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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.

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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.

Box 1. Concepts and definitions

Ecological niches are defined by the relationships between organisms and the physical and biological environment, taking into account both time and space. A particular combination of physical factors (e.g. temperature and moisture) and biological factors (e.g. food resources and natural enemies) at a particular point in time and space defines a point in niche space. A modern definition of a species' ecological niche is the response that the species has to each point in niche space and the effect that the species has at each point [a]. Responses are defined in terms of demographic variables, such as survival and individual growth; but of most importance is the overall outcome of these responses, the per-capita rate of increase. Effects include consumption of resources, interference with access to resources by other organisms, support of natural enemies and occupancy of space.

Organisms respond to resource availability [b], which is the density of unused resource in the environment – soil water content, for example. Resource supply [b] is the net rate at which resources enter the system, discounting use by the organisms present (for example, rainfall minus evaporation and runoff but not transpiration). Resource availability is the net resource result of the effects of all the organisms in a system and the supply of the resource.
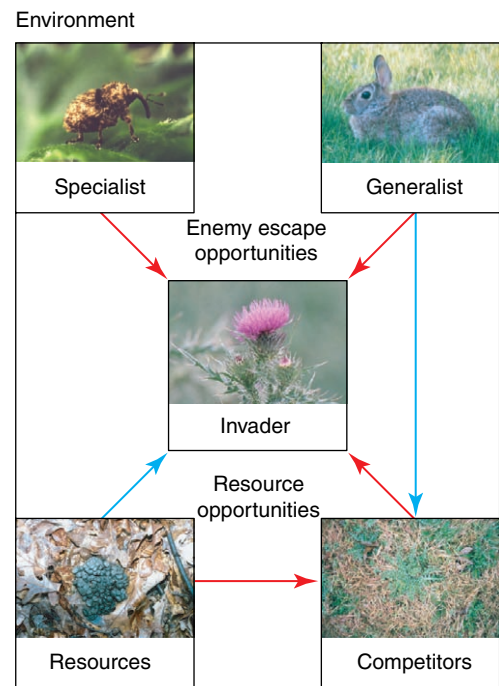
A resource opportunity is defined as a high availability of resources on which a potential invader depends. Resource opportunity includes the effects of mutualists, such as pollinators, because they provide services [c,d] that could also be considered resources. Similarly, a natural enemy escape opportunity is defined as a low level or low efficiency of natural enemies to which invaders might be susceptible.

A niche opportunity is the potential provided by a given community for alien organisms to have a positive rate of increase from low density. This might occur because of a resource opportunity, an escape opportunity or because of some favorable combination of resources, natural enemies and physical environmental conditions, including their fluctuations in time and space (Fig. I). Low levels of niche opportunities lead to invasion resistance of a community – that is, few alien species are able to successfully invade the community.

Maturity is the opportunity a system has had to accumulate species, and for adaptation to the system to have taken place. It depends on the time that the system has had the current climate, including its short-term fluctuations and recurring disturbance events. Maturity depends also on the size of the species pool that has historically served as a source of species to the system [e].

Fig. I. Main components of niche opportunity. Blue arrows are positive effects on the invader; red arrows are negative effects. Arrows from the outer boxes to the inner box represent direct effects of the community on the invader. Arrows between community components represent indirect effects on the invader, and they are colored according to their indirect effect on the invader, which is opposite to their direct effect on the community component. The environment directly affects all components and modifies their interactions with other components. Not shown are the effects of specialist natural enemies of community members. These specialists will limit community members and so have positive indirect effects on the invader. Sometimes generalists might not attack the invader, in which case their effects would be like those of specialists on community members. (Weevil photograph courtesy of CSIRO, Australia.)

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Resource opportunities

Resource opportunities arise when the resources that a species needs are high in availability. This is not simply because resources are supplied at a high rate, but also because the effects of resident species have not reduced resource densities [17–20] or interfered with access to resources too greatly [21].

In cases where a potential invader and a resident species are limited by a single resource, Tilman's $R*$ rule (where R is resource availability; Box 2) predicts that invasion will occur if the resident's $R*$ is greater than the invader's $R*$. For example, invasion would result if the invader had a higher resource acquisition rate than that of the resident species at the same resource densities (e.g. by having a superior foraging technique; Box 2 [11]). Invasion would also occur if the invader had a lower maintenance requirement than that of the resident (Box 2). Simple resource limitation might be approximated in the case of space or food competition of a species invading the habitat of a very similar species [11,22]. Invader success, however, is also predicted for the case of limitation by multiple resources [23], as long as the invader always has a higher response (per-capita growth) than the resident. Most importantly, these conclusions are

Box 2. Resource competition ideas

The per-capita growth rate of a population limited by a single resource is the net effect of the gain from consumption of the resource, and the losses due to metabolism, tissue death (e.g. leaf fall and herbivory) and death of individuals. Thus:

$$\frac{1}{N}\frac{dN}{dt} = af(R) - m \qquad (I)$$

where N is population density, R is resource availability, $af(R)$ defines the gain (the response of the species to the resource), and m (the maintenance requirement) is the total of all losses. The gain consists of the two parts: the constant a defining the overall magnitude of the response to the resource and the function $f(R)$ defining how response to the resource changes with resource abundance. The dynamics of the resource are given by:

$$\frac{dR}{dt} = S(R) - g(R)N \qquad (II)$$

where $S(R)$ is the supply rate of the resource, and $g(R)$ the per-capita effect of the species on the resource. Multiplying $g(R)$ by N gives the total effect of the species and determines the impact of the invader in the invaded community.

Normally, there would be a unique value R^* of R at which equilibrium would occur – that is, $af(R^*) = m$. For an alien species to invade, it must have a smaller value of R^* than does a resident at equilibrium with the resource, because this is the value of resource availability that the alien experiences when it arrives in the system. Only if the resident's R^* value exceeds that of the invader can the invader have a positive growth rate. This is Tilman's R^* rule [a]. An alien might have a smaller R^* value by having a smaller maintenance requirement. Alternatively, it might have a higher response than a resident [i.e. a larger value of $af(R)$]. This might be achieved by taking up the resource at a faster rate or by being more efficient at converting that uptake into gain. Different responses for different species might be modeled by having a vary with the species. In this case, R^* would be an increasing function of m/a, and an invader would be successful if it had a smaller value of m/a than that of a resident.

Although this R^* theory was originally developed as an equilibrium theory [a], in the form where species can differ in a or m, the theory is robust to fluctuations in R and m, with the result being that an alien having a mean of m/a smaller than that of a resident can invade [b]. See Box 3 for situations in which R^* theory does not hold.

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robust to environmental fluctuations [24] and are not restricted to strict equilibrium scenarios, even though the R^* rule was first derived in that context (Box 2). Such uniform superiority of an invader would make it an invader of large effect, because it would depress or displace all resident species relying on the same resources, with the details of the invasion depending on the effect component of the invader's niche (Box 2).

More generally, an invader would not be uniformly superior to any resident species, but instead might have a superior response to a particular resource, certain abundances of resources, or resources found in certain places or times [25]. Any situations in which residents do not keep resources at uniformly low levels are a potential resource opportunity [4,5] (Box 3).

In some situations, the effect aspect of a species' niche can also have a role in its invasion. Where a species has spatially localized effects, as in the case of plants, it will potentially have a strong effect on a small spatial scale, benefiting itself more than other species. For example, allelopathic effects of an invader might reduce densities of other species, increasing resource availability to the invader [26].

Also, some species generate disturbance or alter disturbance regimes, freeing resources and thereby facilitating their own and other invasions [4,27–29].

Natural enemy escape opportunities
Escape opportunities arise when natural enemies, such as diseases, predators and parasites, are in low abundance or are less effective against new species [13,14]. Community ecology theory claims strong symmetries between the effects of natural enemies and the effects of resources on community dynamics [30–32]. Thus, parallel to the R^* rule for resources, there is a P^* rule for natural enemies (where P indicates predator, pathogen or parasite density). Responses to natural enemies include elevated mortality rates and reduced feeding rates, leading to lower per-capita growth rates. Effects of residents on natural enemy densities are parallel to the effects of resident species on resource availability. Although species can vary greatly in resource dependence, natural enemies vary greatly in their specificity [33]. An invader might not be affected by specialist natural enemies preexisting in the invaded community and might gain a considerable advantage because it leaves its own specialist natural enemies behind or loses them early in the invasion process while at too low a density to maintain them [13,14]. This potential forms the basis of biological control of invaders [7,8] (but see Keane and Crawley in this issue [6]). Generalist natural enemies of the invaded community, however, will have effects that vary with their ability to attack the invader [6]. A naive invader might not be well defended against these enemies, in which case they reduce the escape opportunity of that invader [34]. However, generalists of the invaded community might not be equipped to attack the invader, in which case they increase the invader's escape opportunity [6].

Interactions between the physical environment, resources and natural enemies
In some studies, there has been a strong emphasis on the physical environment as a constraint on invasions [15,16]. However, many species have broad environmental tolerances, and the interaction of environmental factors with resources and natural enemies has a potentially important role. For example, with plant species, higher temperatures could mean higher evaporative water loss, lower water-use efficiency and, therefore, higher demand for water as a resource [35]. Similarly, a harsh physical environment could lead to a higher maintenance requirement as a result of higher mortality, higher biomass attrition rates (in plants) or higher metabolic costs (Box 2). A harsher physical environment might therefore require higher resource availability to achieve the same capacity for increase. However, as both residents and invaders respond to environmental harshness, it is the difference in the response of the residents and invader that determines

Box 3. Resource opportunities in fluctuating environments

Community ecology theory predicts that spatial and temporal environmental variation has an important role in species coexistence [a]. For invaders, this can mean spatial and temporal niche opportunities, provided that invaders and residents differ in their responses to varying factors. Most species have periods of relative activity and relative inactivity during a year [b]. Niche opportunities arise during times when resident species are relatively inactive and are not placing high demands on resources. Using the notation given in Box 2, the per-capita growth rate of a species might be represented as:

$$\frac{1}{N}\frac{dN}{dt} = a(t)f(R) - m \qquad \text{[I]}$$

with *a* now a function of time to represent temporally varying growth activity: it is the response of the organism to time. The theory of the storage effect [b] shows that a species can invade even if it has an average value of $a(t)$ less than that of resident species, provided that the invader's $a(t)$ is sufficiently large compared with residents' $a(t)$s some of the time; for example, the activities of the invader and residents might fluctuate out of phase. Fluctuations in $a(t)$ can be deterministic (e.g. seasonal) or stochastic (e.g. in response to yearly weather variation) [b,c]; the key feature is that the invader must show a different temporal pattern of response than that of the residents.

An invader might also gain an advantage by responding differently to changes in resource levels than do residents – that is, by having a function $f(R)$ that differs nonlinearly from that of residents [a,d]. For example, the invader might have a stronger response than residents at both high and low resource availabilities, but not at intermediate resource availabilities. Resource fluctuations between high and low values would then be a resource opportunity for the invader, a mechanism referred to as 'relative nonlinearity of competition' [a].

Spatial variation can also provide niche opportunities, and this can occur through spatial versions of the storage effect and relative nonlinearity of competition [e]. Much emphasized in the literature, however, are competition–colonization tradeoffs [f,g], which can work on a variety of scales. At the level of a local community, the mechanism can be driven by disturbance. In sessile communities, death of an individual is a substitute for disturbance. Most importantly, this mechanism means that an inferior competitor for resources could invade if it had superior colonization or local resource exploitation ability [g].

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whether invasion is promoted or inhibited by harshness [24]. An invader will be at an advantage if its maintenance requirement does not increase as much as that of a resident with environmental harshness, or if it has a stronger response to increased resources than the residents (Box 2).

Environmental fluctuations in time and space also have major effects. The key issues again are differential effects of the fluctuations on invaders and residents, with the added parameter that different species might be favored at different times and in different places [4,5,25] (Box 3).

Environment–resource interactions naturally have parallels in environment–natural enemy interactions, but one should also consider natural enemy–resource interactions. Indeed, important

invader advantage might accrue as a result of these interactions, because residents and invaders could be differentially susceptible to specialist natural enemies of the residents. In particular, high densities of specialist natural enemies should lead to lower densities of resident species, increasing resource availability [24,30,36]. Although generalist natural enemies might have similar effects on resources as the specialists, the increased resource availability for an invader could be countered by a decrease in escape opportunity [24,30]. The net outcome of all these different interactions determines the magnitude and nature of the niche opportunities provided by the community.

How niche opportunities arise

Natural enemy escape opportunities
Most communities provide escape opportunities because they do not have the specialist natural enemies of invaders from geographically distant locations [7]. Although invasions are sometimes compared with range expansions [5,37], escape opportunities imply an important distinction, because specialist natural enemies must be lost at much lower rates during range expansions than they are during invasions of relatively small numbers from great distances.

Invaders that offset losses to natural enemies in their native range by having high fecundity or individual growth (grazed plants and clonal animals) [38] could gain a strong advantage in a system without their specialist natural enemies. Potentially diminishing this advantage are generalist naturalist enemies to which the invader might be particularly vulnerable in the invaded location because it has no evolutionary history with them and might not be adequately protected against them [34]. The spectacular success of biological control for some invaders, however, implies that loss of natural enemies is sometimes an important escape opportunity [7,39].

Escape opportunities can allow a species to win in resource competition in a similar way to a low maintenance requirement (Box 2), potentially allowing an invader to reach high densities and have a large effect on resources. Apparent competition can have a similar outcome. An invader with few specialist natural enemies could rise to a high density, maintaining generalist natural enemies that severely impact the native community.

Resource opportunities
Disturbance is commonly assumed to release resources and provide opportunities for invaders [5], an idea that has been generalized to consider any form of temporal variation in resource availability [4,5]. As emphasized by spatio-temporal resource competition theory (Box 3) an invader still must have some advantage over residents. However, that advantage might occur at particular times or in
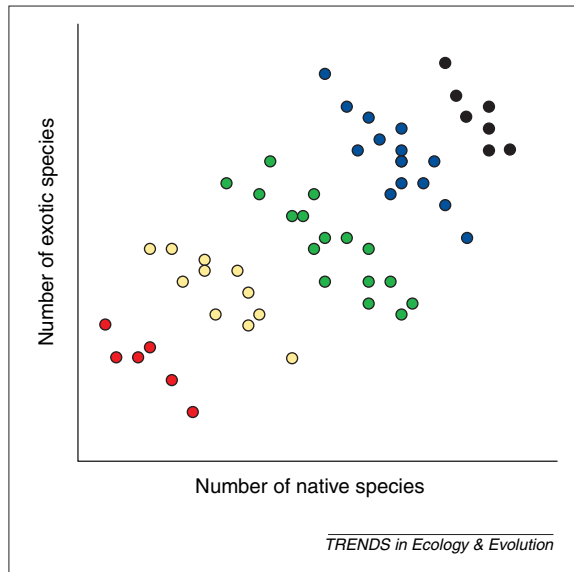
Fig. 1. Reconciliation of relationships between invasion success and species richness on different spatial scales. In this illustration, extrinsic conditions are assumed to be the same within each cluster of points but to differ between clusters. Within any cluster, higher numbers of native species lead to poorer niche opportunities for invaders, generating the negative relationship between the numbers of alien species and native species often observed in models, experiments and at small spatial scales. However, extrinsic factors can vary considerably on broad spatial scales. If extrinsic factors that favor high numbers of native species also directly increase niche opportunity for invaders, changes in these extrinsic factors will lead to clusters of points whose mean numbers of alien and native species are positively related, as depicted. Thus, there is an overall positive relationship between alien and native species when the data are combined on a broad spatial scale.

particular places, or it might be in a life-history trait, such as colonizing ability (Box 3). Sher and Hyatt [4] emphasize that an advantage to invaders commonly arises through disruption of the historical pattern of resource supply and consumption.

There are many ways in which human activities disrupt historical patterns of resource fluctuations, including alteration of patterns of fire [40], harvesting of biomass, nutrient enrichment [12], alteration of patterns of spatial heterogeneity, and climate change [1,41,42]. Resident species might not be adapted to the changed environmental conditions, lessening their ability to reduce resource availability uniformly in time and space, and thus providing resource opportunities for invaders. Some invaders, such as species that inhabit human disturbed environments in their native range, might have critical adaptations to human disturbed environments that resident species lack [43,44], giving them the advantages they need for successful invasion.

Community maturity
Do natural communities vary in the niche opportunities that they provide, independently of the disruptions discussed above? Particular systems and geographical regions have relatively high rates of invasions. Among these are freshwater systems, oceanic islands, regions with a Mediterranean

climate, and North America in comparison with Eurasia [29]. Greater disruption by humans and greater rates of commerce between geographically similar regions might contribute to some of these elevated rates, but particular features of the communities themselves could also contribute [45]. Species in different systems might vary in competitive ability [11,26] or their degree of specialization [29] – that is, the breadth of conditions under which individual members have positive responses to their environment. In the presence of tradeoffs that benefit specialization [46], several specialized species would reduce resources more effectively than one generalist species covering the same range of circumstances.

The maturity concept (Box 1) might explain such community differences: communities that have had less time to assemble, and less time for their constituent species to adapt to the local conditions, are likely to have fewer species with broader niches. Their species might also have lower competitive abilities than those in communities that have had a longer time under their present environmental regime. These communities tend to be less invasion resistant (Box 1). Similar effects on invasion resistance might result from the size of the species pool from which a community has assembled. Maturity undoubtedly also affects invasion resistance through escape opportunities, but clear predictions in this area are not so apparent.

Variation in niche opportunities with resident diversity
Maturity is one theoretical approach to explaining invasion resistance. Ideally, invasion resistance could be predicted from directly observable community properties. In a classic work, Elton [47] proposed that communities with high species diversity should be invasion resistant. Indeed, models and some experimental studies suggest that high species diversity does lead to invasion resistance – that is, there is a negative relationship between invasion success and species diversity [48–51]. However, large-scale observational patterns mostly show that more diverse systems tend to have higher numbers of exotic species [3,51,52]. There have been various attempts to understand these conflicting patterns.

Scale and the role of covarying factors
Species diversity varies widely with physical extrinsic factors, such as latitude, climate (given latitude), soils and the supply rates of physical resources to a system. This observation can help explain the discrepancy between different studies. If extrinsic factors favorable to high species diversity also lower invasion resistance, the positive relationship between species diversity and invasion success seen on broad spatial scales is explained [50]. A negative pattern of invasion success as a function of diversity, for fixed extrinsic conditions, is consistent with this proposal, as illustrated in Fig. 1:

the broad-scale positive relationship is the outcome of combining data from a series of negative relationships, where each negative relationship comes from different extrinsic conditions.

This reconciliation of conflicting patterns is consistent with the outcome of models [51] in which extrinsic factors are not generally varied. Species diversities differ because of different sizes of the species pool colonizing the local system, or different amounts of time for species to accumulate in the local system, or simply due to chance: randomness in the process of community assembly leaves some systems with fewer species than others. In all these ways of varying species diversity, there is a consistent tendency in models for invasion success to decrease with species diversity. Generally, equivalent results have been obtained by experimental studies that carefully control extrinsic factors, or randomize them, and define species diversity as the number of species supplied to the system [53]. By contrast, studies that define species diversity as the number of species successfully established might confound uncontrolled variation in extrinsic factors, including propagule pressure. According to Fig. 1, a positive relationship between invasion success and diversity could result.

The role of positive interactions
An alternative explanation of positive relationships between species diversity and invasion success, which has some support from experiments in agricultural systems, is that high species diversity creates niche opportunities – for example, by mutualisms, both direct and indirect, that facilitate the entry of other species [54]. The modeling and experimental studies that found negative relationships might not have provided the conditions for sufficiently beneficial mutualisms to occur, possibly explaining why invasion success did not increase with diversity.

The role of niche differentiation
Theoretical explanations of why higher species diversity might confer invasion resistance, when extrinsic factors are controlled, depend on how the niches of the various residents and invaders relate to one another. According to the empty niche hypothesis [55], lower species diversity might simply mean the existence of circumstances where resources are not being exploited efficiently because species with suitable niches are lacking. Niche opportunities therefore exist for species able to benefit from resources in those particular circumstances [7]. In this case, it should not be just the diversity of resident species that matters but how their niches differ functionally [56], including their spatial and temporal patterns of effects on resources [48].

At the opposite extreme is the sampling hypothesis, where species are not differentiated functionally but vary in their ability to reduce resources [57], or (presumably) to maintain natural enemies. According to this hypothesis, higher diversity does not broaden the circumstances under which resources are exploited efficiently but instead increases the probability that a high-ranking competitor is present. Invasion success depends not on filling a vacant niche but on being a better exploiter of resources or a better avoider of natural enemies than resident species. However, a competitor's rank might vary in space and time, allowing a high diversity of species to be maintained in the system [25] (Box 3). Thus, invader success depends on finding a time or place where it is superior to resident species, and the distinction between the empty niche hypothesis and the sampling hypothesis is lost [57,58].

Conclusion
Over much of its history, invasion ecology has developed on a relatively separate path from other areas of ecology, potentially to the detriment of the discipline [59]. The framework presented here, however, shows how core issues of invasion ecology can be discussed as topics in community ecology. Recent advances in community ecology theory have made this possible by providing detailed predictions about topics of particular importance in invasion ecology, such as resource and natural enemy interactions [30,32], and disturbance and more general kinds of variation in space and time [24,25,60]. The link between community and invasion ecology is a natural one, because the essential criterion for a species to persist in a community is its ability to increase from low density,

which is also the condition for an alien to be able to invade a community. This means that invasion ecology has the potential to contribute greatly to community ecology. Invasions provide case studies on particular communities subject to perturbation by invaders; they also provide the challenge of explaining invader success and invader impact. Indeed, there is every reason to expect a healthy synergy between invasion ecology and community ecology (Box 4).

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