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ARTICLE

Ecological impacts of alien species: quantification, scope, caveats and recommendations

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Abstract
Despite intensive research on effects of alien species during the past decade, invasion science still lacks capacity to accurately predict impacts and thus provide timely advice to managers on where limited resources should be allocated. This capacity has been limited partly by the context-dependent nature of ecological impacts, research highly skewed toward certain taxa and habitat types, and the lack of standardized methods for detecting and quantifying impact. We review different strategies, including specific experimental and observational approaches, for detecting and quantifying ecological impacts of alien species. These include a four-way experimental plot design for comparing impact studies of different organisms. Furthermore, we identify hypothesis-driven parameters that should be measured at invaded sites to maximize insights into the nature of impact. We also present strategies for recognizing high-impact species. Our recommendations provide a foundation for developing systematic quantitative measurements to allow comparisons of impact across alien species, sites and time.

Keywords: Biological invasions, context dependence, ecosystem functioning, management, prediction.

Introduction

The human-mediated translocation of species to regions outside their native ranges is one of the most distinguishing features of the Anthropocene (e.g., Ricciardi 2007). Although biological invasions are widely recognized as a key component of current global change, there is much debate among scientists and other stakeholders concerning, among other things, the scale of the changes caused by alien species and the extent to which management intervention is warranted (e.g., Richardson & Ricciardi 2013). This controversy is partly rooted in the lack of a widely accepted framework for interpreting impacts and a consolidated terminology for impact to facilitate communication (Blackburn et al. 2014; Jeschke et al. 2014). One reason for this lack of consensus may be that such research has involved only a limited subset of alien species in a restricted number of regions and environments, which has hindered progress towards a predictive understanding of impact in general (Hulme et al. 2013). There are, however, major gaps in our knowledge in particular how species traits and characteristics of the recipient environments interact to determine impact (Drenovsky et al. 2012; Ricciardi et al. 2013), how spatial and temporal scales modulate the interpretation of impacts (Strayer et al. 2006; Powell et al. 2011), how impacts of alien species can be distinguished from other concurrent and potentially synergistic stressors (e.g., climate change, landscape alteration; MacDougall & Turkington 2005; Didham et al. 2007), and how different types of impacts can be evaluated and compared using common metrics and currencies (Parker et al. 1999; Blackburn et al. 2014). Invasion science needs more robust methods for reliably assessing risks associated with alien species introductions – i.e., the likelihood of establishment, spread and impact – but there is a large literature attempting to do this, and on why it has been difficult (see e.g., Leung et al. 2012; Kumschick & Richardson 2013).
The study of impact is not a specifically new phenomenon (see e.g. Lodge 1993; Mack & D'Antonio 1998). However only recently have reviews of the magnitude, scope, and variation of impacts of alien species, as well as their geographic and taxonomic distinctions and biases, greatly expanded our theoretical knowledge and provided a good conceptual framework (e.g., Vilà et al. 2010; Pyšek et al. 2012; Hulme et al. 2013; Ricciardi et al. 2013). However, further progress hinges on the elucidation of general patterns and mechanisms of impacts. Here, we assess approaches for quantifying and prioritizing impacts, and provide recommendations for facilitating the risk assessment and management of alien species.

Specifically, we propose guidelines on (i) what information to collect on the invaded site to better understand the mechanisms of impact and to decide which alien species should be prioritized for management, (ii) how to plan and conduct empirical studies to understand impact, and (iii) steps towards impact prediction. Here, we follow Ricciardi et al. (2013) in defining “impact” as a measurable change in the state of an invaded ecosystem that can be attributed to the alien species. This definition considers any change in ecological or ecosystem properties, but excludes socio-economic effects and human values (cf. Jeschke et al. 2014).

Quantifying ecological impacts in the field: what to measure

Quantitative assessments of alien species impacts are essential to ensure that resources spent on management are prioritized to target the most problematic species, threatened areas and affected ecosystem processes (Hulme et al. 2013). However, in general, the selection of parameters used in quantitative studies of impact does not seem to have been sufficiently driven by hypotheses. Selection of appropriate parameters should account for impacts at different organizational levels, such as individuals, populations, communities and ecosystem functions (Parker et al. 1999; Pyšek et al. 2012; Blackburn et al. 2014) and at different levels of diversity, such as genetic, functional and taxonomic diversity. Quantifying several impact types at the same site allows for the determination of causal links among impacts and the identification of direct and indirect effects (Fig. 1; see also Hulme 2006).
Among the most important metrics is alien species abundance, which is correlated with impact, although not necessarily linearly. The greater the number of individuals or biomass of the alien species, the more resources they will use and the greater the extent and strength of their interactions with native species (e.g., Parker et al. 1999; Ricciardi 2003). Catford et al. (2012) provide a practical way of taking the abundance of alien species into account, by identifying abundance thresholds and using categorical scores.
Time-since-invasion also influences impact, through temporal changes in abundance of the alien species, adaptation by the recipient community, post-invasion evolution, and variation in the physico-chemical environment in the invaded range (Strayer et al. 2006; Dostál et al. 2013). The introduction or establishment date should therefore be noted. The magnitude, direction and type of impact also vary with the spatial extent and grain (resolution) of the study area (e.g., Gaertner et al. 2009). It is therefore important to indicate sampling plot size as well as the area over which plots were sampled, also in light of species-area curves. However, this measure might not always be straightforward, e.g. in the case of migrating animals.

The challenge of context dependence

The impacts of alien species vary across space and time, under the influence of local abiotic and biotic variables (Hulme 2006; Ricciardi et al. 2013). The abundance and performance (e.g. resource uptake, competitive success) of a species can vary predictably along physical environmental gradients (Ricciardi 2003; Jokela and Ricciardi 2008). In addition, the composition of the recipient community moderates impacts in several ways, e.g. through resistance or facilitation by resident species (Ricciardi et al. 2013). Interactions between native and alien species may also vary across physical gradients such that dominance patterns can even be reversed (Kestrup and Ricciardi 2009).
Finally, other anthropogenic stressors that simultaneously alter the physical and biological environment can affect many interactions and obscure the effects of alien species. Figure 1 illustrates this “passenger-driver” problem of impact attribution, which is a major challenge for management (MacDougall and Turkington 2005; Didham et al. 2007); impact attribution could be challenging if the passenger model dominated. In the driver model, interactions *a* (or *c* affecting *e*) are strong; in the passenger model, interactions *d* (or *e* affecting *b*) are strong, whilst *a* is weak. Also illustrated are additive (*a* and *e* are strong) and synergistic models (where *a*, *c*, *d* and *e* are strong).

An increased understanding of context dependence is required to improve our ability to predict impacts. Resource managers can play a valuable role in the initial detection and by providing information on the shifting contexts of impact, through their observation of environmental change. However, *quantifying* these changes requires considerable research and sufficient resources. Governments and land owners and managers, as well as the general public, could profit from the outcomes of such studies. Moreover, funding should be allocated by all these stakeholders to both research institutes and land management agencies. The outcomes can then feed into preventive measures, for example to improve risk assessments and management plans.

Prioritization of management

It is beyond the scope of this study to discuss management prioritisation if the passenger model dominates for a particular system. In the following section we therefore only deal with impacts where the alien species is most likely to be a driver of the impact.

For efficient and cost-effective allocation of management resources, there is a strong need to flag those alien species with potentially high environmental impacts (Blackburn et al. 2014). It has been proposed that species with the potential to force ecosystems to cross biotic and abiotic thresholds – and thus change to alternative states (i.e., causing regime shifts) – should be considered as potentially the most disruptive and given top priority for intervention (Gaertner et al. 2014). Regime shifts are associated with a reorganization of the internal feedback mechanisms that structure an ecosystem, such as plant-soil feedbacks (Scheffer et al. 2012). However, at present, it is difficult to predict whether a given species can alter feedbacks in ways that could lead to a regime shift. Outcomes depend on traits of the alien species, characteristics of the invaded habitat and the invaded community (Pyšek et al. 2012; Kueffer et al. 2013; Figure 1), and interactions between these factors (Ricciardi et al. 2013). One way of tackling these challenges is to identify specific combinations of species traits, ecosystem characteristics and impacts with a high probability of causing changes in ecosystem feedbacks (Gaertner et al. 2014). Such feedbacks are commonly associated with the impacts of ecosystem engineers (Ricciardi et al. 2013; Linder et al. 2012; Table 1 and Appendix S1).

If no quantitative or statistically comparable data are available, as is often the case, impact scoring systems can be used to make very diverse data comparable. Furthermore, they allow comparisons between groups with different impact mechanisms (Kumschick et al. 2012; Blackburn et al. 2014). Scoring systems have been used to identify traits of alien mammals and birds associated with high impacts (Nentwig et al. 2010; Kumschick et al. 2013), and found that the diversity of habitats an alien species can occupy could be a useful parameter in models predicting its impact (Evans et al. 2014).

Implications for prediction and prevention

We need to mitigate not only impacts where aliens are present, but ideally also where they are expected to invade and likely to have an undesirable impact in the future. Pre-border assessments with the purpose of predicting the risk of invasion and impact are used in many parts of the world (Kumschick & Richardson 2013), but the impact assessment is generally not convincingly incorporated, owing mainly to the same inherent difficulties and uncertainties that account for the lack of a robust predictive framework and a lack of data on impacts in general. A potential solution would be to identify predictable patterns via statistical synthesis of data from multiple sites for given species, ideally those with a sufficiently documented impact history (Kulhanek et al. 2011; Figure 2). Such studies can also contribute to the justification of the use of "invasive/impact elsewhere" as an often suggested predictor of invasion success and impact, respectively, in the new range (Leung et al. 2012; Kumschick & Richardson 2013). Figure 2 outlines a logical series of empirical approaches for forecasting impacts, based primarily on impact and invasion history. Vitousek (1990) posited that alien species that have large effects on ecosystem processes differ from the native species by their resource acquisition, resource efficiency, or capacity to alter disturbance

regimes; examples include alien plants that change fire regimes following introduction, such as many invasive grasses (D'Antonio & Vitousek 1992; Yelenik & D'Antonio 2013), or mammalian predators introduced to islands with no evolutionary history of such species or archetypes (e.g., Blackburn et al. 2004). The functional distinctiveness of the alien species may enhance its impact through novel resource use and exposure to ecologically naïve residents or by introducing new ecosystem functions (e.g. nitrogen fixers in communities naturally without such a guild). Taxonomic or phylogenetic distinctiveness can serve as proxy parameters of functional distinctiveness (Ricciardi and Atkinson 2004; Strauss et al. 2006). In some cases, however, alien species may not differ in functional type but in performance and behaviour. For example, alien and native predators may differ in their feeding behaviours towards a common prey, but these differences can be quantified and compared by testing their functional response (Dick et al. 2014).
Finally, one aspect of potentially high predictive value that has not been adequately explored is whether the impacts of alien species are similar to those of phylogenetically closely related or functionally similar alien species. This relationship is often assumed and used to assess the risk of species that have not been introduced elsewhere (e.g., Bomford 2008), but it has rarely been tested. A cursory examination of the freshwater literature indicates that taxonomic affiliation – whether a species is closely related to a proven invader – is not a consistent predictor of impact potential (Ricciardi 2003).

Experimental methods and approaches to investigate impacts

Various approaches have been taken to study impacts of different taxa in different habitat types (Appendix S2 in the Supporting Material). Most of these studies involve comparisons of invaded versus uninvaded reference sites, primarily at the fine resolution of plots and their restricted extent (A in Figure 3). This approach is commonly used to infer impacts of alien species on particular native species, on community structure (i.e., species diversity) and on ecosystem processes such as nutrient pools and fluxes (Vilà et al. 2011). If suitable reference plots are available, it is the simplest observational approach, as it allows large amounts of data to be collected relatively easily and inexpensively. However, it does not demonstrate causality, because the observed outcome can be confounded with between-site differences not related to the introduced species. With this in mind, such studies should select plots that are as closely matched as possible for other abiotic and biotic features (Hejda et al. 2009). One approach is to correlate the magnitude of one or more impacts along a gradient of alien species abundance (B in Figure 3). For instance, herbivore effects on plant fitness are often density-dependent, such that their per-capita effect is correlated with density (e.g., Trumble et al. 1993). However, the relationship between per-capita impact and alien species abundance remains to be examined for a range of taxa, systems and environmental conditions.
Unfortunately, it is often very difficult to find contemporaneous similar but uninvaded reference sites to contrast with invaded sites. Under such circumstances, it would be preferable to study genuine chronosequences that enable analysis of the relationships between time since invasion and the magnitude of impact, provided that there are good historical data to determine when the invasion began (C1 in Figure 3). Of particular interest are comparisons of sites before and after invasion (C2 in Figure 3). This is only feasible under certain circumstances, such as in locations where there have been long-term monitoring programs (Magurran et al. 2010) or monitoring before an anticipated invasion took place (Roy et al. 2012). However, in such cases, the long-term temporal dynamics of the impacts of alien species are generally not sufficiently understood to give recommendations on the optimal time scale of impact studies (Yelenik & D'Antonio 2013). Moreover, time series studies might encounter the same confounding problems as comparisons between invaded and uninvaded sites, given that differences over time might be caused by other (confounding) stressors acting simultaneously during an invasion (Figure 1; Appendix S1).

If direct observations on temporal dynamics of impacts are not feasible, changes in communities or ecosystem processes might not be attributable to the presence and activity of the alien species, but rather to concurrent or preceding changes in the environment (e.g., grazing, eutrophication, changes in climate conditions).

Whether alien species are passengers or drivers of change is difficult to resolve by observation alone (MacDougall & Turkington 2005). For example, the observed decline of native ladybird species in arboreal habitats in the UK after invasion by the alien ladybird *Harmonia axyridis* is also correlated with changes in maximum temperature and rainfall among years (Brown et al. 2011). However, path analysis and structural equation modelling can sometimes be applied to disentangle the relative importance of alien species and other stressors to native species declines (e.g., Light & Marchetti 2007; Hermoso et al. 2011).

Whilst in any aspect of ecology, manipulation of parameters is the best way to demonstrate causality, only a small proportion of studies report on field removal experiments to identify the impacts of alien species (D in Figure 3; Supporting Material Appendix S2). Most prominent examples concern the removal of alien plants, yet field manipulation experiments represent less than 14% of all studies on the impacts of alien plants (data from Vilà et al. 2011). Comparing invaded plots with those from which alien species have been removed offers a straightforward method to demonstrate that ecological differences between these plots are linked to the effects of alien species. However, the outcomes of these experiments can be confounded with disturbance effects due to species removal. Disturbance can be minimized in various ways. For example, if the alien species is an annual plant, the invader can be removed at the seedling stage (Hulme & Bremner 2006). Disturbance is, however, often unavoidable if the invader is a perennial plant species. Consequently, removal plots are often set in an earlier successional stage than intact invaded plots; even if they harbor high species richness, their species composition can be different and therefore not exactly comparable, because many species regenerating in the removal plots are early colonizers that can themselves be alien species (Truscott et al. 2008; Andreu et al. 2010). In such cases, it is advantageous to combine experimental removal of alien species with removal of native species, where appropriate (F in Figure 3), to distinguish the alien/native effect from the disturbance effect. For sessile species, comparing ecological differences between areas where aliens and natives have been removed will elucidate whether the effect of the alien is due to species origin *per se.*

Removal experiments for mobile organisms are difficult to achieve in practice and results from such experiments are highly context-dependent. There have now been many eradications of alien animal species worldwide (e.g., Pluess et al. 2012), with sometimes counterintuitive results on the dynamics of their prey (Rayner et al. 2007). Furthermore, compared to sessile species, the impact of mobile species with large home ranges (e.g. vertebrates) might be spatially diluted and difficult to quantify at the local scale. Eradications can be used for comparisons of invaded communities before and after the removal of the alien (e.g., Monks et al. 2014), but other approaches, such as comparisons with other invaded and uninvaded sites, might also be possible. For mobile species with large home ranges, the use of well-designed enclosures or fences to compare large invaded and uninvaded areas might be one of the most realistic options (Burns et al. 2012).

Removal of an alien species does not necessarily (or not immediately) lead to the restoration of pre-invasion conditions, particularly for some ecosystem engineers that may have a legacy effect on habitat conditions (Magnoli et al. 2013). It is therefore crucial to compare removal plots with uninvaded and unmanipulated reference plots (E in Figure 3). From a restoration perspective, a successful removal strategy would be one in which the ecosystem recovers along a trajectory leading to a state similar to a reference site, not only in terms of species richness but also species composition and ecosystem functioning. For example, following the removal of monkey-flower (*Mimulus guttatus*) from a riparian system, the resident plant community recovered and increased in species richness over time but towards a different community composition than that of uninvaded sites (Truscott et al. 2008). This demonstrates that different methodological approaches can lead to different conclusions regarding impacts.

In some cases, removals of alien species could be compared with removals of closely related natives. For example, field removal experiments that have been conducted in the Bahamas to exclude the alien red lionfish (*Pterois volitans*) and test how the impact of this species compares with that of the coney grouper (*Cephalopholis fulva*; a native predator of similar size and diet) found that the alien species reduced the abundance and richness of small coral-reef fishes more than the native predator (Albins 2013). More studies of this kind are needed to discern whether alien species impacts represent the average effect or a magnified effect of one single species in the community when dominant (F in Figure 3). However, such native-removal studies are only feasible and sensible if no negative conservation implications of removing those natives are expected.

Manipulative species-addition field experiments are technically feasible (Meffin et al. 2010; see also Supporting Material Appendix S2) but highly challenging, as prevention of the establishment and spread of the alien species outside experimental plots has to be a priority in the experimental setting. This is difficult to achieve and might jeopardize the value of an experiment aiming to observe an interaction between the additional alien species individuals and the recipient community. An alternative is to perform species addition experiments in restricted conditions mimicking field conditions as much as possible. Mesocosms have mainly been used to test impacts of soil organisms and aquatic alien species (Supporting Material Appendix S2). Such studies can be informative regarding particular impact mechanisms for species interactions but are problematic for inferring impacts at the community and ecosystem levels. Moreover, mesocosm and common garden experiments are usually too short-term or restricted in scale to predict long-term field conditions.

There are multiple ways to assess alien species impacts, but no single method appears to have a clear advantage. We advocate a four-way-plot experimental design (uninvaded, invaded, removal of natives, removal of aliens, A+D+E+F in Figure 3) – not only to reveal ecological impacts and detect regime shifts, but also to determine the potential success of restoration efforts. The use of large-scale removal programs as a source of experimental data can be highly valuable if carried out in such a way as to allow this recommended design. Spatial and temporal variation in impacts needs also to be taken into account by careful replication and monitoring of sampled sites (Kueffer et al. 2013).

Conclusions

Research on the impacts of alien species is not only necessary to understand why some species are more disruptive than others and why some systems are more susceptible to being disturbed by alien species, but is also of practical importance in determining how limited management resources should be allocated. The better our understanding of impacts, the better equipped we will be to implement effective management. Systematically gathering and synthesising solid evidence of the impacts caused by alien species facilitates communication with the public, and better informs policy and decision-makers. Disputes within the scientific community about the role of alien species increases the perception of them being innocuous or equally likely to have positive effects (but see Richardson & Ricciardi 2013). In fact, many alien species cause substantial and sometimes irreversible impacts but we have not yet achieved a predictive understanding of when, where and by which species these impacts will occur.

Furthermore, our synthesis points out that different experimental methodologies are appropriate for different taxa due to particular properties of the species and ecosystems involved, even though most methods are theoretically possible for most organismal groups (Supporting Material Appendix S2). It is known, however, that using different methodological approaches can lead to different conclusions (e.g., Truscott et al. 2008). Moreover, sessile organisms are more frequently studied than mobile ones, which can potentially introduce bias. Further studies are required to determine the extent to which such issues influence our evaluation and knowledge of impact and perceived differences between organismal groups.

For a more balanced view of impacts, a standardized protocol of how to quantify impacts – that is, which parameters to measure and which metrics to apply at invaded sites – is needed. Hence, we have proposed a set of parameters on which to base the objective quantification of impact. Collation of information on these parameters will contribute to a better understanding of context-dependence and to a robust framework for prioritization.

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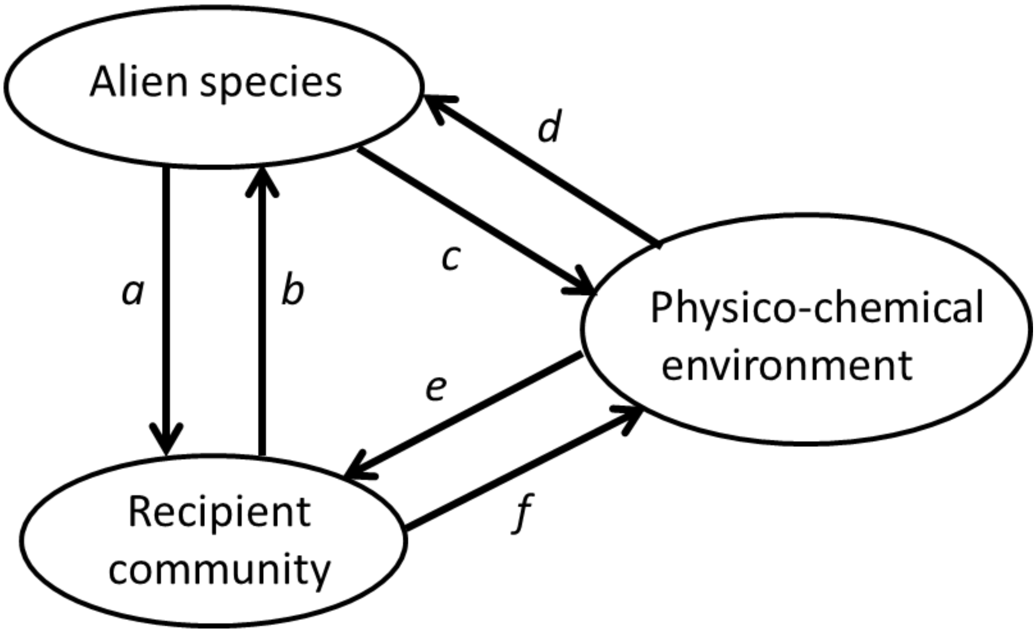

Moderating parameters and scales	**Interactions affected**
Composition of the recipient community	*a, b, e, f*
Abiotic changes	*c, d, e, f*
Abundance of the alien species	*a, c*
Time since introduction	*a, b, c, d, e, f*
Other stressors	*a, b, c, d, e, f*
Spatial scale (extent and grain)	*a, b, c, d, e, f*

Figure 1: The context-dependence of alien species impacts. Knowledge of key interactions and moderating parameters is required to understand and properly quantify impacts. Details of these parameters are given in Table 1 and Appendix S1.

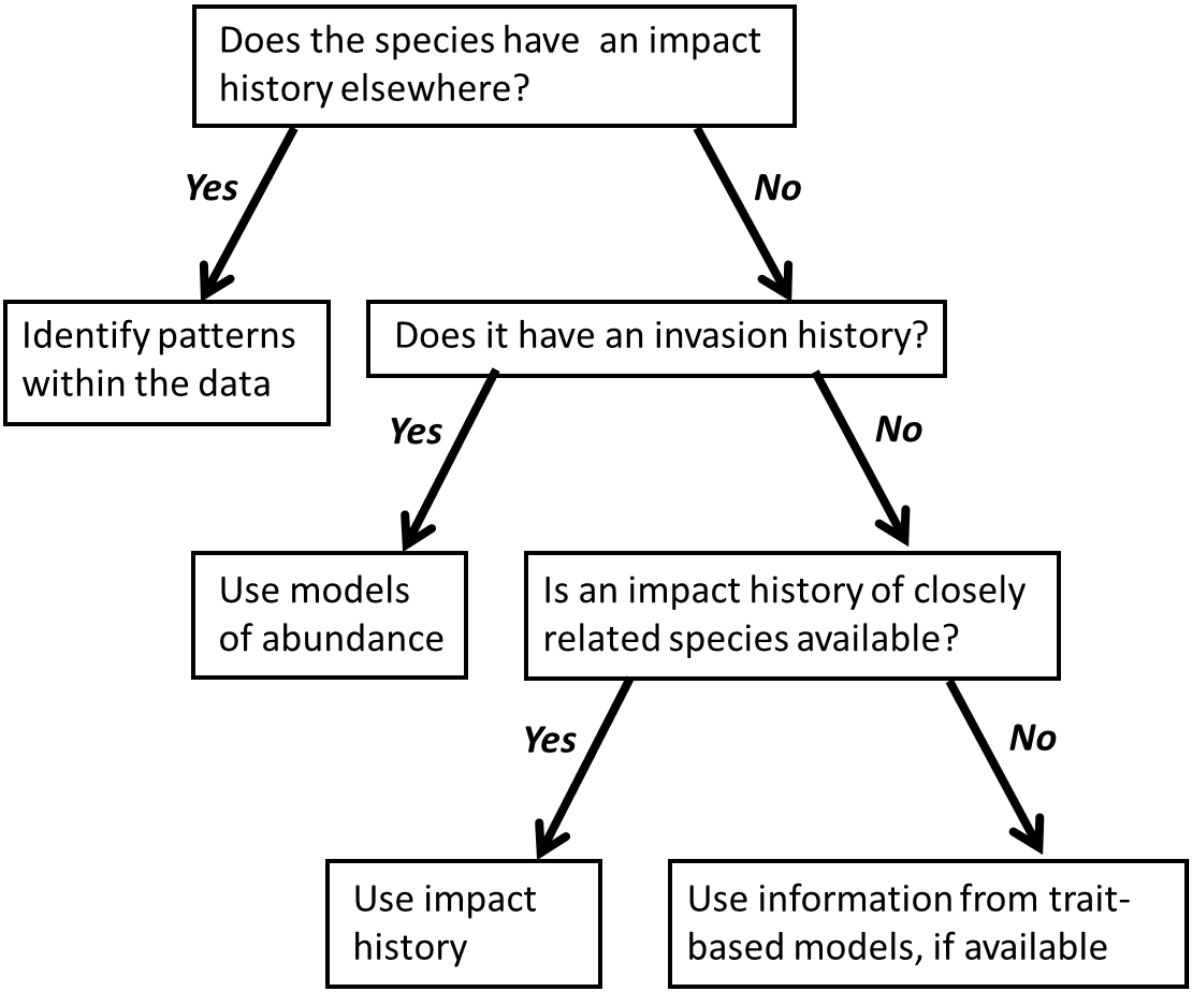

Figure 2: Empirical approaches for forecasting impacts of alien species (adapted from Ricciardi 2003), starting with the most desirable data. If an alien species has a sufficiently documented impact history in its invaded range, then patterns within the data could be analysed statistically (e.g. using multivariate techniques or meta-analysis) to construct quantitative or qualitative models of its impact (e.g., Ricciardi 2003; Kulhanek et al. 2011). In cases where no impact history is available, the invasion history of the species could be used to predict its abundance – a proxy for impact – by relating variation in local abundance across space and time to limiting physico-chemical variables (e.g., Jokela and Ricciardi 2008). Otherwise, predictive information might be obtained from the invasion (impact) history of functionally-similar species, or from trait-based models of high-impact invaders (e.g., Pyšek et al. 2012; Kumschick et al. 2013). Further information on the suggested parameters appears in Appendix S1.

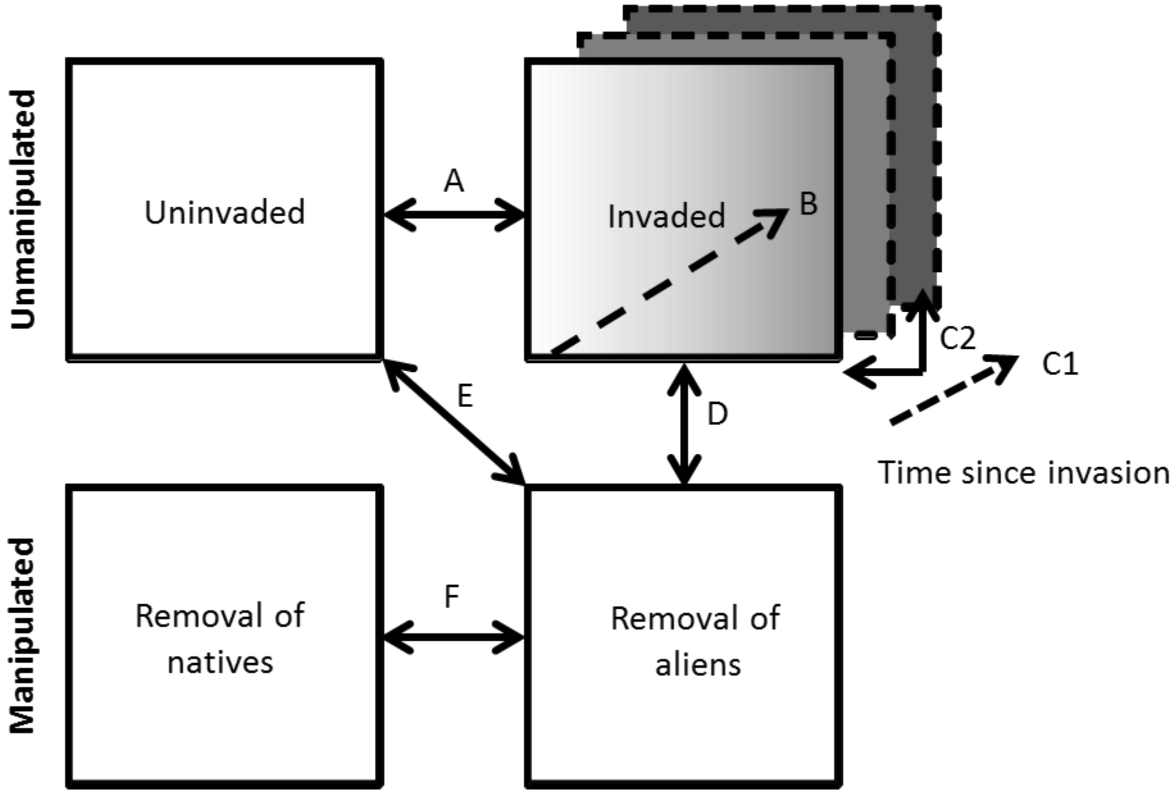

Figure 3: Empirical approaches for studying impacts of invasive alien species using unmanipulated and manipulated plots: (A) observational approach comparing invaded and uninvaded (reference) plots; (B) observational approach along a gradient of alien species abundance (represented here by increased shading); (C1) chronosequence of invasion (stages of different time since invasion shown as discontinuous squares); (C2) a special case of the previous, before-and-after invasion approach comparing only two stages over time; (D) experimental approach comparing invaded and removal plots; (E) experimental approach comparing removal and uninvaded reference plots; (F) experimental approach comparing plots where the alien or the native species have been removed; these can be undertaken to (i) account for the disturbance effect in removal experiments (comparing F, E and D) or (ii) test whether functionally similar native and alien species have different effects.

Table 1: Suggested parameters important for quantifying, predicting and prioritizing management of the impact of alien species. Listed parameters do not cover every potential type of ecological impact (e.g., literature reviews of plant invasions identify at least 15 broad types of impact that are repeatedly measured; see Pyšek et al. 2012; Hulme et al. 2013). Rather, the selection is driven by considerations for the provision of guidance for improving consistency and comparability of the impacts of invasive species among studies (e.g. meta-analysis), and to elucidate context dependency, thus increasing insights into species- and site-related variation, and possibilities for predictions based on impacts previously recorded elsewhere. More detailed information on specific parameters and references appear in Appendix S1.

	Parameter(s)	Rationale
Quantification	Changes to ecosystem function following invasion	Changes to ecosystem functions often affect ecosystem services.
	Per capita effects	Impact is a function of per capita effect (e.g. rate of resource uptake), abundance and interactions between organisms and their environment.
Context dependence	Composition and abundance of native species and traits in the recipient community	Recipient communities can be transformed rapidly by interacting with alien species. Native species may increase or decrease in abundance (or even become extirpated). Food webs may be altered because of the addition or deletion of energy pathways.
	Genetic composition of congeneric native species in the recipient community	Introgression may affect native gene pools.
	Abiotic changes following invasion	Altered physico-chemical processes affect species interactions and ecosystem functions.
	Spatial scale	The overall spatial extent of impact depends on species distribution.
	Time since introduction	Impact varies over time, owing to changes to local abiotic conditions, the abundance of the invader, and the response of the recipient community.
	Other stressors during invasion	Identification of simultaneous biological (e.g. other invaders) and environmental stressors (e.g. climate change, nutrient pollution, land transformations) can have multiple additive or synergistic effects. It is necessary to disentangle these confounding effects to resolve whether the invasion is the cause or the symptom of any impact.
Prediction	Invasion (impact) history of the invader	The invasion history of a species, if well documented, is the most reliable predictor of its impact, although context-dependent influences can cause unexpected outcomes.
	Abundance of the invader	In many cases impact scales with abundance (at least initially). Elucidation of the relationship between abundance and impact will assist in developing species-specific predictive models and for determining thresholds for regime shifts.
	Functional/ phylogenetic novelty (distinctiveness) of the invader respective to native community	Larger impacts are often caused by alien species that are functionally or phylogenetically distinct from the recipient community.

Management prioritisation	Endemism	Native species that have been geographically isolated over evolutionary time scales are naïve to the effects of a broad range of alien species.
	Ecosystem services	Identification of the affected ecosystem services can guide management prioritization and facilitate communication with various stakeholders.
	Rare and Red-listed species	Red-listed species are of priority conservation concern and should be protected against the threat of invasive species.
	Conservation concern of the invaded ecosystem	Prioritization of alien species management depends on the nature of the ecosystem invaded (e.g. protected area, sanctuaries).
	Native biodiversity	Diverse native assemblages are deemed to have more conservation value.
	Ecosystem engineers	Feedbacks, potentially leading to regime shifts, are commonly associated with the impacts of ecosystem engineers.

Supporting Material

Appendix S1: Suggested parameters important for quantifying, predicting and prioritizing management of the impact of alien species.

FOR QUANTIFYING IMPACT UNDER CONSIDERATION			
Parameter(s)	**Rationale**	**Specific metric(s)**	**References**
Changes to ecosystem function following invasion	Changes to ecosystem functions may affect ecosystem services to society.	Various (e.g., productivity, nutrient cycling, contaminant cycling)	Simberloff 2011; Simberloff et al. 2013
Per capita effects	Impact is a function of per capita effect (e.g. rate of resource uptake), abundance and interactions between organisms and their environment.	Resources used and added by the alien species, e.g. functional responses at the individual level	Parker et al. 1999; Dick et al. 2014

FOR CONTEXT DEPENDENCY			
Parameter(s)	**Rationale**	**Specific metric(s)**	**References**
Composition and abundance of native species and traits in the recipient community	Recipient communities can be transformed rapidly by interacting with alien species. Some native species may be extirpated, others may decrease in abundance, and food webs may be altered.	Species and functional richness, evenness, diversity (α, β, γ; depending on the spatial scale of the study)	Hejda et al. 2009; McGeoch et al. 2010; Pyšek et al. 2012; Ricciardi et al. 2013; McKinney & Lockwood 1999; Winter et al. 2008, 2009; Vilà et al. 2006
Genetic composition of congeneric native species in the recipient community	Introgression may affect native gene pools.	Percent of hybrids	Bleeker et al. 2007; Largiadér 2007
Abiotic changes	Physico-chemical processes	Various scale-dependent	Vitousek 1990; Castro-Díez et al.

following invasion		metrics (e.g., habitat structure, fire regime, hydrology)	2009; Simberloff 2011
Spatial scale	The overall spatial area of impact depends on species distribution.	Plot size, sampling unit size	Parker et al. 1999
Time since introduction	Impact varies over time, owing to changes to local abiotic conditions, the abundance of the invader, and the response of the recipient community.	Date of introduction (or establishment)	Strayer et al. 2006; Richardson & Pyšek 2012; Blackburn et al. 2011; Dostál et al. 2013
Other stressors during invasion	Identification of simultaneous biological (e.g. other invaders) and environmental (e.g. climate or land use change) stressors; other invaders can have multiple additive or synergistic effects, e.g. eutrophication. It is necessary to disentangle these confounding effects to resolve the passenger-driver problem.	Various (e.g., disturbance regimes, time series of environmental data, presence/absence of alien species, species interactions, especially measures of the strength of mutualisms and indirect effects)	Simberloff & Von Holle 1999; Didham et al. 2005; MacDougall & Turkington 2005; Didham et al. 2007

FOR PREDICTING IMPACT			
Parameter(s)	**Rationale**	**Specific metric(s)**	**References**
Invasion (impact) history of the invader	The invasion history of a species, if sufficiently documented, is the most reliable predictor of its impact, although context-dependent influences can cause unexpected outcomes.	Literature search of impacts elsewhere. For species with no previous invasion history, information from phylogenetically or functionally similar species may help.	Ricciardi 2003; Kulhanek et al. 2011; Le Maitre et al. 2011
Abundance of the invader	A proxy measure of impact may be abundance. The relationship between abundance and impact will help to find out thresholds for regime shifts.	Biomass, numerical density, cover	Ricciardi 2003
Functional/ phylogenetic novelty (distinctiveness) of the invader respective to native community	Larger impacts are hypothesized to be caused by alien species that are functionally or phylogenetically distinct from the recipient community.	Taxonomic relatedness, phylogenetic distance, functional response, resource consumption rate	Ricciardi & Atkinson 2004; Strauss et al. 2006; Saul et al. 2013; Dick et al. 2014

FOR MANAGEMENT PRIORITIZATION			
Parameter(s)	**Rationale**	**Specific metric(s)**	**References**
Endemism	Native species that have been geographically isolated over evolutionary time scales are naïve to the effects of a broad range of alien species.	Number of endemic native species	Berglund et al. 2009
Ecosystem services	Identification of the affected ecosystem services can facilitate communication with managers and the public.	Socioeconomic valuations of impacts	Van Wilgen et al. 2008; Vilà et al. 2010
Rare and Red-listed species	Red-listed species are of priority conservation concern and should be protected against the threat of alien species.	At the species level: biomass, numerical density, percent cover; at the community level: red-list species richness, diversity	McGeoch et al. 2010
Conservation concern of the invaded ecosystem	Prioritization on alien species management depends on the nature of the ecosystem invaded (e.g. protected area, sanctuaries).	Legal status of the study site	Foxcroft et al. 2013
Native biodiversity	Diverse native assemblages are deemed to have more conservation value.	Native species richness, diversity, functional group richness	McGeoch et al. 2010
Ecosystem engineers	Feedbacks, potentially leading to regime shifts, are commonly associated with the impacts of ecosystem engineers.	Plant and animal species that significantly modify habitats and their functioning	Ricciardi et al. 2013; Gaertner et al. 2014

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Appendix S2: Examples of empirical approaches to quantify the ecological impacts of alien species. Letters (A-F) indicate the approaches according to Figure 3. An X indicates the approach is potentially feasible although not well represented in the literature. We indicate the feasibility level of certain approaches with the following colour code: red = hardly feasible; orange = feasible under certain circumstances; green = highly feasible. Non-field experiments include for example mesocosms, common garden and greenhouse studies. Field experiments can be removals, exclusions or additions. N.A. = not applicable.

		Observational				**Experimental**	
Habitat	**Taxa**	Invaded vs. uninvaded (A)	Abundance gradient (B)	Chronosequence (C1)	Before vs. after (C2)	Non-field	Field (D, E, F)
Terrestrial (above ground, including wetlands)	Vertebrates	Barun et al. 2011; Peay et al. 2013; Dorcas et al. 2011; Rodda & Fritts 1992	Anderson et al. 2006; Strubbe & Matthysen 2007	Carlsson et al. 2010	Phillips & Shine 2006; Koenig 2003; Freed & Cann 2009; Dorcas et al. 2011; Rodda & Fritts 1992	X	Rayner et al. 2007; Fukami et al. 2006
	Arthropods	Rowles & O'Dowd 2007; Tillberg et al. 2007	Bolger et al. 2008	Morrison 2002; Brown et al. 2011	Sanders et al. 2003; Roy et al. 2012	Holway et al. 2002	King & Tschinkel 2006; 2008. Plentovich et al. 2011
	Plants	Vilà et al. 2006; Hejda et al. 2009	Frappier et al. 2003; Schooler et al. 2006	Kwiatkowska et al. 1997	Mills et al. 2009	Dukes 2001	Truscot et al. 2008; Meffin et al. 2010
Terrestrial (soil & epigeous)	Invertebrates	Addison 2009; Bohlen et al. 2004a; Dempsey et al. 2011; Migge-Kleian et al. 2006	Szlavecz et al. 2006	Pop & Pop 2006	Bohlen et al. 2004b	Winsome et al. 2006; Belote & Jones 2009; Snyder et al. 2013	Addison 2009; Bohlen et al. 2004a; Dempsey et al. 2011; Migge-Kleian et al. 2006
Freshwater	Vertebrates	Trumpickas et al. 2011	Marchetti & Moyle 2000	Trumpickas et al. 2011	Zaret & Paine 1973; Trumpickas et al. 2011	Parkos et al. 2003	Knapp et al. 2001
	Invertebrates	Kelly et al. 2006; Strecker et al. 2011	Kelly et al. 2006	Kelly et al. 2006; Strayer et al. 2011	Kipp & Ricciardi 2012	Kestrup & Ricciardi 2009	Strecker & Arnott 2005; Ward &

Habitat	Taxa	Observational				Experimental	
		Invaded vs. uninvaded (A)	Abundance gradient (B)	Chronosequence (C1)	Before vs. after (C2)	Non-field	Field (D, E, F)
							Ricciardi 2010
	Plants/algae	Caralt & Cebrian 2013	Sharma 1984, Dandelot et al. 2005	Olenina et al. 2010	Olenina et al. 2010	N.A.	Bicudo et al. 2007
Marine	Vertebrates	X	X	Green et al. 2012	X	X	Albins 2013
	Invertebrates	Colin et al. 2010	Colin et al. 2010	Colin et al. 2010	Colin et al. 2010	Savini & Occhipinti-Ambrogi 2006	Strain & Johnson 2013; Green & Crowe 2013
	Macroalgae	Jones & Thurber 2010; Byers et al. 2012	X	Davis et al. 1997	Wright & Gribben 2008	Jones & Thurber 2010	Klein & Verlaque 2011; Byers et al. 2012; Wright & Gribben 2008

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