Ecological Impacts of Alien Species: Quantification, Scope, Caveats, and Recommendations

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Despite intensive research during the past decade on the effects of alien species, invasion science still lacks the capacity to accurately predict the impacts of those species and, therefore, to 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 impacts. We review different strategies, including specific experimental and observational approaches, for detecting and quantifying the 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 the impact. We also present strategies for recognizing high-impact species. Our recommendations provide a foundation for developing systematic quantitative measurements to allow comparisons of impacts across alien species, sites, and time.

Keywords: biological invasions, context dependence, ecosystem functioning, management, prediction

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 and Ricciardi 2013). This controversy is partly rooted in the lack of a widely accepted framework for interpreting impacts and a consolidated terminology for impacts 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 toward a predictive understanding of impacts 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 the level of 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 the

impacts of alien species can be distinguished from other concurrent and potentially synergistic stressors (e.g., climate change, landscape alteration; MacDougall and 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 the risks associated with alien species introductions (i.e., the likelihood of their establishment, spread, and impact), but there is ample research in which this has been attempted and on why it has been difficult (see, e.g., Leung et al. 2012, Kumschick and Richardson 2013).

The study of impacts is not a new phenomenon (see e.g., Lodge 1993, Mack and D'Antonio 1998). However, only recently have reviews of the magnitude, scope, and variation of the impacts of alien species, as well as their geographic and taxonomic distinctions and biases, substantially expanded our theoretical knowledge and provided useful conceptual frameworks (e.g., Vilà et al. 2010, Pyšek et al. 2012, Hulme et al. 2013, Ricciardi et al. 2013). Further progress hinges on a more-precise and -comparable quantification of impacts and on an elucidation of the mechanisms behind them, particularly in the context of local factors (coincident stressors,
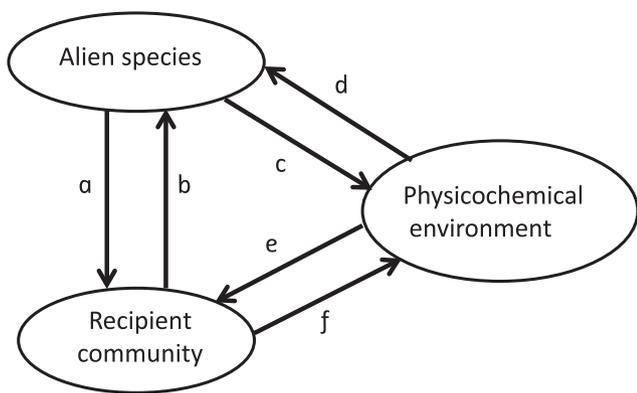
Moderating parameters and scales	Interactions affected
Composition of the recipient community	a, b, e, f
Abiotic changes	c, d, e, f
Abundance of the alien species	a, c
Time since introduction	a, b, c, d, e, f
Other stressors	a, b, c, d, e, f
Spatial scale (extent and grain)	a, b, c, d, e, f

Figure 1. The context dependence of alien species impacts. Knowledge of key interactions and moderating parameters is required to understand and properly quantify impacts. The details of these parameters are given in table 1 and appendix S1.

species interactions, and physicochemical conditions that vary over space and time)—all of which pose challenges for risk assessment and can misguide management decisions. 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 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, on how to plan and conduct empirical studies to understand impacts, and on how to approach impact prediction. We follow Ricciardi and colleagues (2013) in defining an *impact* as a measurable change in the state of an invaded ecosystem that can be attributed to the alien species. This definition includes any change in ecological or ecosystem properties but excludes socioeconomic 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. The 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 (figure 1; see also Hulme 2006).

Among the most important metrics is alien species abundance, which is correlated with the level of impact, although not necessarily linearly. The greater the number of individuals or biomass of the alien species is, the more resources they will use and the greater the extent and strength of their interactions with native species will be (e.g., Parker et al. 1999, Ricciardi 2003). Catford and colleagues (2012) provided a practical way of taking the abundance of alien species into account: identifying abundance thresholds and using categorical scores.

Time since invasion also influences the level of impact, through temporal changes in the abundance of the alien species, adaptation by the recipient community, postinvasion evolution, and variation in the physicochemical 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—for example in the case of migrating animals.

The challenge of context dependence

The impacts of alien species vary both in their location and their duration or frequency, 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, interaction a (or c affecting e) is strong in both directions; in the passenger model, interaction d (or e affecting b) is strong, whereas a is weak. Also illustrated are additive (a and e are strong) and synergistic models (in which a, c, d, and e are strong).

An increased understanding of context dependence is required in order to improve our ability to predict impacts. Resource managers can play a valuable role in their initial detection and by providing information on the shifting contexts of impacts, through their observation of environmental change. However, *quantifying* these changes requires considerable research and sufficient resources. Governments, landowners, and managers, as well as the general public, could profit from the outcomes of such studies. Moreover, funding should be allocated by all of 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.

The prioritization of management

It is beyond the scope of this study to discuss management prioritization if the passenger model dominates for a particular system. In the following section, we therefore only address impacts in situations in which 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, therefore, to change to alternative states (i.e., causing regime shifts)—should be considered as potentially the most disruptive and should be 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. The outcomes depend on the traits of the alien species, the characteristics of the invaded habitat and of the invaded community (figure 1; Pyšek et al. 2012, Kueffer et al. 2013), 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 (table 1 and supplemental appendix S1; Linder et al. 2012, Ricciardi et al. 2013).

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 levels of impact (Nentwig et al. 2010, Kumschick et al. 2013) and have shown that the diversity of habitats that an alien species can occupy could be a useful parameter in models predicting that species' impact (Evans et al. 2014).

Implications for prediction and prevention

We need to mitigate impacts not only when aliens are present but, ideally, also when they are expected to invade and likely to have an undesirable impact in the future. Preinvasion assessments with the purpose of predicting the risk of invasion and impact are used in many parts of the world (Kumschick and 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 (figure 2; Kulhanek et al. 2011). Such studies can also contribute to the justification for labeling a species as a potential invasive or as causing a potential impact elsewhere as an often-suggested predictor of invasion success and impact, respectively, in the new range (Leung et al. 2012, Kumschick and Richardson 2013). Figure 2 outlines a logical series of empirical approaches for forecasting impacts, primarily on the basis of impact and invasion history. Vitousek (1990) posited that alien species that have large effects on ecosystem processes differ from the native species in their resource acquisition, resource efficiency, or capacity to alter disturbance regimes; examples of this include alien plants that change fire regimes following their introduction, such as many invasive grasses (D'Antonio and Vitousek 1992, Yelenik and D'Antonio 2013), and 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 naive 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 differ not in functional type but in performance and behavior. For example, alien and native predators may differ in their feeding behaviors toward 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).

Table 1. Suggested parameters important for quantifying, predicting, and prioritizing the management of the impact of alien species.

| Purpose	Parameter	Rationale
Quantification	Changes to ecosystem function following invasion	Changes to ecosystem functions often affect ecosystem services.
	Per capita effects	The level of impact is a function of per capita effects (e.g., the 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 physicochemical 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	Impact history of the invader	The impact 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, the level of 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 or 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 prioritization	Endemism	Native species that have been geographically isolated over evolutionary time scales are naive 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 alien species.
	Conservation concern of the invaded ecosystem	Prioritization of alien species management depends on the nature of the ecosystem invaded (e.g., protected area, sanctuary).
	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.

Note: The listed parameters do not cover every potential type of ecological impact (e.g., literature reviews of plant invasions have identified 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 the consistency and comparability of the impacts of invasive species among studies (e.g., meta-analysis) and to elucidate context dependency, therefore 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.

Understanding the mechanisms behind an impact is ultimately important to predicting the impacts of new alien species with no alien relatives. Trait-based models can give indications of such mechanisms, but, so far, it has not been explored to what degree traits correlated with impact have a predictive value for new invaders (Evans et al. 2014).

Experimental methods and approaches to investigate impacts

Various approaches have been taken to study the impacts of different taxa in different habitat types (supplemental appendix S2). Most of these studies have involved comparisons of invaded and 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 the 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, because it allows large amounts of data to be collected relatively easily and inexpensively. However, it does not demonstrate causality, because the
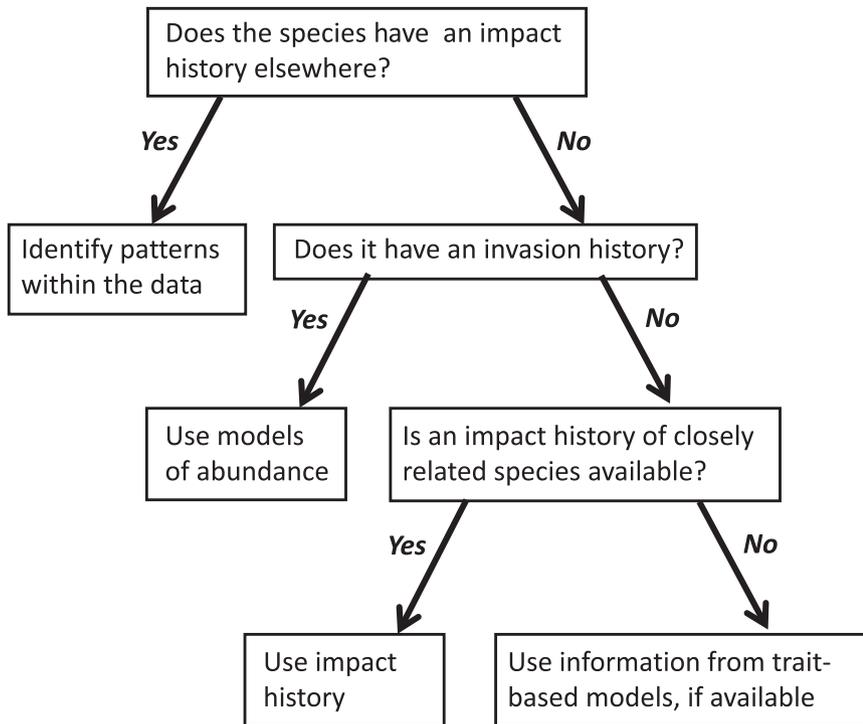
Figure 2. Empirical approaches for forecasting impacts of alien species, starting with the most desirable data. If an alien species has a sufficiently documented impact history in its invaded range, the patterns within the data could be analyzed statistically (e.g., using multivariate techniques or meta-analysis) to construct quantitative or qualitative models of its impact (e.g., Ricciardi 2003, Kulhanek et al. 2011). In cases in which no impact history is available, the invasion history of the species could be used to predict its abundance—a proxy for its level of impact—by relating variation in local abundance to limiting physicochemical variables (e.g., Jokela and Ricciardi 2008). Otherwise, predictive information might be obtained from the impact (invasion) 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. Source: Adapted with permission from Ricciardi (2003).

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 an analysis of the relationships in the time since invasion and the

magnitude of impact, provided that there are good historical data to determine when the invasion began (c_1 in figure 3). Of particular interest are comparisons of sites before and after invasion (c_2 in figure 3). This is only feasible under certain circumstances, such as in locations in which 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 and 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 the 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 and Turkington 2005). For example, the observed decline of native ladybird beetle species in arboreal habitats in the UK after invasion by the alien ladybird beetle *Harmonia axyridis* is also correlated with changes in maximum temperature and rainfall among years (Brown et al. 2011). However, path analysis and structural equation modeling can sometimes be applied to disentangle the relative importance of alien species and other stressors to native species declines (e.g., Light and Marchetti 2007, Hermoso et al. 2011).

Although, in any aspect of ecology, the manipulation of parameters is the best way to demonstrate causality, field removal experiments to identify the impacts of alien species (d in figure 3, appendix S2) have been reported in only a small number of studies. The most prominent examples concern the removal of alien plants, but field manipulation experiments represent less than 14% of the studies on the impacts of alien plants (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
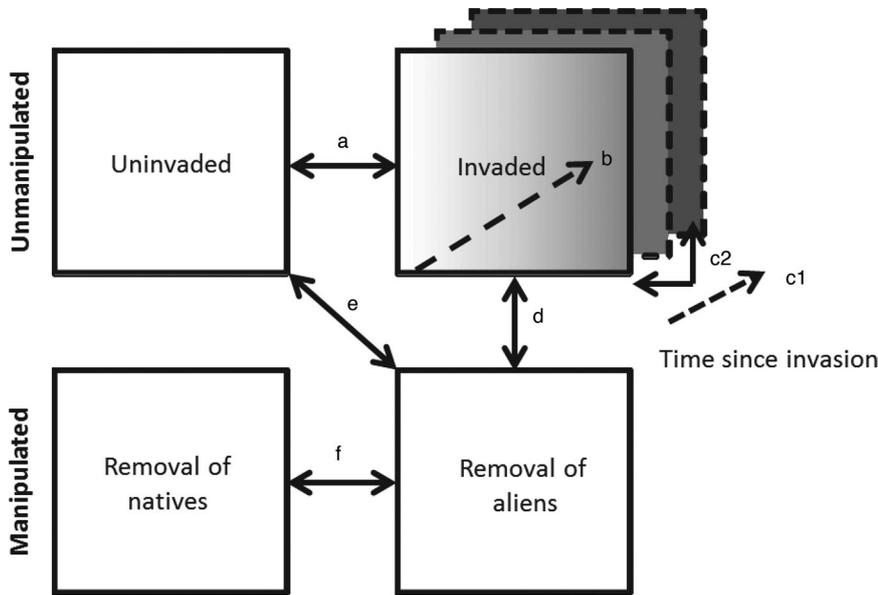
Figure 3. Empirical approaches for studying the impacts of invasive alien species using manipulated and unmanipulated plots: (a) Observational approach comparing invaded and uninvaded (reference) plots. (b) Observational approach along a gradient of alien species abundance (higher abundance is represented here by darker shading). (c1) Chronosequence of invasion (stages of different time since invasion shown as discontinuous squares). (c2) A special case of the previous approach: a 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 from which the alien or the native species has been removed; these can be undertaken to account for the disturbance effect in the removal experiments (comparing panels (f), (e), and (d)) or to test whether functionally similar native and alien species have different effects.

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 and 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 are intact invaded plots; even if they harbor high levels of species richness, their species composition can be different, and they are 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 the experimental removal of alien species with the removal of native species, where that is deemed appropriate (f in figure 3), to distinguish the alien–native effect from the disturbance effect. For sessile species, comparing ecological differences between areas in which 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 the 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 with that of 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).

The removal of an alien species does not necessarily (or not immediately) lead to the restoration of preinvasion 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 that in a reference site, not only in terms of species richness but also in terms of species composition and ecosystem functioning. For example, following the removal of monkey flowers (*Mimulus guttatus*) from a riparian system, the resident plant community recovered and increased in species richness over time but toward a different community composition than that of uninvaded sites (Truscott et al. 2008). This demonstrates that different methodological approaches can lead to different conclusions based on extant 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) showed that the alien species reduced the abundance and richness of small coral-reef fishes more than of 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 a single species in the community when it is 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 (appendix S2; Meffin et al. 2010) but highly challenging, because the 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 intended to obtain observations of 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 the impacts of soil organisms and aquatic alien species (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, and f in figure 3), not only to reveal ecological impacts and to 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 they are carried out in such a way as to allow this recommended design. Spatial and temporal variation in impacts must also be taken into account by careful replication and monitoring of the sampled sites (Kueffer et al. 2013).

Conclusions

Not only is research on the impacts of alien species 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 it 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 synthesizing solid evidence of the impacts caused by alien species facilitates communication with the public and better informs policy- and decisionmakers. 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 and Ricciardi 2013). In fact, many alien species cause substantial and sometimes irreversible impacts, but we have not yet achieved a predictive understanding of when or where these impacts will occur or which species will cause them.

Furthermore, our synthesis points out that different experimental methodologies are appropriate for different taxa because of particular properties of the species and ecosystems involved, even though most methods are theoretically applicable for most organismal groups (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 are 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 impacts and the perceived differences between organismal groups.

A more balanced view of impacts and a standardized protocol of how to quantify impacts—that is, which parameters to measure and which metrics to apply at invaded sites—are needed. Therefore, we have proposed a set of parameters on which to base the objective quantification of impacts. The collation of information on these parameters will contribute to a better understanding of context dependence and to a robust framework for prioritization.

Acknowledgements

Supplemental material

The supplemental material is available online at *http://bioscience.oxfordjournals.org/lookup/suppl/doi:10.1093/biosci/biu193/-/DC1.*

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