

Interspecific interactions and range limits: contrasts among interaction types

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Abstract There is a great deal of interest in the effects of biotic interactions on geographic distributions. Nature contains many different types of biotic interactions (notably mutualism, commensalism, predation, amensalism, and competition), and it is difficult to compare the effects of multiple interaction types on species' distributions. To resolve this problem, we analyze a general, flexible model of pairwise biotic interactions that can describe all interaction types. In the absence of strong positive feedback, a species' ability to be present depends on its ability to increase in numbers when it is rare and the species it is interacting with is at equilibrium.

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This insight leads to counterintuitive conclusions. Notably, we often predict the same range limit when the focal species experiences competition, predation, or amensalism. Similarly, we often predict the same range margin or when the species experiences mutualism, commensalism, or benefits from prey. In the presence of strong positive density-dependent feedback, different species interactions produce different range limits in our model. In all cases, the abiotic environment can indirectly influence the impact of biotic interactions on range limits. We illustrate the implications of this observation by analyzing a stress gradient where biotic interactions are harmful in benign environments but beneficial in stressful environments. Our results emphasize the need to consider the effects of all biotic interactions on species' range limits and provide a systematic comparison of when biotic interactions affect distributions.

Keywords Species' distributions · Biotic interactions · Range limits · Mutualism · Competition · Stress gradient hypothesis

Introduction

One of the grand challenges in ecology is predicting how species' geographical ranges will shift in response to environmental change and, indeed, understanding the factors that lead to range limits in the first place. One dimension of this challenge is teasing apart the impact of biotic interactions, such as competition and predation, from direct effects of abiotic environmental factors in driving range shifts (Elith and Leathwick 2009; Godsoe et al. 2015; Soberón 2007). There is increasing evidence that biotic interactions have strong effects on range margins (Pigot and Tobias 2013; Sexton et al. 2009). However, it is not clear how we can most easily anticipate these effects. There are many ways in which pairs of species interact (as measured for instance by effects of each species on

the fitness or abundance of the other species; Fig. 1), including predation, parasitism, competition, and mutualism. These pairwise interactions are furthermore embedded in webs of interactions, leading to chains of indirect effects, including trait-mediated indirect interactions (Ohgushi et al. 2012). These indirect effects can also affect range margins. Indirect effects may be difficult to distinguish from the direct effects of the abiotic environment on range margins. There has been a tendency in theoretical models to emphasize competition as a driver of range margins (Bull and Possingham 1995; Case et al. 2005; García-Ramos et al. 2000; Goldberg and Lande 2007; MacLean and Holt 1979; Pielou 1974), but models do exist exploring range limits generated by other kinds of biotic interactions such as predation (Holt and Barfield 2009) and mutualism (Afkhani et al. 2014; Hutson et al. 1985; Parker 2001). The effects of asymmetric interactions such as amensalism and commensalism on range margins are mentioned less frequently (Colwell and Rangel 2009; Hirzel and Le Lay 2008; Lavergne et al. 2010).

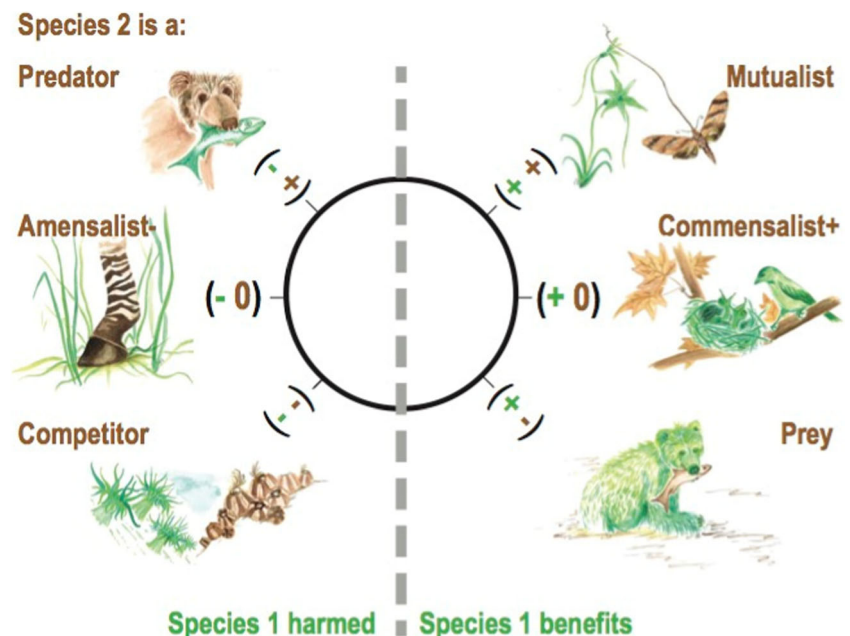
It can be difficult to study the effects of species interactions on range limits because a species' response to other species varies as we move from one context to another (i.e., from one location or environment to another), a phenomenon that we will refer to as context dependency. Most obviously, the growth rates and carrying capacities of each species can change as we move from one location to another (Davis et al. 1998; Holt and Keitt 2000; MacArthur 1972; Samaniego and Marquet 2013). More subtly, the impacts of biotic interactions can change (Chamberlain et al. 2014), both qualitatively and quantitatively. For example, as we move from benign environments to stressful environments, plant species may switch from being competitors to facilitators

(Callaway et al. 2002). It is thought that this trend strongly influences species' range limits (Louthan et al. 2015), but it still is not exactly clear how to analyze the effects of this shift in interaction strength on where a species will be present.

More generally, it is not at all clear which biotic interactions most influence species' range margins, and why. Araújo and Rozenfeld (2014) have recently argued that negative interactions discernible at fine scales fade away at coarser scales of resolution but that positive effects should scale up more broadly. This conclusion is at odds with many previous models where competition has a large effect across environmental gradients (Case et al. 2005; Case and Taper 2000; MacLean and Holt 1979; Pielou 1974). Other authors have explored how positive interactions such as mutualisms can lead to alternative stable states for species along environmental gradients. For instance, Wilson and Nisbet (1997) examined cellular automata models (and mean field approximations) for space-occupying organisms, where in addition to competing for space, individuals could experience reduced mortality when surrounded by neighbors, or neighbors could facilitate recruitment into empty patches. Such positive interactions can lead to abrupt range limits, and alternative states, along gradients (Wilson and Nisbet 1997), even when gradients have complex spatial structures (Buenau et al. 2007). There thus is a need to develop tools that predict the effects of biotic interactions on species' range margins. Such tools can lead to a more general understanding of when biotic interactions affect where a focal species can be present.

Here, we seek to address the effects of biotic interactions on range margins using well-grounded models of population dynamics that flexibly incorporate a wide range of pairwise biotic interactions. To do this, we use a framework developed by

Fig. 1 Compass of interaction types where symbols in parentheses indicate the interaction among the two species. The first symbol indicates the effect of the interaction on species 1; the second indicates the effect of the interaction on species 2. A “+” indicates that a given species benefits from the interaction, while a “-” indicates that the species is harmed, and a “0” indicates no effect of the interaction on a species. So, for example, (+ -) indicates an interaction from which species 1 benefits and species 2 is harmed (i.e., predation)



Holland and DeAngelis (2009) that uses a single set of equations to organize many familiar models of pairwise biotic interactions (Beddington 1975; de Villemereuil and López-Sepulcre 2011; Holland and DeAngelis 2009, 2010; Holling 1959; Kot 2001; May 1973; Pulliam 2000; Rosenzweig and MacArthur 1963). Holland and DeAngelis's framework includes saturating nonlinearities in interaction strengths, and it encompasses predator-prey, consumer-resource, competitive, and mutualistic interactions. As a result, this framework can produce a broad range of dynamics, and it allows us to contrast the effects of biotic interactions with impacts of the abiotic environment across a range of spatial scales.

Studies of species' range limits often distinguish a species' "fundamental niche" (the set of suitable abiotic environments) from its "realized niche," normally defined as that set of environments where a focal species in fact occurs, considering impacts of (e.g.,) other species on that species and the influence of dispersal. Holt (2009) distinguished between what can be viewed two subsets of the realized niche—the "establishment niche" and the "population persistence niche." The former represents locations where we expect the species to be present so long as it has had access to the location. In these environments, the focal species has a positive growth rate when it is rare, given that the rest of the community is at equilibrium (Chesson 2000b; Smith et al. 2011). For our purposes, an "equilibrium" may include fluctuating densities, in a bounded attractor. When these conditions are met at a particular location, the species can colonize the location or recover even when it is close to extinction. Some authors use the term realized niche to denote just the establishment niche as defined here (Thuiller et al. 2014). This use of invasion criteria may be familiar from applications of coexistence theory in community ecology or more generally from persistence theory, a body of mathematics that seeks to determine when species can be present in the face of negative interactions with other organisms (Chesson 2000a; Smith et al. 2011).

But in some circumstances, at a given location, an alternative locally stable equilibrium exists where a species could persist, even if it cannot increase when rare. So, a population may be able to persist, bounded away from low numbers, because of impacts that population has directly on its own growth rates, indirectly on the abiotic environment, or indirectly on biotic interactions. For instance, a generalist predator could exclude a prey species when that prey is initially rare, even though a high density of the same prey species would be able to persist because it can satiate the predator (Sinclair and Krebs 2002). This positive density-dependent feedback can lead to alternative stable states and affect the range limit of a species along a smooth environmental gradient (Donahue et al. 2011). Such alternative states can arise because of a wide range of positive feedbacks of a species on its own growth rate (DeAngelis et al. 2012; Petraitis 2013; Scheffer 2009). These feedbacks may act rapidly and would be represented as

positive density dependence (Courchamp et al. 2008; Keitt et al. 2001) in single species models (Holt 2009). Other examples of positive feedbacks act indirectly and over longer timescales, via impacts on the abundance of other species, or even ecosystem properties (Chase and Leibold 2003). The environmental conditions that promote such positive feedbacks should be viewed as niche dimensions that can determine where a species can be present. The population persistence niche concept highlights that sometimes, a species can persist in a locality, in part because of how that species influences its own environment (including direct density-dependent processes). The model we explore in this paper incorporates such feedback effects.

We aim at developing several results. We present parallel analyses across pairwise interactions, revealing that all may be important in determining range margins. We show that there are similarities among the establishment niches among several different types of biotic interactions. As a result, characterizing a species' establishment niche, after considering biotic interactions, can be a strong predictor of that species' range margin. However, when there is strong positive feedback, a species' persistence niche may extend past its establishment niche increasing the range of conditions where the species may be present. These theoretical results complement the recent review of Wisz et al. (2013) to buttress the proposition that biotic interactions often act jointly with abiotic conditions to set range margins.

The model

The landscape

Our model considers interactions among two species in a study region consisting of locations organized along two spatial dimensions denoted by the vector x (see Table 1 for a list of symbols). Biogeographers might refer to x as geographic space (Elith and Leathwick 2009). As we move from one location to another, the response of each species to the environment and the response of each species to the other can change (Callaway et al. 2002; Hargreaves et al. 2014). Note that the response of one species to another can indirectly reflect changes in the abiotic environment. To represent this, each of the parameters in our dynamic model (see Eq. (4)) can change as we move from one location to another. Our analyses identify the environments that allow a species to be present; this information is then used to identify portions of geographic space where our species can be present. Species interactions change range limits when they change the portion of geographic space where each species can be present. We assume that individual locations are sufficiently small that they can be considered internally spatially homogeneous (but still large enough to ignore demographic stochasticity).

Table 1 List of symbols used in this paper

Symbol	Definition
b_j	Describes the saturation of species i 's ability to obtain a benefit from species j when the density of species j is high. +
c_i	The maximum benefit species i can obtain from interactions with species j
e_i	Describes the saturation of the harm species j inflicts on species i
d_i	Density-dependent mortality of species i
f_i	The effects of species i and j on the per capita growth rate of species i
a_j	Describes the saturation in the harm species j inflicted on species i at high densities of species j
g_i	Density-independent growth of species i
h_j	Describes the saturation in the benefit species i can obtain from species j at high densities of species j
I_i	Zero net growth isoclines for species i
N_i	The density of species i at a location along the environmental gradient
N_i	Equilibrium density of species i in the absence species j
q_i	The maximum harm that species i can receive from
x	A two-dimensional vector representing spatial coordinates (for example, latitude, longitude)

Because we are concerned with the joint effects of biotic interactions and the abiotic environment on geographic range limits, we make a simplifying assumption about dispersal; specifically, we assume that both species can potentially migrate to all locations in the region of interest, but that dispersal rates are low enough that they do not affect local population growth rates. This assumption can arise when individuals disperse through space via a small amount of passive diffusion (i.e., a random walk; Case et al. 2005). However, our results will generalize to many other dispersal mechanisms, for example, the spatial arrangement of locations can be represented either explicitly or implicitly, just so long as dispersal is weak. We revisit the effect of dispersal in the “Discussion” section.

Biotic interactions at a single location

To analyze the presence of species 1 at a single location, we start with a general schematic model for change in the density (N_i) of each of two interacting species ($i = 1, 2$):

$$\frac{dN_1}{dt} = (g_1 + f_1(N_1, N_2))N_1 \quad (1a)$$

$$\frac{dN_2}{dt} = (g_2 + f_2(N_1, N_2))N_2. \quad (1b)$$

Here, g_i represents the density-independent growth rate of species i , while $f_i(N_1, N_2)$ represents the effect of each species on the per capita growth rate of species i , including intraspecific density dependence. We assume that $f_i(N_1, N_2) = 0$ when $N_1 = N_2 = 0$.

In the absence of biotic interactions involving species 2, we expect species 1 to occur in locations within its fundamental niche. These are by definition environments where its density-independent growth rate is positive:

$$g_1 > 0 \quad (2)$$

When the two species interact, species 1 should be present in locations where conditions are inside its establishment niche, which means that species 1 increases in numbers (and hence establishes) when it is rare, and species 2 is present at equilibrium (formally, we define “rarity” as the limit: $\lim N_1 \rightarrow 0$):

$$g_1 + f_1(N_1 \rightarrow 0, N_2) > 0. \quad (3)$$

Here, N_2 is the equilibrium density of species 2 when species 1 is either absent or sufficiently rare to be neglected.

Even if species 1 cannot establish when rare and species 2 is at equilibrium, it still may be able to persist locally under some conditions. The population persistence niche describes these cases. For a location to have conditions within the persistence niche of species 1, there should be some values of N_1 and N_2 that allow species 1 to resist extinction.

To understand the effects of establishment and persistence on range limits, we study an expanded version of the Holland and DeAngelis (2009) model that allows self-interference (i.e., when individuals of a given species are at high density, they interfere with each other, reducing the impact of interactions with other species). Following a suggestion in Fishman and Hadany (2010), we use a Beddington-DeAngelis functional response (Beddington 1975; DeAngelis et al. 1975), a generalization of the type II functional response used by Holland and DeAngelis (2009). There are formal derivations of the Beddington-DeAngelis formulation from mechanistic assumptions for both mutualistic (Fishman and Hadany 2010) and predator/prey interactions (Beddington 1975; Huisman and De Boer 1997). For the predation case, there is substantial support for the Beddington-DeAngelis model over simpler

alternative functional responses (Skalski and Gilliam 2001). Beddington-DeAngelis models have been used to describe competition mediated by behavioral interference among competitors. For example, de Villemereuil and López-Sepulcre (2011) used this model to characterize competition between two predator species (the Trinidadian guppy *Poecilia reticulata* and Hart’s killifish *Rivulus hartii*), each of whom interferes with the foraging of the other.

The model is as follows:

$$\frac{dN_2}{dt} = N_2 \left(\underbrace{\frac{g_2 - d_2 N_2}{}}_{\text{logistic growth}} + \underbrace{\frac{c_2 N_1}{1 + c_2 b_1 N_1 + c_2 h_1 N_2}}_{\text{benefit to 2}} - \underbrace{\frac{q_2 N_1}{1 + q_2 e_2 N_2 + q_2 a_1 N_1}}_{\text{harm to 2}} \right)$$

$$\frac{dN_1}{dt} = N_1 \left(\underbrace{\frac{g_1 - d_1 N_1}{}}_{\text{logistic growth}} + \underbrace{\frac{c_1 N_2}{1 + c_1 b_2 N_2 + c_1 h_2 N_1}}_{\text{benefit to 1}} - \underbrace{\frac{q_1 N_2}{1 + q_1 e_1 N_1 + q_1 a_2 N_2}}_{\text{harm to 1}} \right) \quad (4a)$$

In the absence of biotic interactions, the populations show logistic growth (Gabriel et al. 2005) with a density-independent growth rate of g_i and a density-dependent mortality rate of d_i . These terms could represent the effect of the abiotic environment or diffuse interactions with species other than the focal pair of species including other competitors, consumers, or mutualists. The equilibrium density (“carrying capacity”) of species i in the absence of species interactions (N_i) is g_i/d_i when $g_i > 0$. If the density-independent growth rate of species i is negative, then $N_i = 0$.

Interactions between species 1 and 2 are described by terms denoted *benefit to i* and *cost to i*. For species 1 to be a prey and species 2 a predator, species 1 would receive only harm, whereas species 2 would receive a benefit ($q_1 > 0, c_2 > 0$, but $c_1, q_2 = 0$). This could also formally describe parasitism, such as brood parasitism. The quantity c_i is the maximum benefit species i can obtain from species j per unit time, while q_i is the maximum harm species i can receive from species j per unit time (Huisman and De Boer 1997). The parameters b_2, h_2, e_1 , and a_2 express how the impact of species 2 on species 1 saturates when either species 1 or species 2 is at high densities (see Table 1 for a full list of symbols).

A biological example may help illustrate how species interactions are represented in this model. Van Gils and Piersma (2004) describe a prey species (the blue mussel *Mytilus edulis*). The mussel, species 1, is consumed by a predatory shorebird, the red knot *Calidris canutus*, species 2. The term “harm to 1” in Eq. (4a) describes the cost that blue mussels incur from predation. The

term q_1 describes the maximum per capita harm that blue mussels can receive from predation by an individual red knot. In our model, individual red knots attack individual mussels most efficiently when both species are scarce. Red knots take time to digest captured mussels, so are less efficient consumers (per mussel) at high densities of blue mussels. High values of e_1 correspond to blue mussels experiencing less harm from predation (per capita) when blue mussels are abundant. Red knots

aggregate into dense flocks of tens of thousands of individuals, and individual red knots interfere with each other’s foraging, reducing the harm that red knots inflict on mussels, a process expressed by high values of a_2 .

We model the effect of the interaction on the red knot using the “benefit to 2” term in Eq. (4b). Individual red knots benefit most from individual blue mussels when both species are at low density (modeled by the term c_2). High values of b_1 denote limitations on the benefits red knots can obtain from high mussel densities, while high values of h_1 indicate that interference among knots limits their ability to benefit from consuming prey.

The establishment niche

A location will be a part of species 1’s establishment niche if species 1 can increase in number when it is rare and the other species is at its equilibrium density when alone (denoted N_2). From Eq. (4), this requires

$$g_1 + \frac{c_1 N_2}{1 + c_1 b_2 N_2} - \frac{q_1 N_2}{1 + q_1 a_2 N_2} > 0. \quad (5)$$

Inequality 5 states that species 1’s establishment niche depends on the balance of species 1’s intrinsic growth rate (g_1) and the net effect of species 2 on the growth rate of species 1 (the remaining terms). There are two ways interactions might

alter the establishment niche of species 1, relative to what might be expected considering just the fundamental niche alone. The first is range expansion. This occurs in locations that are otherwise unsuitable to species 1 ($g_1 < 0$) when species 1 benefits sufficiently from its interaction with species 2 to increase in number when rare (inequality 5 holds when $g_1 = 0$). The second possibility is range contraction. This occurs when the environment is inherently suitable to species 1 ($g_1 > 0$), but the effect of species 2 is sufficiently harmful to prevent species 1 from increasing in numbers when rare (inequality 5 is false when $g_1 = 0$).

Because the establishment niche depends only on the ability of species 1 to increase in numbers when rare, considerably less information is needed to model the establishment niche than is needed to model the complete dynamical consequences of biotic interactions. As a result, inequality 5 omits many aspects of the interactions between the two species. Specifically, the establishment niche has the same form for species 1 when it benefits from a commensalist, a prey species, or a mutualist. The establishment niche also has the same form, whether species 1 is harmed by an amensalist, a predator, or a competitor.

The effect of biotic interactions on the establishment niche (inequality 5) reflects how both species respond to the environment. By implication, the effects of biotic interactions on range limits can be strongly mediated by the environment, at least when range limits reflect local conditions. Thus, inequality 5 includes the equilibrium density of species 2 (N_2) and the ability of species 1 to increase in number when it is rare (g_1). Even when biotic interactions strongly shape species 1's range limits, climatic variables might provide an excellent predictor of a focal species' current range limit. The influence of biotic interactions on the establishment niche of species 1 increases with (1) increasing N_2 , (2) increasing maximum benefit or harm (c_1 or q_1), or (3) decreasing mutual interference among individuals of species 2 on their interactions with species 1 (b_2 , a_2).

The population persistence niche

It is difficult to analyze the persistence niche because this requires one to take into account the full gamut of nonlinear interactions and feedbacks a species has on itself, mediated through other species. Using phase portraits, we do find that some of the interactions we consider do not allow species 1's persistence niche to extend past its establishment niche. For other interaction types, the population persistence niche can extend past the establishment niche, at least when special conditions are met. When the persistence niche extends past the establishment niche, changing interaction type typically changes the range of environments where species can persist.

To determine where species 1 can persist, it is helpful to characterize the zero net growth isoclines (conditions where $dN_i/dt = 0$), for each species (which we denote by I_1 and I_2 , respectively). Isoclines for species 1 can take on four distinct shapes (Fig. 2a–d; see Appendix 1 for details). When the interaction has no effect on species 1, I_1 is a vertical line (Fig. 2a). When species 1 benefits from the interaction, I_1 starts at $N_1 = g_1/d_1$, then increases monotonically as N_1 increases (Fig. 2b). When the interaction harms species 1, I_1 can take on one of two shapes. When the following inequality is true:

$$e_1 g_1 q_1 (1 - a_2 g_1) \leq d_1 \quad (6)$$

I_1 decreases monotonically as N_1 increases (Fig. 2c). When inequality 6 is false (Fig. 2d), I_1 increases and reaches a local maximum (Arditi and Ginzburg 1989; Huisman and De Boer 1997). See Appendix S1 for the derivation of Eq. (6). I_2 can take on similar shapes to I_1 , but with the N_1 and N_2 axes switched.

In the case that the focal species benefits from the interaction ($c_1 > 0$, $q_1 = 0$), its persistence niche can only extend past its establishment niche when the two species are mutualists. This occurs when high densities of species 1 benefit species 2, which, in turn, benefits species 1 enough to allow species 1 to persist when otherwise it would disappear (Fig. 3a). A familiar example of this phenomenon would be an obligate pollination mutualism such as that between a yucca and its yucca moth pollinators (Pellmyr 2003). Yuccas cannot establish in the absence of yucca moths and only persist if yucca moths are also present and in sufficient numbers. When species 2 is a commensal (b) or prey (a), in the above model, high densities of

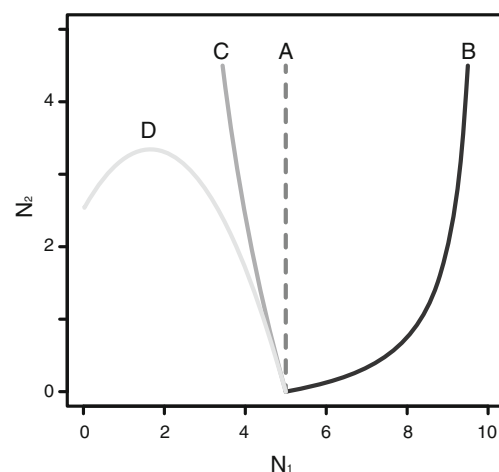
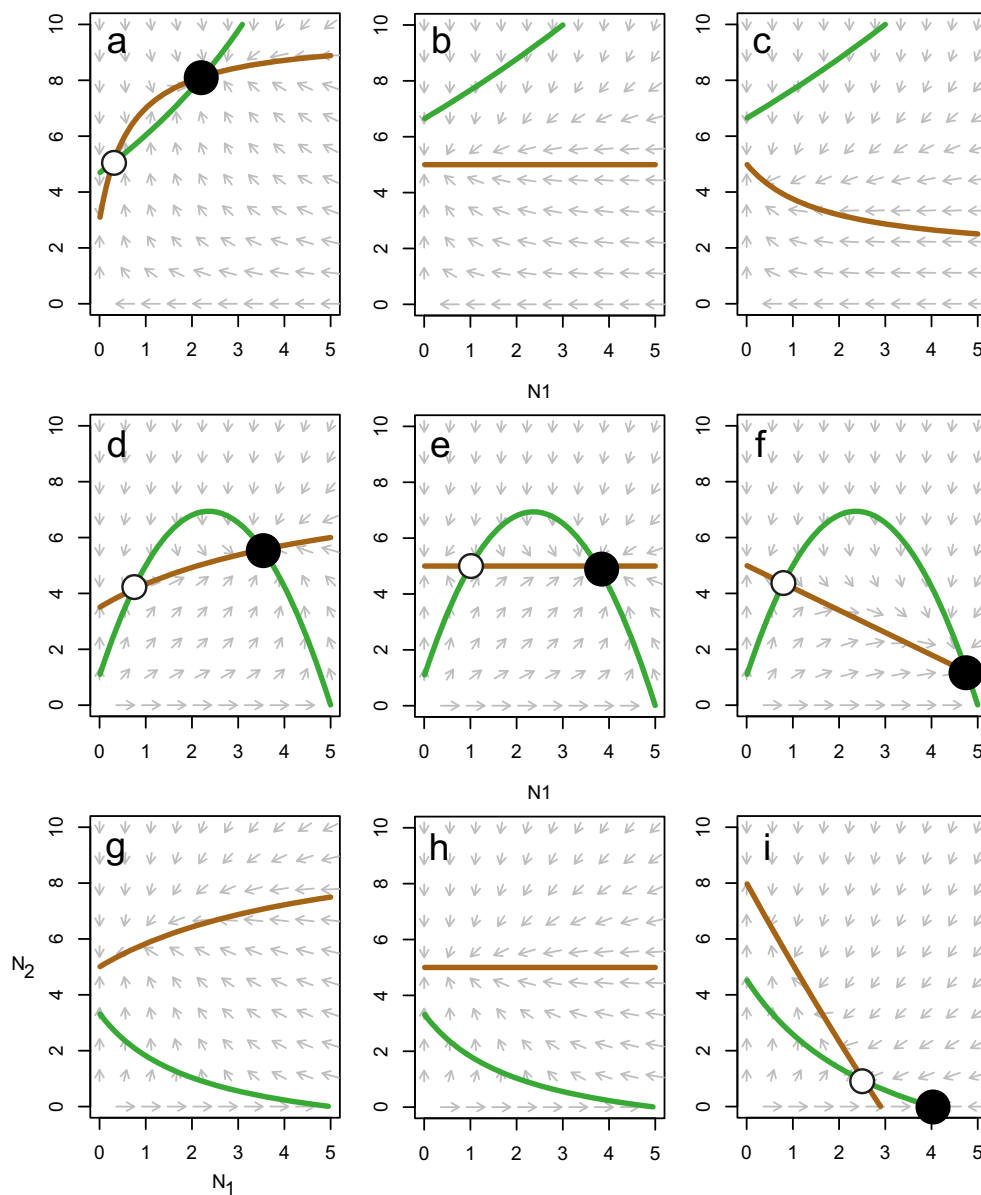


Fig. 2 An illustration of the four qualitatively different isoclines produced by our model for species 1. The isocline for interactions with no effect on species 1, i.e., amensalism (0–) or commensalism (0+) (A). The isocline for interactions that benefit species 1 (B). The isocline for interactions that inflict limited harm on species (C). The isocline with a local maximum from interactions that harm species 1 (D)

Fig. 3 Phase portraits where species 1 cannot increase in number when rare. These illustrations include I_1 (light green), I_2 (dark brown), the change in population density (gray arrows), stable equilibria where species 1 can persist (black circles), and unstable equilibria (open circles). The top row illustrates interactions that benefit species 1 including mutualism (a), commensalism (b), and predation (c; species 1 is predator). Species 1 can persist when both species are mutualists; species 1 will not persist in the commensalism or predation cases. The center row illustrates interactions that harm species 1 when I_1 increases, reaches a local maximum then decreases. It is possible for species 1 to persist when species 2 is a predator (d), an amensalist (e), or a competitor (f). The bottom row illustrates interactions that harm species 1 when I_1 increases monotonically. Species 1 cannot persist when species 2 is a predator (g) or an amensalist (h). It is possible for species 1 to persist in the competition case (i)



species 1 cannot feedback to increase the density of species 2 (in the former case, because by definition, species 2 has no effect on species 1, and in the latter case, because predators typically depress the abundance of their prey, and so, increases in predator numbers should indirectly provide a negative rather than positive feedback on predator growth). As a result, the environment is no more favorable to species 1 (as mediated through species 2) when it is at high densities, than it is when species 1 is at low density.

The observations in the previous paragraph can be demonstrated with a phase portrait. When species 1 benefits from species 2, the establishment niche can only extend past the persistence niche when the phase portrait has three characteristics. First, since the location must be unsuitable for species 1 in the absence of species 2, I_1 must not have a N_1 intercept

when $N_1 > 0$. Second, since species 1 cannot increase in numbers when rare, I_1 must be above I_2 on the N_2 axis (see Appendix 2 for a full explanation). Third, there must be an equilibrium where both N_1 and $N_2 > 0$; this implies that I_1 and I_2 cross in the positive quadrant of the phase portrait. We can meet these criteria when both species are mutualists (Fig. 3a). We cannot meet these criteria when species 2 is a prey species or a commensalist since, in these cases, I_1 must be above I_2 at the N_2 axis and the isoclines move apart to the right of the N_2 axis (Fig. 3b, c).

When the focal species is harmed by biotic interactions ($c_1 = 0$, $q_1 > 0$), our model predicts several cases where the establishment niche extends past the persistence niche. When I_1 reaches a local maximum, species 1 can persist at high densities even if it establishes when species 2 is a predator,

an amensalist, or a competitor (Fig. 3d–f). Oro et al. (2006) provide a concrete example of a system where this could occur in a predator–prey system. Nesting colonies of Audouin's gulls are subject to predation by the larger yellow-legged gull. When a colony has a low density of Audouin's gulls, this species is subject to severe predation. When a colony has a higher density of Audouin's gulls, this species is better able to resist predation, and so, it will have a higher fitness.

When species 1 is harmed by species 2 and I_1 is strictly decreasing (Fig. 2c), the persistence niche can only extend past the establishment niche when species 1 and 2 compete. This occurs when high densities of species 1 depress the density of species 2 sufficiently to allow species 1 to persist. In other words, species 1 indirectly benefits itself, by reducing the numbers of its competitor. In this case, I_2 starts above I_1 at the N_2 axis, and both isoclines may converge as N_1 increases (Fig. 3i). By contrast, when species 2 is an amensalist or a predator, I_2 starts above I_1 at the N_2 axis, but the isoclines do not converge as N_1 increases. As a result, there is no equilibrium with species 1 present (Fig. 3g, h).

The observations we have made about the persistence niche when species 1 is harmed can be demonstrated using phase portraits. When species 1 is harmed by the interaction, the population persistence niche of species 1 will only extend past its establishment niche when three criteria are met. First, the location must be suitable to species 1 in the absence of species 2. On a phase portrait, this implies that I_1 crosses the N_1 intercept when $N_1 > 0$. Second, species 1 must be unable to increase in numbers when rare. This is true when I_1 is below I_2 at the N_2 axis (see Appendix 1 for an explanation). Third, there must be at least one positive equilibrium; this implies that I_1 and I_2 cross in the positive quadrant. For some phase portraits, this positive equilibrium is unstable, while the equilibrium at $(N_1, 0)$ is stable. These conditions can be met when I_1 has a local maximum when species 2 is an amensalist, a predator, or a competitor (Fig. 3d–f). When I_1 decreases monotonically, they can only be met when species 2 is a competitor (Fig. 3i). Changing between predation, amensalism, and competition typically changes whether I_2 is increasing, flat, or decreasing (Fig. 3d–f). This changes the conditions under which the two isoclines intersect, changing the conditions where the focal species can persist.

The stress gradient hypothesis and range limits

The analyses we present helps to clarify which ecological mechanisms shape range limits across environmental gradients. Consider the stress gradient hypothesis which asserts that facilitation (mutualistic interactions) is stronger

in stressful environments, while competitive interactions are stronger in benign environments (Callaway et al. 2002). As a result, stress gradients are believed to produce range limits in benign environments (Louthan et al. 2015), but it is not clear if it can produce other types of range limits.

To analyze this, we present a graphical analysis of where a focal species can establish, when stress depresses the density-independent growth rate of the focal species (g_1 ; solid line Fig. 4a) and changes interactions from harmful to beneficial (dotted line Fig. 4b). A stress gradient can produce range limits in benign environments (Fig. 4c). However, it can produce many other types of range limits, including range limits in harsh environments (Fig. 4d). Expansion of a species' range limit into harsh environments (Fig. 4e) or a "hole" in a species' distribution, with the species relying on beneficial interactions to survive in stressful environments.

The conditions under which a focal species can establish are even more complex when we consider the details of the Beddington-DeAngelis model we have analyzed. Figure 5 considers a relatively simple scenario where the equilibrium density of the nonfocal species (N_2) decreases with x . This detail is enough to make the impact of the nonfocal species on the focal species ($f_1(N_1 \rightarrow 0, N_2)$) curve substantially (Fig. 5a). In the portion of x where species 2 is harmful, much of this curvature arises because the impact of the nonfocal species saturates when N_2 is large. In the portion of the environmental gradient where the nonfocal species is beneficial, its impact switches from highly beneficial to negligible. This is the result of the joint influence of two processes. The nonfocal species is becoming more beneficial, while the density of the nonfocal species that is N_2 is declining towards 0.

Because the impact of the nonfocal species curves along the environmental gradient, there can be many boundaries of the focal species' establishment niche. Recall that each boundary corresponds to an intersection of g_1 and $f_1(N_1 \rightarrow 0, N_2)$ (Fig. 5b). In some cases, the boundaries look like those described above. For example, in Fig. 5c, the focal species can only establish in the most benign environments (small values of x ; gray background). Other potential range limits are much more complex. In Fig. 5d, competition keeps the nonfocal species from establishing in the middle of the environmental gradient, though the species can establish at larger values of x or at smaller values of x . The same gap in the distribution appears in Fig. 5e, but in addition, the distribution of the focal species expands into harsher environments because of facilitation from the nonfocal species. In Fig. 5f, the focal species cannot establish anywhere in its fundamental niche though it can establish in more stressful environments because of facilitation. The ultimate distribution of the focal species can of course be even more complex because it may be able to persist

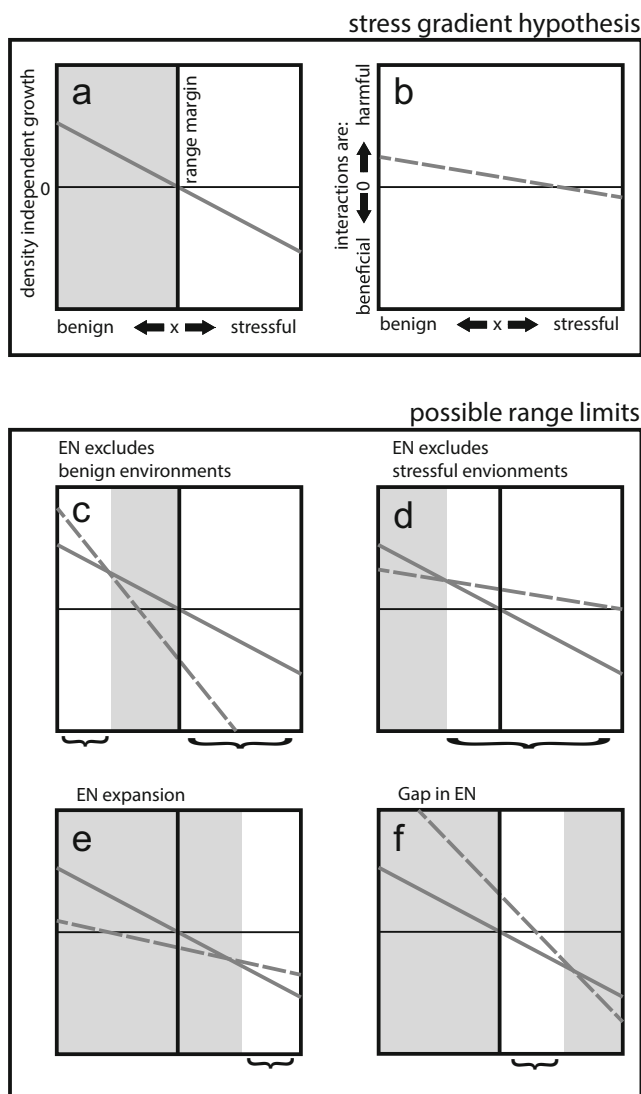


Fig. 4 An analysis of range limits that can emerge from the stress gradient hypothesis. **a** A gradient where environments to the left are benign and environments to the right are progressively more stressful. As a result, the density-independent growth rate of the focal species declines as x increases (*solid line*). The *gray portion* of this panel represents the species' establishment niche in the absence of biotic interactions. The stress gradient hypothesis asserts that as we move from benign to stressful environments, the effects of biotic interactions switch from harmful to beneficial (**b**, *dashed line*). This mechanism can affect a species' distribution by altering its establishment niche (EN). This happens when biotic interactions switch Eq. (3) from negative to positive or vice versa. Graphically, this occurs when the line representing density-independent growth crosses the line representing the effects of biotic interactions. Depending on where exactly biotic interactions switch from harmful to beneficial, they can remove stressful environments from the EN (**c**), remove benign environments from the EN (**d**), expand the species' EN (**e**), or expand a species' distribution past some gap. Under some parameter values and some initial conditions, the species can persist in portions of the environmental gradient indicated with a horizontal “}”

in environments where it cannot establish. Such areas are denoted by the dashed lines in Fig. 5c–f.

Discussion

Ecologists seek to anticipate when biotic interactions affect the presence of individual species (Pigot and Tobias 2013; Sexton et al. 2009; Wisz et al. 2013). When they do so, they confront a tremendous diversity and complexity of biotic interactions. This, in turn, makes it difficult to understand which interactions will most influence species' range margins and why. Our key finding is that seemingly disparate biotic interactions often have comparable effects on species' establishment niches; by implication, they may have similar effects on species' range margins. This emphasizes that information on a diverse range of interaction types could improve predictions of species' range margins and highlights the information needed to make those predictions.

Our most salient result is the value in asking a single, simplified question: Can a species increase in numbers when it is rare and the rest of the community is at equilibrium? If the focal species can increase when rare, the environment in question is a part of the establishment niche and we should expect the species to be present. If it cannot increase in numbers when rare, we should either expect it to be absent or expect its presence to be contingent on initial conditions (and thus be sensitive to history), because of the presence of positive feedbacks of a species upon itself. This question is particularly valuable because well-studied trends in nature such as the stress gradient hypothesis (Callaway et al. 2002; Louthan et al. 2015) can produce very different range limits (Fig. 4). Though community ecologists have long recognized the value in investigating the ability of species to increase in density when rare, particularly in the context of coexistence among competing species (Adler et al. 2007; Chesson 2000b; MacArthur and Levins 1964), this insight is absent from many contemporary reviews of species' interactions and species' range margins (Araújo and Rozenfeld 2014; Holt 2009; Sexton et al. 2009; Wisz et al. 2013).

Our results suggest similarities in how biotic interactions shape species' range margins. The focal species' ability to increase in numbers when rare is comparably affected when it interacts with a mutualist, a commensal, or a prey. Similarly, the focal species' ability to increase in numbers when rare is comparably affected when it interacts with a predator, an amensalist, or a competitor; all make life worse for the focal species. We can also use this approach when the type of interaction changes as we move along an ecological gradient. A focal species may have a range limit at the edge of its establishment niche even if the species it is interacting with switches from being a competitor to an amensalist as we move across other sites in its distribution. We expect these results to generalize to other models of biotic interactions because invasion criteria generalize across many models (Chesson 2000b; Holt 2009). We have only studied pairwise species interactions, but invasion criteria can also be used to determine where

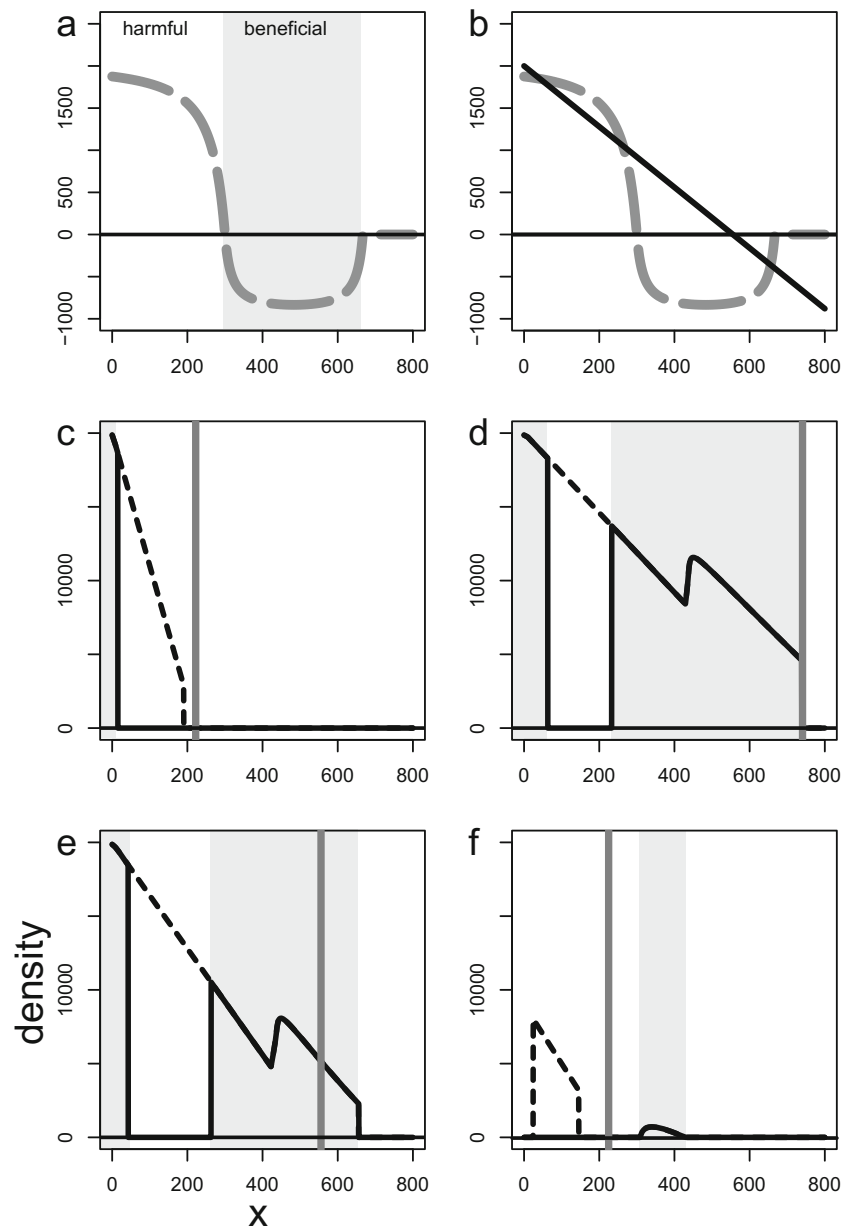


Fig. 5 When competition and mutualism are mediated by Beddington-DeAngelis functional responses, stress gradients can lead to complex range margins. **a** This is easiest to study by considering when the focal species can establish. Even assuming that the density of species 2 changes linearly with x , the impact of species 2 curves (dashed line; $f_1(N_1 \rightarrow 0, N_2)$). As a result, $f_1(N_1 \rightarrow 0, N_2)$ may cross g_1 (black line) several times (**b**). Each of these crossings represents a boundary of the establishment niche of the focal species. **c–f** The panels show how this can produce dramatic differences in environments where the focal species can establish (gray shading), relative to the boundary of its fundamental niche (dark gray line). The black solid line denotes the equilibrium abundance of the focal species when it can establish. The black dashed

line represents the equilibrium abundance of the focal species when initial conditions are favorable to it. These environments are in the focal species' persistence niche. The only difference between **c–f** is how g_1 changes with x . **c** $g_1 = -4x + 2000$. **d** $g_1 = -3.6x + 2000$. **e** $g_1 = -2.7x + 2000$. **f** $g_1 = -9x + 900$. To model the switch from competition to mutualism, we assume that for small x , $c_1 = -0.01x + 3$, until the point where $c_1 = 0$. Past this point, we assume that $c_1 = 0$, but $q_1 = 0.01x - 3$. We used a similar procedure to model the switch from competition to facilitation for species 2. In all simulations, $g_2 = -1.5x + 1000$, $d_1 = d_2 = 0.1$, $b_2 = 0.0005$; all other parameter values were set to 0.001

a species is expected to be present (regardless of initial conditions) in a community consisting of multiple species. As such, invasion analyses like those we present can be used to identify a species' establishment niche in multispecies communities. See Chesson (2000b) for a discussion of when the presence of

a species in a community depends primarily on its ability to invade when rare.

Generalizing our observations regarding the persistence niche would be more difficult. Our analytic results provide some insight into why species 1's persistence niche

is identical to its establishment niche when species 2 is a prey or a commensalist. When species 2 is a predator or amensalist, the persistence niche can only extend past the establishment niche under somewhat restrictive conditions, namely that the isocline for species 1 increases then decreases (implying that inequality 6 is false). There are empirical examples of a persistence niche emerging from mutualism (Dickie et al. 2010; Parker 2001), competition (Hirota et al. 2011; Staver and Levin 2012), and predator-prey interactions (Gascoigne and Lipcius 2004), so this is certainly plausible, but maybe, it is an exception rather than the norm for range limits. This strikes us as a significant question for future studies. To study the persistence niche of a focal species in a multispecies community, it makes more sense to search for a (locally) stable equilibrium where the focal species is present. This approach could be particularly important when competition is intransitive (Soliveres et al. 2015). In this case, there are conditions where a deterministic model would predict that different species will, in turn, cyclically decrease in density to the point where they can go extinct (May and Leonard 1975). As a result, a focal species may ultimately be present, or absent, depending on initial conditions and stochastic effects. However, to understand these cases, it may be necessary to study the effects of stochasticity on population persistence, an important topic beyond the scope of the current manuscript.

We believe that there is much to learn about the importance of the persistence niche at large spatial scales. On one hand, phenomena that are crucial for biogeography such as dispersal often limit the impact of a species' persistence niche on its range margin (Hutson et al. 1985; Shurin et al. 2004); if during the history of a given location, all species initially are rare, being drawn from a sparse rain of colonists from a broader landscape, there is little scope for positive density dependence and impacts on the local environment to exert an influence. However, species might be able to persist in changed circumstances, where they established in different conditions, and became common enough to lead to positive density-dependent feedbacks. There are tantalizing examples in the literature of large-scale influences of species' persistence niches on current distributions. For example, Hirota et al. (2011) and Staver et al. (2011) show that there are large portions of several continents that can be either forest or grassland depending on the history of a particular site. Such sites may be a part of the persistence niche of grassland-associated species and forest-associated species, even though the presence of one species frequently excludes the others. Our work shows that the persistence niche has a limited effect on species' range margins across a swath of well-studied models, but a rigorous assessment of its importance will require a careful integration of empirical systems with theoretical studies.

Our goal has been to understand how biotic interactions and the abiotic environment affect species' range margins. To accomplish this, we used a fairly general model of biotic interactions, and we assumed that biotic interactions happen at a small scale relative to the environmental gradient of interest (Eqs. (4a) and (4b)). We have represented the effects of the environment by studying the growth rate when species are rare in the absence of biotic interactions, the carrying capacities of species, and by recognizing that the consequences of species interactions frequently depend on indirect influences of the environment. This is, at most, a starting point because it provides a simplified representation of space, a representation that can miss outcomes that emerge from more realistic models (Dieckmann et al. 2000). In particular, we have simplified the effects of dispersal among locations, though our results provide insights into dispersal's effects. One of the best-studied mechanisms of dispersal is passive diffusion (i.e., a random walk). This can be modeled by adding a diffusion term to our dynamical models. So long as the region under consideration can support some individuals of each species and so long as the environmental variables change smoothly as we move from one location to another, the analyses we present should hold approximately when dispersal is weak (Cosner 2005). This is because the equilibrium solution of our model typically approaches the solution with no dispersal. Weak dispersal would imply that each species has a small but positive density throughout our study region; in practice though, it would rarely be detected past the range limits we predict. Stronger dispersal could result in the presence of the species past the range limits we predict; sufficiently strong dispersal might change the predictions of our model, say by eliminating a species from across the study region. Our results would also hold if individuals of each species dispersed to maximize their fitness, so that the abundance of individuals was governed by an ideal free distribution (Cosner and Winkler 2014; Kimbrell and Holt 2005). A full synthesis of models that represent space more realistically is a much larger task, particularly because existing models tend to focus on a few interactions, notably predation and competition (Bever et al. 2010; Bolker and Pacala 1999; Chesson et al. 2005; Dieckmann et al. 2000; Snyder and Chesson 2004). Different interactions can operate across different spatial scales, and integrating these into single population models can be.

There are tremendous challenges in identifying the effects of species' interactions on species' range margins. Our work indicates that a diverse range of biotic interactions can have a major effect on species' range margins and that these effects can be predicted by answering a few basic questions, questions that transcend traditional classifications of interaction types (Fig. 1). These results indicate a need to better study some interactions, notably mutualism, commensalism, and amensalism, and the need to study how climate and biotic interactions combine to shape species' range margins.

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