

## SCALE DEPENDENT EFFECTS OF BIOTIC RESISTANCE TO BIOLOGICAL INVASION

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**Abstract.** As nonindigenous species continue to displace native species and disrupt ecosystems, understanding the degree to which native species richness affects the vulnerability of communities to nonindigenous species invasions has grown in importance. Native and exotic species diversity are often positively correlated in large-scale observational studies, but negatively correlated in small-scale experimental studies. This discrepancy suggests that the scale of invasion studies may be an important influence on their outcomes. Using a competition-based model that exhibits a negative relationship on a small scale, we show that changes in the number of available resources across communities can cause invasion success to become positively correlated with native species diversity at larger scales. The strength of the positive correlation, however, depends on the relationship between niche breadth and species diversity in natural communities. Adding species to a community or removing resources has a similar effect—increasing the sum of interspecific interaction strengths, which decreases invasion success.

**Key words:** biological invasion; biotic resistance; community stability; exotic species; interaction strength; invasibility; Lotka-Volterra; species diversity; species richness.

### INTRODUCTION

Species richness has been theoretically and empirically examined as an important variable associated with, and potentially controlling, invasibility of native systems. Species-poor communities have been argued to be more invulnerable primarily for lack of biotic resistance (Elton 1958, Fox and Fox 1986, Pimm 1991, Rejmanek 1996). Yet diverse native communities have also been suggested to accommodate invaders easily because high diversity implies greater resource availability and weak interspecific interactions (Huston 1994, McCann et al. 1998), or because invaders benefit from indirect facilitation of residents competing with shared competitors (Levine 1976, Lawlor 1979, Levine and D'Antonio 1999). As nonindigenous species continue to negatively affect native species and systems (Czech and Krausman 1997, Wilcove et al. 1998) the diversity–invasibility debate has grown in importance as it addresses the degree to which native species richness affects the inherent vulnerability of communities to biological invasions. However, empirical evidence supports both positive and negative correlations between native and exotic species richness. Small-scale experimental manipulations have almost universally demonstrated a negative relationship between native species richness and invasibility (Tilman 1997, Crawley et al. 1999, Stachowicz et al. 1999, Naeem et al. 2000, Lyons and Schwartz 2001). In contrast, large-

scale observational studies have demonstrated positive correlations between native and nonindigenous species richness (Planty-Tabacchi 1996, Lonsdale 1999, Smith and Knapp 1999, Stohlgren et al. 1999). This discrepancy suggests that the scale of invasion studies is an important influence on their outcomes.

To examine invasion success in small-scale experiments, environmental variables are held constant while native species number is manipulated. Hence, observed decreases in invasion success can be definitively attributed to increasing native species richness. Patterns over large spatial scales, however, encompass underlying variation in environmental factors that might be associated with biodiversity. Disturbance, resource availability, propagule pressure, physical stress, climate, percent bare space, competitors, and predators have been argued to covary with diversity in natural systems while also influencing invasibility (Levine and D'Antonio 1999, Levine 2000, Naeem et al. 2000). Thus, failure to control or account for the effect of these covariates on diversity may cause the relationship between invasibility and native species richness that is negative on a small scale to appear positively correlated across a large area that incorporates sufficient changes in these factors (Naeem et al. 2000, Shea and Chesson 2002).

This explanation requires that invasibility increases with such environmental covariates more rapidly than biotic resistance increases with native biodiversity. However, there is no reason to expect a positive correlation a priori—factors that covary with biodiversity could either inhibit or facilitate invasions. Furthermore, if only those covariates that facilitate biodiversity per

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se are considered, we might expect native diversity to have “filled in” the available niche space.

Theoretical studies of the effects of species richness on invasibility have typically supported Elton’s (1958) biotic resistance hypothesis that posits that more diverse communities better resist invading species (Robinson and Valentine 1979, Post and Pimm 1983, Case 1990, 1991, Drake 1990). Support for a negative relationship between native and exotic species diversity might be expected because the models have traditionally employed the same logic as small-scale experiments in that environmental variables are held constant in order to isolate the effects of species number. In this paper we synthesize a model of biotic resistance at the small scale of experiments with theory for the coexistence of competitors when the number of resources varies across large scales. We analyze the simplest possible model of population dynamics at a single trophic level, the Lotka-Volterra competition model. Our decision to use the Lotka-Volterra model was based on a desire to use a simple model whose dynamics are well understood and which has built the base for most of the seminal work in invasion theory (Robinson and Valentine 1979, Case 1990, 1991). In so doing, our results are transparent and readily interpretable and provide the simplest baseline for comparison to previous theory as well as future empirical data.

We ask whether the positive correlation between native and exotic diversity observed in large scale surveys is predicted by the Lotka-Volterra model when interspecific interaction strengths and species richness are determined by the number of resources in the environment. We begin by briefly demonstrating the generation of biotic resistance in the Lotka-Volterra model. (A more detailed analysis can be found in Case [1990, 1991].) We show how invasibility is influenced not only by the number of native species, but also by the number of resources. Then, to derive predictions for the large-scale pattern, we calculate equilibrium native community size as a function of the number of resources and ask how invasibility varies with this equilibrium. We show that the results differ for two assumptions concerning the breadth of resource use by species—one that allows species to exploit all resources in a community, and another where a species’ resource use is independent of the number of resources available.

#### METHODS

The Lotka-Volterra framework consists of a community of  $N$  competing species, with the  $i$ th species characterized by its abundance ( $n_i$ ), intrinsic rate of increase ( $r_i$ ), carrying capacity in the absence of competitors ( $K_i$ ), and a vector of competition coefficients ( $\alpha_{ij}$ ) that represent the strength of interactions between species  $i$  and  $j$ . The population dynamics of species  $i$

are described as follows:

$$\frac{dn_i}{dt} = \frac{r_i n_i}{K_i} \left( K_i - \sum_{j=1}^N \alpha_{ij} n_j \right). \quad (1)$$

We construct random “native” communities and subject them to invasion by randomly constructed “exotic” species. For instance, we simulate invasion of a community of five species with a sixth differential equation for the invader, and then integrate the six equations to determine the outcome. We generate random  $\alpha$  values using the species resource utilization overlap method described by Case (1990; see Levins 1968). This method explicitly links environmental differences to interaction strengths, and allows us to directly manipulate resource availability in our models. Furthermore, native communities constructed in this manner have a single, globally stable equilibrium, which eliminates the effects of multiple domains of attraction in the population dynamics (Case and Casten 1979, Case 1990, 1991).

The resource utilization overlap matrix  $\mathbf{U}$  contains elements  $u_{ik}$  which specify the rate at which species  $i$  utilizes resource  $k$ . An environment contains  $M$  resources which can potentially be utilized by each species. For each species  $i$  we draw  $M$  random numbers from a uniform distribution between 0 and 1. We add each number that is greater than a threshold value  $T$  to  $u_{ik}$ , where  $k$  is determined by drawing from a uniform distribution between 0 and  $M$ . Species  $i$  and  $j$  compete for resource  $k$  at rate  $u_{ik}u_{jk}$ . The competition coefficient is given by the following expression:

$$\alpha_{ij} = \frac{\sum_{k=1}^M u_{ik}u_{jk}}{\sum_{k=1}^M u_{ik}^2}. \quad (2)$$

The equilibrium of Eq. 1 with  $\alpha_{ij}$  values defined by Eq. 2 is stable if feasible, i.e., if all  $N$  native species equilibria are positive. Equilibrium population size  $n_i^*$  is a function of all  $\alpha_{ij}$  and  $K_i$ ; hence, for a given matrix of  $\alpha_{ij}$  values, we require a vector with elements  $K_i$  such that  $n_i^* > 0$  for  $i = 1, \dots, N$ . These  $N$  inequalities define an infinite region in parameter space of all  $K_i$ . We arbitrarily set

$$\sum_{i=1}^N K_i = N \quad (3)$$

which specifies a “slice” of this region, and use the midpoint for the vector  $\mathbf{K}$  (see Case 1990, 1991). This constraint ensures  $E(K_i) = 1$  for all simulations with different values of  $M$  and  $N$ .

The resource utilization overlap procedure is a general technique for calculating interaction strengths in an environment characterized by the number of resources,  $M$ . However, in order to analyze the effects of environmental variation, we must adopt some assumption regarding the relationship between niche breadth

and  $M$ . Here we consider two theoretically plausible possibilities. First, each species could utilize every resource to some degree (niche breadth increases with  $M$ ). Alternatively, the number of resources utilized by each species could be independent of  $M$ . These assumptions result in critical differences in the distribution of  $\alpha$  values; the pattern in natural communities probably lies between these two extremes. We refer to the two resource utilization models as  $RU_{\text{all}}$  (all resources potentially utilized) and  $RU_{\text{fixed}}$  (fixed average number of resources utilized). For the  $RU_{\text{all}}$  model,  $T = 0$ . For the  $RU_{\text{fixed}}$  model, the average number of resources utilized by a species ( $M_u$ ) is held constant by letting  $T$  vary with  $M$  such that  $M(1 - T) = M_u$ . We let  $M_u = 15$ .

We generate competition coefficients for the invaders by adding a row for the invader to the matrix  $\mathbf{U}$  and using Eq. 2 to find the new  $\alpha$  values. We assume that invaders have the same distribution for the elements  $u_i$  (and  $\alpha_{ij}$ ) as the natives and set the carrying capacity of the invader to 1, the average of  $K_i$ 's in the native community (Eq. 3). The values of  $K_i$  affect invasibility only if the invader is drawn from a distribution that differs from that of the native community (Case 1990). Therefore our assumptions represent the simplest case, that potential invaders do not, on average, have an inherent competitive advantage over the native species.

We calculated invasibility by subjecting 500 native communities to invasion by 10 different species. We simulate invasions by numerically integrating  $N + 1$  differential equations (Eq. 1), starting each replicate at the original native community equilibrium for each of the 10 invaders. When the populations have settled to their new equilibria, we place the run into one of the following categories: (1) failure—invader declines to  $n < 10^{-6}$  and all native species return to their equilibria; (2) augmentation—natives and invader coexist at positive population sizes; or (3) replacement—invader reaches a positive equilibrium, but one or more natives decline to  $n < 10^{-6}$ . Within the replacement category we record the number of natives driven to extinction. Invasibility is defined as the proportion of invaders that attain a positive equilibrium abundance in the community, i.e., the probability of augmentation or replacement.

The simple Lotka-Volterra framework allows us to isolate the effects of community diversity, while excluding other factors that contribute to invasion resistance, such as predation and demographic stochasticity. Consequently, the predicted values for invasibility are expected to be higher than the absolute magnitude of invasion success that might be observed in the field (e.g., Case 1990, Williamson 1996).

The model outcome is independent of the invader's initial population size and  $r_i$  has no effect on invasibility. For consistency with Case (1990, 1991), we set the invader's initial population size to 0.001, and  $r_i = 0.5$  for all natives and invaders.

To understand how variation in  $M$  across communities might ultimately affect patterns of exotic and native species richness sampled in large-scale studies, we determined invasibility at the equilibrium community size ( $N^*$ ) for each community of  $M$  resources using the results of the simulations.  $N^*$  is the value of  $N$  for which the rate of colonization of new species is equal to the rate of extinction (Case 1990). Here, colonization is identical to invasion and extinction rate is equal to the expected number of species lost through replacement per invasion event:

$$\text{extinction} = \sum_{k=1}^N k \times \Pr\{\text{replacement of } k \text{ species}\}.$$

This colonization–extinction model is based on the assumption that communities are built up gradually by the arrival of new species and losses to competitive displacement. Such a process is broadly consistent with basic community assembly theory (e.g., Drake 1990).

## RESULTS AND DISCUSSION

In both resource-utilization models, invasion resistance increases with native species diversity,  $N$ . Moving across communities with increasing resources increases the maximum number of species able to coexist within a community and increases invasibility for a given native species richness (Fig. 1). These relationships in Fig. 1 offer theoretical support for the hypothesis that positive associations in large-scale observations are the result of sampling across many negative relationships between invasion success and native diversity manifested at smaller scales (Levine and D'Antonio 1999, Naeem et al. 2000, Shea and Chesson 2002). However, invasibility increases across communities of increasing resources ( $M$ ) only if native species richness is held constant or increases only slightly. In large-scale field observations, the number of native species is not experimentally controlled, and native diversity is likely to respond positively to increases in  $M$ .

Indeed, both  $RU_{\text{all}}$  and  $RU_{\text{fixed}}$  models predict that  $N^*$  increases with  $M$  (Fig. 2a); however, the number of resources has negligible effects on invasibility in the  $RU_{\text{all}}$  model (Fig. 2b). Because equilibrium native species richness increased with  $M$ , the otherwise positive effect of rising resources on invasion rate was negated by the effect of increased biotic resistance. Thus, the weak relationship does not imply that native and exotic species do not interact, just that on average, the sum of interspecific competitive effects ( $\sum \alpha_{ij} n_j$ ) remains nearly constant at equilibrium. In contrast, in the  $RU_{\text{fixed}}$  model invasion success increased more rapidly with  $M$  (and therefore  $N^*$ ), indicating that invasibility rose more rapidly than biotic resistance (Fig. 2b).

The mechanistic differences between the  $RU_{\text{all}}$  and  $RU_{\text{fixed}}$  models are manifested in how competition coefficients depend on  $N$  and  $M$ . In both models, interaction strength for any pair of species is independent

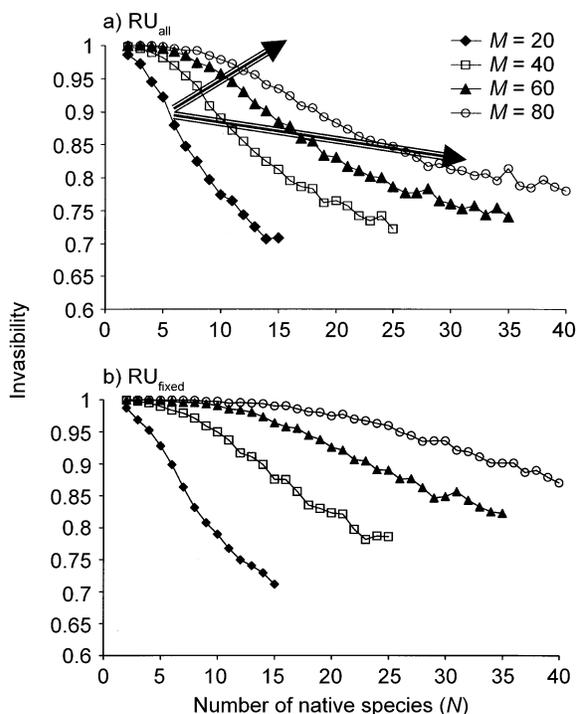


FIG. 1. Simulation results from (a)  $RU_{all}$  and (b)  $RU_{fixed}$  models. Each point represents the probability of successful invasion (invasibility) as a function of community size ( $N$ ). This probability was calculated with 500 communities, each subjected to 10 invaders. Increasing  $N$  for a given value of  $M$  (i.e., small-scale variation in native diversity) enhances biotic resistance to invasion. Increasing  $M$  (large-scale environmental variation) increases invasion success for a given native species richness. Arrows in panel (a) indicate possible outcomes of large-scale surveys of natural communities that encompass natural variation in  $M$ . If native diversity increases slowly with  $M$ , invasibility is positively correlated with native diversity. If native diversity increases rapidly with  $M$ , the correlation is negative. The same argument can be applied to the  $RU_{fixed}$  model in panel (b).

of  $N$  (Eq. 2). Invasibility decreases with increasing  $N$  (Fig. 1) because the sum of native species competitive effects increases, and this reduces the expected initial population growth rate of an invader's propagules. On the other hand, increasing  $M$  does affect the distribution of the  $\alpha$  values, and this effect differs between the two models (Fig. 3). In the  $RU_{all}$  model, the variance of  $\alpha$  decreases with increasing  $M$ , but mean  $\alpha$  is independent of  $M$ . In the  $RU_{fixed}$  model, both the mean and variance of  $\alpha$  decrease with increasing  $M$ . In the latter case, each species, on average, utilizes a constant number of resources, so increasing  $M$  decreases the expected number of resources for which a pair of species competes.

In the  $RU_{all}$  model, the predicted weak correlation between native and exotic species diversity at equilibrium (Fig. 2b) implies that the positive slope often observed in large-scale studies is not driven by intrinsic differences among communities in their susceptibility to invasion. In other words, environmental variables

that directly determine native diversity, represented here by  $M$ , are not solely responsible for differences in invasibility. Instead, extrinsic factors that covary with  $M$ , such as disturbance or propagule pressure, must play a dominant role in determining susceptibility to invasion. For example, propagules of nonindigenous species are often introduced to native habitats as functions of increased human activity or size of habitat (Macdonald et al. 1989, Williamson 1996, Lonsdale 1999, Brown and Peet 2003), which are likely to covary with  $M$  across large spatial scales. Propagule pressure might covary with  $M$  independent of area if, e.g., reserves or parks with the highest rates of human visitation (and thus human-transported propagules) are also the most diverse and resource-rich (Lonsdale 1999).

In contrast, the  $RU_{fixed}$  model predicts that, at equilibrium determined by  $M$ , native communities with high diversity are intrinsically more invulnerable than less diverse communities. Hence, the same factors that promote native diversity also facilitate exotic species (Case and Bolger 1991, Huston 1994, Blackburn and Duncan 2001). The verbal model suggested by Davis et al. (2000) is also consistent with the  $RU_{fixed}$  model's framework. These authors suggest that communities are

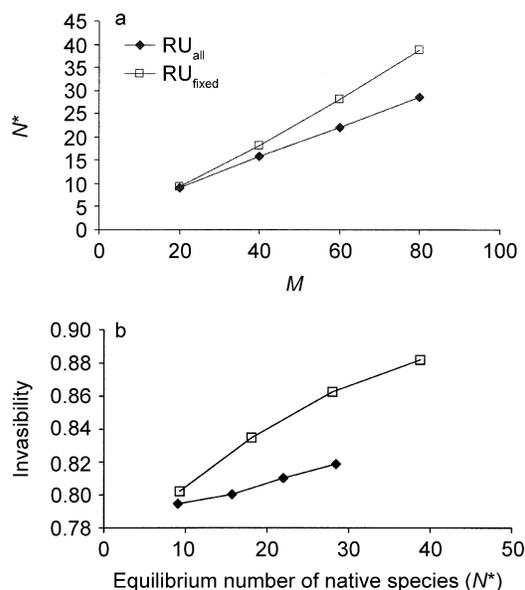


FIG. 2. Invasibility of communities at equilibrium number of species,  $N^*$ , for  $RU_{all}$  and  $RU_{fixed}$  models. (a)  $N^*$  increases with  $M$  in both models. (b) The four points for each model represent, from left to right,  $M = 20, 40, 60,$  and  $80$ .  $N^*$  and equilibrium invasibility increase rapidly with  $M$  in the  $RU_{fixed}$  model in which niche breadth is independent of  $M$ , relative to the  $RU_{all}$  model in which niche breadth increases with  $M$ . Due to the large number of replicates (500), confidence intervals are negligible to within the accuracy of the estimates for each point. Hence, the simulation results represent accurate estimates of the parameters that define the underlying distribution, and we do not perform further statistical analysis.

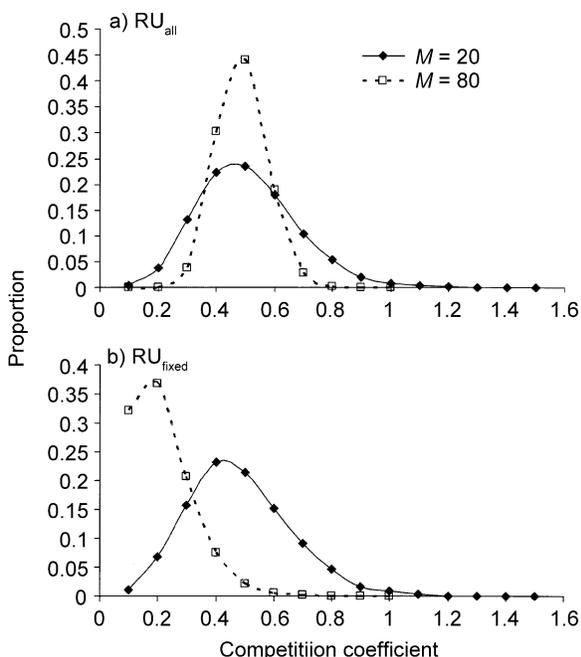


FIG. 3. Distribution of interspecific competition coefficients ( $\alpha$ ) from 500 random communities for  $M = 20$  and  $M = 80$  generated by the (a)  $RU_{all}$  and (b)  $RU_{fixed}$  models with  $N = 5$ . Distributions for  $M = 40$  and  $M = 60$  (not shown) fall between distributions for the two extreme values of  $M$  displayed here.

more invulnerable when resources surge and temporarily go unutilized, providing an opportunity for invaders to capitalize on the free resources. The  $RU_{fixed}$  model does not rule out a role for extrinsic factors; these factors might also be strengthening an observed positive pattern.

The slope of the predicted relationship between native and exotic richness at large scales depends on the model assumption of how the number of resources each species consumes varies with the number of resources available. This assumption determines the predicted relationship between the mean and variance of interaction strengths and the number of species in a community (Fig. 3), and could be tested with empirical data. Measurement of interaction strengths is notoriously difficult and has been the subject of much controversy (Laska and Wootton 1998). Empirical and theoretical research typically supports the assertion that communities are composed of many weak and few strong interactors (Paine 1992, McCann et al. 1998, Kokkoris et al. 1999). Currently, however, the relationship between mean and variance of interaction strengths and species diversity is poorly understood. Limited empirical evidence suggests that mean interaction strength may be independent of diversity (Hallett 1991). A meta-analysis of interaction strengths across communities of different sizes could provide valuable insight into which form of resource use predominates.

Furthermore, differences in the outcomes from the  $RU_{all}$  and  $RU_{fixed}$  model assumptions may suggest how species characteristics contribute to the invasibility of a community at a given trophic level. Because species in the  $RU_{fixed}$  model, on average, use fewer resources than species in the  $RU_{all}$  model for a given value of  $M$ , they may characterize resource specialists. The comparison of the specialist/generalist framework to our  $RU_{fixed}/RU_{all}$  models is not absolute, since a species in the  $RU_{fixed}$  framework could still utilize a large, albeit fixed, number of resources. However to the extent that this comparison is valid, our model suggests that among specialist communities, invasibility will rise with diversity more rapidly than among generalist communities.

We have demonstrated that variations on the well-understood Lotka-Volterra competition model can explain the contrasting patterns of exotic species success across spatial scales. The model predicts that increasing invasibility with native diversity across large scales is the result of decreasing mean interaction strength as resources increase. The strength of the positive relationship between native and exotic species diversity and the relative contribution of factors extrinsic to the community depend on whether niche breadth increases with the number of available resources. However, the same mechanism—the sum of interspecific competitive effects ( $\sum \alpha_{ij}n_j$ )—drives the opposite pattern of decreasing invasibility with native richness at small scales because resource numbers are held constant. Hence, we conclude that Elton's biotic resistance hypothesis, interpreted as a small-scale phenomenon, is consistent with large-scale patterns in exotic species diversity.

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