When is Diversity-Mediated Invasion Resistance Overridden by Highly Competitive Invaders?

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- competition, disturbance, invasion resistance, species diversity, enemy escape hypothesis, novel weapons hypothesis, niche theory, overyielding
When is Diversity-Mediated Invasion Resistance Overridden by Highly Competitive Invaders?

Short Title: Resistance to Invasion by Superior Competitors

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Abstract

Theory predicts and empirical studies have demonstrated diversity-mediated invasion resistance. Whether species-rich communities can resist invasion from species that are competitively superior to the residents remains unclear. We used Lotka-Volterra models to examine the effects of different mechanisms and magnitudes of invader competitive superiority on invasion in relation to species diversity and disturbance. We assumed strong competition between resident species and the invader. Reduced density-dependent mortality in the invader resulted in the greatest invasion success and impact. Low disturbance and high species richness at competitive equilibrium decreased invasion rate, but were not effective at preventing invasion by highly competitive invaders. Differences in invasion success between invaders with different levels of competitive superiority were greatest in diverse equilibrium communities but lowest in diverse non-equilibrium communities. Given that most diversity-invasibility experiments do not consider competitive superiority of the invader, their relevance to management of the most problematic invasive species may be limited.
INTRODUCTION

Non-native species are a paradox in that ecologists have argued that they can both reduce and be reduced by biodiversity. Numerous reviews on the impacts of non-native invaders have revealed that there are at least a few high profile species with strong competitive effects that can lead to significant losses of species diversity (Davis 2003; Levine et al. 2003; Gurevitch & Padilla 2004; Huston 2004; Ricciardi & Cohen 2007; Hejda et al. 2009; Powell et al. 2011; Brewer & Bailey 2014). On the other hand, theory and the results of several experiments have revealed that species-rich assemblages tend to resist invasion (Levine & D’Antonio 1999). These seemingly contradictory conclusions suggest there is a need to better understand how invaders known to be superior competitors affect and are affected by diverse species assemblages.

Competitive superiority of non-native invaders over native species (hereafter, Invader Competitive Superiority or ICS) can occur via a variety of mechanisms. One category is reduced negative density-dependence in the invader relative to native species. One mechanism of reduced negative density dependence is reduced predation or disease as a result of the invader having escaped its coevolved parasites or predators in its home range, hereafter enemy escape (Janzen 1970; Connell 1971; Maron & Vilá 2001; Klironomos 2002; Wolfe 2002; Reinhart & Callaway 2004). Enemy escape by a non-native invader can result in competitive exclusion of natives by the invader if density-dependent mortality of the natives caused by predators or pathogens is substantially high (Bever 2003). Another mechanism is greater tolerance of competition for resources, also known as reduced competitive response (Goldberg & Fleetwood 1987; Suding et al. 2004). As predicted by classic, two-species Lotka-Volterra competition models (Volterra
1926; Lotka 1932), a large disparity in carrying capacity (and thus tolerance of low resource supplies) can result in competitive exclusion of the species with the lower carrying capacity.

A second category of ICS is an advantage in terms of per capita competitive effect. A specific mechanism of per capita competitive advantage associated with invasive species is direct aggression or the production of novel weapons, usually biochemical compounds in plants (Callaway & Ridenour 2004). Described as allelopathic advantages against resident species (AARS), novel chemicals produced by non-native plants result in allelopathic effects on the evolutionarily naïve resident community and thus give non-native invaders a competitive advantage (Callaway & Ridenour 2004). Using competing species of yeast, Gause (1934) demonstrated that such competition could be modeled using two-species Lotka-Volterra competition equations by assuming differences in competition coefficients between the two species.

A third category of ICS is an inherent (genetically-based) advantage in terms of per capita growth rate (Blossey & Notzold 1995). Known as the Evolution of Increased Competitive Ability (EICA) hypothesis, growth rate is assumed to trade off with allocation to defense. Competitive superiority results when a non-native species, having escaped its natural enemies in its home range, evolves increased growth rate as a result of reduced selection for defense in its introduced range. Similar to patch models of competition (e.g., Hastings 1980), Lotka-Volterra competition models can be modified to examine the effect of growth rate differences on competitive outcomes by incorporating continuous density-independent loss (Ricklefs & Miller 1999; Brewer 2011). Competitive exclusion can result when the faster growing invader recovers from the loss
more quickly and interferes with the recovery of the native species from the loss (Brewer 2011).

Despite numerous case studies demonstrating the potential importance of different mechanisms of ICS, the relative importance of different ICS mechanisms to invasion success and community-wide impact is not well understood. Competitive ability of invaders, and thus invasion success and impact, depends on both the competitive response of the invader to the residents and the competitive effects of the invader on the residents (Goldberg & Fleetwood 1987). Invaders that experience reduced density-dependent mortality due to enemy escape or greater tolerance of low resource supplies likely have an advantage over resident species in terms of competitive response. In contrast, invaders that have a growth rate advantage over residents or employ novel biochemical weapons to harm residents likely have an advantage in terms of competitive effect. We are aware of only one empirical study that has explicitly considered the relative importance of ICS in terms of competitive response versus competitive effect (Suding et al. 2004), and predicted differences have not been explored in detail.

In addition to the competitive superiority of invaders, most ecologists agree that reductions in competitive resistance of established communities (e.g., via disturbance and/or resident species losses) tend to promote invasion (Hobbs & Huenneke 1992; Burke & Grime 1996; Davis et al. 2000; Levine 2000; Stohlgren et al. 2001; Huston 2004; Zavaleta & Hulvey 2004; Stachowicz & Byrnes 2006; Brewer & Bailey 2014). Existing theory predicts that species-rich communities at competitive equilibrium can resist invasion due to the combined competitive resistance from multiple resident species (Case 1990; Luh & Pimm 1993; Law & Morton 1996; Tilman 2004), demographic
stochasticity, and reduced Allée effects (Mack 2000). Although numerous experimental
studies at small spatial scales appear to support theoretical predictions (Knops et al. 1999;
Levine 2000; Naeem et al. 2000; Wilsey & Polley 2002; Zavaleta & Hulvey 2004; Maron
& Marler 2007), few have explicitly considered whether the invader was competitively
superior to the resident species (Maron & Marler 2007).

Some ecologists have argued that neither the lack of disturbance nor high resident
species diversity reduces invasion by species that are superior competitors to most or all
of the resident species (Levine & D’Antonio 1999; Ortega & Pearson 2005), and some
empirical studies appear to support that conclusion (Ortega & Pearson 2005; Brewer
2008; Corbin & D’Antonio 2010; Case et al. 2016). Although the theoretical
investigations mentioned above examined diversity-mediated invasion resistance as a
means of understanding community stability and assembly, none of these studies
explicitly examined whether species-rich communities could effectively resist invasion
by very highly competitive invaders. And yet invasions by such species are precisely the
type of invasions that are most likely to cause catastrophic reductions in biodiversity and
are the greatest cause for concern. It is therefore crucial to assess the combined
competitive resistance of species-rich communities to invaders known to be
competitively superior to most or all of the resident species in an assemblage.

In this study, we used Lotka-Volterra competition models to simulate invasion of
established resident communities and to test the relative predicted importance of different
mechanisms of ICS [reduced density-dependent mortality (advantage in K), increased per
capita competitive effect (advantage in c), and increased growth rate (advantage in r)] on
resident communities (Table 1). In addition, we examined how the different ICS
mechanisms interacted with factors that potentially influenced resistance to invasion (i.e., disturbance severity and resident species diversity) to influence invasion success and impact. We examined the effects of varying niche overlap among competitively equivalent resident species, but assumed that equilibrium coexistence of the competitively superior invader and any individual resident species was not possible.

Under the set of conditions examined here, the current study provided answers to the following questions: 1) Which mechanisms of ICS result in the greatest invasion success and the greatest impact on resident species? 2) How do species richness and niche overlap among equally competitive and abundant resident species affect invasion by a competitively superior invader? 3) How do severe disturbance and moderate density-independent loss (mortality) affect invasion and impact of invaders with different mechanisms of competitive advantage? 4) What is the relationship between species diversity in equilibrium and non-equilibrium assemblages and increasing competitive superiority of a potential invader?

MATERIALS AND METHODS

The Model

The model is a simple multi-species extension of the classic two-species Lotka-Volterra competition model, modified to incorporate continuous density-independent loss:

\[
\frac{\Delta N_x}{\Delta t} = r_x N_x \left[ 1 - \frac{N_x}{K_x} \right] - \left( \sum_{j=1}^{n} \frac{c_{xj} N_j}{K_x} \right) - l_x N_x
\]  

(1)
where,

- \( N_x \) is the density of the target species, \( x \)
- \( r_x \) is the per capita growth rate of the target species
- \( K_x \) is the carrying capacity of the target species
- \( N_y \) is the density of each of \( n \) heterospecific competitors, \( y \)
- \( c_y \) is the competition coefficient (per capita competitive effect) of species \( y \) on species \( x \), and
- \( l_x \) is the density-independent instantaneous loss rate of species \( x \).

ICS was modeled by giving the non-resident invader an advantage in one of three parameters, \( K \), \( c \), or \( r \), while holding the others equivalent to those of the resident species. In initial trials, we examined both a 20% and a 40% advantage for the invader in each of the parameters indicated. Because the results were qualitatively similar, we present only the results of 40% ICS when contrasting different mechanisms of ICS. The effects of greater magnitudes of ICS are considered in greater detail with respect to an advantage in \( K \). Reduced density-dependent mortality of the invader, e.g., enemy escape or more efficient resource use, was modeled as \( K_{\text{invader}} > K_{\text{resident}} \) (140% vs. 100% of resident species \( K \)). Higher per capita competitive effect of the invader on resident species, e.g., resulting from novel weapons possessed by the invader, was modeled \( c_{\text{invader}} > c_{\text{resident}} \) (1.4 vs. 1). We chose a baseline per capita effect of the residents on the invader of 1 (equivalent to intraspecific competition) for the simulations, based on the assumption that resident species and the invader competed for the same resources, and that lack of coevolution between resident species and the non-resident invader prevented any
opportunity for character displacement and thus any reduction in niche overlap. Hence, the 40% advantage for the invader was assumed to be the result of non-resource-related competitive superiority (e.g., allelopathy, direct aggression). Simulations with lower baseline competitive effects of residents on invaders, as expected, resulted in weaker competitive resistance to invasion, but otherwise qualitatively similar results and as such are not presented here. Higher intrinsic growth rate in the invader than in resident species, e.g., evolved higher growth rate following introduction and escape from enemies, was modeled as $r_{\text{invader}} > r_{\text{resident}}$ (0.028 vs. 0.02). Density-independent loss was set at 0 or 1%.

Starting Conditions for Simulated Invasions of Assemblages of Resident Species

Invasion success and impact were assessed using simulated invasion experiments (Armstrong & McGehee 1980; Chesson 2000). We introduced a non-resident invader to resident species assemblages at an arbitrarily low starting density of 10% of the resident species’ equilibrium densities. The starting densities for the resident species were either at their equilibrium densities (assuming no severe disturbance) or at 10% of their equilibrium densities (severely disturbed). To examine the effect of species richness on invasion, we constructed 1, 2, 3, 6, and 10-species assemblages of residents. For these simulations, we assumed that all resident species had the same $K$, $r$, and $l$, and the same $c$ with respect to one another [either 0.9 for high per capita competition or 0.54 (40% reduction) for low per capita competition]. Given that all residents had the same $K$, we hereafter refer to $c = 0.9$ as “high niche overlap” among the resident species and $c = 0.54$ as “low niche overlap.” For the scenarios with two or more species, all resident species had equivalent starting densities. All simulations were run for 1000 time steps.
The Relationship between Diversity-Mediated Resistance and the Magnitude of Competitive Superiority of a Potential Invader

To determine how diversity-mediated resistance varied in relation to the magnitude of ICS, we first simulated invasion of undisturbed equilibrium assemblages of 1, 2, 3, 6, and 10 species, using an invader of equal competitive ability or with a $K$ that was either 140%, 200%, or 300% of that of the resident species. The invader was introduced at a starting density of 10% of each resident species’ $K$. We ran simulations for 1000 steps assuming either high niche overlap (0.9) or low niche overlap (0.54). Starting conditions were otherwise the same as described above for the ICS in the $K$ scenario assuming no disturbance or density-independent loss.

To determine the relationship between the relationship between ICS and disturbance-mediated coexistence of resident species, we invaded non-equilibrium assemblages that varied along a continuum of dominance and species richness using an invader of equal competitive ability or with a $K$ that was either 140%, 200%, or 300% of that of the subordinate resident species. Each resident assemblage contained one dominant resident with a $K$ that was 140% of that of the subordinate competitors. We assumed an $r$-$K$ trade-off (100% vs. 140% $K$ combined with 0.028 vs. 0.02 $r$, respectively) among the residents and no continuous density-independent loss. We also assumed complete niche overlap among resident species and between the residents and the invader ($c = 1$), thereby precluding any possibility of stable coexistence. Disturbance-mediated coexistence was simulated by reducing the abundance of the dominant resident and adding subordinate species. For every 10% reduction in the dominant resident an
additional resident was added at 10% of its $K$. After establishing the desired starting
conditions for the resident assemblage, the invader was introduced at 10% of the
subordinate resident species’ $K$ and its growth rate (RGR) followed for 1000 time steps.

Quantification and Analysis of Invasion and Impact

Invasion success and impact were quantified by calculating the log response ratio, i.e.,
the difference in relative growth rates between the invader and the residents:

$$LRR_{500} = \left[ \ln(N_{\text{invader}(t=500)}) - \ln(N_{\text{invader}(t=0)}) \right] - \left[ \ln(N_{\text{resident}(t=500)}) - \ln(N_{\text{resident}(t=0)}) \right]$$  (2)

and

$$LRR_{1000} = \left[ \ln(N_{\text{invader}(t=1000)}) - \ln(N_{\text{invader}(t=0)}) \right] - \left[ \ln(N_{\text{resident}(t=1000)}) - \ln(N_{\text{resident}(t=0)}) \right],$$   (3)

wherein relative growth rate of the invader represented invasion success and the average
relative growth rate of the residents represented invader impact.

RESULTS

Invasion of Assemblages of Resident Species by Invaders with Different
Mechanisms of Competitive Superiority

In the absence of severe disturbances or continuous, modest density-independent loss,
reduced density-dependent mortality in the invader (e.g., as predicted by enemy escape or
more efficient resource use) resulted in the greatest invasion success and impact on the
resident community (Figs. 1a, b; 2a, b; 3a, b). When subjected to modest, density-independent loss, inherently higher growth rates in the invader (ICS from a growth rate, $r$, advantage) resulted in invasion success and impact on the resident community that was comparable to that of ICS from $K$ advantage and substantially greater than that of ICS from $c$ advantage (Figs. 1c, d; 2c, d; 3c, d). In contrast, higher per capita competitive effect (ICS from $c$ advantage; e.g., novel weapons) in the invader was relatively ineffective at promoting invasion success or impact except following severe disturbances in assemblages with few resident species, suggesting that invaders with this type of competitive advantage over resident species have difficulty increasing when rare within an undisturbed community characterized by low niche overlap among residents (Fig. 2).

Increasing the numbers of resident species, especially when niche overlap was relatively low, was effective at decreasing invasion success (Figs. 1-3). The negative effect of resident species richness on invasion success was greatest for invaders with an advantage in $r$ or $c$ and lowest for invaders with an advantage in $K$ (Figs. 1a, c, e; g; 2a, c, e; 3a, c, e; g). In the absence of severe disturbance (with or without continuous loss) and when niche overlap among residents was low ($c = 0.54$), successful invasion by invaders with an advantage in $c$ occurred only when there was just a single resident species (Figs. 2a, c). In contrast, in the absence of severe disturbance but with continuous loss, invaders with an advantage in $r$ or $K$ or were able to successfully invade and displace resident species in assemblages containing two or three species, respectively (Figs. 1a, c; 3a, c).

When niche overlap among residents was high ($c = 0.9$), the effect of species richness on invasion was weak (Figs. 1-3b, d, f, h). The reduced effect of species richness was well illustrated by the example in which the invader had an advantage in $K$, when
there was no disturbance or loss. Low niche overlap among resident species prevented successful invasion when there were three or more species (Fig. 1a). When niche overlap was high, the decline in invasion success with increasing species richness was modest (Fig. 1b). Even 10 resident species were not sufficient to prevent invasion or displacement by the invader (Fig. 1b).

The Relationship between Diversity-Mediated Resistance and the Magnitude of Competitive Superiority of a Potential Invader

Diversity-mediated resistance to invasion decreased greatly with increasing ICS with respect to $K$. The reduction in invasion success with increasing species richness was asymptotic in all cases (Figs. 4a; b). Hence, there were diminishing returns with respect to invasion resistance in response to increasing species richness. The greatest reduction in invasion success with increasing species richness occurred when the potential invader was equal in competitive ability to the resident species (Figs. 4a; b). Indeed, this potential invader was not able to increase in any assemblage, even when niche overlap among resident species was high, but the rate at which its density was reduced increased with increasing species richness, especially when niche overlap among residents was low (Figs. 4a; b). Overall, the reduction in invasion success with increasing species richness was greater when the resident species exhibited low niche overlap (Fig. 4a) than when they exhibited high niche overlap (Fig. 4b). Nevertheless, even when niche overlap among the residents was low, an invader with two times or three times the carrying capacity of the residents could invade all assemblages and displace the residents.
The Relationship between Disturbance-Maintained Diversity, Invasion, and the Magnitude of Competitive Superiority of a Potential Invader

In contrast to the effect of species diversity on invasion resistance in equilibrium assemblages maintained by reduced niche overlap, invasion rate increased with increasing species diversity maintained by reduced competitive dominance by a strong resident competitor (Fig. 5). Invasion was least successful in monocultures of the dominant resident competitor, especially when the invader was equal to rather than superior in competitive ability to the dominant resident competitor (Fig. 5).

DISCUSSION

Invasions by non-native species with differing levels and types of competitive superiority over resident species can improve our understanding of the processes that maintain species diversity and their relevance to management. To date, the primary motivation of most diversity-invasibility studies appears to be to demonstrate the importance of niche complementarity in maintenance of species diversity, rather than relevance to management of invasive species. This is because most diversity-invasibility studies do not explicitly consider whether, how, or to what degree introduced species are competitively superior to resident species (Knops *et al*. 1999; Levine 2000; Naeem *et al*. 2000; Wilsey & Polley 2002; Zavaleta & Hulvey 2004; but see Maron & Marler 2007).

Although our study predicts that biotic resistance (in the form of high resident species richness or lack of disturbance) can reduce invasion rate or even prevent invasion by non-native species known to be superior competitors to all residents, it also predicts that, given sufficient competitive superiority, a potential invader will still successfully invade
and competitively displace resident species even in species-rich and undisturbed communities. Perhaps most importantly, our study predicts that the strength of diversity-mediated resistance to invasion resulting from niche complementary among resident species diminishes as the magnitude of competitive superiority of the invader increases. If invasion is strongly negatively affected by resident species diversity, then resident species diversity may indeed be maintained in part by stabilizing niche differences. Nevertheless, in those cases, the invader is predicted to be a relatively weak competitor that is unlikely to cause significant losses of species diversity. In contrast, if species diversity has more-or-less equal effects on weak and strong competitors, then diversity-mediated resistance is weak (Figure 4b), in which case niche differences among resident species might have little effect on maintaining species diversity. If resident species diversity is maintained primarily by disturbance, then diverse communities will be the most easily invaded due to the lack of competitive resistance by the dominant resident competitor (Fig. 5; Huston 2004). In contrast to responses to equilibrium communities of resident species, differences in invasion success between invaders that differ in the magnitude of competitive superiority would be at their lowest in diverse communities. In all three scenarios, niche complementarity among resident species ultimately would provide little value in terms of resistance to the most competitive invaders and thus the management of non-native species that matter. Rather than simply manipulating resident species diversity and then demonstrating diversity-mediated resistance to introduced species without regard to their competitive ability, we suggest that future studies experimentally contrast invasion success of introduced species known to differ in either the magnitude or the type of competitive superiority over the resident species.
Furthermore, we suggest that these studies contrast invasion success in relation to naturally occurring levels of resident species diversity, in order to assess the relative importance of niche complementarity among resident species and disturbance in maintaining species diversity. Such studies could also indicate if niche complementarity is relevant to the management of problematic non-native species.

In the absence of severe disturbance or continuous density-independent loss, potential invaders that experience reduced negative density-dependence (compared to resident species; i.e., higher $K$) were predicted to be the most successful invaders and have the greatest impact on resident species. Examples of such species with higher carrying capacities include those that have escaped natural enemies (Maron & Vilá 2001; Klironomos 2002; Wolfe 2002; Reinhart & Callaway 2004) and those that are more tolerant of low resource supplies (Suding et al. 2004). Such a prediction has at least three important implications for both ecological theory and management of invasive species. First, if the competitive advantage that a potential invader has at competitive equilibrium derives from enemy escape or more efficient use of limiting resources, then simply minimizing disturbances will not prevent invasion by such a species. Second, because disturbances are not required to promote invasion by species with higher $K$, such species are likely to invade communities that have not experienced severe anthropogenic disturbance and thus are likely to contain rare endemics (Pimm et al. 2014). Hence, such invaders likely represent the greatest threat of invasion to biodiversity (Brewer 2008). Third, potential invaders with higher $K$ than resident species need not have higher intrinsic growth rates than the resident species, nor possess novel biochemical weapons to be effective invaders with strong negative impacts on resident species (Suding et al.)
2004, Corbin & D’Antonio 2010). High intrinsic individual or population growth rate and novel weapons are often argued to be quintessential characteristics of successful invaders that also have strong competitive effects on resident species (Blossey & Notzold 1995, Callaway & Ridenour 2004). The model simulations presented here, however, suggest such species may have difficulty invading undisturbed ecosystems and thus may not represent the greatest threat of invasion to biodiversity. Additional empirical tests or meta-analyses of existing empirical studies are necessary to validate this prediction.

Having an intrinsic growth rate advantage over resident species is likely to be an important characteristic of invaders with large impacts on resident communities that experience continuous, moderate density-independent losses of individuals or biomass (Brewer 2011). Most communities experience some level of continuous density-independent loss from moderate disturbance (Pickett & White 1985). Therefore, having an intrinsic growth rate advantage over resident species is likely to be an important characteristic of invaders of many communities (Grime 1977; Blossey & Notzold 1995; Huston 2004; Brewer 2011). Species with high intrinsic growth rates are often associated with productive ecosystems (Grime 1977). Therefore, it would be interesting to see if the type of competitive advantage experienced by an invader varies from higher $K$ to higher $r$ along gradients of increasing productivity (Brewer 2011).

Severe disturbances increased invasion success in equilibrium assemblages by dramatically reducing population densities of resident species, which in turn reduced the advantage that resident species as a group had over the invader. Such results are consistent with the general empirical observation that invaders that are superior competitors are nonetheless often associated with disturbances (Brewer & Bailey 2014).
Severe disturbances promoted invasion and impact by invaders with a growth rate advantage, provided there was also modest density-independent loss that occurred continuously. In those cases, in which the invader had greater per capita competitive effects on the residents (as assumed in the novel weapons hypothesis), successful invasion only occurred in conjunction with severe disturbance or when there was only one resident species.

Given the parameters of the model examined in this study, the invasion success and impact of competitively superior invaders was reduced by the number of resident species coexisting at equilibrium. In this study, when niche overlap among residents was low, species-rich assemblages produced higher overall assemblage-level densities than did species-poor assemblages, thus demonstrating overyielding (Beckage & Gross 2006). Hence, low and uniform niche overlap among many equally abundant and competitive resident species resulted in significant diffuse (sensu Chesson 2000) competitive resistance to invasion by a non-resident species starting at low density. These findings are similar to those of previous theoretical investigations (Case 1990; Luh & Pimm 1993; Law & Morton 1996; Tilman 2004), which demonstrated that the combined competitive resistance of multi-species assemblages could reduce the likelihood of successful invasion by a non-resident species with a competitive ability equal to that of the best resident competitor. Our results show, however, that such an effect applies also to invaders that are competitively superior to all resident species, although the effect is much weaker when the invader has a higher carrying capacity than the residents. Weak diversity-mediated resistance to invasion and rapid displacement of resident species is consistent with the results of several empirical studies that specifically examined strong
competitors (Ortega & Pearson 2005; Brewer 2008; Corbin & D’Antonio 2010; Case et al. 2016). Given that the most problematic invaders can achieve natural densities in invaded systems that are orders of magnitude higher than any resident species (e.g., Brewer et al. 2015), we would argue that the maximum competitive advantage examined here (300% of resident species’ $K$) was not unrealistic. Furthermore, our results show that the mechanism of competitive superiority matters, at least in theory. In the absence of disturbance or density-independent loss, those invaders that were more tolerant of low resource supplies or less affected by density-dependent enemies (higher $K$) were better able to increase from a low starting density in a multi-species assemblage than those with a per capita competitive advantage (higher $c$), especially when niche overlap among residents was high. Whether such findings apply to natural field situations, however, remains unclear. More empirical work is needed to determine whether the strength of diversity-mediated resistance depends on the mechanism of ICS.

Non-native invaders that are superior competitors to resident species arguably represent one of the greatest threats to biodiversity. Repeated experimental demonstrations of significant diversity-mediated resistance have led some to suggest management practices aimed at minimizing local losses of native species (Levine 2000; Zavaleta & Hulvey 2004; Maron & Marler 2007). While we agree that management that minimizes resident species losses should be encouraged, we argue that such practices should not be viewed as a sufficient or viable means of managing the most problematic invaders. Rather than managing for biodiversity and hoping for the best, a more effective approach to dealing with the most problematic invaders would be to base management decisions on knowledge of the mechanisms and magnitude of ICS. In many cases, early
detection and eradication or containment may be the only effective option for managing such species.

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References


For Review Only


36. Maron, J. & Marler, M. (2007). Native plant diversity resists invasion at both low and
high resource levels. *Ecology*, 88, 2651–2661


Table 1. List of hypotheses of invader competitive superiority (ICS) considered in the current study and associated parameter adjustments for the Lotka-Volterra competition equations.

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<th>Hypothesized Invader Competitive Superiority (ICS)</th>
<th>Model Parameter Adjustment</th>
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<td>Reduced Density-Dependence (Enemy Escape; Greater Tolerance of Competition or of Low Resource Supplies)</td>
<td>Elevated Carrying Capacity ($K$) in the Invader</td>
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<td>Allelopathic Advantage against Resident Species (AARS)</td>
<td>Elevated Per Capita Competitive Effect ($c$) in Invader</td>
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<tr>
<td>Evolution of Increased Competitive Ability (EICA)</td>
<td>Elevated Per Capita Intrinsic Growth Rate ($r$) in the Invader, Combined with Continuous Density-Independent Loss ($l$)</td>
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Figure 1. Invasion of communities by a non-resident species with a 40% advantage over the resident species in terms of carrying capacity ($K$) as a function of severe disturbance, 1% continuous density-independent loss and resident species richness. Left-hand panels represent situations in which per capita competitive effects among residents were low ($c = 0.54$; low niche overlap). Right-hand panels represent situations in which per capita competitive effects among residents were high ($c = 0.9$; high niche overlap). Responses are log-response ratios of population growth of the non-resident invader to that of the average resident species (see text for details of calculation).

Figure 2. Invasion of communities by a non-resident species with a 40% advantage over the resident species in terms of per capita competitive effect ($c$) as a function of severe disturbance, 1% continuous density-independent loss and resident species richness. Left-hand panels represent situations in which per capita competitive effects among residents were low ($c = 0.54$; low niche overlap). Right-hand panels represent situations in which per capita competitive effects among residents were high ($c = 0.9$; high niche overlap). Responses are log-response ratios of population growth of the non-resident invader to that of the average resident species (see text for details of calculation).

Figure 3. Invasion of communities by a non-resident species with a 40% advantage over the resident species in terms of per capita growth rate ($r$) as a function of severe disturbance, 1% continuous density-independent loss and resident species richness. Left-
hand panels represent situations in which per capita competitive effects among residents were low ($c = 0.54$; low niche overlap). Right-hand panels represent situations in which per capita competitive effects among residents were high ($c = 0.9$; high niche overlap). Responses are log-response ratios of population growth of the non-resident invader to that of the average resident species (see text for details of calculation).

Figure 4. Invasion of undisturbed communities by a non-resident species with a $K$ that was 100% (equal), 140%, 200%, or 300% of that of the resident species in relation to resident species richness. The left-hand panel represents the situation in which per capita competitive effects among residents were low ($c = 0.54$; low niche overlap). The right-hand panel represents the situation in which per capita competitive effects among residents were high ($c = 0.9$; high niche overlap). Responses are log-response ratios of population growth of the non-resident invader to that of the average resident species after 1000 time steps.

Figure 5. Invasion of non-equilibrium communities with different levels of dominance and diversity by a non-resident species with a $K$ that was 140%, 200%, or 300% of that of the subordinate resident species. Subordinate residents had a starting density of 10% of their $K$. The competitively dominant resident (whose $K = 140\%$ of that of the subordinates) was present in all communities and had a starting density of 140%, 130%, 120%, 90%, and 50% of the subordinate residents’ $K$ for the 1-, 2-, 3-, 6-, and 10-species communities, respectively. Responses are relative growth rate (RGR) of the non-resident invader for 1000 time steps.
Figure 1.

279x361mm (300 x 300 DPI)
Figure 2.

279x361mm (300 x 300 DPI)
Figure 3.

279x361mm (300 x 300 DPI)
Figure 4.

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Figure 5.

279x361mm (300 x 300 DPI)