

# Exotic plant invasions and the enemy release hypothesis

Ryan M. Keane and Michael J. Crawley

To curb the future economic and environmental impacts of invasive exotic species, we need to understand the mechanisms behind exotic invasions. One commonly accepted mechanism for exotic plant invasions is the enemy release hypothesis (ERH), which states that plant species, on introduction to an exotic region, experience a decrease in regulation by herbivores and other natural enemies, resulting in a rapid increase in distribution and abundance. The success of classical biological control has been used as support for ERH, but this observational evidence does not directly test ERH, and the more experimental evidence is equivocal. Competitive release through greater generalist enemy impact on natives seems to be an important but understudied mechanism of enemy release, but there is a serious need for experiments involving exclusion of natural enemies in invaded plant communities. With a clearer understanding of the role of enemy release in exotic plant invasions, we can begin to build a comprehensive predictive model of exotic plant invasions.

BIOLOGICAL INVASIONS (see Glossary) are believed to be the second largest cause of current biodiversity loss, after habitat destruction [1]. As international trade increases, the number of both accidental and intentional EXOTIC introductions is likely to increase. To limit the impact that exotic species have on natural and man-made communities, we need to understand the major mechanisms that allow exotics to become invasive. For exotic plants, one commonly accepted mechanism of invasions is that proposed by the ENEMY RELEASE HYPOTHESIS (ERH), also referred to as the herbivore escape, predator escape or ecological release hypothesis [2,3].

The ERH states that plant species, on introduction to an exotic region, should experience a decrease in regulation by herbivores and other natural enemies, resulting in an increase in distribution and abundance. This hypothesis is based on a three-point logical argument: (1) natural enemies are important regulators of plant populations; (2) enemies have a greater impact on native than on exotic species; and (3) plants are able to capitalize on a reduction in enemy regulation, resulting in increased population growth.

The validity of these points, and thus the potential for ENEMY RELEASE, varies across species. Enemy release might play a role in some exotic invasions, whereas different mechanisms, such as community disturbance, are important in others [4]. Our main objective here is not to determine whether enemy release is the main mechanism for all exotic plant invasions, but to understand which species will be most likely to benefit from enemy release.

We first examine the underlying assumptions of ERH, and how these assumptions might not apply equally to all species. Second, we review the traditional observational evidence that has been used to support ERH and the experimental evidence that tests it more directly. Finally, we propose an empirical model for testing the importance of enemy release in exotic plant invasions.

## Assumptions of the ERH

Before the assumptions underlying ERH can be assessed, a common framework of how plants and their enemies interact in a community must be established (Fig. 1). In its native community, the study plant (i.e. the species that has been introduced to a new region) competes with other native plant species whilst being attacked by specialist herbivores and pathogens. The competing plant species are attacked by their OWN SPECIALIST ENEMIES, and all the plants are attacked by generalist enemies. The relative strength of each interaction will vary depending on the species and community, allowing for complex indirect effects on the abundance of the study species. When the species is introduced to a new region, the ERH predicts that: (1) the specialist enemies of the study species will be absent from the new region; (2) HOST SWITCHING by specialist enemies of native congeners will be rare; and (3) generalists will have a greater impact on the native competitors.

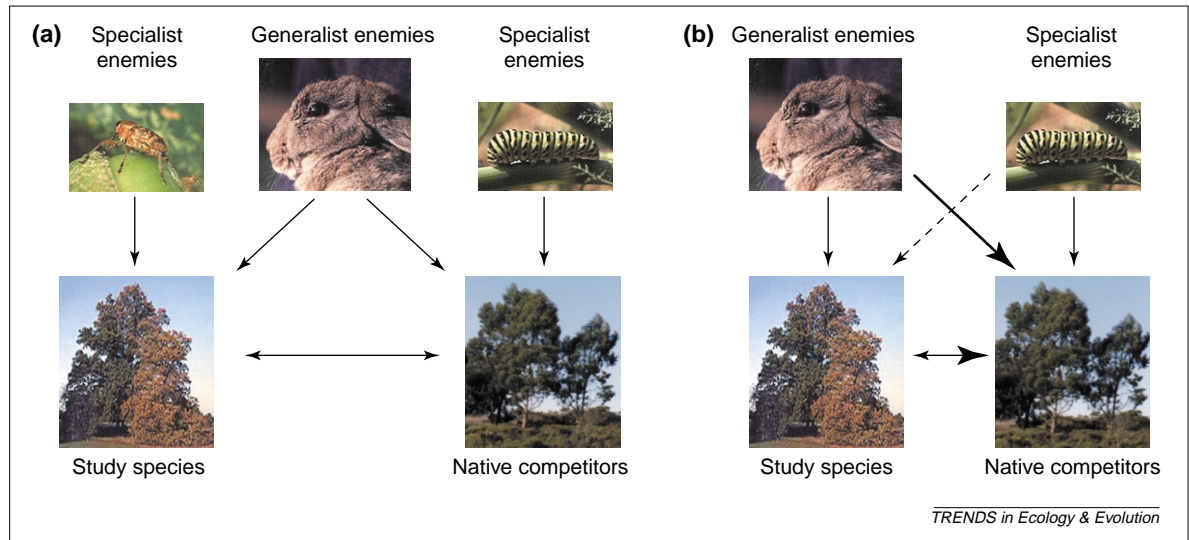
Thus, the loss of the study species to enemies is reduced in the exotic region relative to its loss in the native region, but also the relative loss to enemies is shifted onto the species' competitors, resulting in competitive release. This highlights the fact that interspecific plant competition can be as or more important than enemies in limiting plant establishment.

Similarly, two alternative hypotheses to explain exotic invasiveness focus on how native plant species, through competitive exclusion, prevent exotics from establishing and increasing. First, human perturbations to native communities can reduce the adaptation of native species to the current environment, decreasing their competitive ability relative to better-adapted exotic species (e.g. nutrient enrichment, overgrazing by domestic livestock, decreased water flow and climate change) [5–7]. Second, invasive exotic species might have a greater inherent competitive ability than do the native species as a result of different evolutionary histories (e.g. faster uptake of limiting resources, ability to maintain dense monocultures and high levels of allelopathy) [8–10]. The ERH and these two hypotheses provide different, but not mutually exclusive, mechanisms by which an exotic species can outcompete the natives and become invasive.

*The role of natural enemies as regulators of plants*  
The natural enemies of plants include vertebrate and invertebrate herbivores, fungal pathogens, and

Ryan M. Keane\*  
Michael J. Crawley  
Dept of Biological  
Sciences, Silwood Park,  
Imperial College of  
Science, Technology and  
Medicine, Buckhurst  
Road, Ascot, Berkshire,  
UK SL5 7PY.  
\*e-mail:  
ryan.keane@ic.ac.uk

Fig. 1. Enemy release in a simplified community. (a) The native community consists of the study plant species (the invasive exotic), other competing plant species, specialist enemies, and generalist enemies, with arrows signifying the interactions that directly and indirectly affect the abundance of the study plants. (b) In the exotic community, the enemy release hypothesis predicts that there will be few exotic specialist enemies attacking the study species, host switching by native specialists will be rare, and generalists will have a greater impact on native competitors, resulting in reduced competition against the study species.



bacterial and viral diseases. There has been much study and discussion of how important natural enemies are as regulators of plant populations and community dynamics [11–14]. The source of much discussion is the variation in the importance of enemies depending on the spatial and temporal scale under study. In terms of spatial scale, one can examine the impact of plant enemies at the level of an individual plant, a single population or an entire community. In terms of temporal scale, one can examine the short-term ecological dynamics or the long-term evolutionary dynamics.

Generally speaking, for every plant species, even the most unpalatable, something has evolved to eat them. At the individual scale, herbivory and pathogen attack generally has a negative impact on the fitness of an individual plant. Most plant species, however, have evolved defenses to minimize this impact, either by producing chemicals or structures to deter enemy attack or by developing ways to tolerate the loss of biomass to enemies, resulting in equal fitness with or without enemy attack. For these species, enemies have little impact on individuals in ecological time, but enemies have obviously been important in evolutionary time, selecting for better-defended genotypes. For many species, there is a fitness cost to investing in resistance and tolerance, meaning that defended genotypes would be outcompeted by undefended genotypes in an enemy-free environment [15,16]. These cases are often more complex, with species being well defended against some enemies but poorly defended against others [17,18].

Enemies can have important impacts at the scale of plant populations. However, enemies might impact individuals with little resultant effect on populations. This is because recruitment by new individuals might be limited by other factors, such as microsite availability [19,20]. For example, enemies might remove a large proportion of the yearly seed production of a population, but owing to the low level of microsites available for seedling establishment, the

enemies have no impact on population recruitment. Again, the enemies are still impacting individual fitness and should, over evolutionary time, select for better-defended individuals; but in ecological time, the enemies are not regulating the population.

Enemies can also have serious effects on plant communities. Vertebrate herbivores, such as rabbits and sheep, clearly have serious impacts on vegetation structure, community composition and plant abundance [14,21]. The results of invertebrate exclusion experiments are more equivocal [21–23], and pathogens have rarely been studied in natural communities [24]. However, even in the experiments that show large herbivore impacts, there are plant species that show no change in abundance regardless of whether herbivores are present. Many species even decrease in abundance with the removal of herbivores, probably as a result of changes in the competitive environment (species will benefit in a generalist herbivore environment if their competitors are less well defended). Thus, natural enemies can interact with competition to produce complex patterns, making it difficult to determine the direct impact of enemies on a species.

#### *Greater enemy impact on native species*

The ERH predicts that specialist enemies of an exotic species will be absent in areas where it has been introduced. By definition, specialist enemies that attack a single species (i.e. single-species specialists) do not occur outside the native range of their host. However, there are two main mechanisms through which specialist enemies can be found in the exotic region: host switching and co-introduction of enemies.

If a plant species is introduced to a region that contains closely related native congeners, the specialist enemies of those congeners might switch to attack the exotic species [25,26]. Several studies have shown that specialist insect herbivores can switch to exotic congeners, although their impact is rarely measured [27–29].

Sometimes, plant species will not escape their enemies when introduced to a new region because their enemies might also be introduced to the same area. There are several examples where a plant and its enemy have both been introduced to the same region [28], although most cases involve generalist insect herbivores, such as widespread exotic pests. In general, it will be difficult for an exotic plant to escape from enemies that can survive on the propagules of the plant (e.g. seed-borne pathogens).

Another prediction of ERH is that generalist enemies will have a greater impact on native competitors than on the invasive exotic species. This shift in generalist enemy impact towards the natives should result in less interspecific competition for the exotic in its new region, resulting in invasive behavior. However, there is no obvious reason why generalist enemies should be less likely to attack exotics or to have a lower impact on exotics. The study of local adaptation of enemies to their native hosts provides limited evidence that generalist enemies might be better adapted to attacking native species than to attacking exotics [30]. However, native plants might have evolved better defenses against the native generalists than have exotic plants. A few studies have shown that generalist enemies (grasshoppers and mammals) might prefer natives as food plants [31–33], and some exotic species seem more tolerant to generalist enemy attack than are their native competitors [33].

A common occurrence is the invasion of well-defended exotics into communities that are grazed by domestic livestock, such as sheep and cattle [34]. We might predict that species of Eurasian or African origin would be better defended against such grazers, having had a recent evolutionary history of domestic grazing pressure. This example might be a better case for the human perturbation hypothesis, with the introduction of exotic generalist enemies producing a decreased adaptation of the native competitors to the new environment. However, it is an interesting illustration of how greater impact on natives by generalist enemies can allow competitive release for invasive exotics.

#### *Capitalizing on a reduction in enemy regulation*

If an exotic species is impacted by enemies in its native region and there is a reduction in this impact in its exotic region, the logical conclusion is that the species should be able to capitalize on this with a greater abundance in the exotic region. However, there are several reasons why an exotic might fail to become invasive.

A primary reason for failure might be the unsuitability of the climate of the exotic region, such that an introduced plant species cannot establish in sufficient numbers to capitalize on enemy release. Several models have been developed to determine the exotic areas suitable for establishment by an introduced species, based on its native climatic

range [35,36]. These models can also show where an exotic species can establish but fail to become invasive through enemy release because the climate is only marginally suitable.

An exotic might fail to capitalize on enemy release if it is less competitive than the native species, even when there is a greater enemy impact on the natives. Although invasive exotics are often hypothesized to have a greater inherent competitive ability compared with the natives, through evolution, natives should be better adapted to local conditions than are introduced species. Unless the native community has been perturbed by humans, decreasing the level of local adaptation of the natives, native species should outcompete introduced exotics. If the level of enemy release is not enough to compensate for this greater local adaptation by the natives, an exotic species is unlikely to successfully compete and become invasive.

Species might also fail to capitalize if the first assumption of the ERH is not fulfilled (i.e. natural enemies are regulating the native population). Poorly defended species presumably persist under high enemy impact through high fecundity, and these species would be expected to capitalize on a reduction in enemy regulation. However, a species might be sufficiently well defended such that removal of enemies in the native region does not allow it to increase in abundance. Such a species might fail to become invasive in the exotic region, even with the decreased impact of enemies. However, if generalist enemies are more important than are specialists in structuring the plant community in the exotic region, we would still expect increased abundance of well-defended exotics through competitive release. If specialists are more important, well-defended exotics might not benefit from the relative lack of specialist enemies.

There is another mechanism by which well-defended exotics might indirectly benefit from the lack of specialists and become invasive: Blossey and Notzold [37] hypothesized that, because a plant has limited resources to partition to enemy defense and competitive ability, an exotic in a specialist enemy-free environment will, over time, evolve to invest less in specialist defense. By having more resources to allocate to competitive ability, these new exotic genotypes could become invasive. There is limited evidence that such a mechanism has occurred in the short period of time since most exotics were introduced (<200 years) [38–41]. However, it provides an interesting mechanism by which species with minimal enemy impact in their native region (first assumption false) might still become invasive because of greater impact on natives (second assumption).

#### **Observational and experimental evidence**

##### *Patterns of size, growth and reproduction*

Many studies have compared the size, growth, and reproduction of exotic plant species in their native and introduced regions. Although there is some variation, the general trend is that exotics grow

**Table 1. Abundance and impact of enemies on exotic invasive plants**

Invasive exotic spp.	Exotic region	No. of generalist enemy spp. <sup>a</sup>	Impact <sup>b</sup>	Relative impact <sup>c</sup>	No. of specialist enemy spp. <sup>d</sup>	Impact <sup>b</sup>	No. of introduced enemy spp. <sup>e</sup>	Refs
<i>Betula pendula</i>	South Africa	42	–	<	NA	NA	NA	[50]
<i>Buddleia davidii</i> , <i>B. nivea</i>	UK	37	–	<	NA	NA	NA	[50]
<i>Clematis vitalba</i>	New Zealand	9	–	NA	5	–	1	[51]
<i>Heracleum mantegazzianus</i>	Switzerland	Insects (26)	–	=	8	–	0	[52]
		Molluscs	–	<				
<i>Hieracium</i> spp.	New Zealand	13	–	NA	3	–	8	[53]
<i>Lonicera japonica</i>	S. Carolina, USA	Insects	+	<	NA	NA	NA	[33]
		Mammals	+	<				
<i>Lythrum salicaria</i>	N. America	49	–	NA	6	–	7	[54]
<i>Myriophyllum spicatum</i>	Vermont, USA	1	+	NA	1	+	NA	[29]
<i>Quercus robur</i>	South Africa	36	+	=	NA	NA	NA	[50]
<i>Picea</i> spp. <sup>f</sup>	France	>5	+	Variable <sup>g</sup>	>10	+	3	[28]
<i>Robinia pseudacacia</i>	South Africa	24	+	>	NA	NA	NA	[50]
	UK	28	–	<	NA	NA	NA	
<i>Solanum mauritianum</i>	South Africa	20	–	<	4	–	0	[32]
<i>Solidago altissima</i>	Switzerland	Insects (13)	–	NA	2	–	0	[26]
		Molluscs	+	NA				

<sup>a</sup>Unless otherwise noted, numbers refer to the number of native phytophagous insects found attacking the exotic plant species. None of the studies provided accurate species counts of non-insect herbivores.

<sup>b</sup>In all but the *Lonicera japonica* study (where enclosure treatments were used), impact was measured as visually observed loss of biomass. +, significant impact; –, no significant impact.

<sup>c</sup>Relative impact was based on a comparison of generalist enemy impact on the exotic species versus that on native congener(s). For the species from [50], other native tree species included in the study were used for comparison. <, relative impact lower on the exotic; =, impact equal on both species; NA, data unavailable.

<sup>d</sup>The number of oligophagous insects found attacking the exotic plant species. NA, enemy specialization data unavailable and all enemies considered generalist.

<sup>e</sup>The number of exotic insects found attacking the exotic plant spp. (polyphagous, oligophagous and monophagous). NA, data unavailable.

<sup>f</sup>It is uncertain which exotic *Picea* spp. examined in the study are invasive in France.

<sup>g</sup>Of the 28 exotic *Picea* spp. examined, some had a greater generalist enemy impact than did the native *Picea abies*, whereas others had a lower impact.

larger, reproduce more and live longer in their introduced regions [3,42,43]. Some of these studies have implicated the decreased impact by insect enemies as a possible mechanism for this pattern, and such patterns have generally been proposed as support for the ERH. However, mechanisms of competitive release proposed by the alternative hypotheses could also explain these patterns [3]. Without empirical data on the impact of enemies, it is difficult to attribute these patterns to enemy release.

#### Classical biological control of invasive exotic plants

Stronger evidence for the ERH comes from the successful BIOLOGICAL CONTROL of weeds [44]. Because the abundance of an invasive exotic plant can be rapidly reduced by introducing specialist enemies from the native range of that plant, this is strong circumstantial evidence that enemy release was a factor in the invasion [45]. The biological control literature commonly claims that ERH is a reality [46]. However, there are reasons why classical biological control might not be a proper test of ERH.

Just as invasive exotic plants act differently in their native and introduced regions, introduced exotic enemies might also become invasive, growing faster, reproducing more or attacking their hosts more effectively in the introduced region than in their native region. Biocontrol researchers spend considerable effort ensuring that the introduced enemy is free from any of its own natural enemies, reducing the potential for cointroduction of secondary

enemies. In addition, because the targeted exotic plant presumably has few other enemies, the introduced enemy is free from other competitors for its host [47]. Thus, introduced enemies might themselves benefit from enemy and competitive release, resulting in a greater impact on their host than occurs in the native region [13,48].

The main point is that the relative success of classical weed biocontrol, although showing that introduced enemies can regulate invasive exotic plants, does not provide clear evidence that enemy release plays a part in exotic invasion success [33,47,49]. Just because a control method works does not confirm that absence of the means of control was the mechanism of invasion. An analogy would be the use of herbicides, which are used to control agricultural weeds. It is not the case that the absence of such herbicides was the reason why the weed species became abundant. Our argument is that classical biological control is more similar to a self-persisting herbicide than to natural enemy regulation, and thus it does not provide direct support for the ERH.

#### Experimental evidence for enemy release

We surveyed the literature for studies measuring the enemy impact on invasive exotic plants (Table 1). A large part of the literature consists of only anecdotal mention of the negligible impact of enemies on invasive exotics. The thirteen publications in Table 1 were chosen because they (1) provided quantitative

### Box 1. An empirical model for testing the role of enemy release in exotic plant invasions

The model (Fig. 1) relates the invasiveness of an exotic plant species (abundance in an exotic community) to the level of enemy release occurring in the exotic community. Based on our conclusion that the main mechanism of enemy release is through competitive release from natives, an enemy exclusion experiment can be used to measure enemy release. As many enemies (vertebrates, insects, molluscs, fungi, etc.) as possible are excluded from a natural community, and the abundance of each exotic species is compared in the control and enclosure treatments (level of enemy release = control abundance – enclosure abundance). If enemy release is the main mechanism for exotic plant invasions, few exotic species should fall in the top left or bottom right of the model.

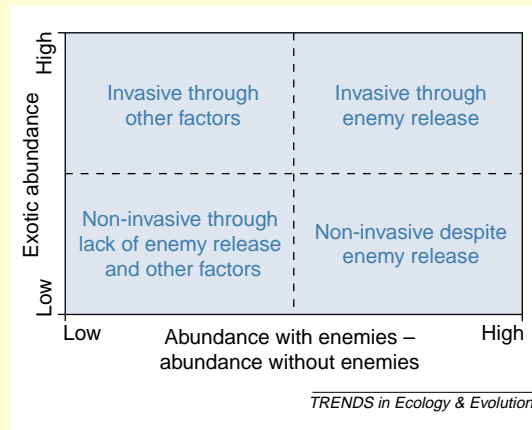


Fig. 1. Relationship between exotic abundance and enemy release.

measurements of impact; and either (2) differentiated between generalist and specialist enemies; or (3) measured enemy impact on natives. However, except for the *Lonicera japonica* study, in which herbivores were experimentally excluded, all measures of impact in Table 1 are based on visual estimates of how much biomass was eaten by a particular enemy. Indirect impacts, such as decreased growth, cannot be detected using this method. Also, none of these studies compared the relative impact of enemies on the exotic species and its native competitors; the measures of relative impact in Table 1 are based on comparisons of impact on the

exotic species and its native congeners, which might or might not be competing with each other.

Given all these problems with the data, they can still be used to test provisionally some of the assumptions of the ERH. Contrary to the assumption that few specialist enemies attack invasive exotics, host switching by oligophagous insects seems relatively common (Table 1). Native specialist insects were found attacking the exotic plant in every study where specialists were differentiated. However, the specialists usually comprised a small percentage of the total insect fauna found on an exotic (22% mean across the studies, ranging from 11% to 67%), and their impact was usually minimal. Introduction of exotic enemies also seemed to be relatively common (found in four out of the seven studies in which native enemy status was available). In relation to the assumption that generalist enemies have a greater impact on native competitors, although we found several cases where generalists impact the invasive exotic, in only two possible cases do the generalists have a greater impact on the exotic species [*Picea* spp. (spruce) in France and *Robinia pseudacacia* (black locust) in South Africa]. Although host switching and co-introduction of exotic enemies appear to occur more often than generally believed, rarely do they result in significant impact. The absence of significant specialist enemies and the lower relative impact by generalist enemies both seem to be playing important roles in the enemy release of invasive exotic plants, but there is evidence that enemy release might not be important in some cases.

#### Empirical model for testing the ERH

Throughout this review, we have placed the impact of enemies within a context of competition and have argued that the importance of enemy release is not so much about the absence of enemies on exotics but about the reduced impact of enemies on exotics relative to that on native competitors. The alternative hypotheses used to explain exotic plant invasions focus on the role of competition, and the level of competitive exclusion of a community seems to be the main factor by which native plant communities successfully or unsuccessfully resist exotic invasions.

Given this focus on competitive release through relative enemy release, the ERH predicts that natives should be more successful at competitively excluding invasive exotics when all natural enemies are excluded. This prediction can be tested empirically by conducting enemy exclusion experiments in natural communities (Box 1). Fencing, insecticide, molluscicide and fungicide can be used to exclude the major groups of enemies. This exclusion will free both native and exotic plant species from enemy attack. Although the exotics might benefit from some reduction in enemy attack, the natives will benefit from a much greater reduction, resulting in greater native competitive ability (Fig. 1). Thus, invasive exotics that were benefiting from enemy release

#### Glossary

**Biological control:** the use of natural enemies to control invasive species; classical biological control specifically refers to the introduction of a specialist exotic enemy to control an invasive exotic species.

**Biological invasion:** the disruption of natural communities and ecosystems by the increase in distribution and abundance of exotic species.

**Enemy release:** a decrease in regulation by herbivores and other natural enemies experienced by an exotic plant species, resulting in an increase in distribution and abundance.

**Enemy release hypothesis:** states that enemy release is an important mechanism for exotic plant invasiveness.

**Exotic:** being outside its native range because of human-mediated transportation.

**Host switching:** the occurrence of a specialist enemy attacking a new host.

**Specialist enemy:** an enemy who attacks only a single species (monophagous) or a few closely-related species (oligophagous), as opposed to generalist enemies who attack a wide range of species (polyphagous).

should decrease in abundance under enemy exclusion, because they are being competitively excluded by natives. There are several complications: beneficial insects and fungi will also be excluded, possibly reducing the observed effect of enemy exclusion; not all native plants will benefit from enemy exclusion; and communities completely dominated by exotics might lack enough native individuals to outcompete the exotics under enemy exclusion. However, this experimental model is a relatively clean, simple test of the role that enemy release plays in exotic plant invasions.

Although enemy release is an intuitively clear and clean explanation of exotic plant invasions, a full understanding of the assumptions underlying ERH is

required to test it properly. The success of classical biological control and patterns of size and reproduction have been used as support for ERH, but this observational evidence does not directly test ERH, whereas our review of the experimental evidence is equivocal. Competitive release through greater generalist enemy impact on the natives seems to be an important and understudied mechanism of enemy release, and experiments involving exclusion of natural enemies in invaded plant communities are seriously needed. Once we have a clearer understanding of the role of enemy release in exotic plant invasions, we can begin to build a comprehensive predictive model of exotic plant invasions.

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# Community ecology theory as a framework for biological invasions

Katriona Shea and Peter Chesson

Community ecology theory can be used to understand biological invasions by applying recent niche concepts to alien species and the communities that they invade. These ideas lead to the concept of 'niche opportunity', which defines conditions that promote invasions in terms of resources, natural enemies, the physical environment, interactions between these factors, and the manner in which they vary in time and space. Niche opportunities vary naturally between communities but might be greatly increased by disruption of communities, especially if the original community members are less well adapted to the new conditions. Recent niche theory clarifies the prediction that low niche opportunities (invasion resistance) result from high species diversity. Conflicting empirical patterns of invasion resistance are potentially explained by covarying external factors. These various ideas derived from community ecology provide a predictive framework for invasion ecology.

Biological invasions are having a major impact on the Earth's ecosystems [1], giving urgency to a better understanding of the factors that affect them. Some recent reviews have considered invasions from a variety of viewpoints, including the characteristics of invaders [2], the characteristics of invaded communities [3], resources [4,5] and natural enemies [6]. As these issues are not independent, it is essential to find a means of considering them jointly. Towards this goal, a theoretical framework for invasion ecology based on community ecology theory is proposed here. We show how this framework applies to the analysis

of the factors promoting invasion, and use it to examine correlations between invasion resistance and species diversity.

Invasion involves two essential stages: transport of organisms to a new location [7,8]; and establishment and population increase in the invaded locality [9]. A third stage, applicable to the most worrisome invasions, is regional spread from initial successful populations [10]. We focus on the second stage, where community ecology theory has most to offer. There is much evidence that the chance of establishment increases markedly with the rate of arrival of an alien species at a potential invasion site [2]. However, for establishment and growth, a species must be able to increase in abundance at the invaded locality. This depends on the opportunities that the particular invaded community provides for the invader in question.

## Niches and niche opportunities

Three main factors contribute to an invader's growth rate: resources [4,5,11,12], natural enemies [7,13,14] and the physical environment [15,16], all of which vary in time and space. How a species responds to these factors, including their spatial and temporal variation, determines its ability to invade. Once an invader has achieved an appreciable density, it will have effects on the invaded locality – for example, by consuming resources and maintaining natural enemies. Such responses and effects are the two defining aspects of an organism's niche, according to a recent definition (Box 1). The response aspect of the niche is fundamental to an alien species' ability to invade, and the effect aspect is fundamental to the impact that the invader has in the invaded community (Box 2). Both effects and responses of resident species in a community determine whether that community provides opportunities for invasion – that is, whether it provides niche opportunities (Box 1). In simple circumstances, niche opportunities can reduce to either resource opportunities or natural enemy escape opportunities.

Katriona Shea\*  
Dept of Biology,  
208 Mueller Laboratory,  
The Pennsylvania State  
University, University  
Park, PA 16802, USA.  
\*e-mail: k-shea@psu.edu

Peter Chesson  
Section of Evolution and  
Ecology, University of  
California, Davis,  
CA 95616, USA.