (2) examine the pattern of overlap of both carnivores with three potential prey species (the big-eared opossum (*Didelphis aurita*), the spotted paca (*Cuniculus paca*) and the tapiti (*Sylvilagus brasiliensis*)); and (3) assess factors influencing the occupancy patterns of rural free-ranging dogs. We hypothesized that the activity and occupancy patterns of the dogs would be affected by the presence of ocelots (which are mainly nocturnal predators; Maffei et al. 2005; Di Bitetti et al. 2006; Massara et al. 2016). Specifically, we expected that, in areas with the presence of ocelots, rural free-ranging dogs would be mainly diurnal (e.g. Boitani and Ciucci 1995; George and Crooks 2006; Srbek-Araujo and Chiarello 2008; Silva et al. 2018), despite the nocturnal activity patterns of their potential prey, as a strategy to avoid the risk of being predated themselves by the ocelots. In addition, the ocelot activity patterns would follow those commonly described (i.e. mostly nocturnal), indicating that dogs have no effect on ocelot activity patterns.

Material and methods

Study area

The study was carried out in the Serra do Japi Biological Reserve (hereafter REBIO Serra do Japi) and its surrounding areas, located in the municipality of Jundiaí, state of São Paulo, southeastern Brazil (23°12' – 23°21'S and 46°30' – 47°05'W) (Fig. 1). REBIO Serra do Japi is located in the Atlantic Plateau, comprises an area of 2,071 ha, and has a strongly seasonal climate with hot-rainy (October to March) and dry-cold (April to September) seasons. Sampling plots were located in altitudes exceeding 1,040 m, covered by altitudinal mesophilic semideciduous forests (Carvalho et al. 2013).

Data collection

Surveys were conducted from July 2006 to February 2007 and July 2009 to February 2010, using seven and 10 camera traps in each period, respectively. The camera traps were located in different sites during each sampling period, but always placed on trails that were already established in the REBIO Serra do Japi (Fig. 1). Camera traps (Trapa Camera), using a 35 mm analog camera (Canon® model BF35), were activated by movement through a passive infrared beam. Sampling sites were approximately 1 km away from each other in each sampling period. Camera traps were set up on a tree trunk 30–40 cm above ground-level, directed across the trail (Srbek-Araujo and Chiarello 2005) and programmed to operate 24 h/day with a minimum inter-photo interval of 60 s (the maximum time period allowed by the device configuration). During 1 month in each of the dry and rainy seasons, each camera trap remained active in the field for 6 days of each week. The traps were removed on Saturdays to avoid camera damage or theft (e.g., by hikers at weekends). Films and batteries were changed during this time, and the cameras were reactivated on Sunday afternoon.

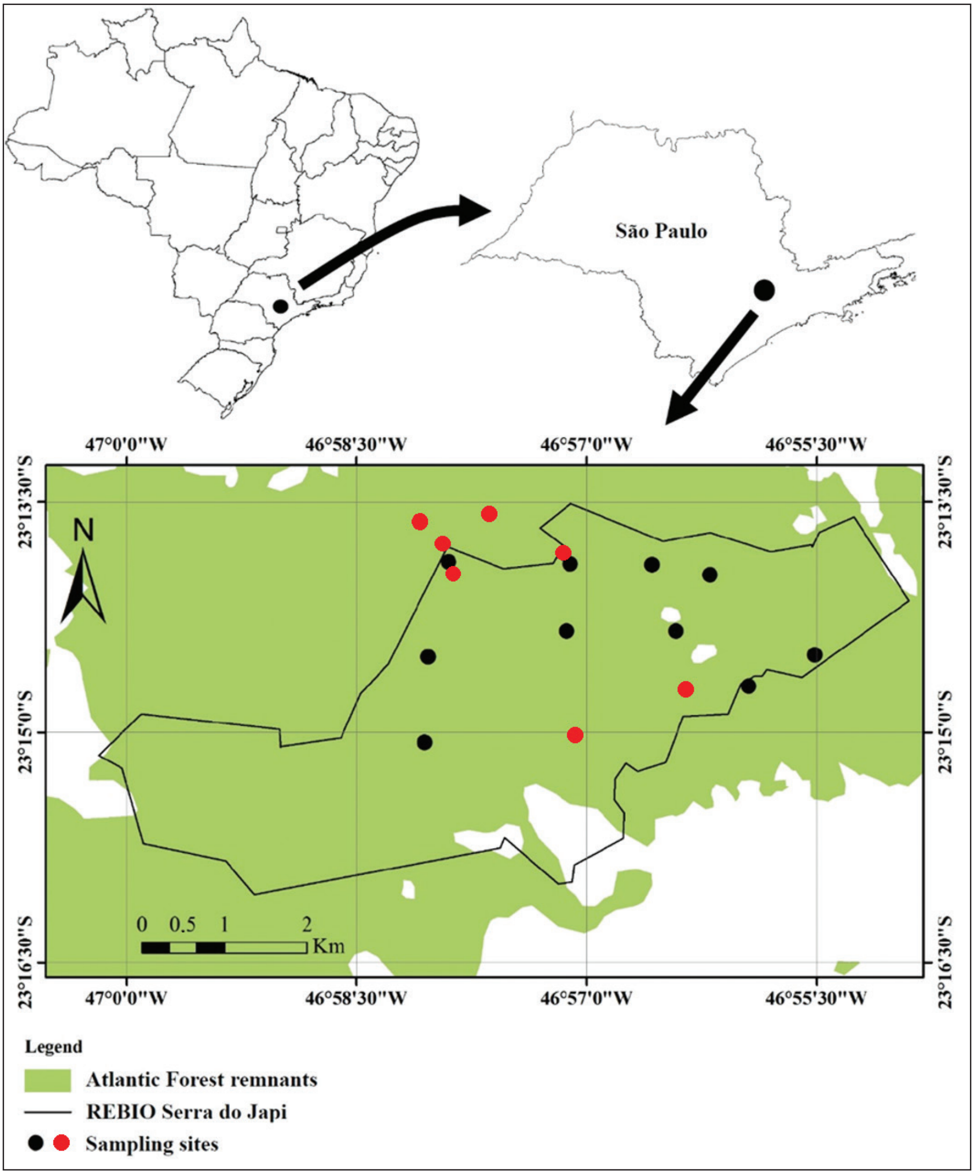

Figure 1. Study area location in São Paulo state, Brazil, and Atlantic Forest remnants in the REBIO Serra do Japi. The circles represent the sampling sites used to place camera traps. Red circles represent the surveys conducted from July 2006 to February 2007 and black circles represent the survey conducted from July 2009 to February 2010.

Data analysis

Sampling effort was defined as the number of camera-traps × number of sampling days (1d = 24h; Srbek-Araujo and Chiarello 2005). In relation to temporal activity, to ensure temporal independence of each detection event, for each camera we considered only the first record of the same species within a 1-hour interval (see Tobler et al. 2008). For the occupancy analysis, we considered only the first record of the same species within a 24-hour period (but as data was transformed to detection/non-detection within each 5-day period, this did not have any influence on the occupancy patterns described). We tested for activity clusters over a specific daily period (24h) for each species using Rayleigh's test and compared the activity patterns between species using Watson-Wheeler's test (Zar 1996). Rayleigh's test provides statistical significance for the average angle of a unimodal distribution, verifying the existence of a uniform circular distribution in a dataset (e.g. circadian activity). Watson-Wheeler's test verifies differences between two datasets that are circular in scale (Zar 1996). We used the data from the two datasets together because there were few records in each sampling period. In addition, when the activity was analyzed separately, considering the period between 2009 and 2010, this did not appear to be discrepant compared to both datasets between free-ranging dogs and the ocelot, and between the free-ranging dogs and the tapiti (see Suppl. material 1). We also used the approach suggested by Linkie and Ridout (2011) to evaluate the relationships between the activity rhythms of the predators (ocelot and rural free-ranging dogs) and prey species (tapiti, spotted paca, and big-eared opossum). We first converted the national time (linked to the Brasilia Standard Time, 3 h behind Greenwich Mean Time) to the solar time in order to correct for discrepancies associated with the daily period perceived by wildlife in the field and that registered in the collected data. We then used the independent detection records, which were considered as a random sample of the continuous temporal distribution of activity, to build a probability density function (Ridout and Linkie 2009) describing the species activity pattern, based on a non-parametrical kernel density (Ridout and Linkie 2009). This analysis was only implemented for cases with more than 10 detections. We also estimated the coefficient of overlap $\Delta 1$, which is most adequate when dealing with small sample sizes (Ridout and Linkie 2009; Linkie and Ridout 2011). $\Delta 1$ ranges from 1 (full overlap) to 0 (no overlap). We adopted the threshold mentioned by Monterroso et al. (2014) to qualitatively classify the degree of overlaps between species (i.e. $\Delta 1 \leq 0.66$, low overlap; $0.66 < \Delta 1 < 0.76$, moderate overlap; $\Delta 1 \geq 0.76$, high overlap; Curveira-Santos et al. 2017). Analyses were performed in Oriana (Kovach 2004) and R software v. 3.3.2 (R Core Team 2011), in which we used the R package "overlap". We did not consider moonlight effect, because camera traps where set under a dense tropical forest canopy which prevented/minimized moonlight penetration.

Due to the asymmetry in activity patterns of dogs and ocelots (see results), we also tested for the influence of ocelot presence, type of habitat (Habitat; Atlantic Forest vs *Eucalyptus* plantations), distance to patch edge (Dist_edge) and distance to human houses (Dist_houses) on the occupancy by dogs (Ψ). In these models, we accounted for variations in detectability (p) by building single-season occupancy models (MacKenzie et al. 2006). Different areas were sampled in each year-period (seven cameras active in 2006–2007 and 10 in 2009–2010, located in different areas). Thus, due to the limited sampling period in each year-period (i.e. 2006–2007 and 2009-2010), we assumed the populations to be closed in each sampling period and region, with reduced probability of immigration and emigration events. Due to the limited number of stations, we assumed that we were assessing the probability of use rather than the probability of occupancy. We pooled the detections of dogs over five consecutive days to generate a presence (dog detection in a five days period)/absence (no detection) matrix. Usually, 5–10 days occasion lengths are recommended for rainforest mammals (Ancrenaz et al. 2012), which will prevent having extremely low detection probabilities that reduce the accuracy and applicability of occupancy models (Ancrenaz et al. 2012).

The habitat type of each camera-trap, the distance between each trapping site and human houses and patch edge were tested as covariates influencing occupancy and detectability. We first tested for spatial autocorrelation in the detection frequency of rural free-ranging dogs in all cameras using Moran's I Index (Legendre 1993) as implemented in the package "ape" (Paradis et al. 2004) in R v. 3.3.2 (R Core Team 2011). We also assessed the correlation between continuous variables (i.e. distance covariates) using the Spearman correlation rank (*r*), and in cases of collinearity, we retained the variable most highly correlated with the dependent variable (dog detection). In the modeling procedure, we adopted the strategy suggested by Doherty et al. (2012) that consisted in building models representing all possible combinations of covariates considered as influential for occupancy (Ψ) and detectability (p). To assess the possible influence of ocelots on occupancy patterns of free-ranging dogs, we also tested the presence of ocelots as a covariate. However, to avoid a bias arising from false negatives of ocelot occupancy, we used the conditional occupancy probability of ocelots (Ψconditional_Ocel) estimated for every camera, as a candidate co-variate in the dog occupancy models (Massara et al. 2016). The conditional occupancy probability was estimated using a single-season occupancy approach (MacKenzie et al. 2002; 2006), considering all combinations of covariates. The same procedure was implemented in modelling ocelot occupancy patterns, but using the conditional occupancy probability of rural free-ranging dogs.

Model selection was performed using the Akaike Information Criterion adjusted for small samples (AICc; but see below the use of QAICc after overdispersion was assessed) to rank models according to the model's Akaike weights and the change in AICc score – ΔAICc (Burnham and Anderson 2002). Based on the models' Akaike weights, we used model averaging to determine variables' coefficients (as suggested by Doherty et al. 2012). Model fit was evaluated using the Pearson chi-square statistic and the model's dispersion assessed by the overdispersion parameter c-hat (č) (MacKenzie and Bailey 2004). Values of č greater than 1 indicate a wider variation in the observed data than expected by the model, and lower than 1 the inverse (MacKenzie et al. 2006). Although the Pearson chi-square statistic was not significant (see Results), the č estimated value was greater than 1 for the free-ranging dog models, indicating some level of overestimation. In such cases, MacKenzie and Bailey (2004) suggested the use of QAICc (quasi-likelihood version of AICc) in model selection and averaging. Thus, we applied a QAICc approach to estimate the models and weights of the covariates included in the free-ranging dog occupancy models. Occupancy modeling was performed using the "unmarked" package (Fiske and Chandler 2011), and model selection was performed using the "AICcmodavg" (Mazerolle 2017) and "MuMin" (Bartón 2014) packages. All packages were uploaded in program R v. 3.3.2 (R Core Team 2011).

Results

Overlap in temporal activity between species

From a total of 714 camera-trap days (17 cameras-trap running for 42 days), we revealed a nocturnal activity pattern for *D. aurita*, *C. paca*, *S. brasiliensis*, and *L. pardalis*, whereas the domestic dog presented a cathemeral pattern (Table 1; Fig. 2). No differences were detected between the activity patterns of *L. pardalis* and its wild prey, with an overlap always greater than 65% (Table 1; Fig. 2). Δ1 values were all above the threshold of 0.66 (low overlap), confirming this pattern. Ocelots had an intermediate overlap of diel activity patterns with big-eared opossums (Δ1 = 0.69) and a high overlap with tapitis (Δ1 = 0.80) and spotted pacas (Δ1 = 0.83) (Table 1; Fig. 2).

Domestic dogs showed a cathemeral pattern, with peak activity at dusk and dawn (Fig. 2). The overlap between this canid and its potential prey was low, reaching a maximum of 44% with the spotted paca (Table 1; Fig. 2). Again, this pattern was confirmed by Δ1 values that indicate a low overlap of activity patterns (i.e. Δ1 ≤ 0.66). The overlap was lower for the spotted paca (Δ1 = 0.24), followed by the big-eared opossum (Δ1 = 0.34) and the tapiti (Δ1 = 0.48) (Table 1; Fig. 2). Both rural free-ranging dogs and ocelots increased their activity at dusk, with a marked decrease in dog activity during the night, as that of ocelots increased. At dawn, dogs again became more active as ocelots greatly decreased their activity (Fig. 2). The coefficient of overlap Δ1 reached intermediate values (Δ1 = 0.69), although very close to the considered threshold (0.66) associated with a low overlap.

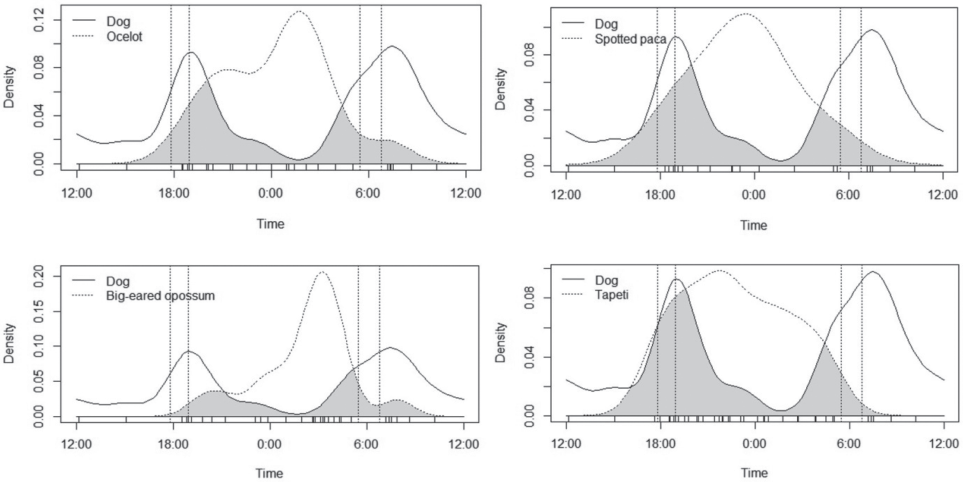

Figure 2. Kernel densities for paired activity patterns of free-ranging dogs and ocelot, spotted paca, big-eared opossum and tapiti in REBIO Serra do Japi. Individual records are shown as short vertical lines above the x-axis. The grey areas represent overlapping activity periods and the vertical dashed lines the approximate time of sunrise and sunset.

Table 1. Number of detections, relative frequency (RF), type of activity and main activity period (Mean Vector in time and angle) of the studied taxa in the REBIO Serra do Japi, Jundiaí, São Paulo: Daur – *Didelphis aurita* (big-eared opossum); Cfam – *Canis lupus familiaris* (free-ranging dogs); Lpar – *Leopardus pardalis* (ocelot); Cpac – *Cuniculus paca* (spotted paca); Sbra – *Sylvilagus brasiliensis* (tapiti). Statistical significance (*p*) of Rayleigh's test for comparing the unimodal distribution of activity patterns and Watson-Wheeler's test for assessing differences in activity between species, as well as the coefficient of overlap between activity patterns (Δ1), are also presented.

Taxa	Number of detections (RF, %)	Rayleigh test (*p*)	Main activity period	Mean Vector in time and angle (μ)	Watson-Wheeler test (*p*) and overlap (%)		Coefficient of overlap Δ1	
					Lpar	*Cfam*	*Lpar*	*Cfam*
Daur	17 (18.28)	<0.001	Nocturnal	02:21 (35.41°)	0.111 (65)	<0.001 (37)	0.69	0.34
Cfam	19 (20.45)	>0.05	Cathemeral	08:47 (131.76°)	<0.001 (43)	–	0.44	–
Lpar	16 (17.20)	<0.001	Nocturnal	00:14 (3.703°)	–	<0.001 (43)	–	0.44
Cpac	11 (11.82)	0.003	Nocturnal	23:12 (348.01°)	0.602 (70)	0.009 (44)	0.83	0.24
Sbra	30 (32.25)	<0.001	Nocturnal	22:41 (340.33°)	0.529 (73)	<0.001 (37)	0.80	0.48
Total	93 (100)	–	–	–	–	–	–	–

Rural free-ranging dog occupancy patterns

We did not detect any significant spatial autocorrelation in detection frequency of rural free-ranging dogs ($I = -0.059$; $p = 0.957$). Distance to human houses (Dist_houses) and to patch edges (Dist_edge) were highly correlated ($r = 0.912$, $p < 0.001$). We, therefore, excluded the distance to edges, as it was the variable less associated with the dependent variable ($rr_{Dist\_edg\text{-}dog} = 0.181$ $r_{Dist\_houses\text{-}dog} = 0.275$). The null occupancy and detection estimates for rural free-ranging dogs were 0.472 (SE = 0.145) and 0.291 (SE = 0.082), respectively.

The full model produced for the rural free-ranging dogs, i.e. considering all the variables influencing detectability and occupancy, showed a good model fit ($\chi^2 = 70.603$, $p = 0.200$), but indicated wider variation in the observed data than expected, i.e. overdispersion ($\check{c} = 1.29$). Thus, model ranking, averaging and estimation of variable coefficients were based on QAICc (see Methods). The total set of 53 models produced (see Suppl. material 2) were ranked according to QAICc values. The most supported model, as evidenced by the lowest QAICc value and highest QAICc weight, was the null model (Table 2). This indicates that the selected covariates were not accounting for much of the variation in the data. However, the analysis of the covariates' cumulative weights shows that the habitat type was the most influential variable for probability of detection and occupancy (Table 3; Suppl. material 3), with the influence of ocelot probability of presence being negligible on both parameters.

Ocelot occupancy patterns

We did not detect any significant spatial autocorrelation in detection frequency of ocelots ($I = -0.070$; $p = 0.920$). Due to correlation problems (see above), we excluded the distance to edges from the analysis. Null occupancy and detection estimates for ocelots were 0.765 (SE = 0.019) and 0.147 (SE = 0.037), respectively.

Table 2. Top ten ranked models for occupancy of rural free-ranging dogs in the Serra do Japi Biological Reserve, Brazil (*N* – Number of parameter in the model; QAICc – quasi-likelihood version of the Akaike Information Criterion, adjusted for small samples (i.e. accounting overdispersion); ΔQAICc – Difference between the lowest QAICc and the model's QAICc; QAICcWeight – quasi-likelihood version of the Akaike weight; Cumulative QAICcWeight – Cumulative weight of the models; psi – occupancy; p – detectability; Habitat – Type of habitat; Dist_houses – distance to Human houses; Ocelot – Conditional occupancy of ocelot in each camera-trap).

Occupancy model	***N***	**QAICc**	**ΔQAICc**	**QAICcWeight**	**Cumulative QAICcWeight**
psi(.)p(.)	2	65.951	0.000	0.484	0.484
psi(.)p(Habitat)	3	68.583	2.632	0.130	0.614
psi(.)p(Ocelot)	3	69.184	3.233	0.096	0.710
psi(.)p(Dist_houses)	3	69.202	3.251	0.095	0.805
psi(Ocelot)p(Dist_houses)	4	72.321	6.369	0.020	0.825
psi(Dist_houses)p(Habitat)	4	72.388	6.437	0.019	0.844
psi(Habitat)p(Dist_houses)	4	72.448	6.497	0.019	0.863
psi(Habitat)p(Ocelot)	4	72.475	6.524	0.019	0.882
psi(Ocelot)p(Habitat)	4	72.513	6.562	0.018	0.900
psi(Dist_houses)p(Dist_houses)	4	72.665	6.714	0.017	0.917

Table 3. Cumulative QAICc weights of the explanatory variables for models of occupancy (Ψ) and detection (p) of free-ranging dogs in Serra do Japi Biological Reserve, Brazil. QAICc – quasi-likelihood version of the Akaike Information Criterion, adjusted for small samples (i.e. accounting overdispersion); Ψ – occupancy; *p* – detectability; Habitat – Type of habitat; Dist_houses - distance to Human houses; Ocelot – Conditional occupancy of ocelot in each camera-trap; b - Covariates coefficient; SE – Standard error of the covariates coefficient; z-value - Wald statistic for testing the hypothesis that the coefficient is zero; p-value – statistical significance.

	Covariate	b	SE	z-value	*p*-value	Cumulative QAICc weights
Detection (p)	Habitat	1.676	19.999	0.084	0.933	0.204
	Dist_houses	-0.088	0.274	0.322	0.748	0.172
	Ocelot	-0.061	0.239	0.255	0.799	0.163
Occupancy (Ψ)	Habitat	0.914	13.904	0.066	0.948	0,077
	Ocelot	-0.412	3.877	0.106	0.915	0,068
	Dist_ houses	0.052	0.272	0.191	0.849	0,067

The full model produced for the ocelots showed a good model fit ($\chi^2 = 34.941$, $p = 0.300$), with negligible overdispersion (č = 0.95), and therefore we used the AICc for model ranking, averaging and estimation of variables coefficients. From the set of 53 models produced, seven (including the null model) had a ΔAICc < 2 (Table 4), and as such could be considered to be part of the set of best models for describing ocelot occupancy patterns (Burnham and Anderson 2002). However, most of the variables had large coefficients and standard errors, (Table 5), indicating that the models were not very robust.

Table 4. Top ten ranked models for occupancy of ocelots in the Serra do Japi Biological Reserve, Brazil (N – Number of parameter in the model; AICc –Akaike Information Criterion, adjusted for small samples; ΔAICc – Difference between the lowest AICc and the model's AICc; AICcWeight – Akaike weight; Cumulative AICcWeight – Cumulative weight of the models; psi – occupancy; p – detectability; Habitat – Type of habitat; Dist_houses - distance to Human houses; Dog – Conditional occupancy of dog in each camera-trap).

Occupancy model	N	AICc	ΔAICc	AICcWeight	Cumulative AICcWeight
psi(Dist_houses+Dog)p(Dist_houses+ Dog)	6	87.87	0.00	0.130	0.13
psi(Dist_houses+Dog)p(Dist_houses +Habitat)	6	88.12	0.25	0.115	0.25
psi(Dist_houses+Dog)p(Dist_houses)	5	88.51	0.64	0.095	0.34
psi(Dist_houses+Dog)p(Habitat)	5	88.77	0.89	0.083	0.42
psi(.)p(.)	2	89.19	1.31	0.068	0.49
psi(Dist_houses+Dog)p(Dist_houses +Habitat+Dog)	7	89.68	1.81	0.053	0.54
psi(.)p(Habitat)	3	89.78	1.91	0.050	0.59
psi(Dist_houses+Dog)p(Dog)	5	89.95	2.08	0.046	0.64
psi(Dist_houses+Dog)p(Habitat+Dog)	6	90.48	2.61	0.035	0.68
psi(Dist_houses+Habitat+Dog)p(Dog)	6	90.86	2.99	0.029	0.70

Table 5. Cumulative AICc weights of the explanatory variables for models of occupancy (Ψ) and detection (p) of ocelot in the Serra do Japi Biological Reserve, Brazil. AICc –Akaike Information Criterion, adjusted for small samples; Ψ – occupancy; p – detectability; Habitat – Type of habitat; Dist_houses - distance to Human houses; Dog – Conditional occupancy of dog in each camera-trap; b - Covariates coefficient; SE – Standard error of the covariates coefficient; z-value - Wald statistic for testing the hypothesis that the coefficient is zero; p-value – statistical significance.

	Covariate	b	SE	z-value	p-value	Cumulative AICc weights
Detection (p)	Habitat	-0.383	0.756	0.506	0.613	0.486
	Dist_houses	0.059	0.201	0.295	0.768	0.521
	Dog	-0.022	0.181	0.120	0.905	0.423
Occupancy (Ψ)	Dist_houses	-8.121	38.734	0.210	0.934	0.679
	Dog	11.951	54.127	0.221	0.853	0.674

Discussion

Temporal activity patterns

In common with our results for the REBIO Serra do Japi, *D. aurita*, *C. paca*, *S. brasiliensis*, and *L. pardalis* have previously been described as having nocturnal habits in South American tropical forests (Alves and Adriolo 2005; Di Bitetti et al. 2006; Michalski and Norris 2011; Blake et al. 2012; Ferreira and Vieira 2014; Massara et al. 2016; Pratas-Santiago et al. 2016; Silva et al. 2018). We found no differences between activity patterns of ocelot and their prey, and they showed high overlap in temporal activity. Similarly, previous studies have shown a substantial overlap between ocelot activity and the foraging period of their potential prey (Emmons et al. 1989; Porfirio et al.

2016; Pratas-Santiago et al. 2016). Moreover, despite the tendency for prey to reduce their activity in periods when predators are more active (Eccard et al. 2008; Gliwicz and Dabrowski 2008), in South America, there seems to be a strong overlap between prey and predator activity patterns (e.g. Blake et al. 2012; Silva-Rodríguez and Sieving 2012; Foster et al. 2013; Pratas-Santiago et al. 2016), suggesting that predators are more efficient in adjusting their activity to reduce energy costs (Foster et al. 2013), than are prey in avoiding the high activity periods of predators.

Here, the free-ranging dogs showed cathemeral activity pattern with peaks at dusk and dawn. This pattern is different to that described by other studies performed within and around protected areas in the Atlantic Forest, in which domestic dogs were mostly reported to be active during the day (Alves and Andriolo 2005; Srbek-Araujo and Chiarello 2008; Silva et al. 2018). Although rural free-ranging dogs present a peak of activity at dusk and dawn, these canids have low overlap with their potential wild prey. As these prey species show similar activity patterns to those already described in other Neotropical areas (see above), the presence of dogs within the REBIO seems to have little or no effect on the activity patterns of these vertebrates.

As ocelots in our study area maintain the activity patterns recorded in preserved environments (e.g. Maffei et al. 2005; Di Bitetti et al. 2006; Massara et al. 2016; Pratas-Santiago et al. 2016), it seems that the presence of rural free-ranging dogs is not having a large effect on their temporal behavior. Other studies have detected a negative influence of the number of dogs within Brazilian Protected Areas on ocelot abundance (Massara et al. 2015). However, we do not consider abundance in our spatial analysis, but only presence-absence data. Inversely, no nocturnal activity was detected for rural free-ranging dogs as mentioned in other regions that present potential nocturnal predators such as coyotes (*C. latrans* - e.g., George and Crooks 2006). In the temperate rainforest of southern Chile, foraging excursions of free-ranging dogs occur mostly during the day (Sepúlveda et al. 2015). There, it is expected that most wild carnivores inhabiting the area (including the puma; e.g., Adania et al. 2017) concentrate their activity at night. These patterns and the fact that the dogs detected in our study area were usually smaller (when compared to ocelots that can reach 18 kg; Paschoal et al. 2012) and often travelled alone (see Figure S1 in the Suppl. material 4), leads us to suspect that the dogs may be avoiding ocelots due to either interference or predation. However, further studies are needed to confirm this trend. Furthermore, the presence of top predators such as pumas (which were detected in our camera-trap set but in low abundance; Carvalho et al. 2013) may directly constrain rural free-ranging dog activity (through predatory pressure). In addition, during fieldwork, we found two carcasses of domestic dogs, one a fresh kill, with signs of predation and partially consumed. Next to the fresh dog carcass, we also found ocelot footprints and no other footprints from any other large predator (e.g. *P. concolor*). Therefore, we consider there was a probability that this kill was carried out by an ocelot. The carcasses were of rural free-ranging dogs of similar size to the individuals recorded on the cameras in the REBIO Serra do Japi (12–15 kg; see Figure S1 in the Suppl. material 4). There are records of ocelots preying upon and consuming wild prey that can reach up to approximately 40 kg (e.g. pampas deer, *Ozotoceros bezoarticus*, and wild boar, *Sus scrofa* – Bianchi et al. 2013; collared peccary, *Pecari tajacu* – Bianchi et al.

2010). Although the consumption of larger prey may be the result of scavenging behavior, several authors have mentioned that ocelot, especially large adult males, can actively prey upon larger prey species (Sunquist and Sunquist 2002; Moreno et al. 2006). Therefore, the ocelot may also have some negative influence on activity of rural free-ranging dogs.

Occupancy patterns of the rural free-ranging dogs and ocelots

Contrary to what we hypothesized, we did not detect any influence of ocelots on patterns of occupancy of rural free-ranging dogs, or vice versa. Occupancy models were not robust enough to allow us to infer what might be constraining or promoting the spatial patterns of dogs or ocelots in the REBIO Serra do Japi. Indeed, given that the most supported model for free-ranging dog occupancy was the null model (i.e. low QAICc/AICc and high QAICc/AICc weight; Tables 2, 4; Suppl. material 2), it would seem that the covariates included had no or a negligible effect on occupancy patterns of dog and ocelots. Our small sample size could be contributing to the lack of discrimination. Therefore, future studies should reanalyze the spatial ecology of rural free-ranging dogs and ocelots within or close to protected areas using a wider data set. Such a strategy would allow for the confirmation (or not) of the detected lack of effect of the covariates tested here, but that were identified elsewhere as important drivers of free-ranging dog occupancy patterns (e.g. Torres and Prado 2010; Paschoal et al. 2016).

Conclusions

Although acknowledging that our data has some limitations due to the small sample size and the grouping of data from two different time periods, which should lead to a cautious interpretation of our results, our study still points out some ecological patterns that should be further investigated. Our data suggest that rural free-ranging dogs adapted their activity to avoid the main activity periods of ocelots, which also reduced the interference of the dogs with wild prey. Therefore, the management of protected areas subjected to incursions by rural free-ranging dogs should prioritize the protection and promotion of resident medium-sized to large felids, as they may inhibit dog activity in those areas and thereby act as a protective measure for threatened prey species.

Acknowledgements

We are grateful for the support of the City Hall and the Secretary of Planning & Environment of Jundiaí, and the Forest Rangers, Tetra Pak of Brazil, and CCR AutoBAn (highway Anhanguera-Bandeirantes). We are also grateful to the staff of Serra do Japi Reserve for granting us a collecting permit and for supporting the fieldwork. The final version of the manuscript was reviewed for English by Karen Mustin. L.M. Rosalino who was funded by post-doctoral fellowships from the Fundação para a Ciência e a Tecnologia & Fundo Social Europeu (III Quadro Comunitário de Apoio) (SFRH/BPD/35842/2007 and SFRH/BPD/101556/2014). We thank the University of Aveiro (Department of Biology) and FCT/MEC for the financial support to CESAM (UID/AMB/50017) through national funds and, co-financed by the FEDER, within the PT2020 Partnership Agreement, and for FCT/MEC funding to cE3c (UID/BIA/00329/2019). W.D. Carvalho was granted a PhD fellowship and sandwich PhD fellowship (process 99999.002169/2014-02) by CAPES. M.S.M Godoy was granted a master scholarship by CAPES. C.E.L. Esbérard has fellowships from the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), and Jovem Cientista Program from Fundação de Amparo à Pesquisa do Estado do Rio de Janeiro 2009 e 2012 (FAPERJ).

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Supplementary material 1

Kernel densities for paired activity patterns of free-ranging dogs and ocelot (A) and free-ranging dogs and tapiti (B) in REBIO Serra do Japi, considering only the sample period of 2009/2010

Authors: William Douglas Carvalho, Luís Miguel Rosalino, Maíra Sant'Ana M. Godoy, Marília F. Giorgete, Cristina Harumi Adania, Carlos E. Lustosa Esbérard

Data type: occurrence

Explanation note: Individual records are shown as short vertical lines above the x-axis. The grey areas represent overlapping activity periods and the vertical dashed lines the approximate time of sunrise and sunset.

Link: https://doi.org/10.3897/neobiota.45.30645.suppl1

Supplementary material 2

Rural free ranging dogs occupancy models for Serra do Japi Biological Reserve

Authors: William Douglas Carvalho, Luís Miguel Rosalino, Maíra Sant'Ana M. Godoy, Marília F. Giorgete, Cristina Harumi Adania, Carlos E. Lustosa Esbérard

Data type: occurrence

Link: https://doi.org/10.3897/neobiota.45.30645.suppl2

Supplementary material 3

Occupancy and detectability probabilities variation of the independent variable included in the best models

Authors: William Douglas Carvalho, Luís Miguel Rosalino, Maíra Sant'Ana M. Godoy, Marília F. Giorgete, Cristina Harumi Adania, Carlos E. Lustosa Esbérard

Data type: statistical data

Explanation note: Variation of occupancy and detection probabilities with changes in distance to houses (km).Variation of occupancy and detection probabilities with changes in ocelot's occupancy probability.

Link: https://doi.org/10.3897/neobiota.45.30645.suppl3

Supplementary material 4

Image of a rural free ranging dog registered in the Serra do Japi Biological Reserve

Authors: William Douglas Carvalho, Luís Miguel Rosalino, Maíra Sant'Ana M. Godoy, Marília F. Giorgete, Cristina Harumi Adania, Carlos E. Lustosa Esbérard

Data type: occurrence

Explanation note: This was a small size individual (ca. 10–15kg), ranging alone.

Link: https://doi.org/10.3897/neobiota.45.30645.suppl4

NeoBiota 45: 75–92 (2019)
doi: 10.3897/neobiota.45.31009
http://neobiota.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
NeoBiota
Advancing research on alien species and biological invasions

Low detectability of alien reptiles can lead to biosecurity management failure: a case study from Christmas Island (Australia)

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Academic editor: *Sven Bacher* | Received 1 November 2018 | Accepted 27 March 2019 | Published 7 May 2019

Citation: García-Díaz P, Ross JV, Vall-llosera M, Cassey P (2019) Low detectability of alien reptiles can lead to biosecurity management failure: a case study from Christmas Island (Australia). NeoBiota 45: 75–92. https://doi.org/10.3897/neobiota.45.31009

Abstract

When we assume that contemporary management actions will be effective against the global rise of emerging alien species, we can develop management complacency, which leads to potentially disastrous outcomes for native biodiversity. Here, we propose the use of the probability of detection as a metric to assess the feasibility of management actions for alien species. We explore how detectability can influence the management of alien reptiles, a group of emergent alien vertebrates globally. We use a Rapid Biological Assessment method (time-limited transects) to estimate the probability of detection for alien reptiles present on Christmas Island (Australia). Across the five species studied, we found low probabilities of detection and poor explanatory capacity of the individual covariates included in our models. These findings indicate that management options to deal with alien reptiles are limited due to the potential high cost and low efficacy associated with low probabilities of detection. Strict preventive strategies, firmly espousing the principles of adaptiveness and precautionary policies, combined with early detection and biosecurity response activities are needed to address the emergence of alien reptiles. Our research was focussed on alien reptiles on islands, but the rise of new pools of alien species from all taxonomic realms across the world suggests that our conclusions may be applicable more generally. Further research is called for to explore the applicability of our conclusions and recommendations to other taxonomic groups and regions of the world.

Keywords
Anticipatory policy-making; Christmas Island; preventive decision-making; probability of detection; Rapid Biological Assessment; uncertainty

Introduction

The global emergence of a new pool of alien species may render existing management actions, ranging from rapid incursion response to the eradication of self-sustaining populations, ineffective (Hulme 2015; Seebens et al. 2018). For example, while the increasingly successful program of invasive alien rodent eradications is well documented (Howald et al. 2007), large-scale attempts to eradicate invasive alien reptiles, a group of emergent alien vertebrates, have failed (Kraus 2009; García-Díaz et al. 2017a). Additionally, the allocation of resources along the management continuum (from prevention to eradication) is complicated by the uncertainties surrounding the costs and benefits of emerging alien species, and the realised efficacy of practical activities (McIntosh et al. 2009; Rout et al. 2014). Assuming that management actions, which have been demonstrated and validated on historical alien species, will work as effectively with novel pools of alien species is risky and can lead to poor management outcomes (or complete failure) in the face of increasing introductions of new alien species (Gregory et al. 2014; Early et al. 2016).

Successful management of alien species depends on the capacity to anticipate the specific transport pathways, which move alien species, and on adapting management actions to address the associated novel risk. While substantial research effort has been invested in understanding the dynamics of changing pathways (Hulme 2015; Seebens et al. 2018), less has focussed on assessing the efficacy and effectiveness of existing management actions. The probability of detection (or capture) of an individual, provides a simple quantitative measure of the likely effort needed to manage new alien species. In turn, the capacity to assess management efforts needed to contend with new alien species provides an indicator of the estimated efficacy of candidate management actions. Critical alien species management actions such as: (i) quarantine; (ii) early detection and either rapid containment, control, or suppression of recent introductions; and (iii) eradication, cannot proceed unless the individuals of an alien species can be reliably detected (Christy et al. 2010; Holden et al. 2016; García-Díaz et al. 2017b). To complicate matters further, during quarantine and early detection activities the presence of a new alien species and the identity of such are not necessarily known *a priori*. This undermines the possibility of designing and planning species-specific surveillance approaches and implies a need for a multi-purpose surveying methodology, which is reliable across a broad range of taxa.

Rapid Biological Assessments (RBAs) are a widely used tool for conducting biodiversity inventories and monitoring, balancing reliability in sampling biological communities with time and resource constraints to conduct the surveys (Sutherland 2006; Larsen 2016). These features make RBAs a prime candidate for conducting standardised surveys in a timely and cost-effective manner, fitting well the need for rapid detection of new alien species to trigger management actions. However, the reliability of standardised RBAs to suit the needs of alien species management activities needs to be evaluated before they are adopted. In particular, it is essential to establish the capacity to detect the presence of alien species during RBAs (Catenazzi et al. 2016; García-Díaz et al. 2017a).

Reptiles are a notable group of emergent alien species responsible for serious environmental impacts in recipient regions worldwide, especially on islands (Rodda et al. 1999; Christy et al. 2010; Powell 2011; Smith et al. 2012a; Kraus 2015). Alien reptiles are frequently transported both unintentionally (i.e., as stowaways) and intentionally (e.g., through the pet trade), and the accelerating volume of global traffic has increased their opportunities for introduction into new regions (Kraus 2009; Powell 2011; Helmus et al. 2014; Capinha et al. 2017; Moser et al. 2018). In this work, we use a candidate survey methodology (RBAs) to detect alien reptiles. Given the key importance of detecting alien individuals, we explore how detectability can lead to challenges to the effective management of alien reptiles. Taking our findings into account, we suggest policy directions for the effective management of new and emergent alien species.

We investigated a standardised RBA using the case study of the detection of alien reptiles on Christmas Island (Fig. 1). The introduction of five species of invasive alien reptiles on Christmas Island provides the opportunity to investigate how the probabilities of detection could influence the feasibility of management actions for four of the most commonly transported and introduced families of alien reptiles worldwide, including on islands (Kraus 2009; Helmus et al. 2014; Capinha et al. 2017). To date, Christmas Island has been invaded by two species of geckos (family Gekkonidae; common house gecko, *Hemidactylus frenatus*, and stump-toed gecko, *Gehyra mutilata*), a skink (Scincidae: grass skink, *Lygosoma bowringii*), and two snakes (family Typhlopidae: flowerpot snake, *Indotyphlops braminus*: and family Colubridae: wolf snake, *Lycodon capucinus*).

Methods

Study area and survey sites

Christmas Island is an Australian oceanic territory located in the Indian Ocean, 10º 30’ S 105º 40’ E (Fig. 2). The island has an area of 135 km^2, of which approximately 63% is a National Park. The island has a tropical climate, with rainforest covering most of it, although phosphorus mining has transformed some areas (Fig. 1). The island’s landscape and habitat features are described in greater detail elsewhere (Claussen 2005; Smith et al. 2012b). The island’s native biota has suffered a catastrophic extinction crisis since its human colonisation in the 1890s, with most of its terrestrial vertebrate species, except birds, extinct as a consequence of the impacts caused by humans and alien species (Wyatt et al. 2008; Smith et al. 2012b).

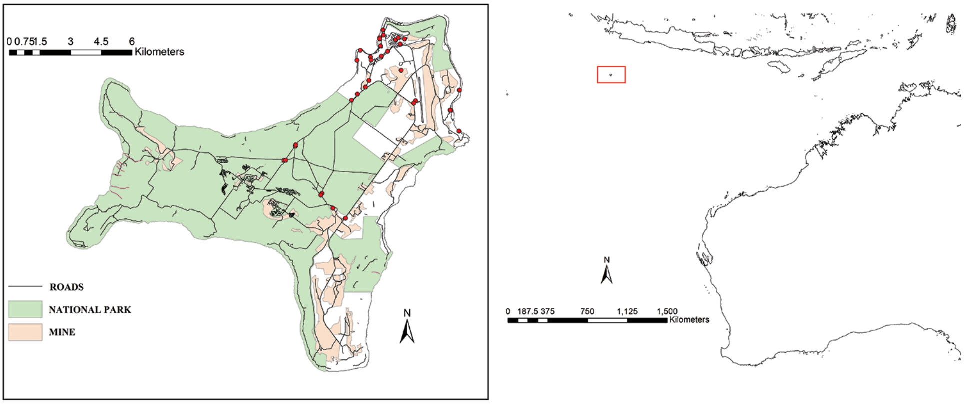

Figure 1. Major land uses on Christmas Island and the geographical distribution of the 34 survey sites (red dots), left panel, and geographical location of Christmas Island (box in right panel map) illustrating its remoteness and position with respect to Australia and Indonesia.

We identified 34 survey sites (Fig. 1) through expert consultation with representatives of the Christmas Island National Park and Natural Resource Management Board (S. Flakus, B. Tiernan, D. Maple, M. Misso) and the Australian Government Department of Agriculture and Water Resources (J. Matthews). These sites are representative of the current distribution of all five alien reptiles, and include potential entry points for new alien reptiles, such as the port and the airport. We concentrated our survey efforts on the western part of Christmas Island because all five species of alien reptiles occur mostly around the more disturbed and human-altered locations (see distribution maps in Smith et al. 2012b). These 34 survey sites encompass the variety of environmental conditions and different alien reptile abundances (Table 1 and see data available at https://figshare.com/s/e85ac13693bc6272437f).

Standardised Rapid Biological Assessment: a time-limited approach

We surveyed for alien reptiles during the dry season, 8th July to 7th August 2015, to minimise disturbances caused by the inclement weather conditions of the wet season. Each of the survey sites was surveyed using the time-limited transect approach; a standardised RBA for reptiles and amphibians (Catenazzi et al. 2016). In each of the survey sites, we intensively searched for alien reptiles during 10 minutes along a linear transect (mean ± standard error: 182.71 ± 72.59 m; range: 60–384 m). Our models indicated that the wide range of distances surveyed did not influence the results of the surveys (Table 1). We intensively searched for alien reptiles under rocks or other fallen structures (e.g., logs), and in the vegetation, during both day and night surveys (using a Led Lenser H14R.2 head torch during night surveys). Each site was surveyed on six occasions, three after sunset (during night time 18:20–20:40), and three after sunrise

Table 1. Goodness of fit (Bayesian *p*-values), summary statistics of the covariates (before standardisation; mean ± standard deviation, and range), and posterior coefficient estimates (mean ± standard error, and 95% Credible Intervals) of the abundance-detection models for five species of alien reptiles on Christmas Island.

	Covariate summary statistics (original units)	**Common house gecko (*Hemidactylus frenatus*)**	**Stump-toed gecko (*Gehyra mutilata*)**	**Grass skink (*Lygosoma bowringii*)**	**Flowerpot snake (*Indotyphlops braminus*)**	**Wolf snake (*Lycodon capucinus*)**
Bayesian p-value		0.51	0.49	0.44	0.29	0.31
Estimated mean abundance (across survey sites)		67.27 ± 27.15 (34.68, 152.85)	24.19 ± 78.86 (1.50, 265.14)	1.83 ± 2.25 (0.77, 6.94)	0.62 ± 0.24 (0.35, 1.24)	5.43 ± 10.93 (0.53, 32.18)
Probability of individual detection (across survey sites)						
Day		0.007 ± 0.008 (0.002, 0.03)	0.001 ± 0.007 (0.00, 0.001)	0.22 ± 0.15 (0.03, 0.60)	0.15 ± 0.13 (0.05, 0.53)	0.02 ± 0.04 (0.00, 0.15)
Night		0.08 ± 0.05 (0.02, 0.21)	0.11 ± 0.11 (0.005, 0.42)	0.009 ± 0.02 (0.001, 0.06)	0.02 ± 0.04 (0.00, 0.53)	0.03 ± 0.04 (0.003, 0.12)
Probability of individual detection: logit model						
Intercept (day)		-5.31 ± 0.50 (-6.46, -4.50)	-8.61 ± 6.12 (-25.47, -4.83)	-1.30 ± 0.88 (-3.30, 0.16)	-1.67 ± 0.65 (-2.69, -0.40)	-4.01 ± 1.51 (-7.94, 1.92)
Intercept (night)		-2.06 ± 0.5 (-3.25, -1.18)	-2.21 ± 1.26 (-5.35, -0.43)	-4.70 ± 1.22 (-7.69, -2.89)	-1.42 ± 0.59 (-2.69, 0.40)	-4.32 ± 1.51 (-8.19, -2.19)
Ground temperature (standardised)	Degree Celsius 26.75 ± 3.61 (20.0-48.0)	0.10 ± 0.10 (-0.11, 0.29)	-0.11 ± 0.56 (-1.64, 0.70)	-0.15 ± 0.19 (-0.55, 0.19)	-0.08 ± 0.34 (-0.92, 0.47)	0.12 ± 0.34 (-0.56, 0.79)
Temperature 10cm above ground (standardised)	Degree Celsius 26.40 ± 2.47 (21.0-33.5)	0.10 ± 0.14 (-0.19, 0.37)	-0.09 ± 0.16 (-1.29, 0.61)	-0.29 ± 0.37 (-1.18, 0.22)	0.05 ± 0.40 (-0.75, 0.91)	0.02 ± 0.44 (-0.88, 0.96)
Temperature 10cm underground (standardised)	Degree Celsius 26.40 ± 2.41 (21.6-33.8)	-0.11 ± 0.09 (-0.29, 0.06)	0.12 ± 0.28 (-0.34, 0.81)	0.07 ± 0.33 (-0.64, 0.71)	0.35 ± 0.42 (-0.26, 1.37)	0.43 ± 0.41 (-0.18, 1.39)
Temperature 120cm above ground (standardised)	Degree Celsius 26.25 ± 2.29 (21.40-33.80)	0.52 ± 0.16 (0.22, 0.84)	0.13 ± 0.47 (-0.54, 1.39)	0.50 ± 0.52 (-0.25, 1.73)	0.02 ± 0.44 (-0.96. 0.89)	-0.26 ± 0.54 (-1.62, 0.49)
Abundance: Negative Binomial regression						
Distance to port (standardised)	Metres 1937.0 ± 2876.45 (138.0, 8575.0)	0.01 ± 0.21 (-0.39, 0.43)	0.26 ± 0.32 (-0.36, 0.98)	0.15 ± 0.32 (-0.48, 0.79)	0.01 ± 0.15 (-0.29, 0.35)	-0.04 ± 0.27 (-0.61, 0.44)
Cover of trees	Scale 2.00 ± 1.82 (0-5.00)	0.12 ± 0.15 (-0.17, 0.43)	0.07 ± 0.27 (-0.40, 0.70)	-0.25 ± 0.26 (-0.78, 0.23)	0.01 ± 0.12 (-0.21, 0.27)	-0.27 ± 0.26 (-0.91, 0.10)
Cover of bush	Scale 2.00 ± 1.63 (0.00-5.00)	-0.11 ± 0.18 (-0.47, 0.47)	-0.13 ± 0.30 (-0.79, 0.62)	-0.32 ± 0.27 (-0.88, 0.19)	-0.05 ± 0.14 (-0.40, 0.18)	-0.01 ± 0.21 (-0.43, 0.44)
Cover of grass	Scale 4.00 ± 1.52 (0.00-5.00)	0.48 ± 0.12 (0.24, 0.73)	0.17 ± 0.25 (-0.28, 0.74)	0.06 ± 0.19 (-0.33, 0.43)	-0.05 ± 0.11 (-0.28, 0.18)	0.22 ± 0.26 (-0.12, 0.89)
Cover of rocks and stones	Scale 2.00 ± 0.97 (0.00-4.00)	-0.01 ± 0.24 (-0.48, 0.47)	-0.05 ± 0.35 (-0.80, 0.62)	0.27 ± 0.34 (-0.32, 1.03)	-0.01 ± 0.15 (-0.33, 0.32)	0.03 ± 0.27 (-0.48, 0.65)
Cover of human structures	Scale 3.50 ± 1.74 (0.00-5.00)	0.69 ± 0.13 (0.46, 0.97)	0.31 ± 0.24 (-0.07, 0.88)	0.05 ± 0.21 (-0.31, 0.51)	-0.07 ± 0.12 (-0.35, 0.12)	0.10 ± 0.19 (-0.26, 0.54)
Transect length (standardised)	Metres 175.00 ± 72.59 (60.00-384.00)	-0.01 ± 0.20 (-0.40, 0.41)	-0.01 ± 0.31 (-0.64, 0.62)	0.33 ± 0.37 (-0.24, 1.18)	0.01 ± 0.16 (-0.31, 0.35)	0.14 ± 0.26 (-0.28, 0.74)
Elevation (standardised)	Metres above sea level 194.5 ± 94.25 (10.00, 303.00)	-0.05 ± 0.21 (-0.47, 0.36)	-0.01 ± 0.32 (-0.65, 0.64)	-0.69 ± 0.38 (-1.47. -0.01)	-0.05 ± 0.17 (-0.48, 0.21)	0.01 ± 0.27 (-0.57. 0.55)
Overdispersion parameter Θ		0.97 ± 0.30 (0.54, 1.70)	0.31 ± 0.25 (0.12, 0.98)	3.78 ± 15.17 (0.19,47.20)	23.69 ± 14.70 (1.11, 48.68)	24.97 ± 14.32 (1.66, 48.75)

(during the daytime 8:00–11:30) (see Table 2 for a summary of the counts of each species during our surveys). The combination of transect and visual encounter surveys is known to be effective in detecting reptiles in tropical environments (Doan 2003; McDiarmid et al. 2011; Smith et al. 2012a).

Table 2. Summary of the counts (number of observations per each 10-minute survey) of five species of alien reptiles on Christmas Island across the 34 survey sites (mean ± standard deviation, and range). Three repeated surveys were conducted during each day and night time conditions in each survey site. The raw data are available at https://figshare.com/s/e85ac13693bc6272437f

Species	Day surveys	Night surveys
Common house gecko (*Hemidactylus frenatus*)	0.74 ± 1.44 (0.00–7.00)	6.51 ± 7.84 (0.00–35.00)
Stump-toed gecko (*Gehyra mutilata*)	0.00 ± 0.00 (0.00–0.00)	0.58 ± 1.45 (0.00–7.00)
Grass skink (*Lygosoma bowringii*)	0.31 ± 0.84 (0.00–5.00)	0.01 ± 0.10 (0.00–1.00)
Flowerpot snake (*Indotyphlops braminus*)	0.08 ± 0.44 (0.00–2.00)	0.11 ± 0.31 (0.00–1.00)
Wolf snake (*Lycodon capucinus*)	0.06 ± 0.28 (0.00–2.00)	0.05 ± 0.26 (0.00–2.00)

Time-limited transects do not neccesarily require repeated survey occasions (Catenazzi et al. 2016), but our repeated surveys allowed us to estimate both the abundance and the probability of individual detection of alien reptiles via hierarchical models (Royle 2004; Kéry and Royle 2016; Ficetola et al. 2018). Our time-limited approach was a minor modification of the methodology employed by Christmas Island National Park Staff to survey for both native and alien reptiles on the island (Smith et al. 2012a, 2012b). Therefore, our time-limited methodology aligns well with pre-existing protocols, which can be easily adapted to inform the management of alien reptiles. Only wolf snakes, found on the last survey occasion, were captured and relinquished to National Parks Australia as required in the conditions of our permits (see Acknowledgements). All other individuals were either not captured or left in the same place where they were found when handling was necessary for identification purposes.

During each survey occasion, we recorded the number of individuals of each alien reptile species detected, and the temperature (ºC) at four different heights in the habitat (Table 1). These four temperatures were used to model the probabilities of detection. For each survey site, we collected information on eight covariates believed to influence the site abundance of alien reptiles; including vegetation cover and geographical features (Table 1). We defined the cover of different microhabitat characteristics in each site following the semiquantitative Braun-Blanquet scale (Sutherland 2006). We gathered information on the altitude (metres above sea level; sourced from the National Park digital elevation map), and the Euclidean distance from the survey site to the port (metres). The port has been the point of entrance for all the alien reptiles to the island and closer sites might be more likely to have higher abundances (Fritts 1993; Smith et al. 2012b). The four temperature measures, the elevation, the transect length, and the distance to the port were standardised (centred by their mean and scaled by their standard deviation). All the detection data, temperatures and the covariates used in the models are available from https://figshare.com/s/e85ac13693bc6272437f. We assumed that the number of animals counted ($Nd_{i,z}$) at survey site i during surveying occasion z follows a Binomial distribution with parameters N_i and $p_{i,z}$:

$$Nd_{i,z} \sim \text{Binominal}(N_i, p_{i,z}) \quad (1)$$

where N_i is the abundance of the species, and $p_{i,z}$ is the probability of individual detection (Kéry and Royle 2016).We modelled the abundance of a species at a survey site, N_i, as a function of the micro-habitat features, the distance to the port, and the elevation via a Negative Binomial regression. The abundance model was defined as follows:

$$N_i \sim \mathrm{NB}\left(\theta, \frac{\theta}{(\theta + \lambda_i)}\right) \tag{2}$$

$$\log(\lambda_i) = \sum_{j=1}^{8} \beta_j X_{i,j} \tag{3}$$

where β_j ($j = 1, \ldots, 8$) are the slopes of the model of the mean abundance, λ_i, in survey site i and X_i is a vector of the eight covariates used for modelling the mean abundance (Table 1), and Θ is the overdispersion parameter of the Negative Binomial regression. Note that we did not include an intercept in our log-regression (eq. 3) as it is not possible for all micro-habitat variables to equal zero. We modelled the probability of individual detection using a logit model:

$$\mathrm{logit}(p_{i,z}) = \alpha_d + \sum_{\mathrm{r}=1}^{4} \beta d_r T_{i,z,r} \tag{4}$$

where α_d are the time-of-day specific intercepts (day and night), βd_r ($r = 1, \ldots, 4$) are the slopes of the model of the probability of individual detection, $p_{i,z}$, during survey occasion z at survey site i, and $T_{i,z}$ is a vector of the four temperature covariates used for modelling the probability of individual detection (see Table 1). It is important to note that in our model the probability of individual detection is independent of the abundance of the species in the surveyed site (Royle 2004; Kéry and Royle 2016). That is, the probability of individual detection does not vary with abundance (McCarthy et al. 2013; Kéry and Royle 2016). Our modelling approach permits the extrapolation of our probability of individual detection estimates to scenarios with unknown but estimable abundances, typical of novel alien reptile management situations.

We employed Bayesian regularisation to construct robust model structures for the abundance and the probability of individual detection as a function of the covariates (Hooten and Hobbs 2015). Models were constructed and fitted independently for each of the five alien reptile species on Christmas Island. The models were fitted using the NIMBLE package in the R software environment (R Development Core Team 2015; de Valpine et al. 2017). We used relatively uninformative priors for the intercepts in the model, $\sim N(0, \sigma^2 = 10)$, and uninformative priors for all the slopes to construct regularised models, $\sim N(0, \sigma^2)$, $\sigma^2 \sim Exp(0.5)$. All the models were run using three chains with 1,000,000 iterations each, and no thinning. After checking for convergence and mixing of the chains, using trace plots and the Gelman-Rubin diagnostic test, we discarded the first 200,000 iterations via a burn-in time, resulting in 2,400,000 draws of the posterior distribution for all the parameters in the models. We used Bayesian p-values, based on the Freeman-Tukey goodness-of-fit statistic, residual QQ-plots, and simulations to evaluate the fit and identifiability of our abundance-detection models (Dunn and Smyth 1996; Kéry and Royle 2016; Conn et al. 2018; Kéry 2018) (see Supplementary Methods for details). Bayesian *p*-values within the range between 0.05 and 0.95 indicate a model that fits the data adequately (Hobbs and Hooten 2015; Kéry and Royle 2016). The model script is available from https://figshare.com/s/e85ac13693bc6272437f.

Results

Probabilities of individual detection of alien reptiles on Christmas Island

Our Bayesian regularised models were an adequate fit to the count data (Bayesian *p*-values close to 0.5 and non-skewed Q-Q plots in all cases; see Supplementary Methods), and revealed that the survey time (day vs night) was the main driver of the probability of individual detection across the five alien reptiles (Table 1; Fig. 2). For three of the five alien reptiles the detection probabilities were higher during

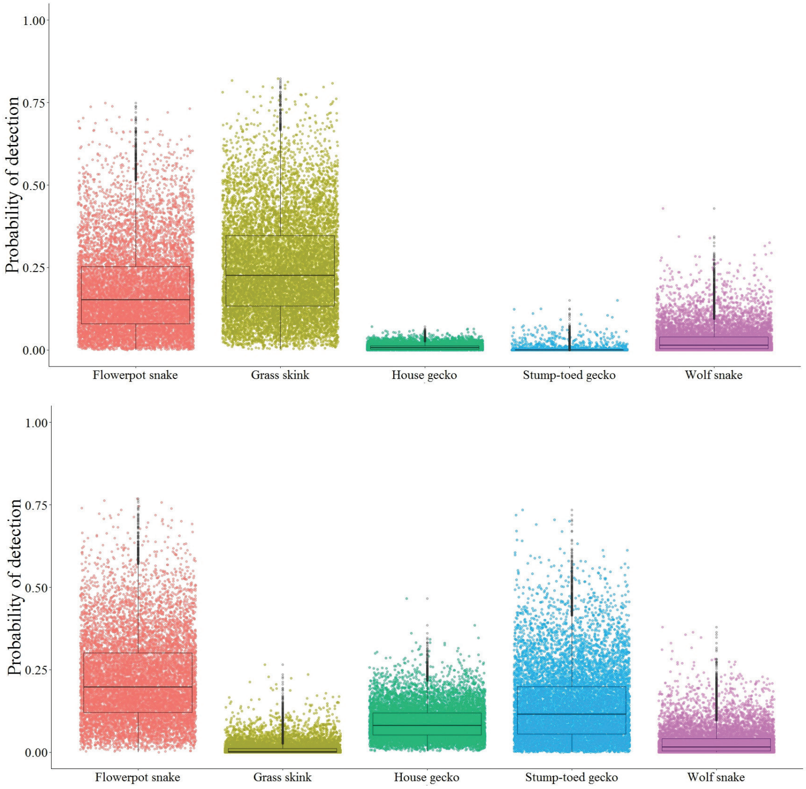

Figure 2. Estimated probabilities of individual detection of five invasive alien reptiles on Christmas Island (Australia) during day time (top panel) and night time surveys (bottom panel). Estimates correspond to the probability of individual detection during a 10-minute survey across the 34 surveying sites. Each dot represents a realisation from 1000 simulations.

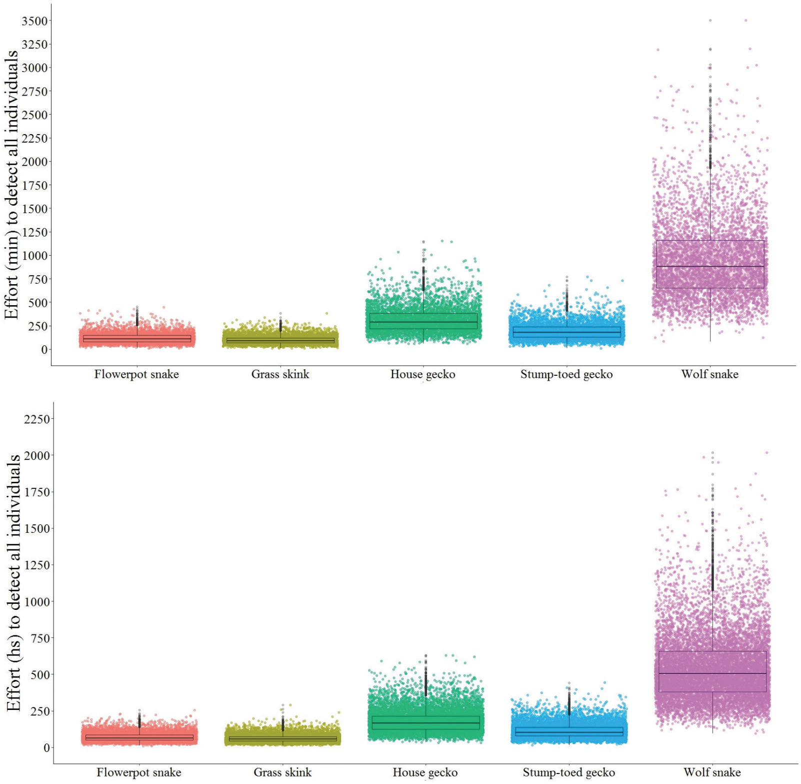

Figure 3. Estimated surveying effort required to detect all 10 individuals of each species of five alien reptiles in two situations and under a best-case detection scenario (i.e., sites surveyed during the time of the day when detection probabilities are higher). Top: surveying effort (minutes) to detect 10 individuals known to be present in one surveying site when only those 10 individuals are present; bottom: surveying effort (hours) to detect 10 individuals distributed at random across 34 surveying sites, where each occupied site harbours one individual, and only ten individuals are present across the 34 surveying sites. We used 10 individuals as an example to showcase and compare detection efforts across different situations. Best-case detection scenarios are night time surveys (common house gecko, stump-toed gecko, and flowerpot snake) and daytime surveys (grass skink and wolf snake). Each dot represents a realisation from 1000 simulations.

night time surveys, whereas only for the grass skink was the detection probability higher during daytime surveys (Table 1; Figs 2, 3). There were virtually no differences between day and night time surveys for the wolf snake. Only in the case of the common house gecko was the probability of individual detection influenced by any of the four covariates included in the models; positively associated with the temperature 120 cm above ground (mean ± standard error: 0.52 ± 0.16; 95% Credible Intervals: [0.22, 0.84]).

All the posterior estimates of the probabilities of individual detection were relatively low, with the upper 95% Credible Interval estimates of daytime surveys of the grass skink and night time surveys of flowerpot snakes being the only values exceeding 0.5 (Table 1). Accordingly, the highest probability of individual detection was for the grass skink during daytime surveys (0.22 ± 0.15; 95% CIs: [0.03, 0.60]). The smallest median probability of individual detection was estimated for stump-toed geckos during daytime surveys (0.001 ± 0.001; 95% CIs: [0.001, 0.01]).

Abundance of alien reptiles on Christmas Island

Common house geckos were the most frequently encountered species, followed by stump-toed geckos during night time surveys and grass skinks during daytime surveys (Table 2). Likewise, our posterior estimates of the abundance of the five species showed that the two species of alien geckos were the most abundant species on Christmas Island (Table 1). Wolf snakes were the third most abundant species and flowerpot snakes were the rarest (Table 2).

Our Negative Binomial regressions revealed that common house geckos were more common in sites with higher grass and human structure cover (positive relationships), and that grass skinks tended to become rarer in higher elevation sites (negative relationship with elevation). Across the five alien reptiles, all the covariates had uncertain effects on the estimated alien reptile abundances and probabilities of detection, with wide posterior estimates overlapping zero (Table 1).

Discussion

The probabilities of detecting individuals using a standardised RBA were consistently low across all the alien reptiles found on Christmas Island. Both the detectability and the abundance of those alien reptiles were difficult to explain given the rather uncertain effects of the covariates tested in our models, even when our surveys explored a representative and variable sample of environmental conditions (Table 1). Only common house geckos were more detectable with increasing temperature 120 cm above ground, which is concurrent with the species habit of occupying buildings and being found active on the walls of those buildings during our surveys. Low detection probabilities, and the difficulty in predicting both abundance and detection, indicate that managing novel pools of alien reptiles, of yet unknown taxonomic identity, will prove a challenge on both Christmas Island and, by extension, in other places subject to increasing pressure of novel alien reptiles.

It is particularly important to protect island ecosystems, where alien reptiles have produced substantial negative impacts and whose native biodiversity is highly exposed to the threat of alien species (Rodda et al. 1999; Powell 2011; Smith et al. 2012b; Silva-Rocha et al. 2015; Bellard et al. 2017; Moser et al. 2018; van Wilgen et al. 2018). Management activities on islands, excluding targeted eradication post-introduction, will need to be able to detect any potential alien reptiles that arrive on the island, to provide effective protection against these novel alien species (García-Díaz et al. 2017b;

Scott et al. 2017). However, even well-resourced management programs cannot detect and intercept every single alien individual arriving at a new location (Jarrad et al. 2011; Scott et al. 2017). We found important differences in the probability of individual detection of different species of alien reptiles, which implies that one survey method and surveillance effort cannot fit all. It is of particular concern that the posterior estimates of the probability of individual detection of wolf snakes were very low (mean < 0.02; Table 1). This is unfortunate, because alien snakes represent, amongst all the alien reptiles, some of the worst threats to native species in the recipient communities, including islands (Dorcas et al. 2012; Kraus 2015; Silva-Rocha et al. 2015). Our posterior estimate of the detection probability of wolf snakes was very similar to that reported for other snakes in places around the world and surveyed using different techniques (Kéry 2002; Christy et al. 2010; Durso et al. 2011; Sewell et al. 2012; Durso and Seigel 2015), suggesting that regardless of the location, species and surveying method, snakes are very difficult to detect in the field. In order to properly address the differences between species, and in anticipation of future changes in pathways and species transported, we recommend that management activities base their surveying efforts on species with the smallest detection probability. This approach will maximise the number of new alien reptiles detected and intercepted, even when accepting that not all individuals can possibly be detected.

The compounded effects of low detection probabilities and uncertain effects of covariates will hinder effective measures to manage the emergence of alien reptiles, a conclusion reinforced by previous species-specific research into the management of invasive brown snakes (*Boiga irregularis*) in Guam (Christy et al. 2010), invasive Burmese pythons (*Python bivittatus*) in Florida (Reed et al. 2011), and invasive red-eared slider turtles (*Trachemys scripta elegans*) in the Iberian peninsula (García-Díaz et al. 2017a). Unfortunately, the detectability of alien reptiles remains a challenge to both management and research activities even when sufficient resources are available, as shown by long-term detectability research conducted in Guam (Rodda et al. 2015). In conclusion, managing alien reptiles already established on islands, and future pools of new invasive alien species, will be costly and with no guarantee of success due to both the low detectability of individuals and the difficulty to predict the likely abundance and detectability of alien reptiles.

Framed in this context of overarching uncertainties and high costs, strong preventive policies should be a priority to address the emergent threat of alien reptiles on islands and elsewhere (Jarrad et al. 2011; Rout et al. 2014; Lodge et al. 2016; Scott et al. 2017). As a first step, public agencies tasked with preventive policies for managing alien species (e.g., environmental protection and primary industries agencies) should implement strict quarantine measures and biosecurity regulations (Meyerson and Reaser 2002; Brenton-Rule et al. 2016; Early et al. 2016). These measures and regulations should be aimed at detecting incoming alien reptiles at quarantine border controls before those individuals can escape containment into the wild (Meyerson and Reaser 2002; Jarrad et al. 2015; Brenton-Rule et al. 2016; Chapple et al. 2016; Scott et al. 2017). Australia and New Zealand have biosecurity arrangements in place, even if imperfect, to achieve these two management goals and islands elsewhere could draw lessons from these two countries to implement their own preventive strategies (Jarrad et al. 2011; Brenton-Rule et al. 2016; Chapple et al. 2016; García-Díaz et al. 2017b; Scott et al. 2017).

Preventive management activities should be complemented with early detection surveys aimed at detecting new populations of alien reptiles promptly (Vander-Zanden et al. 2010; Jarrad et al. 2015; Scott et al. 2017). Again, the costs incurred by early detection surveys will be high due to the need for large survey efforts to overcome low probabilities of detection of alien reptiles. A combination of citizen-science surveys, public education programs, and strategic surveys by biosecurity agencies is an avenue worth continuing to invest in to implement effective early detection surveys within environmental budgets, which are heavily constrained by limited funding (Gallo and Waitt 2011; Lawson et al. 2015; Scott et al. 2017). Our results and methodology can be extended by incorporating additional quantitative tools, such as Baye's rule, to estimate the surveying effort needed to confidently declare the absence of new alien reptiles given no individuals are detected (Ramsey et al. 2009; Anderson et al. 2013; García-Díaz et al. 2017a). Additionally, the adequacy—particularly, the rates of false positives and negatives—of novel detection methods, such as environmental trace DNA, should be thoroughly explored; although indirect surveillance techniques do not replace the need for capturing alien individuals implicit to many management actions (Hunter et al. 2015; Guillera-Arroita et al. 2017).

More broadly, biosecurity regulations, strict quarantine, and early detection activities should be considered within the framework of robust anticipatory policy-making (Boston 2016, 2017). Anticipatory policy-making for emerging alien species is to be guided by the philosophies of adaptiveness and the precautionary principle (Conroy and Peterson 2013; Boston 2016, 2017). Adaptiveness will require frequently evaluating the performance of preventive tools and policies, such as risk assessments and quarantine, against indicators of risk reduction, and updating the management actions as necessary (Rout et al. 2014; Lodge et al. 2016). The precautionary principle should be central to policy and decision-making to prevent the establishment and spread of emergent alien vertebrates. This is particularly important given the scant knowledge about the impacts of most new alien reptiles and the low likelihood of succeeding in eradicating established, self-sustaining, alien reptile populations (Kraus 2015; García-Díaz et al. 2017a; van Wilgen et al. 2018).

The implementation of stringent preventive policies and early detection activities might be more straightforward on oceanic islands, where their remoteness commonly requires all goods and commodities to be imported via shipping and air traffic routes arriving in a small number (usually one) of ports and airports, limiting the number of potential pathways of transport and points of entry into the island (Kraus 2009; Helmus et al. 2014; Moser et al. 2018). The situation is different on continents and mainland contexts, where there are multiple pathways of transport and many points of entry (Hulme et al. 2008; Leung et al. 2014; Hulme 2015; Yemshanov et al. 2015; García-Díaz et al. 2017b). Further research could explore how well our findings and conclusions transfer to mainland scenarios. Research into the detectability of invasive snakes in Florida suggests that they are similarly difficult to detect in mainland settings (Reed et al. 2011).

We have focussed on alien reptiles on islands in this research, but our conclusions are likely applicable to other groups of emergent alien species globally; such as vertebrates in the pet trade (Hulme 2015; Seebens et al. 2018). Building on the realisation of the cornerstone importance of detectability to manage alien species, future work should investigate the extent to which our findings and recommendations hold for different groups of emergent alien species and under other conditions such as mainland environments. In any case, the lack of research and the abundant uncertainties do not preclude the implementation of good preventive policies to manage alien species, an urgent task considering the lack of preventive and early detection capacities in most countries of the world (Early et al. 2016).

Acknowledgements

This work would not have been possible without the support provided by the all the staff of the Christmas Island National Park, the Christmas Island Natural Resource Management Board, and the Department of Agriculture and Water Resources (Indian Ocean). This research was conducted under permit number CIN_2015_5 (Christmas Island National Park, Director of National Parks, Australian Government) and a Licence to undertake research activities on regulated crown land. The research was approved by the University of Adelaide Animal Ethics Committee (S-2014-155). Andrew Robinson, John Measey, and an anonymous reviewer provided constructive feedback that helped improve this manuscript. PG-D was supported by an IPRS/APA scholarship (DET), an Invasive Animals CRC PhD scholarship, and the IA CRC Student Grant. This work was supported by an ARC Discovery Grant (DP140102319) to JVR and PC and ARC Future Fellowships to PC and JVR (FT0991420, FT130100254).

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Supplementary material 1

Model evaluation and estimability

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Data type: measurement

Link: https://doi.org/10.3897/neobiota.45.31009.suppl1

NeoBiota 45: 93–115 (2019)
doi: 10.3897/neobiota.45.33866
http://neobiota.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
NeoBiota
Advancing research on alien species and biological invasions

Alien plants in Central European river ports

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Academic editor: *Ingo Kowarik* | Received 14 February 2019 | Accepted 27 March 2019 | Published 7 May 2019

Citation: Jehlík V, Dostálek J, Frantík T (2019) Alien plants in Central European river ports. NeoBiota 45: 93–115. https://doi.org/10.3897/neobiota.45.33866

Abstract

River ports represent a special type of urbanized area. They are considered to be an important driver of biological invasion and biotic homogenization on a global scale, but it remains unclear how and to what degree they serve as a pool of alien species. Data for 54 river ports (16 German, 20 Czech, 7 Hungarian, 3 Slovak, and 8 Austrian ports) on two important Central European waterways (the Elbe-Vltava and Danube waterways) were collected over 40 years. In total, 1056 plant species were found. Of these, 433 were alien, representing 41% of the total number of species found in all the studied Elbe, Vltava, and Danube ports. During comparison of floristic data from literary sources significant differences in the percentage of alien species in ports (50%) and cities (38%) were found. The number of alien species was closely related to port size, but the proportion of alien species expressed as a percentage of the total number of species did not depend significantly on port area. The proportion of alien species in both studied waterways decreased with distance from the sea and was highest in the Hungarian ports and lowest in the Czech Republic, Austria and Bavaria. Lower levels of shipping towards inland regions due to decreased river flow are likely the reason for this trend. The dissimilarity in the species composition of alien and native flora between individual river ports increased with increasing inter-port distance. Neophytes presented a stronger distance decay pattern than did either native species or archaeophytes of the Danube inland ports, potentially due to the different cargoes of individual ports, which may affect the introduction of different neophytes from different geographic areas. The results show that river ports in Central Europe should be regarded as a type of industrial area and deserve full attention with regard to the distribution and spread of alien plants.

Keywords

Alien plants, Central Europe, river ports, waterway

Introduction

Many studies have demonstrated that cities are hotspots of alien plants (e.g. Pyšek 1998; Sukopp 2002; Wittig 2002; Clemants and Moore 2003; Zerbe et al. 2004; Ricotta et al. 2009; Zhao et al. 2010; Lososová et al. 2012; Aronson et al. 2014). A main reason for this is that urbanized areas provide suitable environments for alien species, with superior conditions for their development compared to those available in rural areas (e.g. Kühn and Klotz 2006; von der Lippe and Kowarik 2008). This suitability of urbanized areas especially applies to neophytes (taxa introduced after AD 1500), whose presence among urban flora over the last 100 years or longer has increased significantly (Godefroid 2001; Chocholoušková and Pyšek 2003; DeCandido 2004; Knapp et al. 2010).

The development of international trade and transport and the related global dispersal of invasive alien species have had significant impacts on the spread of alien species among urbanized areas (Levine and D'Antonio 2003; Dehnen-Schmutz et al. 2007; Westphal et al. 2008). Traffic junctions and transshipment points of goods have had an important role, as they represent the sources of occurrence and spread of invasive plants (Jehlík and Hejný 1974; Forcella and Harvey 1988; Kornaś 1990; Jehlík et al. 1998; Song and Prots 1998). For this reason, urban-industrial areas are regarded as the main drivers of biological invasions (Wittig 2010).

Within urban-industrial environments, port areas represent introduction hubs for alien species whose seeds are spread with shipping (Wittig 2004; Adhikari et al. 2015). Some cargoes provide excellent means for the transportation of seeds or entire plants (e.g., food and animal feed, minerals, coal, solid ballast). Port areas have been extensively explored with respect to marine invasive species (Molnar et al. 2008). Attention has also been paid to terrestrial plant species, which can also benefit from marine/freshwater transportation routes (Anastasiu et al. 2011; Jehlík 2013). The presence of alien plants among the flora of seaports in the north of Europe has been reported for Poland (Ćwikliński 1970; Misiewicz 1985), Norway (Ouren 1978, 1980, 1983, 1987), Germany (Jehlík 1981, 1989, 1994a), the Netherlands (Jehlík and Dostálek 2015), and Ireland (Reynolds 1990). Information on the occurrence of alien plants in the Black Sea ports in the territory of Ukraine is reported by Petryk (1993), and the role of ports in the spread of alien plants along the Romanian Black Sea was analysed by Anastasiu et al. (2011). In addition, the relationship between the occurrence of alien plants and urban habitat type in the port of Trieste on the Adriatic coast was explored in detail by Tordoni et al. (2017).

Marine ports are typically connected to inland waterway networks; the connections facilitate the inland spread of alien plants, especially through river ports. Port-Juvénal, the port of Montpellier (France) on the river Lez, is a classic case for the role of inland ports for the introduction of alien plants. Thellung (1912) reported the arrival of many alien plant species, most of which have been introduced into the area through imports of wool (see details: Kowarik and Pyšek 2012). Most data on the occurrence of alien plants in the river ports of central Europe come from Germany (Ludwig 1957; Stricker 1962; Schäfer 1965; Runge 1965; Stieglitz 1980, 1981; Klotz 1984; Brandes 1989; Jehlík 1994b; Brandes and Sander 1995; Lotz 1998; Düring 2004). Additional data come from Poland (Szotkowski 1978), Belgium (Verloove 1992), Switzerland (Baumgartner 1973, 1985), the Czech Republic and Slovakia (Eliáš 1985; Jehlík 1985, 2008; Jehlík et al. 2005). River ports typically occur in industrial areas that are part of the urban matrix and whose alien flora has not yet been systematically studied. Using data from a 40-year study of flora and vegetation in 54 river ports of Central Europe (Jehlík 2013), this paper presents detailed information on alien plants that occur in this specific type of industrialized area.

The following questions are addressed:
1. What is the proportion of alien species in the flora of Central European river ports, and does it differ from the proportions in other urbanized areas? 2. To what extent does the size of a port influence the abundance of alien plants? 3. Does the amount of alien species differ among various river systems (regions)? 4. Is the floristic composition in river ports related to the distance of the port from the sea or the distance between ports?

Methods

The data used for the analysis were collected over the course of long-term floristic research activities conducted during 1968–2009 in 54 river ports in five countries in Central Europe (Czech Republic, Germany, Austria, Slovakia, Hungary) by the first author (Jehlík 2013). The ports were studied in two different river systems belonging to the most important waterways of Central Europe. A total of 32 ports were located in the Elbe-Vltava waterway between 50° and 53° N, and a total of 22 ports were located on the Danube River between 45° and 49° N (Table 1, Fig. 1).

The ports were visited several times during various periods of the growing season to maximize the possibility of sampling the full species composition (see Appendix 2). After 41 years, lists of taxa from all 54 locations were compiled. To record the abundances of plant taxa, a five-degree scale (sporadic, rare, scattered, abundant, highly abundant) derived from the Braun-Blanquet approach (Braun-Blanquet 1964; Westhoff and van der Maarel 1978) was used. To calculate the floristic dissimilarity between ports and the difference in individual species representation between waterways, the degrees of the scale were transformed into numeric values: sporadic (one or two individuals) = 1, rare = 2, scattered = 3, abundant = 5, and highly abundant = 7. To statistically evaluate the effect of port size on species richness for all focal species groups, the area of each port locality was measured using Google Earth Pro 7.1. To compare the presence of alien species between the investigated river ports and other urbanized areas, previously published floristic data for 29 cities were compiled and analyzed (Pyšek 1998; Table 2), and the data were tested for differences using the Mann-Whitney U test.

Table 1. Native and alien plant species in the flora of 54 Central European river ports, including the total number and proportion of species of different categories, identified in each port.

River port (country)	Number of species					Proportion of species [%]			
	Total	Native	Total aliens	Archaeophytes	Neophytes	Native	Total aliens	Archaeophytes	Neophytes
Elbe and Vltava Rivers									
1. Hamburg (Germany)	360	153	207	98	69	48	52	31	21
2. Wittenberge (Germany)	197	79	118	75	37	41	59	39	20
3. Tangermünde (Germany)	170	76	94	60	33	45	55	35	20
4. Magdeburg-Rothensee (Germany)	133	48	85	52	32	36	64	40	24
5. Magdebur, Industriehafen (Germany)	283	120	163	98	58	43	57	36	21
6. Magdeburg, Handelshafen (Germany)	353	150	203	117	74	44	56	34	22
7. Schönebeck-Frohse	229	100	129	90	37	44	56	40	16
8. Aken, Handelshafen (Germany)	250	123	127	93	34	49	51	37	14
9. Torgau (Germany)	245	121	124	78	36	51	49	33	16
10. Riesa-Gröba, Industriehafen (Germany)	354	174	180	111	62	50	50	32	18
11. Riesa, transshipment point at mill houses (Germany)	282	133	149	87	50	49	51	32	19
12. Dresden, Albertshafen (Germany)	333	158	175	103	56	50	50	32	18
13. Děčín-Loubí (Czech Republic)	336	147	189	92	59	49	51	31	20
14. Děčín-Staré Loubí (Czech Republic)	279	161	118	73	39	59	41	27	14
15. Děčín-Staré Město (Czech Republic)	153	82	71	46	25	54	46	30	16
16. Děčín-Rozbělesy (Czech Republic)	267	184	83	54	29	69	31	20	11
17. Ústí nad Labem-Krásné Březno (Czech Republic)	323	142	181	100	55	48	52	34	18
18. Ústí nad Labem, Central Port (Czech Republic)	251	125	126	81	43	50	50	33	17
19. Ústí nad Labem, Western Port (Czech Republic)	327	140	187	101	54	47	53	34	19
20. Ústí nad Labem, Větruše (Czech Republic)	227	121	106	60	38	55	45	28	17
21. Ústí nad Labem-Vaňov (Czech Republic)	234	127	107	71	35	55	45	30	15
22. Lovosice, Canal Port (Czech Republic)	232	85	147	85	49	39	61	39	22
23. Lovosice-Prosmyky (Czech Republic)	246	110	136	93	39	45	55	39	16
24. Mělník-Pšovka (Czech Republic)	333	148	185	110	57	47	53	35	18
25. Mělník, Transshipment Point (Czech Republic)	266	144	122	79	43	54	46	30	16
26. Kolín, Transshipment Point (Czech Republic)	225	101	124	84	39	45	55	38	17
27. Týnec nad Labem, Ro-Ro-Transshipment Point (Czech Republic)	216	138	78	52	26	64	36	24	12
28. Chvaletice (Czech Republic)	178	125	53	34	19	70	30	19	11
29. Miřejovice Ro-Ro-Transshipment Point (Czech Republic)	236	138	98	66	30	59	41	28	13
30. Praha-Holešovice (Czech Republic)	388	187	201	119	69	50	50	32	18
31. Praha-Smíchov (Czech Republic)	216	93	123	80	37	44	56	38	18
32. Praha-Radotín (Czech Republic)	162	68	94	65	26	43	57	41	16
Danube river									
33. Mohács, Transshipment Point (Hungary)	183	79	104	65	36	44	56	36	20
34. Baja (Hungary)	305	134	171	106	59	45	55	35	20
35. Dunaújváros (Hungary)	250	105	145	95	45	43	57	39	18
36. Budapest-Csepel (Hungary)	280	93	187	109	64	35	65	41	24
37. Budapest-Ferencváros (Hungary)	205	78	127	83	38	39	61	42	19
38. Györ, Transshipment Point (Hungary)	249	108	141	87	46	45	55	36	19
39. Györ, Commercial Port "Iparcsatorna" (Hungary)	166	61	105	69	34	37	63	42	21
40. Komárno (Slovakia)	338	135	203	123	70	41	59	38	21
41. Bratislava-Pálenisko (Slovakia)	322	150	172	106	57	48	52	34	18
42. Bratislava-Nivy (Slovakia)	411	182	229	133	78	46	54	34	20
43. Wien-Lobau (Austria)	293	167	126	85	37	58	42	29	13

River port (country)	Number of species					Proportion of species [%]			
	Total	Native	Total aliens	Archae-ophytes	Neo-phytes	Native	Total aliens	Archae-ophytes	Neo-phytes
44. Wien-Albern (Austria)	295	128	167	117	46	44	56	40	16
45. Wien-Freudenau (Austria)	307	138	169	113	54	45	55	37	18
46. Krems an der Donau (Austria)	294	140	154	105	42	49	51	36	15
47. Ennsdorf, Hafenbecken Ost, Silos (Austria)	276	150	126	76	43	56	44	28	16
48. Enns (Austria)	389	231	158	92	52	62	38	24	14
49. Linz, Tankhafen (Austria)	229	138	91	66	25	60	40	29	11
50. Linz, Handelshafen /Stadthafen (Austria)	324	169	155	99	51	53	47	31	16
51. Passau-Racklau (Germany)	252	135	117	80	35	54	46	32	14
52. Deggendorf (Germany)	202	124	78	56	22	61	39	28	11
53. Regensburg, Osthafen (Germany)	308	164	144	95	43	54	46	32	14
54. Regensburg Westhafen/Luitpoldhafen (Germany)	296	146	150	96	47	51	49	33	16

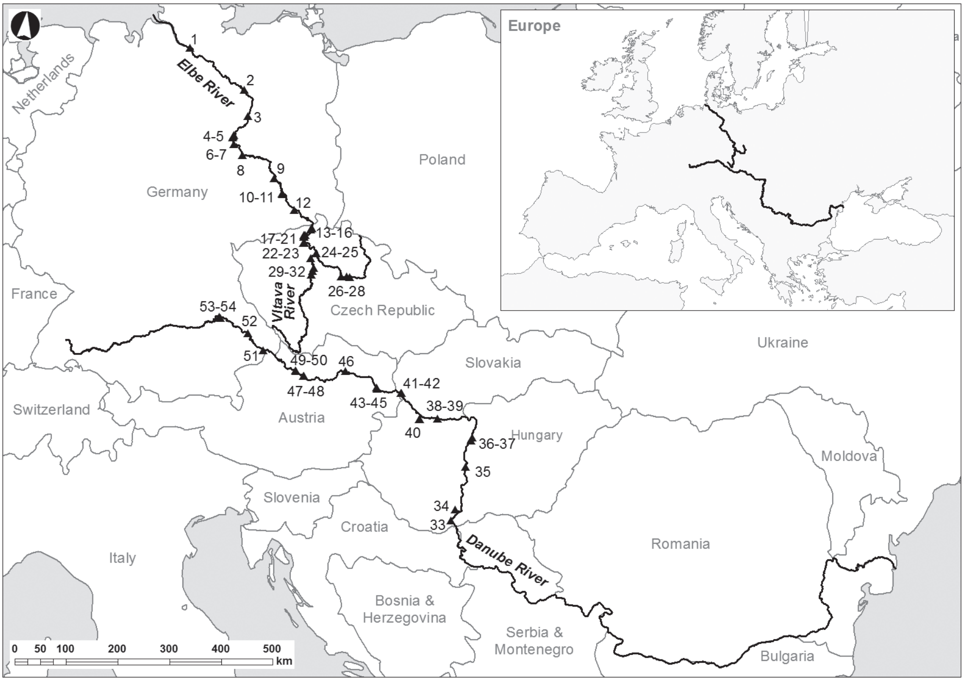

Figure 1. Map of Central European river ports whose floras were used in the analysis. Detailed information about individual ports is presented in Table 1.

The species were classified according to their immigration status (for details, see Pyšek 1995; Richardson et al. 2000; Pyšek et al. 2002; Blackburn et al. 2011): (i) A native (indigenous) species is a species that evolves in the area or arrives there either before the beginning of the Neolithic period or after the beginning of that period but in a way entirely independent of human activity (Webb 1985); (ii) An alien (introduced, exotic, adventive) species is a species that reaches the area as a consequence of man or the presence of domestic animals. Two main categories of alien species were used in the

Table 2. Presence of alien species in ports and cities. Means ± SD or range in parenthesis are given. Statistically significant differences of proportions between ports and cities are indicated by different letters (Mann-Whitney U test).

	Ports	Cities
Number of cases	54	29
Total number of species	260 ± 59	747 ± 321
Number of aliens	131 ± 34	294 ± 160
Number of archaeophytes	86 ± 22	96 ± 33
Number of neophytes	45 ± 14	198 ± 135
Proportion of aliens	50 (30–65) ^{a}	38 (20–56) ^{b}
Proportion of archaeophytes	33 (19–42) ^{a}	13 (8–19) ^{b}
Proportion of neophytes	17 (11–24) ^{b}	25 (11–42) ^{a}

analysis: (i) archaeophytes (introduced to Central Europe before the year 1500, mostly from the Mediterranean region) and (ii) neophytes (introduced after the year 1500). Casuals, which do not form self-replacing populations, were not considered. The classification of alien species followed the national lists of alien plants and specialized databases (Klotz et al. 2002; Pyšek et al. 2002, 2012; DAISIE 2009).

Floristic pairwise dissimilarity was calculated as the percentage dissimilarity (Gaugh 1982) separately for the ports of the Elbe-Vltava waterway and Danube waterway. The significance of the correlation coefficients of the relationship between geographical distance and floristic dissimilarity of the ports was tested by Mantel test. The significance of differences between regression coefficients was assessed by the self-made algorithm according to Diem (1960: 178–180). The relationship between species richness and port size was examined by regression analysis (non-linear power function was used). Differences in the abundance of alien species between waterways were tested using Mann-Whitney U test. The program STATISTICA 9.0 (StatSoft Inc. 2009) was used for the analyses. A Principal Components Analysis (PCA) (program CANOCO; ter Braak and Šmilauer 2012) was performed to examine the relationship between the proportion of the number of alien and native species and both waterways and individual regions.

Results

Richness of alien species in the river ports

Overall, 1056 plant taxa were found in the 54 studied river ports. Of these, 193 species were present only in the Elbe-Vltava waterway, and 249 species occurred only in the Danube waterway. The remaining 614 species were found in both river systems.

Of the total number of species, 433 were alien, representing almost half (41%) of the total number of species in the studied Elbe, Vltava, and Danube ports. Sixty-five alien species were found only in the ports of the Elbe-Vltava waterway (i.e., 15% of the total number of alien species), and 72 were found only in the Danube ports (i.e., 17% of the total number of alien species).

On average, there were 125 alien species per river port in the Elbe-Vltava waterway and 140 alien species per port in the Danube waterway. The number of alien species in individual ports ranged between 53 and 191 in the Elbe-Vltava waterway and between 78 and 211 alien species in the Danube waterway (Table 1). The total proportion of alien species in the Elbe-Vltava waterway averaged 50%, with archaeophytes contributing 33% and neophytes contributing 17%. The total proportion of alien species in the Danube waterway averaged 51%, with archaeophytes contributing 34% and neophytes contributing 17%.

Regarding species-area relationships, there were more species in larger ports than in smaller ones [SPECIES NUMBER = 149 * (PORT AREA $m^2)^{0.046}$; $R^2 = 0.171$; $p = 0.005$]. This was also true when considering alien species alone [ALIEN SPECIES NUMBER = 69 * (PORT AREA $m^2)^{0.053}$; $R^2 = 0.173$; $p = 0.005$]. However, the proportion of alien species expressed as a percentage of the total number of species did not vary significantly with port area ($R^2 = 0.0175$; non-significant).

Role of a distance to the sea and other ports

The relationship between the number of alien species in a port and the distance of the port from the sea is presented in Figure 2. The proportion of alien species in both studied waterways decreased with increasing distance from the sea. This pattern was also observed when considering the archaeophytes and neophytes separately.

The floristic dissimilarity values for the 496 unique pairwise combinations of flora in 32 river ports of the Elbe-Vltava waterway and for the 231 combinations of flora in 22 Danube inland ports presented divergent decay patterns for the native species, archaeophytes, and neophytes (Fig. 3). In general, the similarity in species composition between individual river ports of both waterways decreased with inter-port distance in the case of both alien and native flora. All correlations were significant (Mantel test, $p = 0.008–0.0001$). However, in the ports of Elbe-Vltava waterway native and allien species dissimilarity expressed similar slope (i.e. the regression lines are parallel), while in the ports of Danube waterway archaeophytes and native species presented the weakest pattern of distance decay, whereas neophytes presented the strongest pattern. The difference between the regression coefficients was significant ($p = 0.016$ and 0.015 for the comparison of archeophytes × neophytes and native species × neophytes, respectively).

Comparison with urban floras

The data presented in Table 2 show that the percentage of the total number of alien species reported from the ports (50%) is significantly higher than that observed in the cities (38%). However, significant differences in the proportions of archaeophytes and neophytes were found between ports and cities. The percentage of archaeophytes in ports (33%) was significantly higher than that in cities (13%), whereas the percentage of neophytes in ports (17%) was significantly lower than that in cities (25%).

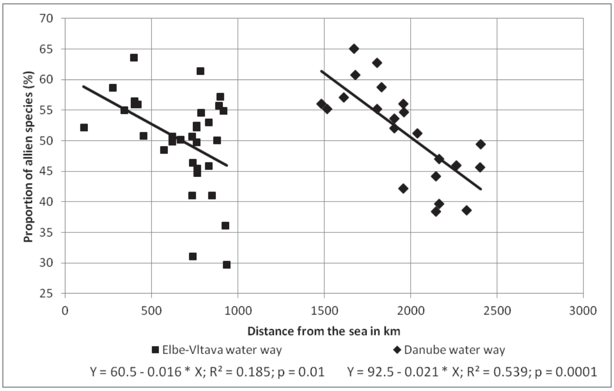

Figure 2. Relationship between the proportion of the number of alien species in studied river ports and the distance from the sea.

Comparisons between the Elbe-Vltava and Danube waterways

Results of Principal Component Analysis (PCA) shown in Figure 4 do not indicate remarkable difference in the proportion of alien species between the Elbe-Vltava and Danube waterways. The ratio of alien and native species decreases with the distance from the sea. The highest proportion of alien species was found in Hungarian ports (especially archaeophytes), followed by the ports in the northern parts of Germany and Slovakia with higher proportion of neophytes. The lowest proportions of alien species were found in the upper parts of the rivers; specifically, in the Elbe and Vltava ports in the Czech Republic and in the Danube ports in Austria and Bavaria.

Most alien species (only species that occurred in at least five ports were tested) were similarly distributed in both waterways. However, some species occurred more frequently in the Elbe-Vltava waterway, whereas other species were more often observed in the Danube waterway. The number of alien species that were significantly more abundant in the Danube ports than in the Elbe-Vltava ports was higher than the number of alien species that were significantly more abundant in Elbe-Vltava ports (see Appendix 1).

Discussion and conclusions

The results of this study demonstrate that river ports contain high proportions of alien plant species. The abundance of alien species increases with port area. This pattern exists because small ports do not have as many large and diverse sites that are suitable for vegetation cover to develop as large ports. In addition, smaller ports have less shipping activity, which contributes less to the intensive spread of alien plants. The proportion of alien species in both studied waterways decreased in relation to port distance from the sea. Consistent with this finding, a higher proportion of alien species was observed

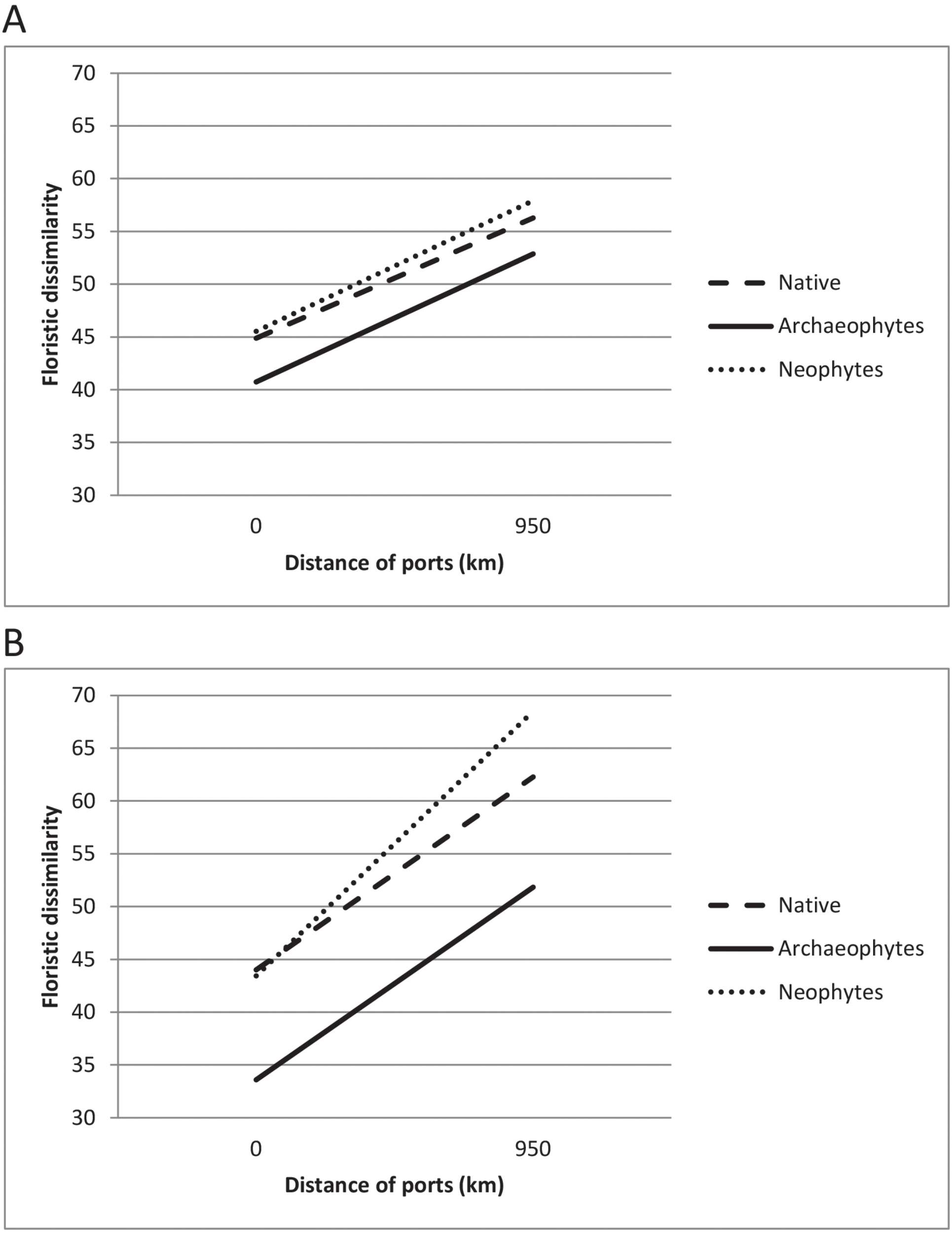

Figure 3. Relationship between the floristic dissimilarity of native and alien floras of studied river ports and the geographical distance of ports of the individual waterways. A. Elbe-Vltava waterway. Regression lines for native species ($Y = 45 + 0.012X$; $R^2 = 0.111$; $p = 0.0025$) and two categories of alien species: archaeophytes ($Y = 41 + 0.013X$; $R^2 = 0.081$; $p = 0.007$) and neophytes ($Y = 46 + 0.013X$; $R^2 = 0.082$; $p = 0.0082$). B. Danube waterway. Regression lines for native species ($Y = 44 + 0.019X$; $R^2 = 0.292$; $p = 0.0001$) and two categories of alien species: archaeophytes ($Y = 34 + 0.019X$; $R^2 = 0.279$; $p = 0.0001$) and neophytes ($Y = 43 + 0.026X$; $R^2 = 0.420$; $p = 0.0001$).

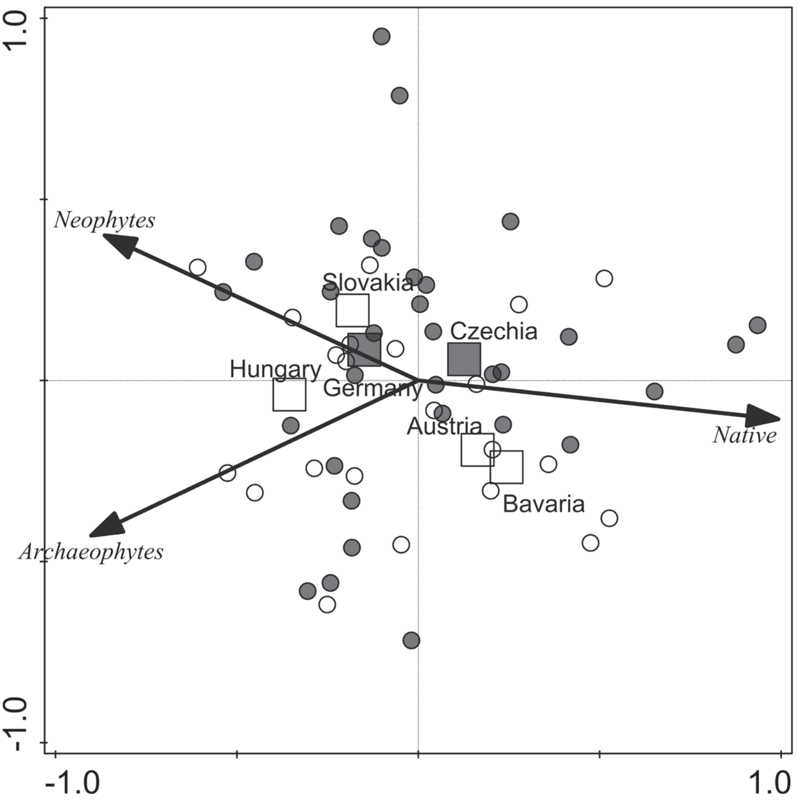

Figure 4. Ordination diagram (PCA) of proportion of the number of alien and native species in the river ports. The first two axes explain 99% of the total variation, individual regions account for 33% of variation. Circles = ports, squares = countries; closed symbols = ports and regions on the Elbe-Vltava waterway; open symbols = ports and regions on the Danube waterway.

in countries whose river ports are more closely connected to the sea. Lower levels of shipping towards inland regions due to decreased river flow are likely the reason for this trend. The importance of traffic in the spread and subsequent naturalization of alien plants in urbanized areas has been documented, e.g. by von der Lippe and Kowarik (2007), Hulme (2009), and Lembrechts et al. (2015).

The similarity in the species composition of alien flora between individual river ports decreased with distance in the same way as the similarity in native flora. In case of the Elbe-Vltava waterway, the slope of the regression lines is the same and the correlation dissimilarity/distance of all three groups of species was weaker, whereas in the case of the Danube waterway, the neophyte dissimilarity increases with the distances of ports much faster than the dissimilarity of the archaeophytes and native species. In addition, in the case of the Danube waterway, the correlation dissimilarity/distance of all three groups of species is closer. The differences in the correlation power of groups of species between both waterways might be due to the different abiotic factors and historical land use (see Deutschewitz et al. 2003). The stronger distance decay patterns observed in neophytes of the Danube waterway supports the findings of La Sorte et al. (2008), showing that archaeophytes present the weakest distance decay patterns. In contrast, neophytes presented the strongest distance decay patterns, whereas native species presented intermediate decay patterns. La Sorte et al. (2008) attributed this trend to the fact that the European archaeophytes that exist today represent a set of species that developed successful associations with anthropogenic activities over several millennia. In the case of ports, this scenario implies that archaeophytes have had more time than other alien species to disperse among anthropogenic harbor sites, which are often similar. No significant differences in species richness were found between the two river systems. In addition, the proportion of alien species did not differ between the climatically warmer region (the Danube waterway) and the colder northwestern region (the Elbe-Vltava waterway) of southeastern Central Europe. The data differ in this regard from those of Lososová et al. (2012) and Schmidt et al. (2014), who, after analyzing floristic data from Central European cities, concluded that the proportion of native species decreased with increasing mean annual precipitation. The number of alien species with a significantly stronger relationship to one waterway was higher for the ports on the Danube River than for those on the Vltava and Elbe Rivers, which indicates a favorable influence of warmer climate on the success of alien species in urbanized areas (e.g. Pyšek 1998; Lososová et al. 2012). This influence can also be explained by the higher presence of species from southeastern Europe. A number of these thermophilous species have found suitable habitats in the ports of Central Europe. To a great extent, the differences in species richness and presence of alien species among the individual ports are likely dependent on the size, type, and treatment of port localities.

Our results also indicate that the proportion of the total number of alien species is significantly higher than the proportions reported from urbanized areas in larger European cities and summarized by Pyšek (1998). However, the proportion of archaeophytes in ports was significantly higher than that in cities, while the proportion of neophytes in ports was significantly lower than that in cities. The higher proportion of archaeophytes, which represent a heterogeneous group in terms of the degrees of adaptation to local conditions (see Pyšek and Jarošík 2005), is likely supported by the presence of a high number of diverse habitats with different levels of disturbance in ports. The lower proportion of neophytes reflects the smaller area of port habitat that is suitable for their development (see Celesti-Grapow et al. 2006). These observations demonstrate that a high number of alien species are present in a relatively small area in the river ports.

The results of the flora composition analysis of the studied ports showed that in Central Europe, the river ports belong to the species-rich urbanized areas, with a high presence of alien species. Our results support the findings of Ricotta et al. (2010), indicating that aliens tend to have different environmental requirements than natives. Ports must be regarded as a unique type of species-rich industrial area, deserving full attention with regard to the control of invasive alien plants as well as nature conservation (Jehlík et al. 2016). When planning port development, both of these aspects should be considered.

Acknowledgements

This study was funded by the Silva Tarouca Research Institute for Landscape and Ornamental Gardening (research project no. VUKOZ-IP-00027073) and the Institute of Botany, Academy of Sciences of the Czech Republic (project no. RVO 67985939). Special thanks go to Ingo Kowarik and Thomas Gregor for helpful comments on the previous version of the text. American Journal Experts edited the manuscript for English language.

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Appendix 1

Overview of the distribution of the alien plants in the inland ports of the river Elbe-Vltava and the river Danube

Statistical significance was tested using 5-degree abundance scale. Only species that occurred in at least 5 ports were tested. For the species statistically differently distributed between the waterways, frequency (%) of the occurrence in the ports of Elbe-Vltava / Danube waterway follows the species name.

The species (taxa) significantly more abundant in the Elbe-Vltava waterway ports:

Aethusa cynapium 22/0
Ambrosia trifida 22/0
Arctium tomentosum 44/14
Asparagus officinalis 44/9
Atriplex oblongifolia 72/45
Atriplex sagittata 91/36
Bidens frondosa 100/77
Carduus crispus 75/32
Chelidonium majus 88/59
Chenopodium pedunculare 84/55
Chenopodium striatiforme 50/14
Chenopodium suecicum 84/41
Datura tatula 31/5
Erysimum cheiranthoides 94/23
Fumaria officinalis 38/14
Galinsoga ciliata 81/45
Galinsoga parviflora 94/73
Hordeum jubatum 25/0
Hyoscyamus niger 47/14
Impatiens glandulifera 44/9
Iva xanthiifolia 53/23
Lamium album 94/14
Leonurus intermedius 25/0
Lepidium latifolium 19/0
Linum usitatissimum 47/14
Lycopsis arvensis subsp. *arvensis 31/0*
Malva pusilla 19/0
Papaver dubium 50/9
Papaver somniferum 44/14
Rumex thyrsiflorus 88/45
Setaria viridis subsp. *pycnocoma 47/18*
Sisymbrium loeselii 100/82
Sisymbrium officinale 81/55
Tanacetum vulgare 97/82
Thlaspi arvense 91/45
Tripleurospermum inodorum 100/100
Xanthium albinum 72/9

The species (taxa) significantly more abundant in the Danube waterway ports:

Amaranthus albus 44/82
Amaranthus blitoides 9/36
Amaranthus powellii 88/95
Ambrosia artemisiifolia 53/86
Amorpha fruticosa 0/23
Anagallis arvensis 31/64
Anthemis austriaca 9/36
Anthemis ruthenica 3/23
Anthriscus caucalis 19/59
Anthriscus cerefolium subsp. *trichosperma 0/36*
Atriplex tatarica 19/59
Bromus hordeaceus subsp. *hordeaceus 97/95*
Bromus japonicus 9/36
Bromus tectorum 75/91
Buddleja davidii 0/41
Camelina microcarpa subsp. *sylvestris 9/41*
Cannabis ruderalis 13/41
Cardaria draba 59/86

Chenopodium ambrosioides 0/23
Chenopodium botrys 6/50
Chenopodium strictum 91/95
Consolida regalis 28/59
Conyza canadensis 100/100
Crepis foetida subsp. *rhoeadifolia 13/50*
Cuscuta campestris 9/36
Cynodon dactylon 22/77
Daucus carota subsp. *carota 81/100*
Descurainia sophia 84/86
Diplotaxis muralis 9/36
Diplotaxis tenuifolia 34/77
Echinochloa crus-galli 91/91
Echium vulgare 94/95
Eragrostis minor 44/100
Erigeron annuus 66/100
Erodium cicutarium 50/91
Erucastrum gallicum 0/36
Fraxinus pennsylvanica 6/32
Galeopsis angustifolia 0/23
Geranium pussilum 50/95
Geranium pyrenaicum 16/41
Juglans regia 22/55
Lamium amplexicaule 22/64
Lamium purpureum 66/91
Lathyrus tuberosus 38/82
Lepidium campestre 22/50
Lepidium densiflorum 34/59
Lepidium virginicum 16/45
Lithospermum arvense 9/36
Medicago lupulina 91/100
Medicago sativa 56/86
Melilotus officinalis 84/86
Microrrhinum minus 44/73
Morus alba 0/41
Onobrychis viciifolia 3/64
Oxalis corniculata 3/23
Papaver rhoeas 81/91
Parietaria officinalis 0/27
Pastinaca sativa subsp. *sativa 38/82*
Petrorhagia prolifera 25/59
Populus alba 13/64
Populus cf. × *canadensis 78/86*
Portulaca oleracea 22/55
Reseda lutea 69/91
Rumex patientia 13/50
Setaria pumila 44/73
Setaria verticillata 31/68
Setaria viridis subsp. *viridis 72/91*
Sisymbrium orientale s.l. 22/55
Solidago gigantea 25/82
Stachys annua 3/41
Torilis arvensis 0/23
Tragopogon dubius 41/73
Verbena officinalis 3/86
Veronica arvensis 59/95
Veronica persica 50/82
Vicia angustifolia agg. 41/100
Vicia villosa 25/50
Vulpia myuros 28/64
Xanthium saccharatum 0/32

The species (taxa) showing no significantly different distribution between the individual waterways:

Abutilon theophrasti
Acer negundo
Acorus calamus
Aesculus hippocastanum
Ailanthus altissima
Alopecurus myosuroides
Amaranthus blitum
Amaranthus hybridus
Amaranthus × *ozanonii*
Amaranthus retroflexus
Anchusa officinalis
Anethum graveolens
Anthemis arvensis
Antirrhinum majus
Apera spica-venti
Arctium minus
Armoracia rusticana
Arrhenatherum elatius

Artemisia absinthium
Artemisia annua
Asperugo procumbens
Aster simplex
Atriplex patula
Avena fatua
Avena sativa
Ballota nigra subsp. *nigra*
Bellis perennis
Berteroa incana
Brassica napus subsp. *napus*
Brassica nigra
Bromus inermis
Bromus sterilis
Bryonia alba
Bryonia dioica
Bunias orientalis
Calendula officinalis
Capsella bursa-pastoris
Carduus acanthoides
Centaurea cyanus
Chenopodium ficifolium
Chenopodium glaucum
Chenopodium hybridum
Chenopodium missouriense
Chenopodium murale
Chenopodium polyspermum
Chenopodium probstii
Cichorium intybus subsp. *intybus*
Cirsium arvense
Cirsium vulgare
Commelina communis
Conium maculatum
Consolida orientalis
Convolvulus arvensis
Cornus sericea
Crepis biennis
Crepis capillaris
Crepis tectorum
Cymbalaria muralis
Datura stramonium
Digitaria ischaemum
Digitaria sanguinalis subsp. *pectiniformis*
Digitaria sanguinalis subsp. *sanguinalis*
Dipsacus fullonum
Echinops sphaerocephalus
Epilobium ciliatum
Eryngium campestre
Euphorbia helioscopia
Euphorbia peplus
Fagopyrum tataricum
Geranium dissectum
Helianthus ×laetiflorus
Helianthus annuus var. *macrocarpus*
Helianthus tuberosus
Hibiscus trionum
Hordeum distichon
Hordeum murinum
Hordeum vulgare subsp. *vulgare*
Impatiens parviflora
Isatis tinctoria
Kochia scoparia subsp. *densiflora*
Kochia scoparia subsp. *scoparia*
Lactuca serriola
Lapsana communis
Lathyrus latifolius
Lepidium ruderale
Leucosinapis alba
Linaria vulgaris
Lolium multiflorum
Lycium barbarum
Malus domestica
Malva neglecta
Malva sylvestris
Matricaria discoidea
Matricaria recutita
Medicago × varia
Melilotus albus
Mentha × rotundifolia
Mentha arvensis
Mercurialis annua
Myosotis arvensis
Myosotis stricta
Oenothera depressa
Oenothera glazioviana
Oenothera pycnocarpa
Onopordum acanthium
Oxalis dillenii

Oxalis fontana
Panicum capillare subsp. *capillare*
Papaver argemone
Parthenocissus inserta
Phacelia tanacetifolia
Phalaris canariensis
Pisum sativum subsp. *sativum*
Plantago major subsp. *major*
Polygonum arenastrum
Potentilla intermedia
Prunus cerasus
Prunus domestica
Pyrus communis
Raphanus raphanistrum
Raphanus sativus
Reseda luteola
Reynoutria japonica var. *japonica*
Robinia pseudacacia
Rubus armeniacus
Salvia verticillata
Saponaria officinalis
Secale cereale
Sedum rupestre subsp. *erectum*
Sedum spurium
Senecio inaequidens
Senecio vernalis
Senecio vulgaris
Silene latifolia subsp. *alba*
Silene noctiflora
Sinapis arvensis
Sisymbrium altissimum
Sisymbrium volgense
Solanum decipiens
Solanum lycopersicum
Solanum nigrum s.s.
Solidago canadensis
Sonchus arvensis
Sonchus asper
Sonchus oleraceus
Sorghum halepense
Syringa vulgaris
Tilia × euchlora
Torilis japonica
Trifolium hybridum
Triticum aestivum
Urtica urens
Verbascum densiflorum
Veronica polita
Vicia hirsuta
Vicia tetrasperma
Viola arvensis
Viola odorata
Xanthium strumarium

Appendix 2

Table 3. Summary of the port localities areas and years of investigation of 54 Central European river ports used in the study.

River port (country)	Port locality area [m^2]	Years of investigation
Elbe and Vltava Rivers		
1. Hamburg (Germany)	74 400 000	1980, 88, 91, 95
2.Wittenberge (Germany)	5 143	1979, 85, 87, 97
3.Tangermünde (Germany)	36 423	1987, 97
4. Magdeburg-Rothensee (Germany)	906 672	1997, 98
5. Magdebur, Industriehafen (Germany)	2 017 555	1980, 85, 87, 97, 98
6.Magdeburg, Handelshafen (Germany)	268 722	1979, 80, 85, 87, 97, 98
7. Schönebeck-Frohse	128 203	1979, 80, 85, 87, 97, 98
8. Aken, Handelshafen (Germany)	93 547	1987, 97
9. Torgau (Germany)	100 048	1979, 87, 97
10. Riesa-Gröba, Industriehafen (Germany)	2 194 650	1979, 80, 87, 97, 98
11. Riesa, transshipment point at mill houses (Germany)	15 398	1979, 80, 87, 91, 97
12.Dresden, Albertshafen (Germany)	337 191	1979, 87, 91, 97

River port (country)	Port locality area [m²]	Years of investigation
13.Děčín-Loubí (Czech Republic)	51 630	1968, 74, 75, 78, 79, 81, 82, 83, 84, 85, 86, 87, 88, 89, 90, 91, 92, 93, 95, 96, 97, 98, 99, 2000, 03, 04, 05, 06, 07
14. Děčín-Staré Loubí (Czech Republic)	20 241	1968, 74, 87, 93, 95, 96, 97, 98, 99, 2000, 04, 05
15. Děčín-Staré Město (Czech Republic)	3 524	2000
16. Děčín-Rozbělesy (Czech Republic)	553 337	1974, 87, 90, 91, 92, 95, 2005, 07, 08, 09
17. Ústí nad Labem-Krásné Březno (Czech Republic)	17 285	1968, 74, 75, 78, 79, 80, 81, 82, 83, 84, 85, 86, 87, 88, 89, 90, 91, 92, 93, 95, 96, 97, 98, 99, 2000, 04
18. Ústí nad Labem, Central Port (Czech Republic)	151 096	1990, 91, 92, 93, 94, 95, 96, 97, 98, 99, 2000, 04, 05
19. Ústí nad Labem, Western Port (Czech Republic)	113 993	1968, 74, 75, 78, 79, 80, 81, 82, 83, 84, 85, 86, 87, 88, 89, 90, 91, 92, 93, 94, 95, 96, 97, 99, 2000, 03, 04, 05, 06, 07
20. Ústí nad Labem, Větruše (Czech Republic)	27 885	1968, 73, 74, 75, 79, 80, 81, 82, 83, 84, 85, 86, 87, 88, 89, 90, 91, 92, 95, 97, 2000
21. Ústí nad Labem-Vaňov (Czech Republic)	37 598	1974, 75, 89, 92, 93, 95, 97, 2000, 04
22. Lovosice, Canal Port (Czech Republic)	49 346	1968, 69, 72, 74, 75, 76, 78, 79, 80, 81, 82, 83, 84, 85, 86, 87, 88, 89, 90, 91, 92, 95, 96, 97, 2000, 04, 05, 07
23.Lovosice-Prosmyky (Czech Republic)	772 847	1996, 97, 2000, 09
24. Mělník-Pšovka (Czech Republic)	118 689	1968, 69, 71, 72, 74, 75, 76, 78, 79, 81, 82, 83, 84, 85, 86, 87, 88, 89, 90, 91, 92, 93, 95, 99, 2000, 04, 05, 06, 08, 09
25. Mělník, Transshipment Point (Czech Republic)	56 487	1972, 73, 74, 75, 78, 79, 80, 81, 82, 83, 84, 85, 86, 87, 88, 89, 90, 91, 92, 93, 95, 99, 2000, 09
26. Kolín, Transshipment Point (Czech Republic)	12 584	1987, 91, 92, 93, 95, 96, 97, 2000, 04
27. Týnec nad Labem, Ro-Ro-Transshipment Point (Czech Republic)	5 585	1992, 95, 97, 2000
28. Chvaletice (Czech Republic)	19 376	1987, 88, 91, 92, 95, 2000
29. Miřejovice Ro-Ro-Transshipment Point (Czech Republic)	31 313	1992, 95, 97, 2000
30. Praha-Holešovice (Czech Republic)	122 402	1968, 69, 70, 71, 72, 73, 74, 75, 76, 78, 79, 80, 81, 82, 83, 84, 85, 86, 87, 88, 89, 90, 91, 92, 93, 94, 95, 98, 99, 2001, 06
31. Praha-Smíchov (Czech Republic)	20 044	1996, 97, 99, 2000, 05, 06, 08, 09
32. Praha-Radotín (Czech Republic)	16 727	1992, 93, 94, 96, 99, 2006
Danube river		
34. Baja (Hungary)	362 773	1982, 89, 94
35. Dunaújváros (Hungary)	60 591	1994
36. Budapest-Csepel (Hungary)	2 640 118	1982, 89, 94
37. Budapest-Ferencváros (Hungary)	3 013 144	1982, 89, 94
38. Györ, Transshipment Point (Hungary)	960 530	1982, 89, 94
39. Györ, Commercial Port "Iparcsatorna" (Hungary)	140 892	1989, 94
40. Komárno (Slovakia)	210 567	1968, 73, 76, 79, 80, 81, 82, 83, 84, 85, 86, 87, 88, 89, 90, 91, 92, 98, 99, 2000, 03, 04, 05
41. Bratislava-Pálenisko (Slovakia)	842 843	1986, 87, 88, 90, 91, 92, 98, 2003, 04, 05, 08
42. Bratislava-Nivy (Slovakia)	415 605	1968, 73, 74, 79, 80, 81, 82, 83, 84, 85, 86, 87, 88, 89, 90, 91, 92, 98, 2003, 05, 08
43. Wien-Lobau (Austria)	1 915 257	1990, 92, 93, 98
44. Wien-Albern (Austria)	119 731	1990, 92, 93, 98
45. Wien-Freudenau (Austria)	862 591	1990, 92, 93, 98
46. Krems an der Donau (Austria)	529 067	1990, 92, 93, 98
47. Ennsdorf, Hafenbecken Ost, Silos (Austria)	152 737	1997, 98
48. Enns (Austria)	711 666	1997, 98
49. Linz, Tankhafen (Austria)	1 636 055	1990, 92, 93, 94, 97
50. Linz, Handelshafen /Stadthafen (Austria)	1 375 666	1900, 92, 93, 94, 97
51. Passau-Racklau (Germany)	36 308	1989, 97
52. Deggendorf (Germany)	408 775	1989, 97
53. Regensburg, Osthafen (Germany)	435 161	1989, 91, 97
54. Regensburg Westhafen/Luitpoldhafen (Germany)	724 553	1989, 91, 97

Supplementary material 1

Electronic data set

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Data type: species data

Link: https://doi.org/10.3897/neobiota.45.33866.suppl1