

REVIEW AND SYNTHESES

Eight questions about invasions and ecosystem functioning

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Abstract

I pose eight questions central to understanding how biological invasions affect ecosystems, assess progress towards answering those questions and suggest ways in which progress might be made. The questions concern the frequency with which invasions affect ecosystems; the circumstances under which ecosystem change is most likely; the functions that are most often affected by invaders; the relationships between changes to ecosystems, communities, and populations; the long-term responses of ecosystems to invasions; interactions between biological invasions and other anthropogenic activities and the difficulty of managing undesirable impacts of non-native species. Some questions have been answered satisfactorily, others require more data and thought, and others might benefit from being reformulated or abandoned. Actions that might speed progress include careful development of trait-based approaches; strategic collection and publication of new data, including more frequent publication of negative results; replacement of expert opinion with hard data where needed; careful consideration of whether questions really need to be answered, especially in cases where answers are being provided for managers and policy-makers; explicit attention to and testing of the domains of theories; integrating invasions better into an ecosystem context; and remembering that our predictive ability is limited and will remain so for the foreseeable future.

Keywords

Alien species, biodiversity, ecological engineering, ecosystem function, ecosystem management, exotic species, invasive species, long-term studies, non-native species, traits.

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INTRODUCTION

More than 20 years have passed since Vitousek (1990) highlighted the large role that biological invasions can play in ecosystem function, yet the link between biological invasions and ecosystem function seems not to have been enthusiastically embraced by either invasion ecologists or ecosystem ecologists. Invasion ecologists have studied the responses of ecosystems far less often than they study populations or communities, and understand them less well (e.g. Parker *et al.* 1999; Ruesink *et al.* 2005; Lovett *et al.* 2006; Kenis *et al.* 2009; Cucherousset & Olden 2011). Although ecosystem ecologists do study invasions, the field does not appear to put biological invasions on par with factors such as climate change, nutrient loading, land use change and disturbance when considering what drives the structure and function of 21st century ecosystems (e.g. Ågren & Andersson 2012). Furthermore, in contrast with the population and community ecology of invasions, which are guided by a large number of influential hypotheses, theories and frameworks (see Catford *et al.* 2009; Foxcroft *et al.* 2011; Gurevitch *et al.* 2011 for an introduction), much of the work on the effects of invaders on ecosystems consists of case studies and demonstrations of impacts, rather than tests of theories.

If biological invasions are important in determining the structure and function of ecosystems, as I argue below, then we will be unable to satisfactorily understand or manage ecosystems without considering invaders and their impacts, any more than we could expect to understand or manage ecosystems without taking nutrient inputs into account. Likewise, a satisfactory accounting and management of the effects of biological invasions must consider the effects on ecosystem processes, just as it considers effects on populations,

communities or human economies. Thus, understanding how biological invasions affect ecosystems may be central to understanding and managing both ecosystems and invasions.

In this article, I propose a series of eight questions that I think are central to understanding the link between species invasions and ecosystem functioning. After introducing each question, I will assess how well it has been answered, evaluate the prospects for achieving a better answer and suggest ways in which progress might be made. I hope that this exercise will stimulate discussion about how invasion ecologists and ecosystem ecologists might better work to define and answer questions of mutual interest.

I use the term ‘nonnative species’ to describe species that were moved out of their native range by some human action (deliberate or accidental) and established a population in this new range. Although I recognise that ‘ecosystem function’ is validly used to cover a wide range of ecological processes (e.g. Likens 1992; Simberloff 2011), here I will adopt a narrower definition simply to make the subject more tractable. By ‘ecosystem function’, I mean processes that determine the amount, forms, distribution, fluxes, import and export of energy and various materials, including (but not limited to) carbon, macronutrients such as nitrogen and phosphorus, important trace materials and toxins.

EIGHT QUESTIONS

Can species invasions affect ecosystem functioning?

This is the most fundamental question about species invasions and ecosystem functioning, and it has been adequately answered. Even if we set a very high threshold for ‘affect’, we know that all kinds

of invaders (plants, vertebrates, invertebrates and microbes) can cause large changes to all kinds of functions in all kinds of ecosystems throughout the world (Crooks 2002, Dukes & Mooney 2004, Ehrenfeld 2010, Simberloff 2011 provided extensive catalogues of examples). In particular, invasions have been shown to affect the amount and quality of primary and secondary production; decomposition; pools and flows of materials (nutrients, toxins, sediments or soils, and water); production and destruction of engineered structures such as reefs and burrows; frequency and severity of fires and other disturbances; availability of light; and temperature. Many changes in ecosystem functioning caused by biological invasions have been greater than two-fold in size and have covered large geographic areas for long periods of time (at least decades) (e.g. Crooks 2002; Dukes & Mooney 2004; Liao *et al.* 2008; Ehrenfeld 2010; Simberloff 2011; and references cited therein). Thus, the effects of species invasions on ecosystem functioning can be as large as those of any human actions (e.g. addition of nutrients and toxins, changes to disturbance or hydrologic regimes, harvest of organisms), and can affect most ecosystem functions.

There has been some interest in the related question about how species affect ecosystem functioning. The usual answer is that a species affects ecosystem functioning if it is functionally distinctive in how it acquires key resources, is placed in the food web, affects disturbance regimes or responds to environmental factors, through either direct or indirect pathways (Vitousek 1990; Chapin *et al.* 1997; Wardle *et al.* 2011). This answer covers so many possibilities that it provides little insight except to emphasise that non-native species, like native species, can affect ecosystems in the most varied ways.

How frequently do species invasions affect ecosystem functioning?

Given that species invasions can affect ecosystem functioning, are they a major determinant of contemporary ecosystem function, or just a striking but rare occurrence? This question usually has been formulated as 'what fraction of established invaders affect ecosystem functioning?' Several authors have suggested that the answer to this question is ~10% (e.g. Mills *et al.* 1993; Ruiz *et al.* 1999; Richardson *et al.* 2000; Vilà *et al.* 2010). These analyses typically have several important flaws: they usually are based on some form of expert opinion (species are simply scored as having a substantial impact or not, without any actual species-by-species study of impacts), this expert opinion is usually based on a few studies of some functions of the more conspicuous invaders and no studies at all of the less conspicuous invaders, these studies often have low statistical power to detect impacts, there is rarely any quantitative definition of what constitutes an impact, and impacts usually are assessed at one point in time rather than over the long-term. A rigorous answer to this question would require careful definition of 'impact' (in terms of magnitude and spatial and temporal extent) and actual studies of a representative sample of the invaders in a region. Nevertheless, as Simberloff (2011) concluded in his recent review, it seems safe to conclude that a large minority (I would say 3–30%) of established invaders substantially affect ecosystem functioning, given any typical definition of what constitutes an impact. This answer tells us that at the current rate of invasions (often 0.1–1 new species/year; e.g. Mills *et al.* 1993; Ruiz *et al.* 1999; Hulme *et al.* 2009), invaders are likely to affect the functioning of many

ecosystems around the world, and pose a challenge to the management of goods and services from those ecosystems. The fact that most invaders apparently are benign (e.g. Davis *et al.* 2011) does not affect this conclusion. A more precise answer probably is not needed for most purposes.

An alternative way to pose this question that may sometimes be more useful than focusing on species would be to ask 'How many ecosystems are substantially affected by nonnative species?' This formulation of the question focuses on the degree of change to ecosystems, rather than on the likelihood of impact by a typical invader, and may be more tractable than the more common formulation of this question. Answers to parallel questions about how many ecosystems are substantially affected by other anthropogenic activities (e.g. dams: Nilsson *et al.* 2005; nonpoint-source pollution: Brown & Froemke 2012) have been very useful and influential in showing the extent and severity of those effects, and allowing comparison with other drivers of ecosystem functioning.

A first-order answer to this question might be obtained by summing the number of known high-impact invaders across the ecosystems of interest. Alterations to ecosystem function would be possible at all sites that contain at least one high-impact invader, and ecosystems containing several such high-impact invaders would be very likely to have been affected by species invasions. This exercise seems not to have been carried out, although maps showing the total number of invaders (e.g. Leprieur *et al.* 2008) could be easily modified to include only species known or thought to have substantial impacts. This level of analysis would be feasible for many regions and many kinds of invaders.

A better approach would be based on the abundance of the invader, rather than simply its presence. An example is shown in Fig. 1, which shows the abundance of zebra mussels across a group of European lakes (Strayer 1991). Judging that ecosystem impacts are

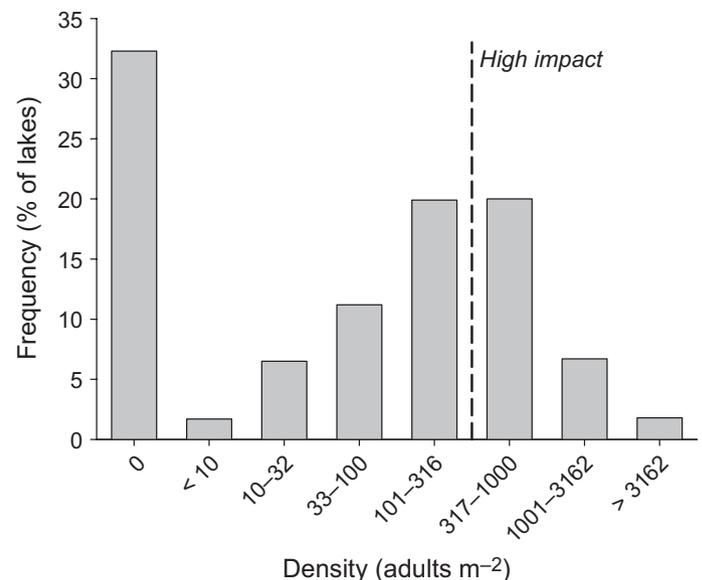


Figure 1 Frequency of densities of zebra mussels in European lakes (based on the study of Strayer 1991). The vertical dashed line indicates the population density above which significant ecosystem impacts might be expected (cf. Higgins & Higgins & Zanden 2010).

likely in any lake where densities exceed $\sim 300 \text{ m}^{-2}$ (cf. Higgins & Vander Zanden 2010), we could conclude that $\sim 30\%$ of European lakes in this group have been affected by the zebra mussel. If this exercise were repeated for many or all suspected high-impact invaders in a region, and the results summed, we could obtain a good estimate of what proportion of ecosystems have been strongly affected by non-native species. Zaiko *et al.* (2011) published a semi-quantitative version of such an analysis for the Baltic Sea that suggested strong regional differences in invasion impacts. Such an analysis may be feasible for other well-studied regions.

A more rigorous approach would be to actually measure the change in a specified ecosystem function (e.g. primary production, denitrification) caused by invaders. Although simple in concept, this approach would be difficult to implement in most situations. Such a measurement would have to account for the combined direct and indirect effects of multiple invaders, as well as their interactions with other factors. Experiments to answer this question would have to include all relevant invaders (and the different combinations of invaders that occur in the region of interest), and run over long enough time-scales and large enough spatial scales to provide meaningful answers. An analysis of long-term field data would require good data on the ecosystem function of interest extending back before the invasions, as well as data on invaders themselves and other variables that affect the ecosystem; such data sets are vanishingly rare. As a result of these difficulties, this approach probably will be feasible only in circumscribed research settings, and probably will not be practical for broad-scale assessments.

Although the second formulation of this question appears not to have been answered, I suspect that we'll find that impacts of species invasions on ecosystem function are as widespread as those of any of the well-known human impacts on ecosystems (e.g. disturbance, nutrient loading, toxification) for many regions. I do think that this formulation of the question would be worth answering *approximately*, because it could show the very broad impact of species invasions, identify regions in which species invasions have had large or small effects, and perhaps have the same sort of influence as parallel analyses on other leading human impacts. However, I again would question whether we need a really *precise* answer to this question, or whether an approximate answer would suffice for the purposes just mentioned, as well as most other purposes.

Which invasions will change ecosystem function?

There are two common forms of this question: What sorts of non-native species are most likely to affect ecosystem function?; and What sorts of systems are most sensitive to species invasions, from the viewpoint of ecosystem functions? Most answers to both forms of this question have been related to the familiar framework of Parker *et al.* (1999):

$$\text{Impact} = \text{Range} \times \text{Abundance} \times \text{Per Capita Effect}$$

(It is perhaps worth noting the Zavaleta *et al.* 2009 proposed similar criteria for determining whether ecosystem functions would change as the result of the loss of a species.) In general terms, ecologists have suggested that species have high per capita impacts if they are functionally distinctive in some way related to the acquisition of key resources, their position in the food web, their effect on disturbance regimes or their responses to environmental factors (e.g. Vitousek 1990; Chapin *et al.* 1997; Wardle *et al.* 2011). Although these ideas are simple and appealing, it has not proven to be easy to estimate either the abundance or the per capita impact of an invader before the invasion has actually happened.

Most invasion ecologists seem to have focused on the last term in the Parker equation, identifying powerful invaders as those that have high per capita impacts because they are functionally distinctive. The iconic example is the transformative impact of the nitrogen-fixing tree *Morella faya* on the Hawaiian ecosystems that it invaded (Vitousek *et al.* 1987; Vitousek & Walker 1989). Likewise, insular ecosystems such as oceanic islands and lakes, which are thought often to have low functional diversity, may be sensitive to the arrival of new invaders that bring new traits into the ecosystems (cf. Ricciardi & Kipp 2008; Ricciardi & MacIsaac 2011; Vilà *et al.* 2011; Pyšek *et al.* 2012). Perhaps because of the difficulty in quantifying functional distinctiveness *a priori*, such work has typically been used mostly in *post hoc* explanation rather than prediction, however. The study of Wright *et al.* (2006), which showed that use of conventional functional groups did not predict ecosystem function any better than random groups, should serve as a caution to invasion ecologists that trait-based analyses, however, logically appealing, may fail to perform in practice and must be tested.

It may be useful to examine these ideas a little further. Consider members of a native guild that have a certain distribution of traits

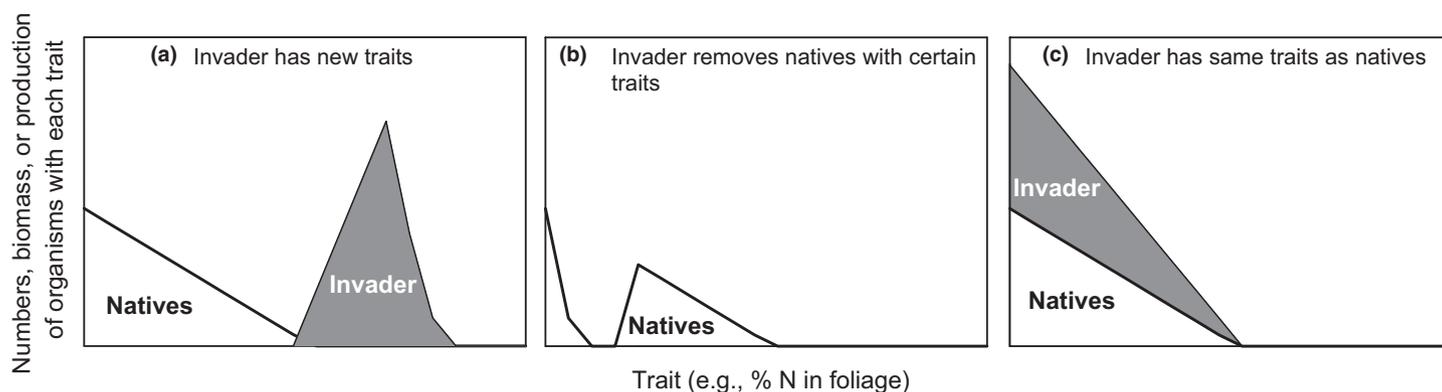


Figure 2 Three idealised examples of how an invader can affect the distribution of traits (the 'trait spectrum') in an ecosystem: (a) the invader has different traits from the natives; (b) the invader selectively displaces natives that have certain traits; (c) the invader has the same traits as the natives, but increases the overall abundance of individuals with those traits in the ecosystem.

(I mean effect traits; i.e. traits that determine the effects of the organism on the ecosystem) along some trait axis (Fig. 2). The trait could be body size, or C : N ratio, or the size of particles eaten in the diet or any trait of interest. The height of the distribution represents the abundance (or biomass, or production) of each trait in the guild. This might be called the 'trait spectrum' for that ecosystem (cf. D'Antonio & Hobbie 2005; Wardle *et al.* 2011). This trait spectrum can be affected by the invasion of a new species in three non-exclusive ways (Fig. 2): the invader could bring entirely new traits into the ecosystem (Fig. 2a), it could change the trait spectrum of native species by altering their abundance or composition (Fig. 2b), or by virtue of its abundance, it could change the height of all or part of the trait spectrum (Fig. 2c). Although real invaders probably have all three of these effects to some extent, only the first has received much attention from invasion ecologists (but see Fig. 1 of Ruiz *et al.* 1999).

In the simple world of Fig. 2, the effect of the invader on ecosystem function will be proportional to the change in the trait spectrum following the invasion. But an examination of Fig. 2 also reveals the complexities of even this simple trait-based approach. First, the difference between the pre- and post-invasion trait spectra depends on the traits already contained in the ecosystem before invasion, so 'functional distinctiveness' depends on the invaded system as well as the invader. Thus, as others have pointed out (e.g. de Moura Queirós *et al.* 2011), distinctiveness and therefore impacts can be highly context-dependent. Second, the abundance of the invader also usually is very context-dependent, and there have been few successful attempts to predict the abundance of new invaders (e.g. Mellina & Rasmussen 1994). Third, the trait spectrum of the invaded community itself changes as the invader interacts with the species already present in the ecosystem. Such changes may be idiosyncratic and very hard to predict. Fourth, the characteristics of the ecosystem determine the relevance of the trait axis chosen. A trait axis (say, nitrogen content) that is highly relevant in determining function in one ecosystem (e.g. a nitrogen-limited system) may be totally irrelevant for another function or another ecosystem (a non-nitrogen limited system). Thus, the domains of any such trait-based analysis will have to be carefully defined.

As an alternative to focusing explicitly on traits, taxonomic distinctiveness may be used as a surrogate for functional distinctiveness (Lockwood *et al.* 2001; Ricciardi & Atkinson 2004; Strauss *et al.* 2006). All of these studies showed that taxonomically distinctive invaders had stronger effects than those with close relatives in the native biota. A difficulty with this otherwise appealing approach is that it considers only the invaders that establish, and so is not as useful as a screening tool to identify potentially problematic invaders before they invade. It seems natural to suppose that species highly dissimilar to the native biota would be less likely to succeed in an invasion because of a poor match to environmental conditions at the invasion site. This would suggest that distinctive species might be more likely to have an impact if they establish, but might be less likely to establish if introduced. The overall probability of an impact if introduced (the quantity of interest for screening) might therefore be hard to predict.

Finally, invasion history can be used to predict the impacts of invasions. This may be the strongest tool for predicting the impact of an invader, but is severely limited by the inadequacy of existing data. In an analysis of the ecological impacts of 19 of the 20 most problematic aquatic invaders in the world, Kulhanek *et al.* (2011a)

found that the sign of the impact of an invader (positive vs. negative) was almost always consistent across invasion sites, suggesting that invasion history is at least a qualitatively robust predictor of impacts. However, they found adequate data to support a quantitative analysis of impacts for only a few impacts of a few species, even for some of the world's most high-profile aquatic invaders (Fig. 3). Consequently, it is possible to do a quantitative analysis of impacts (and answer questions about what characteristics of the site determine impacts, for example) for only a handful of the best-studied invaders (Ricciardi 2003; Ward & Ricciardi 2007; Higgins & Vander Zanden 2010; Kulhanek *et al.* 2011b).

Although invasion ecologists have devoted a great deal of attention to answering various forms of this question, it has not been answered. It seems likely that it will be difficult to provide general answers, although it may well be possible to provide satisfactory answers over limited domains (fire-prone grasslands, suspension-feeding bivalves). One practical consequence of our inability to predict the impacts of invaders is that we should be very careful about new introductions.

Which ecosystem functions are affected most often or most severely by invaders?

This question seems to have received little attention from invasion biologists, even though it would be of great interest to ecosystem ecologists to know if some functions are more robust than others against species invasions. One might hypothesise, for example, that functions like primary production that can be performed by many species might be more robust against species change than specialised functions such as nitrogen fixation or litter shredding (e.g. Levin *et al.* 2001). Good data about the relative change in different functions are available for some important groups of invaders, most notably plants (Fig. 4; Liao *et al.* 2008; Ehrenfeld 2010; Vilà *et al.*

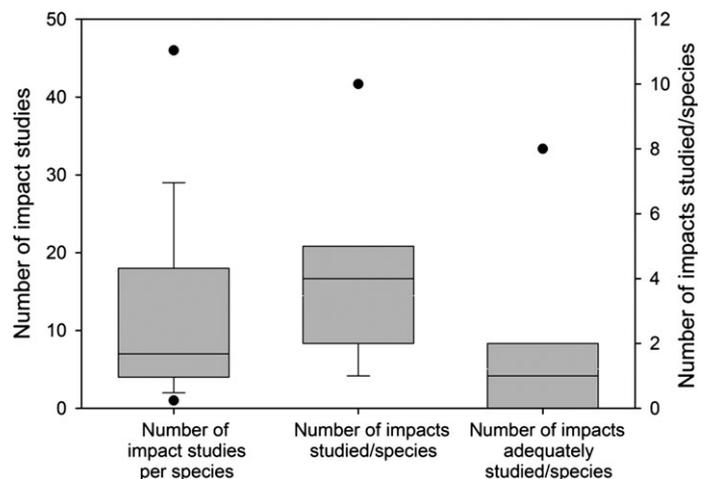


Figure 3 Amount of information available on the ecological impacts of 19 of the 20 most problematic aquatic invaders in the world. From left to right, the boxes-and-whiskers show the total number of studies of any kind of ecological impacts for each species (left y-axis), the number of kinds of impacts studied per species (right y-axis), and the number of impacts per species that have been adequately studied (i.e. ≥ 5 studies) to allow for quantitative analysis of impacts (right y-axis). Impacts include all kinds of ecological impacts, not just ecosystem impacts as defined here, so the available database on ecosystem impacts is even smaller than shown here. From data of Kulhanek *et al.* (2011a).

2011; see also Higgins & Vander Zanden's 2010 review of zebra mussel impacts). It is clear, at least for these groups, that some ecosystem functions are affected more frequently and more severely than others. The reasons for these differential impacts have not yet been explained. It seems entirely feasible to conduct meta-analyses like that of Liao *et al.* (2008) for various important functional groups of invaders (e.g. suspension-feeding bivalves, reef-builders, etc.) to document the typical effects (if any) of that group, and compare one ecosystem function to another. The diversity of invaders and invaded systems may make it difficult to find broader generalisations, but it certainly seems worth looking. For instance, based on the literature on plant invasions (e.g. Liao *et al.* 2008; Ehrenfeld 2010), one might hypothesise that invaders typically speed up cycling of limiting materials. How robust is this pattern? Does it apply to animals and microbes as well as plants?

How are changes in ecosystem functioning related to changes in populations and communities?

Impacts of biological invasions on populations and communities have been much better studied than impacts on ecosystems (e.g. Parker *et al.* 1999; Ruesink *et al.* 2005; Lovett *et al.* 2006; Kenis *et al.* 2009; Cucherousset & Olden 2011). Does this mean that ecosystem impacts are less frequent than those on populations and communities (and therefore less worthy of study), or that impacts on ecosystems can simply be extrapolated or predicted from impacts on populations and communities (so that the more difficult studies on ecosystems can be avoided)? These expectations could arise from viewing the effects of biological invasions on ecosystems as shown by the solid arrows in Fig. 5, in which invasions affect populations, which alters community structure, which in turn affects ecosystem structure and function (Cucherousset & Olden 2011 presented a similar diagram). In this interaction chain, we might expect the ecosystem impacts of an invader to be correlated with its impacts on populations and communities, but attenuated by complementarity and redundancy among species (cf. Schindler 1987; Frost *et al.* 1995).

However, it is well known that the solid arrows in Fig. 5 do not adequately describe how non-native species affect ecosystem function. Many invading species, called ecosystem engineers, affect ecosystem characteristics directly (Crooks 2002), without being mediated by populations or communities in the invaded region. Such engineering effects can then have strong effects on populations and communities (as well as the invader itself), reversing the direction of causation in Fig. 5. Examples of non-native engineers with strong effects on ecosystems are common, and are known from all kinds of ecosystems, and include such well-known examples as eucalyptus (*Eucalyptus* spp.), Australian pine (*Casuarina equisetifolia*) and other trees, cordgrass (*Spartina* spp.) in coastal wetlands,

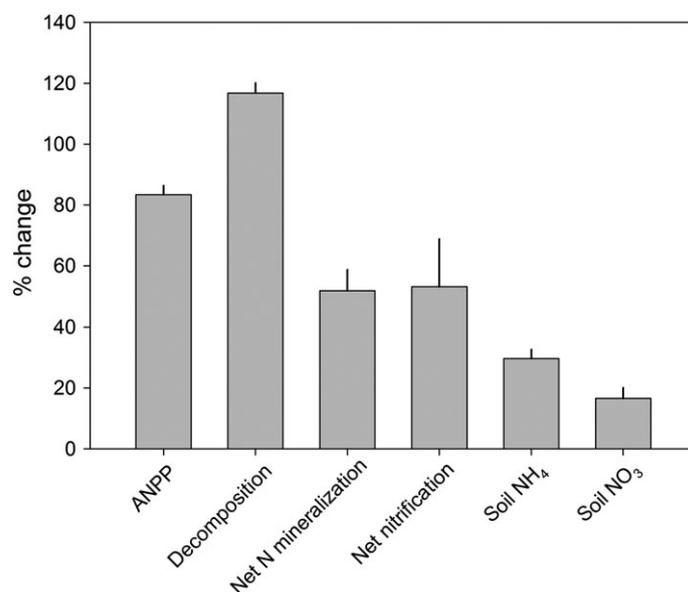


Figure 4 Effects of non-native plants (mean and 95% confidence limit) on selected ecosystem variables (ANPP = aboveground net primary production), from data of Liao *et al.* (2008).

beavers (*Castor canadensis*) in Patagonia and elsewhere, various species of freshwater and marine mussels, wild boars (*Sus scrofa*), common carp (*Cyprinus carpio*), and so on (e.g. Crooks 2002; Anderson & Rosemond 2007; Kulhanek *et al.* 2011b). Thus, there is certainly no reason to expect ecosystem-level impacts to be smaller or less frequent than population- or community-level effects. Both the interaction pathways shown in Fig. 5 suggest the possibility of correlations in the strength of these different levels of impacts, although such correlations are not a logical necessity. The time-constants of the two pathways shown in Fig. 5 may be quite different, especially in cases involving soil formation, sediment accumulation or other slow processes, leading to uncoupling of ecosystem and community/population impacts (Vilà *et al.* 2011). If this question is regarded as worth answering, I think that it would be feasible to answer through careful field studies and meta-analyses.

How do effects on ecosystem functioning change through time?

This is a question that many people assume has been answered, but which I think is still largely unanswered. Many scientists assume that the impacts of an invader decrease over time, as shown in Fig. 6a. This figure makes intuitive sense – the system and the invader come to terms with one another, and something catches up with the invader. Furthermore, this graph is consistent with a number of hypoth-

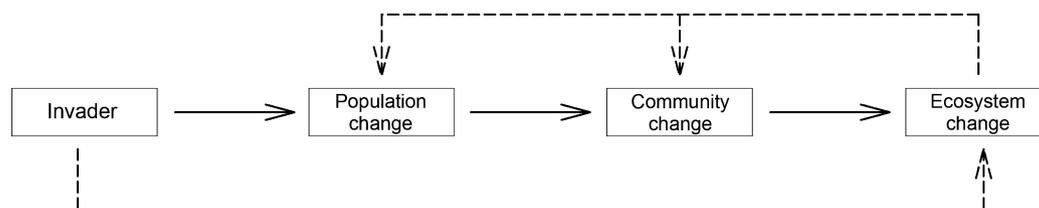


Figure 5 Alternative pathways by which biological invasions affect ecosystems: solid lines = traditional view; dashed line = ecological engineering.

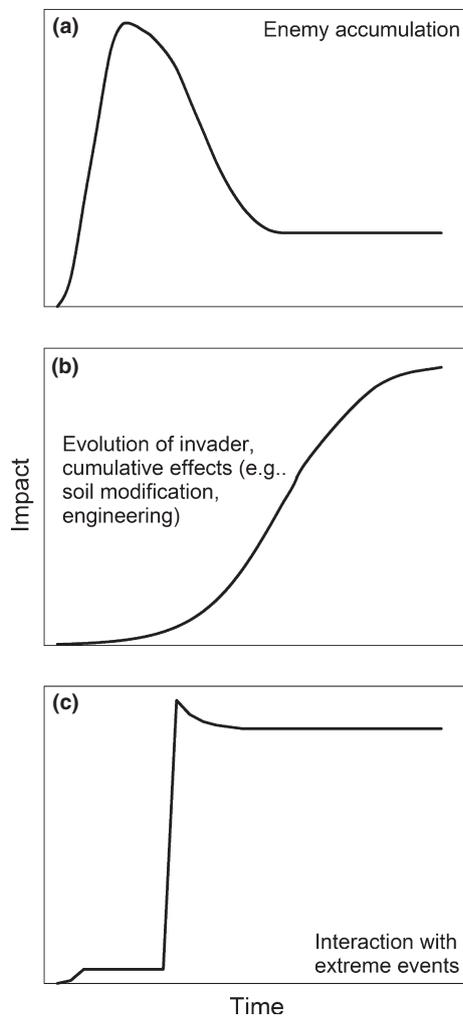


Figure 6 Three possible time-courses for the effects of a non-native species, along with examples of mechanisms that might produce those time-courses.

eses in invasion ecology that postulate that invaders are successful initially because they escape their enemies, and that enemies gradually accumulate over time (e.g. Carlsson *et al.* 2009; Diez *et al.* 2010; Mitchell *et al.* 2010; Wardle *et al.* 2011). This graph also offers a hopeful perspective on invasions – after an initial period of high impact, the impacts of the invader will drop to tolerable levels. Management can focus on mitigating just the short-term impacts of the invader; there may be no large long-term impacts to worry about. In this view, the invasion is a short-term annoyance, not a profound problem.

There are four problems with this answer. First, the x -axis of Fig. 6a does not have a time-scale, so we don't know whether the impacts of the invader moderate after 10 years or ten thousand years. The time-scale of the x -axis is critical for determining whether impacts are tolerably short-lived or long-lasting and effectively permanent, and therefore guiding management. Second, the y -axis does not have a label either. Even if Fig. 6a is correct, it matters a great deal whether the impacts of the invader moderate by 90% from their peak, or by 9%. While an academic researcher may be fascinated by a long-term decline in impacts of 9%, it is unlikely that a manager would be equally impressed.

Third, although there are examples of invasions that follow the trajectory shown in Fig. 6a, support for Fig. 6a seems to rest largely on folk wisdom rather than scientific data. When one tries to track down the source of information about supposed declines in invader impacts, one often finds that the trail ends in an unsupported statement or in the widely cited paper of Simberloff & Gibbons (2004), which in turn is based largely on a small number of stories about invasions. These stories may be correct, but they are not a good substitute for data.

Fourth, other temporal trajectories are as logically appealing and well supported as the boom-bust scenario. For example, the impacts of an invader may rise over time (Fig. 6b) because of evolution in the invader (e.g. Ainouche *et al.* 2009; La Sorte & Pyšek 2009; Dormontt *et al.* 2011; although evolution may also reduce the impacts of invaders – Lankau *et al.* 2009). Impacts may rise through time if they are cumulative (long-term changes in soil characteristics such as carbon sequestration – Gomez-Aparicio & Canham 2008; Peltzer *et al.* 2010). Also, remembering that the Parker *et al.* (1999) equation includes geographic range as one determinant of impact, and that ranges typically expand for decades to centuries after establishment (e.g. Pyšek & Jarošik 2005), there should be a strong general tendency for impacts to increase over time (if we are considering total impacts rather than impacts/area).

On the other hand, impacts may change abruptly if the invader interacts with rare events (Fig. 6c). Non-native flammable grasses are the best known example (e.g. D'Antonio *et al.* 2011). These invaders establish at relatively low abundance and impact until a fire occurs (perhaps as a result of an unusually dry year or a rare ignition), which can take decades. Once a fire occurs, these grasses rapidly become dominant, and abruptly change fire frequency and other ecosystem characteristics. This sort of mechanism can produce sudden drops in the impacts of an invader as well, as must have occurred when unusually high freshwater flows apparently eliminated the non-native mussel *Musculista senhousia* from an Australian estuary (McDonald & Wells 2010).

I conclude that we don't know if there is a general pattern like that shown in Fig. 6a, a manageably small number of patterns for different combinations of species, invaded systems, and ecosystem functions (as in Fig. 6a–c), some general tendencies, or an unmanageably large series of idiosyncratic stories about how the impacts of invasions change through time. I do think that this question is answerable if we can collect more good data sets on the long-term impacts of invaders, either from long-term studies or chronosequences.

How do invasions interact with other anthropogenic changes to ecosystem functioning?

This question is interesting because we know that human actions are causing strong directional changes to many ecosystems, which might interact with invasions. Climate change is leading to predictable changes in temperature and precipitation, many ecosystems have been subjected to increased rates of disturbance and nutrient loading, populations of top predators have declined in many places, and so on. If we could predict how species invasions interact with such drivers, we could better understand the net effect of human impacts on ecosystems, and presumably be better able to manage them.

Ecologists have thought about interactions between invaders and other human impacts on ecosystems in at least two distinct ways (Fig. 7). In the great majority of cases, invasion ecologists have simply asked whether human impacts on ecosystems would tend to increase the success of invaders and thereby increase their impacts (e.g. Dukes & Mooney 1999; Walther *et al.* 2009; Bradley *et al.* 2010; i.e. Fig. 7a). Most invasion ecologists have suggested that there is likely to be a positive interaction between invasions and other global anthropogenic changes. Thus, many studies show that invaders are favoured under conditions of high nutrients (Holdredge *et al.* 2010; Dukes *et al.* 2011; Gennaro & Piazzini 2011; see Jewett *et al.* 2005 for a hypoxia-mediated example), high disturbance (Davis *et al.* 2000; Polce *et al.* 2011), warmer temperatures (Sorte *et al.* 2010; Verlinden & Nijs 2010; Huang *et al.* 2011) and higher CO₂ (Dukes *et al.* 2011; Manea & Leishman 2011). Furthermore, it has been suggested (e.g. Hellmann *et al.* 2008) that climate change will open up new pathways for species invasions, thereby bringing new suites of species into receiving regions. Of course, there are counterexamples (e.g. Peterson *et al.* 2008; Bradley *et al.* 2009), and the great majority of this work has been on plants, so the generalisation that most global change favours invaders (and therefore increases their impacts) is not universally true.

Another sort of interaction between species invasions and other human impacts is when both affect the same ecosystem function (Fig. 7b). Although interactions of this kind have not received much attention from invasion ecologists, a few examples will show that they can be very important. In the 1980s, San Francisco Bay was invaded by the Asian clam *Corbula* (formerly *Potamocorbula*) *amurensis*, which became very abundant and substantially changed the structure of the food web (Carlton *et al.* 1990). One of the more surprising effects of this invasion was the appearance of selenium toxicity in fish and wildlife (Fig. 8; Linville *et al.* 2002; Stewart *et al.* 2004). The problem with selenium toxicity resulted from the interaction between the selenium load (insufficient by itself to cause a problem), selenium accumulation by the invader (insufficient by itself to cause a problem) and the invasion-altered structure of the food web (also insufficient by itself to cause the problem).

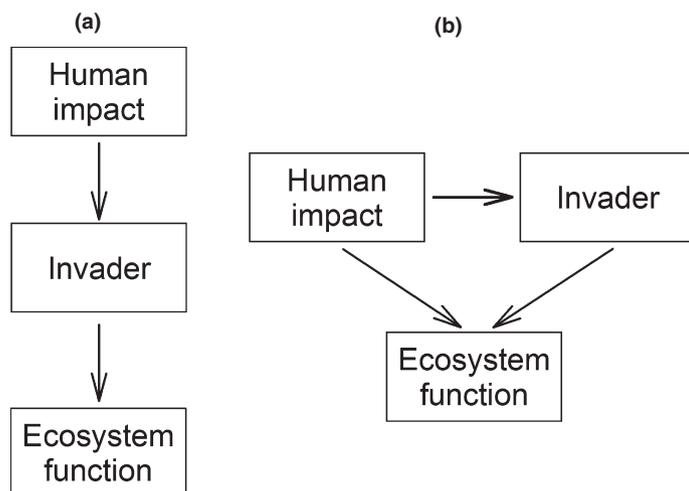


Figure 7 Two views of interactions between species invasions and other human activities on ecosystems.

We have documented strong interactions between freshwater flow and grazing by the non-native zebra mussel in the Hudson River (Strayer *et al.* 2008). One interesting aspect of these interactions was that the zebra mussel made the littoral ecosystem, which was formerly nearly insensitive to freshwater flow, very sensitive to freshwater flow (Fig. 9). That is, this species invasion changed the identity and strength of other controls on the ecosystem.

As a third example, consider interactions between invasions, sea level rise and damage to coastal areas. As sea level rises and extreme weather events become more frequent, we expect more severe damage to ecosystems and human infrastructure in coastal regions. Biological invasions may either greatly exacerbate or reduce this damage. The invasion of the semiaquatic mammal *Nutria* destroyed 10 000s of ha of wetland vegetation along the US Gulf Coast, vastly increasing losses of coastal lands and increasing the future risk of coastal lands to erosion (Pyke *et al.* 2008). On the other hand, invasion of dune grasses (*Ammophila* spp.) to the Pacific Northwest resulted in the formation of large dunes that will protect the coast from erosion arising from sea level rise and extreme events (Hacker *et al.* 2012). In an interesting wrinkle, the two non-native species of *Ammophila* have significantly different effects on dune formation as a result of subtle differences in morphology, even though they are closely related and superficially similar.

Examples such as these suggest that interactions between invasions and other human impacts in which both invasions and other human impacts affect the same ecosystem function (Fig. 7b) are common, strong and varied. They deserve more attention from invasion ecologists. Although it remains to be seen whether there are general patterns to such interactions, it seems likely that more or less general patterns do exist. For example, climate warming and the tendency of plant invaders to have high decomposition rates (Fig. 4) may interact to increase decomposition rates and decrease carbon sequestration, and the generally high nutrient content of plant invaders may interact with increased nutrient loading from other anthropogenic sources to enrich ecosystems.

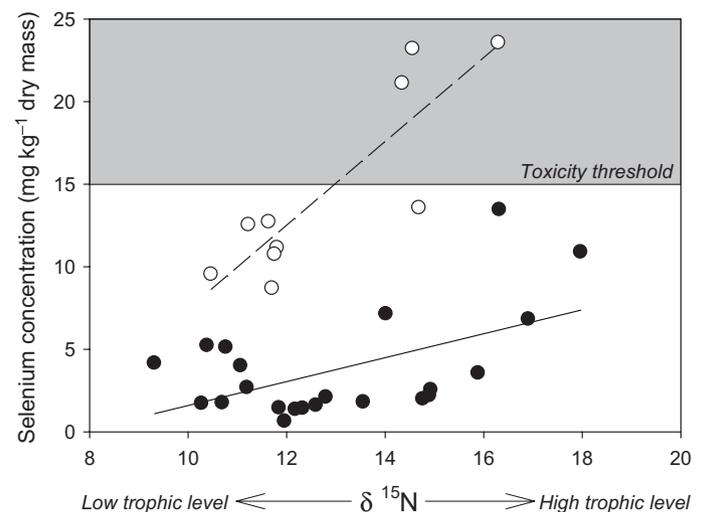


Figure 8 Selenium (Se) content of various species in San Francisco Bay as a function of their trophic position (indicated by ¹⁵N content) and whether they feed primarily on crustaceans (closed circles) or the non-native clam *Corbula amurensis* (open circles) (redrawn from Stewart *et al.* 2004).

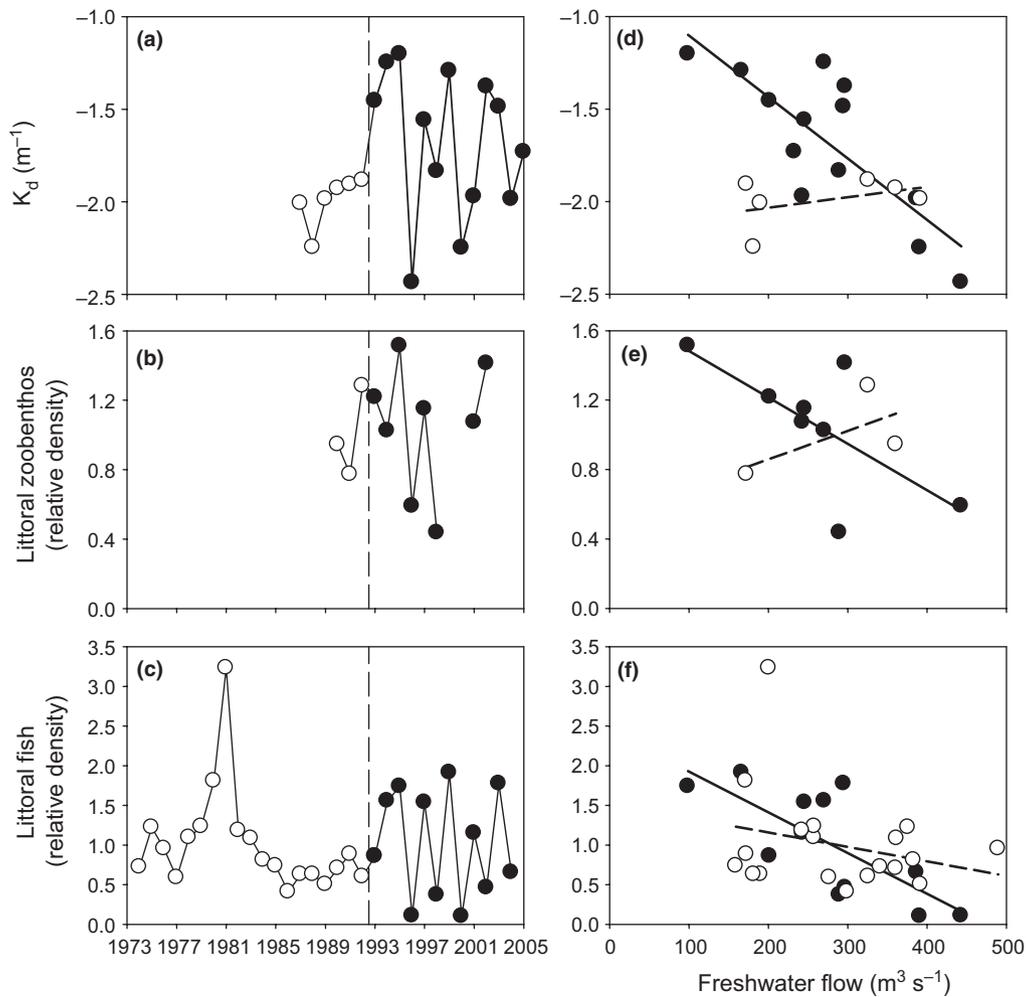


Figure 9 Changes in the response of the littoral food web of the Hudson River to flow following the zebra mussel invasion (vertical dashed line in panels a c). Panels a c show the time-courses for the extinction coefficient K_d (with less negative values indicating clearer water), littoral zoobenthos and littoral fish recruitment; panels d f show relationships between these same variables and freshwater flow before (white circles) and after (black circles) the zebra mussel invasion. Correlations with flow strengthened after the zebra mussel invasion for all these variables (Strayer *et al.* 2008).

Which changes to ecosystem function can be managed or mitigated, and which are unmanageable?

When assessing the importance of invasions for environmental managers, invasion ecologists seem most often to focus on the size of the impacts. Although managers must care about the size of the impacts, they may also care about whether the undesirable effects

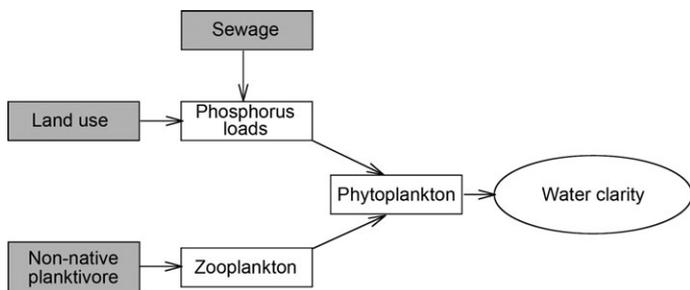


Figure 10 Simplified diagram of mechanisms controlling water clarity in lakes.

of an invasion are easy or difficult to manage. In the linear world-view of Fig. 7a, the only option for controlling the undesirable effects of an invasion is to control the invader (which may not always reverse the effects of an invasion; e.g. Brooks *et al.* 2004; Kardol & Wardle 2010; Yelenik & Levine 2010). Thus, the question about whether the effects of an invasion are manageable reduces to the question of whether the invader is manageable.

The interaction diagram of Fig. 7b suggests additional possibilities for managing the undesirable effects of an invasion – human activities other than the invasion that affect the target ecosystem function can be managed. For instance, water clarity (which is controlled by phytoplankton) is a key management variable for many lakes around the world. Planktivorous fishes such as tilapia, cyprinids, or herrings are commonly introduced to lakes, where they may decrease water clarity by eating the zooplankton that help to control phytoplankton (Cucherousset & Olden 2011). As Fig. 10 suggests, a lake manager trying to improve water clarity could try to manage the planktivore population, reduce inputs of phosphorus from sewage and land use, or both. Although these actions may be difficult, at least the manager has options other than controlling the invader. Situations in

which there are multiple management options for managing the undesirable effects of an invasion could exist in other systems as well. It may be useful to distinguish these situations from those in which there truly are no options for managing the impacts of an invader other than controlling the invader. Because so little attention has been focused on this question, it is too early to know whether general answers might be possible. It seems likely that at least answers that apply to limited domains (types of invaders and ecosystems) might be attainable.

SEVEN SUGGESTIONS FOR INVASIONS AND ECOSYSTEMS

Based on this assessment of the current status of knowledge about biological invasions and ecosystem functioning, I offer the following suggestions to encourage progress in understanding how invasions affect ecosystem functioning.

Critically apply trait-based approaches to understand or predict the effects of invasions on ecosystem functioning

Trait-based approaches may hold great promise. However, it is important to remember that response traits (i.e. traits that determine a species' response to environmental conditions, and which may control the ability of a species to invade) are not always the same as effect traits (which may control the ability of a species to change an ecosystem) (see Suding *et al.* 2008 for a discussion). In early, influential studies on the effects of species invasions on ecosystem function, these traits were congruent (e.g. *Morella's* ability to fix nitrogen is both a response trait and an effect trait), but they are not necessarily so. Indeed, studies showing a lack of correlation between invasion success and invasion impacts (e.g., Ricciardi & Cohen 2007; Engelhardt *et al.* 2009; Vilà *et al.* 2011) suggest that the response traits of invaders must generally be different from their effect traits. For example, traits that favour dispersal by humans appear to be important for determining invasion success, but are not especially likely to determine ecosystem impacts (e.g. Ricciardi & Cohen 2007; Engelhardt *et al.* 2009). In addition, much of the literature on traits and ecosystem effects consists of *post hoc* explanations of invasions that did or did not have effects. Such explanations are appealing, and they may even be correct, but they should be regarded as hypotheses to be tested rather than well supported conclusions. Finally, the idea of trait spectra (Fig. 2), which has appeared in the literature several times in one form or another (e.g. D'Antonio & Hobbie 2005; Wardle *et al.* 2011) might be worth exploring more thoroughly.

Think more strategically about collecting and publishing new data

I highlight just three of many possible issues. First, if long-term changes in invasion impacts on ecosystems is an important scientific and management problem, as I have argued, we need to collect many more data on the long-term impacts of invaders on ecosystems, using directed long-term studies, chronosequences or some other alternative (see Likens 1989 for a discussion of alternatives). Second, if we really want general answers to the big questions in invasion ecology, then we may need to deliberately study a representative sample of species, functions and ecosystems, and not just the dramatic species that have invaded sites convenient to our universities. This may be difficult and expensive to do, so we should think carefully if we really need a general, precise answer before undertaking

such studies, and then use efficient sampling designs to choose species and systems for study. Third, we need to try to minimise bias arising from the tendency to publish studies showing large invasion effects and bury studies that show less dramatic effects (cf. also Thomsen *et al.* 2011). This means that we all need to publish studies showing small or no effects of invaders (Thomsen *et al.* 2011), even if they are not 'sexy', and that we all need to encourage such papers through the peer review process, and not favour studies showing big effects over equally solid studies showing no effects.

Be cautious about using expert opinion

Contemporary invasion ecology relies to a great extent on expert opinion rather than data in determining which species have 'impacts' on ecosystems. Typically, researchers and managers score species as having large, moderate and low impacts without having rigorous definitions for these categories, and often lack actual data on impacts with which to make such decisions. Such an approach probably is sufficient to sketch out broad, approximate answers, but it certainly is not precise, and may even be very wrong (Burgman 2005; Sutherland 2006). In cases where we need firm, reliable or precise answers, we need to work hard to replace expert opinion with actual data, or at least test the expert opinion for reliability.

Do not waste effort answering questions that we do not really need to answer

For instance, much research in the field has been justified on the basis that managers or policy-makers need to know some bit of scientific information. However, what managers and policy-makers need to know may be quite different from what scientists think that they need to know. At least, it might be worth surveying managers and policy-makers who work on non-native species to see what they need to know. Then we could avoid answering questions for them that they are not asking us. Other questions are likely to be unanswerable in their usual form. These questions should either be abandoned or reformulated in a tractable form.

Pay careful attention to defining and testing domains of prediction

Most theories, generalisations, or patterns about species invasions and ecosystem function will be valid over some range (domain) of species, systems, functions and scales of space and time. It is important to stretch those theories, generalisations or patterns as far as we can over these ranges, testing the firmness of the ground as we move forward. Plant ecologists have been very good about developing and testing general theories about how either all plants, or certain functional groups of invaders (e.g. flammable plants), affect ecosystems (e.g. D'Antonio & Vitousek 1992; Levine *et al.* 2003; D'Antonio & Hobbie 2005; Liao *et al.* 2008; Ehrenfeld 2010; Pyšek *et al.* 2012). Animal ecologists could copy this model by trying to define broad functional groups of animals (e.g. suspension-feeding bivalves, folivorous animals and bioturbators) for which ecosystem impacts might reasonably be predicted, then testing those predictions with field studies and meta-analyses. Currently, much of the literature on animal invaders seems to be focused either on individual species (e.g., Higgins & Vander Zanden 2010; Kulhanek *et al.* 2011b) or on groups too broad to have functional meaning

(vertebrates, invertebrates). In addition, invasion ecologists could probably be more explicit about linking functional groups to specific functions in ecosystems, then to the sensitivity of different kinds of ecosystems to changes in those functions.

Put invasions more explicitly into an ecosystem context

Instead of focusing narrowly on how a single invader affects a chosen ecosystem function, consider how it works with other drivers (including other invaders) to determine ecosystem functioning. If we are going to understand and manage the impact of species invasions on modern ecosystems, which are subject to numerous human impacts, we need to understand how invasions interact with these other drivers to determine the functions and services provided by these ecosystems. This means that our focus will have to be the ecosystem rather than the invasion.

Plan for imprecision and surprises

As others have noted (e.g. Ricciardi & MacIsaac 2011), both invaders and ecosystems are highly varied, pathways of interaction are numerous and complex, and our database on the effects of invaders is still very incomplete, so even the best predictive models will be burdened with large errors and will produce mistakes. Thus, we should be very careful when evaluating management actions where the consequences of an error are long-lasting or irreversible, because the best science will be imperfect for the foreseeable future. It would be hard to improve on Harley's (2003) advice about predicting which species can safely be lost from an ecosystem without affecting function, if we simply invert the language to ask which species can safely be added to an ecosystem.

'The desire for a metric of expendability is understandable; such a metric would allow planners and resource managers to make better-informed decisions regarding a variety of human actions. However, assigning an 'expendability quotient' to species should not be undertaken lightly. The cost of error can be high, as extinctions and their corresponding losses of genetic material are irreversible. Because expendability can vary substantially through time and space, estimating expendability is risky if done poorly but expensive if done well....'

I hope that this brief survey demonstrates that biological invasions are major drivers of functioning in many contemporary ecosystems, and that large, interesting questions underlie the relationships between invasions and ecosystem function. Even if the questions identified here are not really the 'right' questions, I hope that laying them out here will stimulate discussion about the fundamental questions in the field and how best to answer them, and ultimately spur progress.

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