

## ESSAY REVIEW

# Plant invasions and the niche

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## Summary

1. For plant invaders, being different is often equated with being successful, yet the mechanistic connection remains unclear.
2. Classic niche theory predicts that invaders with niches distinct from the native flora should coexist with little interaction with native species, yet such invaders often have substantial impacts. Meanwhile, invaders that overlap in niche space with native species should either be repelled or dominate, yet these invaders often naturalize with little effect. Such discrepancies between theory and observation raise questions about how species differences influence invader establishment and impact.
3. Here, we review these issues in light of recent work on coexistence theory, which shows how niche and fitness differences between natives and invaders interact to determine invasion outcomes. We show how successful invader establishment depends on either a fitness advantage or niche difference from resident species, but that only the former allows invaders to become dominant.
4. By identifying the role of niche and fitness differences in leading invasion hypotheses, we unify their predictions for invasion success while highlighting new approaches for evaluating the importance of species differences for invasion.
5. *Synthesis.* Situating the invasion process within a recent coexistence framework broadens our understanding of invasion mechanisms and more tightly links problems in invasion ecology with our more general understanding of community dynamics.

**Key-words:** coexistence, diversity, equalizing mechanisms, exotic species, invasive species, niche theory, stabilizing mechanisms

## Introduction

Ecologists have long argued that differences between biological invaders and the residents of the communities they invade determine invasion success. Darwin hypothesized that successful biological invaders would tend to be distantly related to the taxa in the invaded community (Darwin 1859). Elton argued that unique traits allowed the invaders to exploit 'empty niches' in species-poor island communities (Elton 1958). More contemporary theories of invasion success are numerous and diverse, but many share the prediction that successful invaders are somehow fundamentally different from native species (MacArthur & Wilson 1967; Daehler 2003; D'Antonio & Hobbie 2005).

The predicted importance of invader differences is largely due to the overriding influence of classic niche theory on invasion ecology (Levine & D'Antonio 1999). Classic niche

theory proposes that each species can persist under a limited set of conditions (Hutchinson 1959) and that large overlap in limiting factors can prevent a species from establishing in a community (MacArthur & Levins 1967; Diamond 1975; Case 1983). As such, common interpretations of this theory suggest that successful invasion requires the invader to occupy different niche space than the resident species. For example, invading species that are highly novel are predicted to be more successful because they use untapped resource pools (Fargione *et al.* 2003). Less functionally diverse communities are considered to be more easily invaded (Mack 2003; Stachowicz & Tilman 2005) because invaders are more likely to possess traits (e.g. novel phytochemicals) not already found in the resident community (Elton 1958; Levine & D'Antonio 1999; Fridley *et al.* 2007).

Despite its central role in ecology, however, classic niche theory demonstrates several shortcomings when applied to biological invasions. The theory provides little guidance for how invaders without niche differences establish, yet in many

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empirical examples the functional characteristics of invading and native plants are strikingly similar (Bruno *et al.* 2005). For example, many invasive and native plants in Hawaii possess the same ecophysiological strategies for exploiting low-resource environments (Funk & Vitousek 2007). Moreover, some invasion hypotheses suggest that similarities between invaders and residents are sometimes beneficial; successfully establishing invaders are predicted to possess similar adaptations to climate as the native species.

Classic niche theory also poorly predicts those invaders that produce large impacts. It suggests that if invaders utilize different niche space than the native species, their interactions with the native species should be minimal. However, functionally unique invaders, such as nitrogen fixing plants, often have substantial impacts (D'Antonio & Hobbie 2005). Meanwhile, niche theory predicts that functionally similar invaders should impose the greatest harm on native communities, but case studies often counter this prediction, with similar invaders entering habitats with little impact (Mitchell & Power 2003; Bulleri *et al.* 2008). In total, these shortcomings reveal an explanatory gulf between the importance of being different and the niche-based mechanistic pathways by which these differences determine invasion success (Bruno *et al.* 2005; Stachowicz & Tilman 2005).

Here, we show how recent developments in coexistence theory clarify our expectations about the influence of species differences on invasion from establishment through impact. By separating 'niche differences' from 'fitness differences', this framework organizes the expectations of existing theories of invasion success. It emphasizes that successful invasion can result from either fitness differences that favour the dominance of the invader, or niche differences that allow the invader to establish despite lower average fitness. We highlight the promise of recently developed approaches for predicting invasion outcomes and raise new questions with hope for greater generality in invasion ecology.

### Niche versus fitness differences

When evaluating the role of species differences in driving invasions, it is helpful to distinguish 'niche differences' from 'fitness differences,' two concepts developed in the coexistence literature. Theory developed by Peter Chesson (2000) shows how these differences have opposing effects on the outcome of competition. Recognizing the importance of niche and fitness differences has already helped unify niche and neutral theories of coexistence (Adler *et al.* 2007) and stands to have similar benefits for invasion ecology.

In Chesson's framework, niche differences, or more formally, stabilizing processes, cause species to limit themselves more than they limit their competitors, benefiting coexistence. For example, differences between plants in rooting depth will cause a deeper-rooted species to limit itself more than it limits shallow-rooted competitors. Such differential limitation also arises from species-specific interactions with consumers, pathogens, mutualists, or spatial and temporal environmental heterogeneity (Chesson 2000; Chesson & Kuang 2008).

Density-dependent specialist enemy attack, for example, as in the Janzen–Connell hypothesis (Janzen 1970; Connell 1971), functions as a niche difference (Chesson & Kuang 2008). Chesson's definition of niche differences closely parallels its use in classic theory, and several hypotheses in the invasions literature invoke these differences (Table 1). However, not all species differences are niche differences – only those that cause species' per capita population growth rates to increase as they become rare. For example, a deep-rooted plant has its highest population growth rate when surrounded by shallow-rooted competitors. Given that invaders must increase when rare, niche differences facilitate their establishment. Moreover, the influence of stabilizing niche differences can be approximated by the degree to which an invader's per capita growth rate decreases as it becomes more common (Adler *et al.* 2007).

Fitness differences, by contrast, are those species differences that drive competitive dominance. These include differences between species that, on average, favour one competitor over the other. Examples include differences in the species' abilities to draw down common limiting resources (e.g.  $R^*$  (Tilman 1988)), differences in predator susceptibility or variation in the number of offspring produced per parent. Differences between species in these traits are not niche differences – the advantage does not depend on the invader being rare. For example, escaping natural enemies provides exotic species an advantage over native competitors regardless of their commonness or rarity (Keane & Crawley 2002; Mitchell & Power 2003). Rather than stabilizing coexistence, such fitness differences drive competitive exclusion and can be approximated by species average growth rate differences (Adler *et al.* 2007). The species with the highest average fitness displaces all competitors in the absence of niche differences. The notion that some species simply outperform others is well-established in ecology, and fitness differences are the basis of several leading invasion hypotheses (Table 1). Fitness differences in this coexistence context differ from their typical use in evolutionary biology (but see Endler 1986).

### Species differences and the outcome of invasions

With fitness differences driving systems toward competitive exclusion and niche differences favouring coexistence, the outcome of biological invasions depends on the relative strength of these two types of species differences (Box 1). Figure 1 graphically displays the lessons from the theory. The key message is that successful invasions can result from either fitness differences that favour the dominance of the invader, or niche differences that allow the invader to establish despite lower average fitness. In region A, the invader has lower average fitness than the resident community and the niche difference is not large enough to prevent the residents from repelling the invader. In region B, niche differences are sufficient to allow successful invasion despite the lower average fitness. In region C, the invader is at a fitness advantage relative to the resident community, but niche differences allow the residents to

**Table 1.** Leading invasion hypotheses and their relationship to niche and fitness differences

Hypothesis	Prediction	Examples
<b>Niche differences</b>		
Empty niche	Invader successful when occupying niche space unused by the resident community	Stachowicz & Tilman (2005)*†
Diversity-resistance	More diverse communities have less unused niche space, preventing invasion	MacArthur & Levins (1967)†; Levine (2000)*; Kennedy <i>et al.</i> (2002)*
Negative soil feedbacks	Species alter soil pathogens or biogeochemical cycles in ways that harm themselves more than others	Bever <i>et al.</i> (1997)†; Klironomos (2002)*
<b>Fitness differences</b>		
Novel weapons	Invader negatively impacts natives through novel pathways, such as allelopathic chemicals	Callaway & Aschehoug (2000)*†
Enemy escape	Native populations are depressed by pathogens and herbivores that do not prey on the invader	Keane & Crawley (2002)†; Mitchell & Power (2003)*; although see Van Kleunen & Fischer (2009)
Climate matching	Invaders are at a disadvantage relative to natives due to climate differences between home and invaded regions	Broennimann <i>et al.</i> (2007)*
<b>Both niche and fitness differences</b>		
Fluctuating resources	Invaders maintain populations through short-term increases in resources	Davis <i>et al.</i> (2000)†; Walker <i>et al.</i> (2005)*
Novel niches	Invader is better able to exploit new niches created by anthropogenic changes	Shea & Chesson (2002)†; MacDougall & Turkington (2005)*
Darwin's naturalization hypothesis	Invader that is phylogenetically distinct from natives will be more successful due to greater niche differences and less predation	Darwin (1859)†; Strauss <i>et al.</i> (2006)*

\*Empirical test of theory.

†Development of theory.

**Box 1.** Chesson theoretical framework

In Chesson's theoretical framework, niche differences (more formally called stabilizing processes) and fitness differences are quantified by their contributions to population growth rates when a species is rare. In many mathematical models of competing species, the number of individuals produced per individual (logged) when the invader is rare and the resident community is at its stochastic equilibrium can be expressed as follows:

$$r = s[\text{FitnessDifference} + \text{Niche Difference}] \quad \text{eqn 1}$$

where  $r$  is the per capita growth rate and  $s$  is a scaling term that converts the units of the niche and fitness differences to per capita growth rate units. The fitness difference term can be positive or negative, depending on whether the invader or the resident community has the greater average fitness. The niche difference term is always positive, because it describes advantages due to the resident community limiting itself more than the invader. See Chesson & Kuang (2008) for a specific model decomposed into niche and fitness differences.

Successful invasion requires that the invader has a positive growth rate when rare, which in turn requires the term in bracket to be positive. Invasion can thus result from a fitness advantage (a positive fitness difference term) or a niche difference strong enough to exceed the fitness disadvantage. These two scenarios form the basis of the 'niche opportunities' in Shea & Chesson (2002).

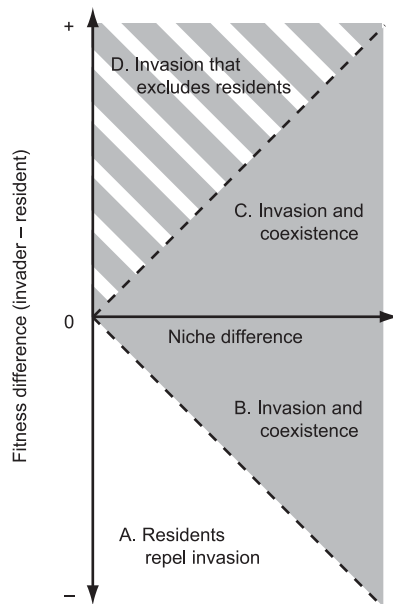
Equation 1 can be used to understand impact by treating the invader as the abundant resident and evaluating native species growth when rare. If positive, the latter persist. If the invader has greater average fitness, native persistence rests on the niche difference term being sufficiently positive. More generally, the native residents and exotic invader will coexist if both can increase when rare, which depends on a positive niche difference term.

persist with the successful invader. In region D, the fitness advantage of the invader outweighs the niche difference, causing the successful invader to displace residents.

This framework emphasizes that species differences can have a diversity of effects on the outcome of invasion. But these outcomes are not contradictory once one acknowledges that the invader or residents can have the fitness advantage and that niche differences modulate the outcome of this

advantage. The theory formalizes several points that help resolve confusion over species differences and invasion.

**1.** As long noted by ecologists, niche differences ( $x$ -axis of Fig. 1) increase the probability of invader establishment. Less appreciated is that niche differences also increase the chance that residents will persist with the invader once successful (Melbourne *et al.* 2007). Thus, theory predicts that some species differences enhance invader establishment but reduce



**Fig. 1.** The influence of niche and fitness differences on the outcome of biological invasions following the theory in Box 1. See Adler *et al.* (2007) and Chesson & Kuang (2008) for similar figures from the coexistence literature.

impacts. This prediction is supported by a poor correlation between the ability of invaders to establish and their impact on native species (Ricciardi & Cohen 2007).

2. Species differences that increase invader fitness relative to the native species ( $y$ -axis of Fig. 1) increase both establishment and impact. Sometimes maximizing fitness requires the invader to be similar to resident species in certain ways. For example, successful invaders ideally tolerate the climate of their new range equally well as locally-adapted native species.

3. Integrating points 1 and 2, high-impact invasions require similarity along the niche difference axis but a fitness advantage for the invader. For example, the invader must use resources required by the resident (little niche difference) but the invader should be much more effective at obtaining those resources (large fitness difference). Some invaders therefore do not require niche differences to invade. By contrast, those invaders that do require niche differences to establish (Fig. 1, region B) are unlikely to exert major impacts. Thus, results showing how niche differences facilitate invader establishment (Levine 2000; Kennedy *et al.* 2002) may not apply to the most damaging invaders.

### A unifying framework for species differences and invasion

The Chesson framework shows how the entire course of an invasion, from establishment to impact, is influenced by niche and fitness differences. In this theoretical framework, all mechanisms known to influence invasion success do so via their influence on one or both of these differences. The framework thus presents an opportunity to organize and unify the

wide diversity of hypotheses on the biotic controls over biological invasions. A recent review identified twenty hypotheses linking biotic interactions to plant invasions (Mitchell *et al.* 2006). Although this diversity reflects the numerous mechanisms that control biological invasions, it also demonstrates the challenge of generality in this research area. It can be difficult to identify the commonalities between the hypotheses and determine which make similar predictions for the outcome of invasions. Placing these hypotheses along the niche and fitness difference axes of Fig. 1 helps unify their influence on invasion dynamics.

In Table 1, we categorize leading invasion hypotheses into those that predict niche differences and those that predict fitness differences, following Chesson's definition of these terms (Chesson 2000). Interestingly, most invasion hypotheses invoke either niche or fitness differences but not both. The observation that exotic species seem more aggressive than their native counterparts has motivated several of the hypotheses for fitness differences that favour the invader. For example, the novel weapons and enemy release hypotheses describe frequency-independent advantages that invaders have over native species. Hypotheses such as these predict successful invader establishment and the displacement of native residents (Fig. 1).

Other invasion hypotheses fall squarely on the niche difference axis of Fig. 1, as they generate advantages when the invader is rare, but disadvantages when it is common via negative frequency-dependent dynamics (Adler *et al.* 2007). These include feedbacks where native and exotic species influence soils in ways that are disproportionately harmful to themselves (Klironomos 2002), as well as all of the hypotheses where invaders capitalize on niche space underutilized by resident species (Table 1). As discussed earlier, these hypotheses can explain successful invader establishment, but leave open the question of how impacts are exerted. The reverse is true for the positive-frequency dependence that arises when invaders influence ecosystem processes in ways that favour their growth over natives (Callaway *et al.* 2004). Such mechanisms may contribute to the high-density growth and impacts of already abundant invaders, but have little role in their initial establishment.

While the individual hypotheses in Table 1 have tremendous heuristic value, empirically observed differences between invaders and native species almost always involve both niche and fitness differences. Thus, relating the establishment and impacts of natural invasions to theory requires considering both axes of Fig. 1 simultaneously. For example, nitrogen (N) fixers are some of the most successful invaders. Their difference from residents in acquiring nitrogen is well-known to facilitate invasion (Vitousek *et al.* 1987; D'Antonio & Hobbie 2005), supporting the empty niche hypothesis; but because they utilize a different nitrogen pool than non-fixing residents (which should facilitate coexistence), this hypothesis does not explain how N-fixers exert large impacts on community composition (Vitousek *et al.* 1987). Instead, impacts often arise because of a fitness difference; N-fixation allows invaders to grow large and better intercept lighter than the residents,

an advantage when light is limiting. Indeed, the impacts of N-fixing invaders on resident species are often mediated via above-ground competition and not elevated soil nitrogen (Holmes & Cowling 1997; but see Stock *et al.* 1995).

Lastly, we point out that niche and fitness differences are a function of the spatial and temporal scale of inquiry. For example, habitat conversion might alter the relative advantages of native and exotic species at the scale of the converted habitat, but introduce habitat heterogeneity at the landscape scale. This is the case in the 'novel niche hypothesis', where anthropogenic changes to the landscape create niche opportunities for invaders (Shea & Chesson 2002). Abandoned fields and urban areas, for example, host a number of exotic species that cannot survive in adjacent forests (Lonsdale 1999). Similarly, eutrophication and alteration of the trophic structure in a community, both commonly caused by anthropogenic disturbance, can favour invaders (Byers 2002). When novel environments are created in small patches within a broader landscape, the novel niche hypothesis involves increased environmental heterogeneity, favouring invasion and coexistence via niche differences. By contrast, eutrophication of an entire region or global climate change influences the overall favourability of the landscape for native and exotic species.

### New questions and approaches

The coexistence framework put forth by Chesson raises the interesting question of where real invasions fall along niche and fitness difference axes: How strongly do niche differences stabilize the interactions between exotic and native species? How different are native and exotic species in their average fitness? These questions encompass multiple mechanisms for invasion success (Table 1), and addressing them is complementary to current studies focused on individual invasion hypotheses. We conjecture that the answers may be quite general across systems. For example, numerous authors have pointed out that most introduced species that establish remain at low density and exert little impact (Simberloff 1981; Williamson & Fitter 1996). These fall within regions B and C of Fig. 1. We infer that while niche differences between invaders and resident species are not always obvious, they are typically sufficient to allow coexistence. Support for the notion that fitness differences generally favour the invader is more ambiguous. Although there are some spectacularly successful invaders with high impact, the large number of failed invasions (Williamson & Fitter 1996) may indicate that mechanisms favouring native species over invaders commonly overwhelm mechanisms that do the reverse.

How can ecologists more formally test the influence of niche and fitness differences in stabilizing the interactions between native and exotic species? Here we describe recent phylogenetic, experimental and observational approaches for doing so.

The first approach uses phylogenetic distance as a proxy for species differences and evaluates patterns of relatedness between the invader and the native community. Darwin

hypothesized that phylogenetic distance benefits invaders by minimizing overlap in resource use with the resident species, a niche difference in Fig. 1. He also hypothesized that phylogenetic distance favours invaders by decreasing their susceptibility to shared natural enemies, and disfavors invaders by decreasing the likelihood that they possess adaptations for the new climate (Darwin 1859). These latter two hypotheses concern fitness differences in our framework. Because Darwin's three hypotheses predict niche differences, fitness advantages and fitness disadvantages, recent studies evaluating these hypotheses could help locate invasions in Fig. 1.

While several phylogenetic studies have found no association between invasion success and the relatedness of the exotic and native species (Daehler 2001; Lambdon 2008), those that do support the overwhelming influence of fitness differences on invasion success. Analyses of the flora in New Zealand, one of the few places where unsuccessful plant invasions have been quantified, show that introduced species that are more phylogenetically similar to native species are more likely to naturalize (Duncan & Williams 2002; Diez *et al.* 2008). Assuming that both fitness and niche differences can increase with phylogenetic distance, these results suggest that minimizing a potential fitness disadvantage is more important than niche differences in determining invader establishment. Meanwhile, Strauss *et al.* (2006) found that phylogenetically distant grass invaders in California were more likely to become noxious weeds. Given that niche differences cannot explain large impacts (Fig. 1), the Strauss *et al.* result suggests that fitness advantages primarily underlie these particular invasions.

Experimental approaches can exploit the principle that niche differences cause species to limit themselves more than competitors, which in turn cause species' per capita growth rates to increase at low relative abundance. The strength of niche differences in stabilizing the interactions between native and exotic species can thus be assessed by the degree to which species' per capita growth rates increase when rare versus common. Recent published articles have proposed experiments manipulating species frequency to understand the strength of niche differences (Adler *et al.* 2007; Eppstein & Molofsky 2007). A similar approach was used by Seabloom *et al.* (2003) to understand the outcome of interactions between native and exotic grasses in California. They found that exotic grasses could increase in plots where native grasses were dominant, and native grasses could increase when exotic grasses dominated. The interaction between these species thus falls within regions B or C of Fig. 1.

Lastly, natural experiments or observational approaches can be used to infer the degree to which niche differences stabilize the interaction between native and exotic species. One can measure the change in per capita population growth rate of the invader as it becomes abundant and its competitors become rare through time. If time-series studies are impractical, a chronosequence approach can be used. Here the investigator would compare invader per capita growth rate, moving from the invasion front towards its interior (Dwyer & Morris 2006). Common pitfalls to studies using natural and

experimentally created gradients of species' relative abundance have recently been evaluated (Levine *et al.* 2008).

## Conclusions

In this article, we have introduced an over-arching framework for thinking about the individual processes regulating the outcome of biological invasions. We distil numerous invasion hypotheses down to two key species differences that generate specific predictions for the establishment and impact of invasions. The framework helps resolve the apparent conflict between classic niche theory and our observations of invasions, and identifies a path towards generality in this field. Of course, future work on individual invasion hypotheses is essential for fully understanding biological invasions. But organizing these hypotheses in the terms of contemporary thinking on coexistence more tightly links problems in invasion ecology with our more general understanding of the maintenance of species diversity. Both fields have much to gain by further strengthening these linkages.

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