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Impact: toward a framework for understanding the ecological effects of invaders

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Abstract

Although ecologists commonly talk about the impacts of nonindigenous species, little formal attention has been given to defining what we mean by impact, or connecting ecological theory with particular measures of impact. The resulting lack of generalizations regarding invasion impacts is more than an academic problem; we need to be able to distinguish invaders with minor effects from those with large effects in order to prioritize management efforts. This paper focuses on defining, evaluating, and comparing a variety of measures of impact drawn from empirical examples and theoretical reasoning. We begin by arguing that the total impact of an invader includes three fundamental dimensions: range, abundance, and the per-capita or per-biomass effect of the invader. Then we summarize previous approaches to measuring impact at different organizational levels, and suggest some new approaches. Reviewing mathematical models of impact, we argue that theoretical studies using community assembly models could act as a basis for better empirical studies and monitoring programs, as well as provide a clearer understanding of the relationship among different types of impact. We then discuss some of the particular challenges that come from the need to prioritize invasive species in a management or policy context. We end with recommendations about how the field of invasion biology might proceed in order to build a general framework for understanding and predicting impacts. In particular, we advocate studies designed to explore the correlations among different measures: Are the results of complex multivariate methods adequately captured by simple composite metrics such as species richness? How well are impacts on native populations correlated with impacts on ecosystem functions? Are there useful bioindicators for invasion impacts? To what extent does the impact of an invasive species depend on the system in which it is measured? Three approaches would provide new insights in this line of inquiry: (1) studies that measure impacts at multiple scales and multiple levels of organization, (2) studies that synthesize currently available data on different response variables, and (3) models designed to guide empirical work and explore generalities.

Introduction

While a great deal of recent progress has been made both deriving and critiquing generalizations about the traits that confer invasiveness (Bergelson and Crawley 1989; Perrins et al. 1992; Rejmánek and Richardson 1996; Reichard and Hamilton 1997), less attention has been placed on developing either theoretical or operational generalizations about which invasive species cause the greatest ecological impacts. One of the few accepted generalizations is that the greatest impacts often occur when a nonindigenous species performs an entirely novel function in the recipient community (Simberloff 1991; Ruesink et al. 1995), such as when a mammalian predator invades an oceanic island (Elton 1958) or a nitrogen-fixing plant invades a region with nitrogen-poor soil (Vitousek and Walker 1989). But exactly what impact is, or how we decide that the impact of one nonindigenous species exceeds that of another, or how we decide that the impact of a particular nonindigenous species is greater in one place than in another, is rarely discussed in a general framework.

There can be surprising disagreement over the magnitude of impact caused by even the most celebrated invasions. It is an undisputed fact that the invasion of *Cryphonectria parasitica*, the chestnut blight fungus, decimated populations of its host over millions of hectares (Anagnostakis 1987; von Broembsen 1989). However, ecologists disagree over whether or not that invasion had a biologically significant impact on the Eastern deciduous forest as a whole (von Broembsen 1989; Day and Monk 1974; Shugart and West 1977). Such disagreement can be attributed in part to the fact that for many historical invasions we do not have good baseline data on the distribution and abundance of the original species assemblage, or on basic ecological processes like energy flow or nutrient dynamics. However, our inability to agree on the impact of historical invasions also reflects the fact that we have no common framework for quantifying or comparing the total impacts of invaders. This dilemma represents more than an esoteric academic issue, because we need to be able to rank order nonindigenous species in terms of their impact in order to prioritize management efforts.

This paper attempts to provide the beginnings of a synthetic approach to defining, evaluating, and comparing the impacts of nonindigenous species. First, we begin by setting out a brief framework for what factors should be included in a composite ‘score’ of impact. Second, we summarize the myriad ways that impact has been measured empirically and then make some specific suggestions for new approaches and for ways to extend and strengthen current approaches. Third, we argue for the usefulness of mathematical models, and we review how community invasion models have measured impacts. As might be expected, historically the common ground between theoretical and empirical measures of impact has been quite narrow. In an attempt to break with this tradition, we explore how models might lead to better empirical measures as well as a clearer understanding of the relationship among those measures. Fourth, we turn to the applied realm and identify some particular challenges, as well as insights, that come from the need to prioritize particular invasions for management and policy actions. With hopes of going beyond a simple recounting of the types of ecological impact, we end with some recommendations about how the field of invasion biology might proceed in order to facilitate a search for generalities.

What should be included in an integrative measure of impact?

Calculating the economic cost in terms of damages or eradication/control is one useful approach to measuring the impact of an invader (US Congress 1993; Williamson 1998), and enjoys the simplicity of a common currency. However, most ecologists feel that such an anthropocentric approach does not capture everything we would like to know about the effects of adding a species. Unlike monetary cost, many different types of ecological metrics can be used to assess impacts on native populations and ecosystems (as we will summarize below). Some authors have tried to consider several different measures simultaneously, at least in an anecdotal way (Schmitz et al. 1997). Quantifying areal extent or a change in ecosystem function, if not easy, is at least conceptually straightforward, but how to combine such lists of metrics into a single number representing impact is not at all obvious.

On a geographic scale, three factors will determine the overall impact of an invasive nonindigenous species: the total area occupied, abundance, and some measure of the impact per individual. It is helpful to think about the units and implications of this statement more formally with the equation:

$$I = R \times A \times E$$

where overall impact, I, is defined as the product of the range size R (in m^2) of a species, its average abundance per unit area across that range (A, in numbers, biomass, or other relevant measure per m^2), and E, the effect per individual or per biomass unit of the invader. It can then be compared among species, among continents for the same species, etc.

Range

Because we have good monitoring data for the spread of many pest species, in management settings impact is often used synonymously with areal distribution

(Dombeck 1996; Schmitz et al. 1997). However, simply measuring impact in square kilometers can be misleading. Species introduced to multiple sites provide a telling illustration. For example, the small Indian mongoose (*Herpestes javanicus*) was introduced to South America shortly after it was introduced to the West Indies. While the range occupied by the mongoose on islands is less extensive than its range on the South American mainland, this voracious carnivore is implicated in the extinction of at least 18 species or subspecies of reptiles on islands, compared to zero known extinctions on the mainland (Roots 1976). Similarly, largemouth bass (*Micropterus salmoides*) may cause some declines in native fish abundance in large lake systems, but this impact is minor when compared to the total elimination of the Owens pupfish (*Cyprindon radiosus*) by bass in small refuge ponds (Minckley et al. 1991).

Abundance

It seems intuitively reasonable that the impact of an invader is correlated with its own population abundance or biomass. One rationale for using invader abundance as a measure of impact is that any biomass (or space, or energy) controlled by the invader constitutes resources no longer available to competitors or prey. Some studies have tracked the abundance of an invader at a single site as a measure of the increasing impact at that site (e.g., Anable et al. 1992). However, for comparing different invaders, abundance alone cannot represent impact, especially in comparisons among dissimilar taxa; e.g., Norway rats vs. chestnut blight.

Effect

While R and A may be straightforward and (at least relatively) easy to quantify, the per-capita or per-biomass effect E is not. The focus of most basic ecological research has been this local effect (or, more accurately, an unspecified combination of local per unit effect and local abundance). For most of the remainder of this paper, we will focus primarily on exploring the definition and measurement of local, per-capita impacts, but we will return to the bigger picture when we discuss the application of impact measurement to resource management decisions.

Part of the confusion over defining impacts has been caused by the fact that most studies use only one of these three factors to represent ‘impact’, while actually all three are separate parts of a greater whole. Related to this confusion is the argument over whether the large impacts of the most noxious invasive species are due primarily to their ‘quirks’ (Simberloff 1985), that is, the special aspects of their biology (e.g., nitrogen fixation in the shrub *Myrica faya* in Hawaii (Vitousek and Walker 1989)), or simply to their sheer numbers (e.g., the zebra mussel *Dreissena polymorpha* at 4500 individuals/m^2 (Hebert et al. 1991)) caused by high demographic rates and high carrying capacities. Quirks vs. density is in fact an argument over whether E or A dominates the overall impact of an invader. A species may have a large impact owing to one of many combinations of the three factors, although an important research question in itself is how well the separate components of impact are correlated with each other. Do invaders with the biggest ranges also have the highest densities? We know from other contexts that widespread species often are also locally abundant (Gaston et al. 1997; Newton 1997).

Separate from the question of what to include in a measure of impact is how to combine the factors, and the linear way we have formulated the equation $I = R \times A \times E$ is probably a gross oversimplification. For example, a positive correlation between range R and per-unit impact E could occur if metapopulation dynamics are important in the persistence of native species, as, one-by-one, individual populations of the native succumb to the expanding invader. Density dependence could result in a negative correlation between E and abundance A. These types of correlations among factors would make impact a non-linear rather than linear combination and therefore greatly complicate the estimation of current impact, let alone the extrapolation of future impact.

How do we currently measure impacts?

Much of the discussion of ecological effects of invaders has been purely anecdotal in nature (e.g., Elton 1958; Cronk and Fuller 1995; Bright 1998); as a result, the case against introducing nonindigenous species is often poorly supported even for some of the most infamous invaders (e.g., purple loosestrife *Lythrum salicaria*, (Hager and McCoy 1998)). Those studies that have attempted to quantify impacts have often done so in a largely correlative manner (Figure 2; also see Parker and Reichard 1998), either comparing one site before and after an invasion, or comparing different sites, with and without an invader present, at the same time. Some elegant studies combine invaded vs. uninvaded patterns with detailed experiments to elucidate the mechanisms

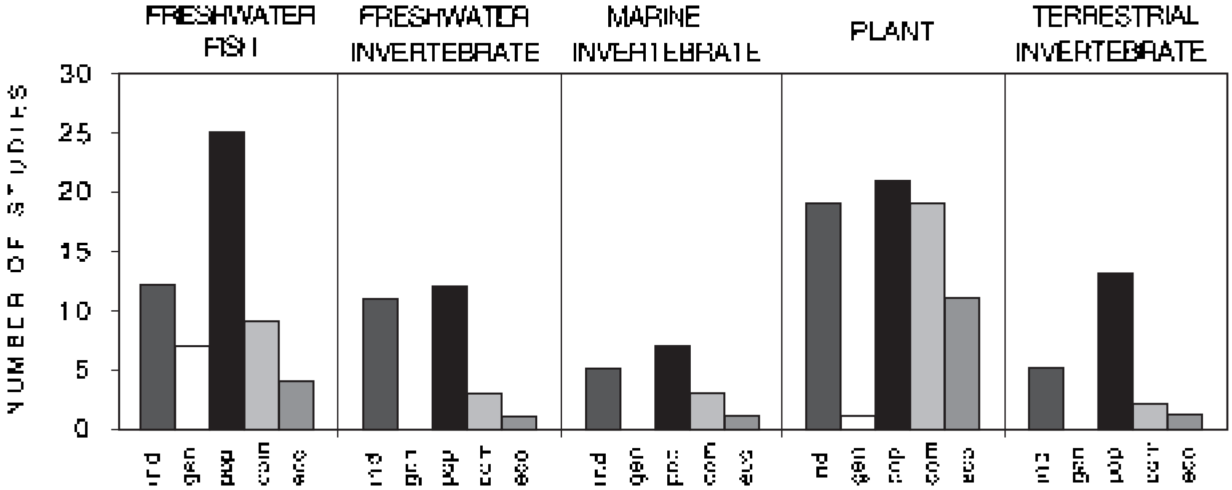

Figure 1. The number of published studies reporting quantitative data on impacts at five different biological levels: individual [ind], genetic [gen], population [pop], community [com], and ecosystem function [eco]. Papers were identified using systematic computerized searching strategies over 10 years of Biological Abstracts (1988–1993) and Biosis (1994–1997) or, for marine invertebrates, over 16 years of Aquatic Sciences and Fisheries Abstracts (1980–1997). We focused on five guilds of invading species: freshwater fish, freshwater invertebrates, marine invertebrates, plants (and algae), and insects and other terrestrial invertebrates. Single studies that reported impacts at more than one level were tallied more than once.

involved. Unfortunately, these are a small minority (Figure 2). Here we review some of the best examples of studies, both experimental and observational, that have quantified impacts.

The impact of an invader can be measured at five levels: (1) effects on individuals (including demographic rates such as mortality and growth), (2) genetic effects (including hybridization), (3) population dynamic effects (abundance, population growth, etc.), (4) community effects (species richness, diversity, trophic structure), and (5) effects on ecosystem processes (nutrient availability, primary productivity, etc.). Some of these impacts are documented much better in the literature than others (Figure 1). Population-level effects on native species, primarily declines in abundance or percent cover, were the most commonly tested impacts for five guilds of organisms we surveyed (Figure 1). Effects on individuals were described fairly well in most groups. Studies documenting invader effects on a composite property of a community were common only for plant invaders, while ecosystem changes were even less extensively documented. The most understudied impacts, except in freshwater fish, were genetic changes and long-term evolutionary effects.

Effects on individuals

The immediate impacts of invaders on the performance or traits of individuals of native species can often be quickly and easily measured. The obvious examples are changes in individual demographic rates, such as reduced growth or reproduction, in the face of predators or competitors (e.g., Cowie 1992; Fraser and Gilliam 1992). Morphology of individual organisms may also change in response to an invader (e.g., Crowder 1984; Busch and Smith 1995).

Behavioral impacts occur when individuals change habitat use or activity patterns in response to new predators or competitors. For example, Brown and Moyle (1991) demonstrated major shifts in microhabitat use of several species of fish in California’s Eel River in response to the invasion of a piscivorous pikeminnow (*Ptychocheilus grandis*). Such shifts can be measured as decreases in the use of some resource, in this case habitat space, but there is also the potential for expanded resource use if an invader causes a release from some limiting factor. Power (1992) has demonstrated that experimental introduction of the California roach (*Lavinia symmetricus*) in the Eel River resulted

Figure 2. The type of data collected in 139 published studies reporting quantitative data on impacts for five guilds of invading species: freshwater fish, freshwater invertebrates, marine invertebrates, plants (and algae), and insects/terrestrial invertebrates. Papers were identified using systematic computerized searching strategies over 10 years of Biological Abstracts (1988–1993) and Biosis (1994–1997) or, for marine invertebrates, over 16 years of Aquatic Sciences and Fisheries Abstracts (1980–1997). Categories were: experimental, comparative (before vs. after invasion, or uninvaded sites vs. invaded sites), or both.

in cascading effects on the abundance of the benthic invertebrates and algae. Invasion of the pikeminnow, which causes a shift in microhabitat use by the roach, will presumably result in the re-expansion of use of food and space by aquatic insects whose distribution and abundance are now regulated by roach predation.

Genetic effects

Genetic impacts of invading species on native species can either be indirect, as a result of altered patterns of natural selection or gene flow within native populations, or direct, through hybridization and introgression. When they exert strong selective pressures, nonindigenous species can be expected to alter allelic frequencies in natural populations; however, proven examples are few (e.g., Burdon et al. 1981; Adalsteinson 1985). In addition to changing selection regimes, nonindigenous species can change the course of evolution in more subtle ways, for example by fragmenting populations of native species and thereby disrupting gene flow (Krueger and May 1991; Leary et al. 1995).

Hybridization between an invader and a native species can have several possible consequences. (1) Creation of a new invasive hybrid genotype: for example, the North American cordgrass, *Spartina alterniflora*, has hybridized with the European *S. maritima* to produce a new polyploid species (*S. anglica*) that is more invasive in Great Britain than the original form (Thompson 1991; Williamson 1996). (2) Production of sterile hybrids, which then compete with native species for resources and can result in the waste of gametes from rare populations (Trenham et al. 1998). (3) Production of a hybrid swarm and widespread introgression, leading to a virtual extinction of native taxa through ‘genetic pollution’ (Echelle and Connor 1989; Rhymer and Simberff 1996). In fact, three of the 24 federally listed species in the United States that have gone extinct since the enactment of the Endangered Species Act did so through hybridization with nonindigenous species (McMillan and Wilcove 1994).

Population dynamic effects

Because we grant species special status in ecology and conservation, it is natural to focus on the impact an invader has on the abundance and dynamics of particular native species, the most extreme impact being complete extinction (e.g., Murray et al. 1988; Braithwaite et al. 1989). Population-level impacts are the most commonly documented for all taxonomic groups we surveyed (Figure 1). Many standard methods of measuring population parameters can be used to determine the impact of an invader. Populations may respond with changes in abundance, distribution, structure (age or size), or population growth rate. For example, Juliano (1998) used the finite rate of increase as a metric to quantify the impact of an introduced mosquito on a resident species.

Population effects can be caused by either direct or indirect mechanisms. Apparent competition, mediated through shared pathogens or parasites, is a common example (e.g., Settle and Wilson 1990). The introduction of the gypsy moth in eastern North American forests illustrates the remarkable, cascading indirect impacts that can occur when communities are tightly linked (Jones et al. 1998). When gypsy moth outbreaks occur, the white-footed mouse populations that eat them also peak, driving up tick populations and consequently the incidence of lyme disease.

A subtlety in quantifying population responses concerns the spatial scale of a measured impact. The fact that one can measure a large response to an invader in a few small quadrats constituting a tiny fraction of a species' range may have little to do with a true population impact. For example, if impacts are measured on species with marginal or 'sink' populations (Watkinson and Sutherland 1995; Hoopes and Harrison 1998), extrapolating from a local impact could greatly exaggerate the real threat to global persistence.

Community effects

When community-level impacts are measured (which is not often (Figure 1)), they are usually framed in terms of species number. High-profile invaders are usually assumed to cause overall reductions in biodiversity. In a classic example, *Mimosa pigra* in northern Australia converted thousands of hectares of open sedge wetland to shrubland, accompanied by a loss of particular native flora and fauna (Braithwaite and Lonsdale 1987; Lonsdale and Braithwaite 1988). However, many invasions may actually increase total species richness, as in the introduction of marine invertebrates into estuaries on the west coast of North America (Cohen and Carlton 1998). Here it is worthwhile to point out a difference between basic and applied research in terms of relevant measures of impact. Total species number is a community response variable of interest in both models of invasion and general ecological theory. In contrast, in the applied realm we make a distinction between the species we care about and those we do not. In agriculture we care about crop and pest species; in conservation we care about native species in natural systems. This difference between basic and applied perspectives leads to a great deal of confusion in the discussion of impacts, especially in forging a link between theory and empirical studies. Many published studies fail to mention basic information such as which species were monitored to calculate diversity indices, much less whether those species are native or introduced (M. Wonham, K. Goodell, B. Von Holle, and I.M. Parker, unpublished data).

Composite community measures include species richness, evenness, and various indices of diversity (e.g., Holmes and Cowling 1997). These indices of community richness or diversity are single numbers that can be compared easily; however, they ignore much information. A more substantial multivariate analysis may be more informative. Principal component analyses and related ordination techniques can usually reduce community data to a few dimensions that capture a substantial proportion of the variation in species composition or abundance (or abiotic characteristics). These dimensions can then be a tool for evaluating impact (Williamson 1987). For example, Gilbert et al. (1993, 1996) studied the response of microbial communities to the introduction of the biological control agent *Bacillus cereus* UW85; they used discriminant analysis to determine that the impact of the control agent on community composition was as great as the (substantial) difference between root-associated soil and root-free soil. Holmes and Cowling (1997) applied principal components analysis to plant communities with and without nonindigenous *Acacia saligna*, specifically to compare the impact of the invader on community composition of the seedbank to impact on the composition of vegetative plants.

Effects on ecosystem processes

Impacts on ecosystem functions or processes can be broken down into changes in (1) resource pools and supply rates, (2) rates of resource acquisition by plants and animals, and (3) disturbance regimes (Vitousek 1986, 1990; Chapin et al. 1996). For example, by increasing nitrogen availability through N-fixation, the introduced tree *Myrica faya* has the potential to affect successional processes on nutrient-poor volcanic soils (Vitousek 1990). Some have argued that the biggest ecosystem impact of invaders is their effect on disturbance regimes (Mack and D'Antonio 1998). Fire-adapted Old World grasses have come to dominate many North American and Hawaiian grasslands, and, by greatly increasing the intensity or frequency of fires, have eliminated or reduced the abundance of native species over vast areas (D'Antonio and Vitousek 1992). Invading species can also change the physical habitat in ways that drastically change ecosystem functioning. For example, non-native herbivores such as goats may not only denude hillsides of vegetation but cause massive erosion and siltation, thereby increasing variability in flows to stream ecosystems (Platts 1991).

Measuring impacts: what are we missing?

The problem of spatial and temporal variation

Both the population dynamics of an invader and the dynamics of the response variable (e.g., species abundance) are expected to vary over space and time. The estimate of an invader's impact may depend, therefore, on the spatial and temporal scale of a study. Some successful invaders increase steadily to a stable equilibrium density, but others exhibit more complex behavior, initially reaching very high densities but then declining to lower levels. These 'boom and bust' dynamics have been described for invading terrestrial mammals (Williamson and Fitter 1996), aquatic plants (Creed and Sheldon 1995), and marine invertebrates (Allmon and Sebens 1988; Zaitsev and Marnaev 1997), among others. One of the best-studied example of variation in the population dynamics of an invader, with sixty years of monitoring, is that of the zebra mussel (*Dreissena polymorpha*) in Eastern Europe. The mussel showed marked boom and bust dynamics in some lakes but steady logistic increase in others (Ramcharan et al. 1992; Karatayev et al. 1997). In addition, some invaders exhibit oscillatory behavior (Ross and Tittensor 1986; Elkinton and Liebhold 1990) or dramatic spatial variation in population dynamics (Moulton 1993).

Responses of native species to invasion are expected to be similarly variable, and background fluctuations in population size could increase the difficulty of detecting a directional change. In addition, one impact of invasions may be to change the magnitude of variability within resident populations. For example, an invasive filter feeding clam, *Potamocorbula amurensis*, has reduced the amplitude of the periodic plankton blooms in San Francisco Bay to a fraction of their former magnitude (Alpine and Cloern 1992). So far, little research has been done on how variation might be either summarized or incorporated as a measure of impact in its own right. It would be possible to construct matrices of the covariances between the population sizes of all pairs of species, one for the covariances before the invasion and one after. Comparisons of the changes in these covariances may provide information about changes in the structure and dynamics in the community.

In the face of spatial and temporal variability, it is no easy task to quantify the impacts of an invader, especially over its entire range. Small-scale studies may inadequately control for natural variation in the response variable over space and time, and large-scale studies may be confounded by spatial gradients or temporal trends in the environment such as pollution, harvesting, or climate change. An ideal study design incorporating both before/after and control/impact comparisons bolstered by experimental manipulations (additions and removals of the invader) may not even be possible in many cases. Well-controlled, replicated studies are difficult to conduct in part because we usually become motivated to study invasions only after they have spread extensively, and only in species that already seem to be having an impact. In addition, there may be time lags between the time of introduction and the appearance of a measurable impact (Kowarik 1995). A general increase in the temporal and spatial scale of invasion studies would be helpful.

Beyond species richness: capturing impacts at the community level

Information on changes in composition and abundance of the resident species can be synthesized in a variety of ways to produce a composite measure of impact. There are three simple measures of change in abundance: (1) mean change in abundance. (2) the number of species that are changed by some critical threshold level, such as 50% or two standard deviations from the mean (this type of measure implies that not all changes in abundance are large enough to be biologically significant). (3) the change in total abundance of the community as measured by numbers or biomass (which could also be linked to a change in overall productivity).

An invader may simply decrease the abundance of all members of a community (for example, by usurping space), or it may have differential impacts on different species, resulting in a fundamental change in community composition. Measures such as ranked order of species by abundance could indicate this sort of fundamental change, and would be relatively easy to calculate and test statistically. Such an approach has potential for measuring the degree to which an invader 'changes the rules of the game' (Vitousek 1990).

How does one get an accurate, synthetic view of the total magnitude of ecological change caused by an invasion? As we have discussed, an interesting approach is to use ordination techniques to capture the change of a community through multidimensional ecological 'space'. However, because results from ordination are usually evaluated visually and qualitatively, this approach may not be compelling as a form of clear communication of results where the impacts of different species must be compared quantitatively. Another way of summarizing data from these sorts of multivariate analyses would be to measure change as the Euclidian distance moved through multivariate space (Digby and Kempton 1987); one advantage of Euclidian distance is that all of the information is retained, and it can be used easily in comparisons (does invader *X* have a larger impact in habitat A or habitat B?). Also, it will tend to weight large changes in a few species more heavily than many small changes; with respect to pest management or extinctions, these large changes are what matter most. Such multivariate approaches can also be applied to ecosystem-level properties such as carbon and nitrogen fluxes, and can even combine information from individual population impacts with ecosystem impacts into a single metric.

Skirting the multivariate problem: bioindicators, biotic integrity, and functional importance

One alternative to trying to capture the complete, multidimensional response of a community is to search for 'bioindicators', whose presence and abundance (or even individual traits such as behavior or hormone levels) reflect changes occurring at the whole community or ecosystem level. Many different groups of taxa have been used as bioindicators of community-level degradation caused by pollution, including birds (Burger 1997), spiders (Maelfait and Baert 1997), and mycorrhizae (Leyval et al. 1997). Bioindicators have also been used to measure restoration success (Andersen and Sparling 1997). The choice of a bioindicator species or guild is an important area of research in its own right (Rodriguez et al. 1998; Parks et al. 1991); characteristics of ideal bioindicators depend upon the specific monitoring goals but usually include (1) practicality in monitoring, (2) sensitivity to the 'stressor' of interest, (3) ubiquity, (4) short generation time, and sometimes (5) a key role in the functioning of the community (i.e., keystone species).

Measurements of 'biotic integrity', now commonly used in aquatic systems, may have some potential as simple indicators of the impact of invaders. Indices of biotic integrity essentially use a hypothetical unaltered assemblage of organisms as the standard for comparison with measured conditions (Karr et al. 1986; see Simberloff 1997 for a critical view). Usually 8–12 metrics (number of native species, abundance of species sensitive to pollution, etc.) are compared between the current state and the reference state. Indices of biotic integrity were originally developed to measure effects of pollutants on stream ecosystems but have been shown to reflect the impact of invaders to a certain extent as well (Moyle and Marchetti 1999). Because the mere presence of an invader usually lowers the biotic integrity score, their use can be circular. Yet it may be possible to compare the index score at the very beginning of an invasion (when the invader is present but has not yet exerted its full impact) with the score after the impact has occurred.

A relevant attempt to define a metric for the 'functional importance' of any species in a community was suggested by Hurlbert (1971, 1997). Although conceived with specific reference to the removal of an existing species, functional importance could also apply to the impact of an invader. This metric compares the sum of the productivity (or biomass, or photosynthetic rate, etc.) of each species in a community before and after the addition of an invader. As a measure of impact, importance value thus defined takes no special account of extinction; an extinct species is reflected only by the absence of productivity (or biomass) of that species. Therefore functional importance by itself may not adequately capture what we think is the fundamental biology of the systems involved.

Nonlinearities and thresholds: might repeated invasions lead to 'invasional meltdown'?

One assumption of our discussion to this point is that the impacts of different invaders are independent of each other. However, if a natural community constitutes any sort of nonrandom assembly of species that is the outcome of a sorting and adjustment process, then it may be that once some threshold of invasion pressure is exceeded, the whole structure of the community collapses. More specifically, relentless and repeated invasion may produce two synergistic effects:

(1) as the cumulative number of *attempted introductions* increases, each one disrupting abundances to some extent (even if ultimately unsuccessful), the community may become more easily invaded.
(2) as the number of *established invaders* increases, future invasions may both succeed more easily and produce more dramatic impacts.

The combination of these two effects defines the 'invasional meltdown hypothesis' (Simberloff and Von Holle 1999). Case studies documenting particular instances in which the presence of one invader facilitated subsequent invasions or exaggerated impacts of a second invader suggest that invasional meltdown is biologically reasonable. For example, feral pigs (*Sus scrofa*) in the Hawaiian islands disperse a large number of harmful nonindigenous plants (Stone 1985). Invasional meltdown is an issue with important conservation implications; critics of strict regulations often argue that since invasions are inevitable and can never be halted entirely, we gain little by expensive efforts aimed at slowing down their rate of occurrence. However, if chronic exposure to nonindigenous species leads to invasional meltdown, then even a partial reduction in introduction pressure could produce major benefits.

The alternative view, termed ‘biotic resistance’, is that communities become more resistant to additional invasions, or additional impacts, as successful invaders are added to the species pool (e.g., Moulton and Pimm 1983). The idea is that successful additions are also more likely to be strong competitors, well-defended prey, etc., that can then more readily impede new introductions. Both hypotheses are plausible. Current documentation of invaders facilitating other invaders is too limited to assess the generality of the meltdown hypothesis empirically. While we wait for additional data, community assembly models could be used to distinguish between patterns of ‘invasional meltdown’ and ‘biotic resistance’, as well as to provide some insight into the mechanisms behind the buildup or breakdown of community resistance.

Despite a lack of realism, models could contribute to our understanding of impacts

The limited number of theoretical models of invasion impact may be one of the reasons for the scarcity of generalizations about impacts. Abrams (1996) argued that current theory is unable to predict changes in abundance caused by either the introduction or deletion of species. We advocate the development of theory in this area because models of impact could provide significant advances in several areas. In addition to their purely theoretical value, new modeling approaches could greatly improve the efficiency and quality of our collection of data on impacts. One problem in developing and assessing reliable measures of impact is the empirical difficulty of collecting the necessary information. In contrast, models permit the calculation and comparison of an essentially unlimited range of measures, because they are not subject to the logistic constraints of collecting empirical data. Such exercises can provide information about which measures are redundant and which measures identify independent effects. With a better understanding of the correlation among impact metrics, we will be able to design more effective and efficient empirical studies and monitoring programs.

Previous models of invasion relevant to impact

Theoretical treatments of the effects of invasions on resident communities have been few, in part perhaps because such models, to be useful, should incorporate both the complexity of a community and the often complicated biological relationships between an invader and the residents.

The stability/complexity debate of the 1970s is tangentially relevant to the issue of the impacts of invasions. One of the major results of that modeling effort was the conclusion that species-rich communities are less likely to be stable (May 1973), where stability is defined as returning to equilibrium when perturbed. A second important result is that stability can shift to instability quickly and unexpectedly; that is, the boundary between high likelihood of stability and near certainty of instability can be a very sharp function of species number and connectance (Gardner and Ashby 1970). Because invasion by one or more species at least initially increases the number of species in that community, invasion is likely to increase the probability of instability.

Case (1990, 1991) directly addressed the issue of invasions using simulated communities and defining impact as the number of extinctions. As May’s results might lead one to expect, larger initial communities had a higher probability of extinction of residents following invasion. One non-intuitive result that came out of Case’s models was that an invasion may produce extinctions but then fail itself: that is, invaders may have an impact even when they do not persist (Case 1995). However, these models describe equilibrium communities structured only by competitive interactions, which means their relevance to multi-trophic level dynamics or non-trophic interactions remains unsubstantiated.

Using models to inform and augment empirical studies: the challenge of connecting models to data

All previous models of the impacts of invaders have measured impact exclusively as the number of species lost from a community; however, many alternative measures of impact may be interesting or useful. Most of these measures, such as abundance of the invader, abundance of each resident species, or total species diversity, correspond directly to the empirical approaches we discussed earlier. Others can be investigated only with models. In general, response variables that are highly derived, or that incorporate complex spatial or temporal variation, are perhaps most fruitfully the domain of modeling efforts.

As discussed in the context of ordination in empirical studies, one derived metric is Euclidean distance in multidimensional ‘species space,’ where each species is represented by its abundance, and the impact on a community is measured by the Euclidean distance between ‘before’ and ‘after’ points in this multidimensional space. Euclidean distances provide a way to handle changes in the abundance of large numbers of species simultaneously, and they are elegant in that they can be generalized across a wide range of communities and hypothetical invasions. This measure will be most easily interpretable in the context of models, where the number and characteristics of resident species are controlled, invasions can be replicated, and outcomes can be analyzed probabilistically.

Historically, response variables in invasion models (e.g., species number) have been evaluated at equilibrium, an assumption that certainly raises the question of relevance for natural systems. However, a species’ mean abundance over a long enough time interval may provide a reasonable substitute to tie field data into model predictions. Alternatively, many response variables can be formulated in ways that require no equilibrium assumption. In fact, models provide an excellent tool for investigating patterns of temporal variability that are biologically important, such as time lags, boom and bust establishment, and changes in the magnitude of variability itself.

The number of extinctions has been used as a response variable in most theoretical studies of invasions (Case 1995; Morton et al. 1996; Morton and Law 1997). While earlier work focused on the number of species extinct at the new equilibrium, an alternative is the number of species going below an extinction threshold as the community moves to its new equilibrium. As the community changes, population trajectories may temporarily pass close to zero even though the equilibrium may be further away. The corresponding extinctions (in a model with stochasticity or a non-zero extinction threshold) would not be predicted from a simple calculation of equilibrium abundance. Extinction is a problematic metric in empirical studies because of the logistical difficulty of verifying that a species has truly gone extinct. However, a nonzero threshold could be used to determine local extinction in the field, as with model systems. Such an approach is especially appropriate for ‘living dead’ species, with long-lived individuals experiencing declines that, though protracted, are inevitable (owing to Allee effects, for instance). Focusing on the dynamics of extinctions rather than snapshot diversity indices would allow empirical studies to be more closely tied to theoretical results.

A role for models in generating new theoretical insights

Models could be used to explore the relationship between specific mechanisms of impact and the consequences of those mechanisms. The idiosyncratic character of each invader’s particular impacts on other species, that is, its role in the community (e.g., eats a keystone predator) is incorporated as a set of parameters of a model, while more integrative measures of impact such as change in species richness or Euclidean distance form the model’s generalizable output. Models could then be the avenue for asking whether impact is dominated by quirks and therefore inherently unpredictable (Simberloff 1985), or whether generalizations are possible. In the context of our original framework, models could also be a valuable tool for investigating the relationship between per-capita effect and abundance in determining total impact at a site.

In order to evaluate the significance of particular traits to the impact of an invading species, or to compare the impacts of different guilds of invaders, we need to be able to isolate all other factors; that is, we need to be able to compare the effects of different invasions into the same community. However, the reality of biological systems is that one cannot compare different kinds of species invading perfectly identical communities. Models can provide such comparisons. Taking advantage of the ability of models to vary characteristics of either the invader or the community independently may put ecologists in a much better position to understand and to predict the impacts of a wide range of invaders.

Impact from a policy or management perspective

Impact measurement is a tool for setting priorities

A community ecologist interested in invasions seeks measures of impact that help test hypotheses about how communities function and what factors inhibit or facilitate invasions. In contrast, a reserve manager may need to measure impact in a way that identifies target species and locations most in need of control actions. Thus, impact measurement for a manager or a policymaker is about priorities, and the key is generating a rank-ordering of major risks to ecosystems and natural communities. Measures of impact for applied ecology can afford to be wrong for minor and even modest impacts, but must be sure to capture (or ideally to foreshadow) those major impacts such as the cactus *Opuntia* sweeping across the Australian rangeland or the extinction of reptiles by the small Indian mongoose.

The opportunities and challenges of working at a large scale in space and time

Control of harmful nonindigenous species is increasingly being dealt with at national and international levels, because species do not recognize administrative boundaries. As soon as one begins to consider pest problems at a strategic level, the potential for effective and efficient action against them increases markedly. For example, Australia is working to control potential outbreaks of screw-worm fly (*Chrysomya bezziana*) before they occur, by rearing sterile males in a cooperative international program in Malaysia (Anonymous 1997, p. 38). As the potential for creative solutions increases, so too does the complexity of the decision-making process. How should a government decide the allocation of funding between weeds, vertebrate pests, tree diseases, marine invertebrates, and so on? We are only now beginning to grapple with these questions, and we have as yet few tools for doing so.

When we move from the perspective of an ecologist interested in local processes affecting diversity to that of a resource manager trying to determine priorities for control of nonindigenous species, we need to expand our view beyond specific local impacts. To return to our conceptual framework, range (R), abundance (A), and local per-capita or per-kg effect (E) all contribute to the global impact of a species. What is the prognosis for using this conceptual framework in management decisions currently, and where are we most likely to run into difficulties estimating impact? Clearly, all three quantities are sometimes difficult to estimate and are likely to vary over orders of magnitude. Range will vary over as much as seven orders of magnitude, but it is also the easiest component of impact to measure and probably has the smallest estimation error (on the order of 10%). Abundance or biomass is more problematic, having a fairly wide range (four orders of magnitude) and a large estimation error (on the order of 50%). The variable with perhaps the greatest interspecific range in values and a potential for enormous errors in estimation is the local per-unit Effect. Studies that have assessed interaction strengths of large numbers of food web links suggest that they may vary over six or seven orders of magnitude (Rafaelli and Hall 1996; Wootton 1997). For example, E of a single individual of an invasive tree species like melaleuca (*Melaleuca quinquenervia*) is probably orders of magnitude greater than E of a single stem of an herbaceous weed like purple loosestrife (*Lythrum salicaria*) (although that may not be the case if equal biomasses are considered). If we are ever to be able to compare overall impact among a set of species, it seems likely that we are going to have to get a much better feeling for how E varies among species, as well as for its possibly complex relationship with R and A.

To assess impact, then, we need to measure R, A, and E, and these measurements may be hard enough to make. The difficulties are compounded in attempting to predict future impact. We might need to know how per-capita E varies in different environments (e.g., will the impact of a weed alter as it moves from wetlands to uplands?), and over time (e.g., do native species learn to evade an introduced predator? Will an invading pathogen evolve the ability to exploit new hosts?). In addition, our projections for the future would have to include potential changes in abundance and range size. Such knowledge would require a daunting and perhaps unattainable level of sophisticated ecological prediction. However, it is worth learning what we can of these relationships and incorporating greater knowledge into our attempts at management.

Working examples of how impact can be measured and monitored

Biological control projects are a form of planned invasion, and assessments of the desirability of proposed biological control introductions offer some lessons for the measurement of invasion impacts in general. Here the goal is to predict the impact of one organism on just one or a few other species. The fact that we so rarely have quantitative measures of impact of the control agent on the pest (let alone on non-target organisms) is some indication of the difficulties of measuring impacts even in systems that are fairly simple. For example, comparatively few recent publications dealing with biological control of weeds have presented quantitative evidence of effects of the control agent (but see Burdon et al. 1981; McEvoy et al. 1991; Lonsdale et al. 1995; Louda et al. 1997). Even in these cases, impacts are often demonstrated on a small scale that may or may not extrapolate to regional landscapes. One exception to the generally poor status of the data in this area involves the release of nonindigenous organisms for the control of human health epidemics (or potential ones), with the intent of creating an impact on disease vectors. Although impacts on nontarget species are usually ignored, at least the target impacts are closely monitored and well quantified (Laird 1981). Examples include crayfish introduced to control snail populations that harbor the trematode fluke *Schistosoma mansoni* (Hofkin et al. 1991) and mosquitofish to control malaria-carrying mosquito populations (Gerberich and Laird 1968).

What kind of effort is required in the applied realm if we really want an accurate assessment of long-term, multitrophic ecological impact? In Kakadu National Park, northern Australia, a team of scientists monitored the impact of a uranium mine on a tropical wetland ecosystem. For more than a decade, 20 researchers studied water chemistry and ecological effects on a variety of trophic levels (Finlayson 1990). Unfortunately, nothing like this level of investment has gone into monitoring any environmental weed or pest.

The realities of setting priorities: risk assessment

In reality, the impact of the organism, even if perfectly known and even if weighted by public values, forms only one part of the information used by a resource manager faced with limited funding and a need for prioritization. In fact, feasibility and cost of control are just as important in determining how to allocate funds (CSIRO 1990). The core structure of a decision system can be thought of as a two dimensional ordination, ranking species by impact (current or projected) on the one hand, and the ease with which they can be controlled on the other (Figure 3). With monetary resources as a common currency, one could envisage earmarking high impact, high feasibility species as top priority species for our major control efforts, while high impact, low feasibility species would be a focus for research into control techniques. To complicate matters, we have focused on impacts of invaders as defined by the degree of ecological change produced by an initial invasion; however, a different type of impact could be defined by the feasibility, not of control, but of restoration of a site once the invader is removed. These two views are not necessarily concordant. Invaders that have large but reversible impacts (i.e., full restoration is possible, as in the case of water hyacinth (*Eichhornia crassipes*) in Florida, Schardt 1997) would be high priority for both halting spread and for eradication. In contrast, invaders with the potential for long-lasting or permanent effects on communities, such as the extinction-causing brown tree snake, *Boiga irregularis* (Wiles et al. 1995), might receive high priority for prevention of initial spread, while being considered a lower priority for eradication once the impacts have occurred.

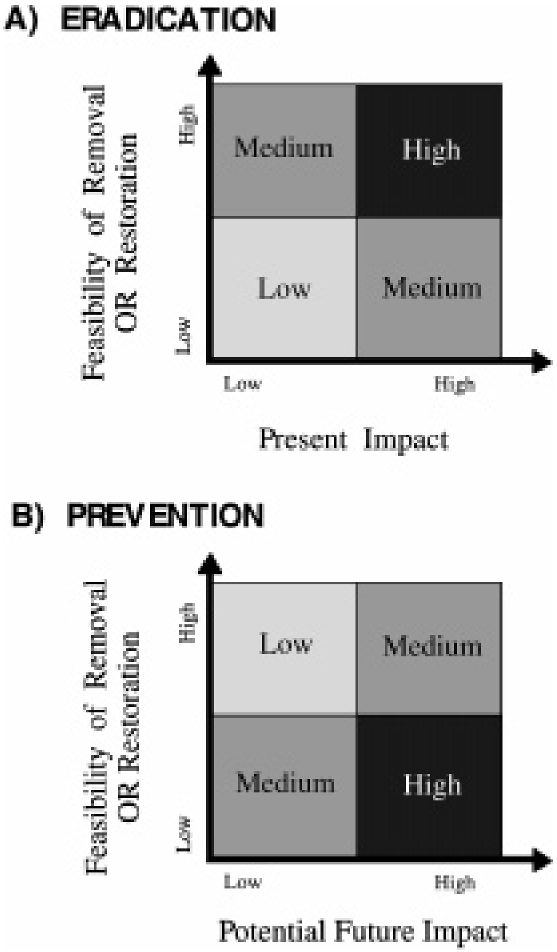

Figure 3. Schematic for the process faced by policy-makers and managers who must decide which nonindigenous species to A) eradicate or control, once already present in the system, or B) keep out, if not already present in the system.

Finally, ranking the impact of different invasive species is much like doing a risk assessment. A risk assessment typically involves three stages: identifying the hazards, quantifying them, and then allowing for values and the perception of risk (Royal Society of London 1992). Similarly the challenge of identifying impact measures that are useful in an applied context is threefold: first determining metrics that reflect all the potentially important biological as well as social, economic, aesthetic, etc., changes that can accompany invasions; second, synthesizing these into a composite measure or algorithm that can be compared and generalized; and then finally, applying public perceptions and values (for example, weighting extinctions over simple changes in abundance) to determine how the metrics will be used to prioritize species for control or removal.

Managers and policy-makers also have to consider that the risks associated with certain invaders, particularly invaders that cause human health hazards, can have a 'psychological impact' out of proportion to their real impact, such as the africanized 'killer' honey bee (*Apis mellifera scutellata*), which is notorious in North America despite causing relatively few deaths or injuries. Esthetic factors can similarly distort the assessment of impacts by the public, either by flagging an invader with an undesirable visual effect, or conversely reducing the perception of impact for invaders that have a pleasing appearance or simply 'seem to belong' (e.g., *Eucalyptus* trees in California). With some invaders, economic factors may completely overshadow the ecological side of the equation. However, as public awareness of biological invasions increases, and as societies place increasing value on conserving biodiversity, more sophisticated and science-based information on the ecological impacts of invaders should play a greater and greater role in practical decision-making.

Conclusions

One of our goals in this synthesis is to spur the identification and measurement of the threat of particular nonindigenous species to native populations, species, communities, and ecosystems. Despite the considerable attention invasive species receive, our lamentable paucity of data on impacts leaves us largely ignorant about the ecological changes they have brought about. We need to build up a catalogue of such studies and encourage collection of data in a standardized manner, in order to coordinate and improve both control and research efforts for existing invaders. A hope for the even more distant future is a general framework for predicting the impacts of future introductions.

On a landscape scale, impacts are determined by the range and abundance of a nonindigenous species, as well as its local per capita effect. The focus of most basic ecological research has been the local effect (without distinguishing per unit effect from abundance). In contrast, regional resource managers often think primarily in terms of distributional range, or of the financial cost of control or remediation. Linking these different approaches through simple theory and statistical or empirical studies would constitute a major contribution to invasion biology.

There is, as always, a conflict between what might be the best or most informative metric of impact and what is practical and useful. Which measures give us the same information, and therefore are a waste of time and money? We suggest that, for the near future, the primary focus for research on the impacts of invaders should be to explore the extent to which the many measures of impact we have described are correlated or redundant. This area is rife with questions that are both important from an applied perspective as well as fascinating from a basic perspective:

(1) Do impacts on individuals or single populations, which are more tractable for both experimental and observational studies, adequately predict the response of community measures of diversity? More specifically, are there useful bioindicators for invasion impact?

(2) Do impacts assessed via simple composite measures such as species richness capture the more complex picture of community change that can be obtained by multivariate methods such as ordination or Euclidean distance?

(3) How closely correlated are impacts on population or community characteristics with impacts on ecosystem functions? Do changes in the community drive changes in ecosystem function, or vice versa? Is it possible to have a large ecosystem impact without an easily measured community or population impact?

(4) Are invaders with large local effects also, on average, those that have large ranges, or that spread rapidly, or that develop the greatest abundance or collective biomass? In addition, how closely correlated are ecological impacts as traditionally measured? Further, how well do ecological impacts correlate with economic impacts (Williamson 1998)?

(5) To what extent does the quantitative measure of the impact of an invasive species depend on the community or ecosystem in which it is measured? On what level can we generalize across systems? How often does the impact of an invader depend on the presence of other nonindigenous species (the Invasional Meltdown Hypothesis)?

We advocate three approaches for gaining insight into the correlation among measures of impact. The first is by synthesizing the quantitative data currently published on different impact response variables estimated for the same suite of species. For example, for introduced plants in Great Britain, Williamson (1998) found significant rank correlations among six estimates of impact, including geographic distribution, herbicide-related costs in agricultural systems, local abundance, cost of control in nature reserves, and a subjective score of ‘perceived weediness’. While the current state of the empirical data will not allow such a comparison for very many species or many types of impact at this time, we expect the information to accumulate rapidly as invasions enjoy a higher public profile. Meta-analysis (Gurevitch et al. 1992) is one potentially fruitful approach for addressing these sorts of questions in a statistically formalized manner (M. Wonham, K. Goodell, B. Von Holle, and I.M. Parker, unpublished data).

Second, while most empirical studies have focused on a single measure of impact, or a single response variable such as one native species’ abundance, we encourage studies that measure impacts at multiple scales and multiple levels of organization. For example, in a single study of *Acacia saligna*, Musil (1993) measured soil mineral enrichment as well as regeneration probabilities for all resident native plant species. Single studies that integrate across levels will provide an even better estimate of the relationship among impact measures than will a formal metaanalysis on an amalgam of studies.

Finally, more attention to models of impact could provide a wealth of new insights and help guide much-needed empirical work. One role for models will be to reveal which measures of impacts in theory carry the greatest information, and the extent to which different measures of impact are correlated with one another. Within simple Lotka-Volterra type community models, the calculation and comparison of a large number of response variables is easy because they are not subject to the practical constraints of empirical work. In addition, by linking community models to models that track ecosystem functions such as carbon budgets or nutrient cycling, we could make the same kinds of comparisons between community and ecosystem metrics. Predictions based on these correlations among model impacts could then be tested explicitly in the field.

There is a great opportunity for the development of a theoretical framework for invasion impacts, and an important application waiting for such a framework. Priorities based on assessment of impact need to be set at all scales, from management of local reserves to national and international policy decisions. In order to proceed we will need standardized rules of thumb for how to measure the impacts of invaders. Furthermore, a steady accumulation of standardized data on impacts coupled with theoretical investigations will allow us to generalize, and perhaps even predict, which species will be most likely to have the greatest impacts.

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References

Abrams PA (1996) Evolution and the consequences of species introductions and deletions. Ecology 77: 1321–1328

Adalsteinson S (1985) Possible changes in the frequency of human ABO blood groups in Iceland due to smallpox epidemic selection. Annals of Human Genetics 49: 275–281

Allmon RA and Sebens KP (1988) Feeding biology and ecological impact of the introduced nudibranch, *Tritonia plebeia*, New England, USA. Marine Biology 99: 375–385

Alpine AE and Cloern JE (1992) Trophic interactions and direct physical effects control phytoplankton biomass and production in an estuary. Limnology and Oceanography 37: 946–955

Anable ME, McClaran MP and Ruyle GB (1992) Spread of introduced Lehmann lovegrass *Eragrostis lehmanniana* Nees in Southern Arizona, USA. Biological Conservation 61: 181–188

Anagnostakis SL (1987) Chestnut blight: the classical problem of an introduced pathogen. Mycologia 79: 23–37

Andersen AN and Sparling GP (1997) Ants as indicators of restoration success: relationship with soil microbial biomass in the Australian seasonal tropics. Restoration Ecology 5: 109–114

Anonymous (1997) The Australian National Weed Strategy. Australian Government, Canberra

Bergelson J and Crawley M (1989) Can we expect mathematical models to guide biological control programs?: a comment based on case studies of weed control. Comments on Theoretical Biology 1: 197–216

Braithwaite RW and Lonsdale WM (1987) The rarity of *Sminthopsis virginiae* in relation to natural and unnatural habitats. Conservation Biology 1: 341–343

Braithwaite RW, Lonsdale WM and Estbergs JA (1989) Alien vegetation and native biota in tropical Australia: the impact of *Mimosa pigra*. Biological Conservation 48: 189–210

Bright C (1998) Life out of Bounds. W.W. Norton, New York

Brown LR and Moyle PB (1991) Changes in habitat and microhabitat partitioning within an assemblage of stream fishes in response to predation by Sacramento squawfish (*Ptychocheilus grandis*). Canadian Journal of Fisheries and Aquatic Sciences 48: 849–856

Burdon JJ, Groves RH and Cullen JM (1981) The impact of biological control on the distribution and abundance of *Chondrilla juncea* in south-eastern Australia. Journal of Applied Ecology 18: 957–966

Burger J (1997) Heavy metals and selenium in herring gulls (*Larus argentatus*) nesting in colonies from eastern Long Island to Virginia. Environmental Monitoring and Assessment 48: 285–296

Busch DE and Smith SD (1995) Mechanisms associated with decline of woody species in riparian ecosystems of the southwestern US. Ecological Monographs 65: 347–370

Case TJ (1990) Invasion resistance arises in strongly interacting species-rich model competition communities. Proceedings of the National Academy of Sciences 87: 9610–9614

Case TJ (1991) Invasion resistance, species build-up and community collapse in metapopulation models with interspecies competition. Biological Journal of the Linnean Society 42: 239–266

Case TJ (1995) Surprising behavior from a familiar model and implications for competition theory. American Naturalist 146: 961–966

Chapin FS III, Reynolds HL, D'Antonio CM and Eckhart VM (1996) The functional role of species in terrestrial ecosystems. In: Walker B and Steffen W (eds) Global Change and Terrestrial Ecosystems, pp 403–428. Cambridge University Press, Cambridge

Cohen AN and Carlton JT (1998) Accelerating invasion rate in a highly invaded estuary. Science 279: 555–558

Cowie RH (1992) Evolution and extinction of Partulidae, endemic Pacific island land snails. Philosophical Transactions of the Royal Society of London B 335: 167–191

Creed RP and Sheldon SP (1995) Weevils and watermilfoil: did a North American herbivore cause the decline of an exotic plant? Ecological Applications 5: 1113–1121

Cronk QCB and Fuller JL (1995) Plant Invaders. Chapman & Hall, London

Crowder LB (1984) Character displacement and habitat shift in a native cisco in southeastern Lake Michigan: evidence for competition? Copeia 1984: 878–883

CSIRO (1990) CSIRO Priority Determination: Methodology and Results. CSIRO Australia, Canberra

Day FP Jr and Monk CD (1974) Vegetation patterns on a southern Appalachian watershed. Ecology 55: 1064–1074

D'Antonio C and Vitousek PM (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual Review of Ecology and Systematics 23: 63–87

Digby PGN and Kempton RA (1987) Multivariate Analysis of Ecological Communities. Chapman & Hall, New York.

Dombeck M (1996) Noxious and invasive weeds: should we have a national policy for a national problem? Proceedings of the Western Society of Weed Science 49: 5–9

Elkinton JS and Liebhold AM (1990) Population dynamics of gypsy moth in North America. Annual Review of Entomology 35: 571–596

Elton CS (1958) The Ecology of Invasions by Animals and Plants. Methuen, London

Echelle AA and Connor PJ (1989) Rapid, geographically extensive genetic introgression after secondary contact between two pupfish species (Cyprinodon, Cyprinodontidae). Evolution 43: 717–727

Finlayson CM (1990) Plant ecology and management of an internationally important wetland in monsoonal Australia. In: Kusler JA and Day S (eds) Wetlands and River Corridor Management, pp 90–98. The Association of State Wetland Managers, Chester, VT

Fraser DF and Gilliam JF (1992) Nonlethal impacts of predator invasion: Facultative suppression of growth and reproduction. Ecology 73: 959–970

Gardner MR and Ashby WR (1970) Connectance of large dynamical (cybernetic) systems: critical values for stability. Nature 228: 784

Gaston KJ, Blackburn TM and Lawton JH (1997) Interspecific abundance-range size relationships: an appraisal of mechanisms. Journal of Animal Ecology 66: 579–601

Gerberich JB and Laird M (1968) Bibliography of papers relating to the control of mosquitoes by the use of fish. An annotated bibliography for the years 1901–1966. FAO Fisheries Technical Paper No. 75. FAO, Rome

Gilbert GS, Parke JL, Clayton MK, Handelsman J (1993) Effects of an introduced bacterium on bacterial communities on roots. Ecology 74: 840–854

Gilbert GS, Clayton MK, Handelsman J and Parke JL (1996) Use of cluster and discriminant analyses to compare rhizosphere bacterial communities following biological perturbation. Microbial Ecology 32: 123–147

Gurevitch J, Morrow LL, Wallace A and Walsh JS (1992) A meta-analysis of competition in field experiments. American Naturalist 140: 539–572

Hager HA and McCoy KD (1998) The implications of accepting untested hypotheses: a review of the effects of purple loosestrife (*Lythrum salicaria*) in North America. Biodiversity and Conservation 7: 1069–1079

Hebert PDN, Wilson CC, Murdoch MH and Lazar R (1991) Demography and ecological impacts of the invading mollusc *Dreissena polymorpha*. Canadian Journal of Zoology 69: 405–409

Hofkin BV, Mkoji GM, Koech DK and Loker ES (1991) Control of schistosome-transmitting snails in Kenya by the North American crayfish *Procambarus clarkii*. American Journal of Tropical Medicine and Hygiene 45: 339–344

Holmes PM and Cowling RM (1997) Diversity, composition and guild structure relationships between soil-stored seed banks and mature vegetation in alien plant-invaded South African fynbos shrublands. Plant Ecology 133: 107–122

Hoopes MF and Harrison S (1998) Metapopulation, source-sink and disturbance dynamics. In: Sutherland WJ (ed) Conservation Science and Action, pp 135–151. Blackwell, Oxford

Hurlbert SH (1971) The nonconcept of species diversity: a critique and alternative parameters. Ecology 52: 577–586

Hurlbert SH (1997) Functional importance vs. keystoneness: reformulating some questions in theoretical biocenology. Australian Journal of Ecology 22: 369–382

Jones CG, Ostfeld RS, Richard MP, Schauber EM and Wolff JO (1998) Chain reactions linking acorns to gypsy moth outbreaks and lyme disease risk. Science 279: 1023–1026

Juliano SA (1998) Species introduction and replacement among mosquitos: interspecific resource competition or apparent competition? Ecology 79(1): 225–268

Karatayev AY, Burlakova, LE and Padilla DK (1997) The effects of *Dreissena polymorpha* (Pallas) invasion on aquatic communities. Eastern European Journal of Shellfish Research 16: 187–203

Karr JR, Fausch KD, Angermeier PL, Yant PR and Schlosser IJ (1986) Assessing biological integrity in running waters: a method and its rationale. Illinois Natural Historical Survey Special Publication 5. Champaign, IL

Kowarik I (1995) On the role of alien species in urban flora and vegetation. In: Pýsek P, Prach K, Rejmánek M and Wade M (eds) Plant Invasions: General Aspects and Special Problems, pp 85–103. SPB Academic Publishing, Amsterdam

Krueger CC and May B (1991) Ecological and genetic effects of salmonid introductions in North America. Canadian Journal of Fisheries and Aquatic Sciences 48: 66–77

Laird M (1981) Biocontrol of Medical and Veterinary Pests. Praeger, New York

Leary RF, Allendorf FW and Sage GK (1995) Hybridization and introgression between introduced and native fish. American Fisheries Society Symposium 15: 91–101

Leyval C, Turnau K and Haselwandter K (1997) Effect of heavy metal pollution on mycorrhizal colonization and function: physiological, ecological and applied aspects. Mycorrhiza 7: 139–153

Lonsdale WM and Braithwaite RW (1988) The shrub that conquered the bush. New Scientist 120: 52–55

Lonsdale WM, Farrell G and Wilson CG (1995) Biological control of a tropical weed: a population model and an experiment for *Sida acuta*. Journal of Applied Ecology 32: 391–399

Louda SM, Kendall D, Connor J and Simberloff D (1997) Ecological effects of an insect introduced for the biological control of weeds. Science 277: 1088–1090

Mack MC and D'Antonio CM (1998) Impacts of biological invasions on disturbance regimes. Trends in Ecology and Evolution 13: 195–198

Maelfait JP and Baert L (1997) Spiders as bio-indicators for nature conservation in Flanders. Levende Natuur 98: 174–179

May RM (1973) Stability and Complexity in Model Ecosystems. Princeton University Press, Princeton, NJ

McEvoy PB, Cox CS and Coombs E (1991) Successful biological control of ragwort *Senecio jacobaea* by introduced insects in Oregon. Ecological Applications 1: 430–442

McMillan M and Wilcove D (1994) Gone but not forgotten: Why have species protected by the Endangered Species Act become extinct? Endangered Species UPDATE 11(11): 5–6

Morton RD and Law R (1997) Regional species pools and the assembly of local ecological communities. Journal of Theoretical Biology 187: 321–331

Morton RD, Law R, Pimm SL and Drake JA (1996) On models for assembling ecological communities. Oikos 75: 493–499

Moulton MP (1993) The all-or-none pattern in introduced Hawaiian passeriforms: the role of competition sustained. American Naturalist 141: 105–119

Moulton M and Pimm S (1983) The introduced Hawaiian avifauna: biogeographic evidence for competition. American Naturalist 121: 669–690

Moyle PB and Marchetti MP (1999) Application of indices of biotic integrity to California streams and watersheds. In: Simon TP and Hughes R (eds) Assessing the Sustainability and Biological Integrity of Water Resources Using Fish Communities, pp 367–380. CRC Press, Boca Raton, FL

Murray J, Murray E, Johnson MS and Clarke B (1988) The extinction of *Partula* on Moorea. Pacific Science 42: 150–153

Musil CF (1993) Effect of invasive Australian acacias on the regeneration, growth and nutrient chemistry of South African lowland fynbos. Journal of Applied Ecology 30: 361–372

Newton I (1997) Links between the abundance and distribution of birds. Ecography 20: 137–145

Parker IM and Reichard SH (1998) Critical issues in invasion biology for conservation science. In: Fiedler PL and Kareiva PM (eds) Conservation Biology for the Coming Decade, 2nd ed, pp 283–305. Chapman & Hall, New York

Parks JW, Craig PJ, Neary BP, Ozburn G and Romani D (1991) Biomonitoring in the mercury-contaminated Wabigoon-English-Winnipeg River (Canada) system: selecting the best available bioindicator. Applied Organometallic Chemistry 5: 487–495

Perrins J, Williamson M. and Fitter A (1992) A survey of differing views of weed classification: implications for regulation of introductions. Biological Conservation 60: 47–56

Platts WS (1991) Livestock grazing. In: Meehan WR (ed) Influences of Forest and Rangeland Management on Salmonid Fishes and Their Habitats, pp 389–423. American Fisheries Society Special Publication 9. American Fisheries Society, Bethesda, MD

Power ME (1992) Habitat heterogeneity and the functional significance of fish in river food webs. Ecology 73: 1675–1688

Rafaelli DG and Hall SJ (1996) Assessing the relative importance of trophic links in food webs. In: Polis GA and Winemiller KO (eds) Food Webs: Integration of Patterns and Dynamics, pp 185–191. Chapman & Hall, New York

Ramcharan CW, Padilla DK and Dodson SI (1992) Models to predict potential occurrence and density of the zebra mussel, *Dreissena polymorpha*. Canadian Journal of Fisheries and Aquatic Science 49: 2611–2620

Reichard SH and Hamilton CW (1997) Predicting invasions of woody plants introduced into North America. Conservation Biology 11: 193–203

Rejmánek M and Richardson DM (1996) What attributes make some plant species more invasive? Ecology 77: 1655–1661

Rhymer JM and Simberloff D (1996) Extinction by hybridization and introgression. Annual Review of Ecology and Systematics 27: 83–109

Rodriguez JP, Pearson DL and Barrera RR (1998) A test for the adequacy of bioindicator taxa: are tiger beetles (Coleoptera: Cicindelidae) appropriate indicators for monitoring the degradation of tropical forests in Venezuela? Biological Conservation 83: 69–76

Roots C (1976) Animal Invaders. Universe Books, New York

Ross J and Tittensor AM (1986) The establishment and spread of *Myxomatosis* and its effect on rabbit populations. Philosophical Transactions of the Royal Society of London B 314: 599–606

Royal Society of London (1992) Risk: analysis, perception and management. Report of a Royal Society Study Group. Royal Society, London

Ruesink JL, Parker IM, Groom MJ and Kareiva PM (1995) Reducing the risks of nonindigenous species introductions: guilty until proven innocent. Bioscience 45: 465–477

Schardt JD (1997) Maintenance control. In: Simberloff D, Schmitz DC and Brown TC (eds) Strangers in Paradise: Impact and Management of Nonindigenous Species in Florida, pp 229–244. Island Press, Washington, DC

Schmitz DC, Simberloff D, Hofstetter RH, Haller W and Sutton D (1997) The ecological impact of nonindigenous plants. In: Simberloff D, Schmitz DC and Brown TC (eds) Strangers in Paradise: Impact and Management of Nonindigenous Species in Florida, pp 39–61. Island Press, Washington, DC

Settle WH and Wilson LT (1990) Invasion by the variegated leafhopper and biotic interactions: parasitism, competition, and apparent competition. Ecology 71(4): 1461–1470

Shugart HHJ and West DC (1977) Development of an Appalachian deciduous forest succession model and its application to assessment of the impact of chestnut blight. Journal of Environmental Management 5: 161–180

Simberloff D (1985) Predicting ecological effects of novel entities: Evidence from higher organisms. In: Halvorson HO, Pramer D and Rogul M (eds) Engineered Organisms in the Environment/Scientific Issues, pp 152–161. American Society for Microbiology, Washington, DC

Simberloff D (1991) Keystone species and community effects of biological introductions. In: Ginzburg LR (ed) Assessing Ecological Risks of Biotechnology, pp 1–19. Butterworth-Heinemann, Boston, MA

Simberloff D (1997) Flagships, umbrellas, and keystones: Is single-species management passé in the landscape era? Biological Conservation 83: 247–257

Simberloff D and Von Holle B (1999) Positive interactions of nonindigenous species: invasional meltdown? Biological Invasions 1: 21–32 (this issue)

Spencer CN, McClelland BR and Stanford JA (1991) Shrimp stocking, salmon collapse, and eagle displacement. Bioscience 41: 14–21

Stone CP (1985) Alien animals in Hawai'i's native ecosystems: Toward controlling the adverse effects of introduced vertebrates. In: Stone CP and Scott JM (eds) Hawai'i's Terrestrial Ecosystems. Preservation and Management, pp 251–297. Cooperative National Park Resources Studies Unit, University of Hawaii, Honolulu, HI

Thompson JD (1991) The biology of an invasive plant. Bioscience 41: 393–401

Trenham P, Shaffer HB and Moyle PB (1998) Biochemical identification and assessment of population subdivision in morphologically similar native and invading smelt species (*Hypomesus*) in the Sacramento-San Joaquin Estuary, California. Transactions of the American Fisheries Society 127: 417–424

United States Congress, Office of Technology Assessment (1993) Harmful Non-indigenous Species in the United States. Washington, DC

Vitousek PM (1986) Biological invasions and ecosystem properties: Can species make a difference? In: Mooney HA and Drake JA (eds) Ecology of Biological Invasions of North America and Hawaii, pp 163–176. Springer-Verlag, New York

Vitousek PM (1990) Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. Oikos 57: 7–13

Vitousek PM and Walker LR (1989) Biological invasions by *Myrica faya* in Hawaii: plant demography, nitrogen fixation, ecosystem effects. Ecological Monographs 59: 247–265

von Broembsen SL (1989) Invasions of natural ecosystems by plant pathogens. In: Drake JA, Mooney HA, di Castri F, Groves RH, Kruger FJ, Rejmánek M and Williamson M (eds) Biological Invasions: A Global Perspective. Scientific Committee on Problems of the Environment (SCOPE) of the International Council of Scientific Unions, pp 77–83. John Wiley, New York

Watkinson AR and Sutherland WJ (1995) Sources, sinks and pseudo-sinks. Journal of Animal Ecology 64: 126–130

Wiles GJ, Aguon CF, Davis GW and Grout DJ (1995) Status and distribution of endangered animals and plants in northern Guam. Micronesica 28: 31–49

Williamson M (1987) Are communities ever stable? Symposia of the British Ecological Society 26: 353–371

Williamson M (1996) Biological Invasions. Chapman & Hall, London

Williamson M (1998) Measuring the impact of plant invaders in Britain. In: Starfinger U, Edwards K, Kowarik I and Williamson M (eds) Plant Invasions: Ecological Consequences and Human Responses, pp 57–68. Backhuys, Leiden, The Netherlands

Williamson MH and Fitter A (1996) The characters of successful invaders. Biological Conservation 78: 163–170

Wootton JT (1997) Estimates and tests of per capita interaction strength: diet, abundance, and impact of intertidally foraging birds. Ecological Monographs 67: 45–64

Zaitsev Y and Marnaev V (1997) Biological Diversity in the Black Sea: A Study of Change and Decline. United Nations Publications, New York