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Acknowledgements

Abstract

30

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'

35   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. This insight leads to counterintuitive conclusions. Notably we often

40   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

45   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

50   comparison of when biotic interactions affect distributions.

Introduction

55   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

60   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

65   abundance of the other species; Figure 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

70   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

75 predation (Holt and Barfield, 2009) and mutualism (Afkhami 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

80 because a species' response to other species vary 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

85 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 isn't exactly

90 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

95   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

100   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

105   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.

110   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

Holland and DeAngelis (2009) that uses a single set of equations to organize many

familiar models of pairwise biotic interactions (Beddington 1975; de Villemereuil

115   and López-Sepulcre 2011; Holland and DeAngelis 2009; Holland and DeAngelis

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

120   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

125   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

130   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

135   "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).

140   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

145   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

150   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

155   longer time scales, 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

160   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 b 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 terms)*.* 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

185   model (see Equations 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

190   individual locations are sufficiently small that they can be considered internally

spatially homogeneous (but still large enough to ignore demographic stochasticity).

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

195   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

200   represented either explicitly or implicitly, just so long as dispersal is weak. We

revisit the effect of dispersal in the Discussion.

Biotic interactions at a single location

205   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):

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

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

210   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

215   to occur in locations within its fundamental niche. These are by definition environments where its density independent growth rate is positive:

$$g_1 > 0 \text{ (2).}$$

When the two species interact, species 1 should be present in locations where conditions are inside its establishment niche, which means species 1

220   increases in numbers (and hence establishes) when it is rare, and species 2 is present at equilibrium (formally, we define "rarity" as the limit: $\lim N_1 \rightarrow 0$):

$$g_1 + f_1\left(N_1 \rightarrow 0, \widehat{N}_2\right) > 0. \text{ (3)}$$

Here $\widehat{N}_2$ is the equilibrium density of species 2 when species 1 is either absent, or sufficiently rare to be neglected.

225   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.

230   To understand the effects of establishment and persistence on range limits we study an expanded version of the Holland-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-

235   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

240   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

245   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:

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

250

$$\frac{dN_2}{dt} = N_2 \left(\underbrace{g_2 - d_2 N_2}_{logistic\ growth} + \underbrace{\frac{c_2 N_1}{1 + c_2 b_1 N_1 + c_2 h_1 N_2}}_{benefit\ to\ 2} - \underbrace{\frac{q_2 N_1}{1 + q_2 e_2 N_2 + q_2 a_1 N_1}}_{harm\ to\ 2} \right) \text{(4b)}$$

In the absence of biotic interactions, the populations show logistic growth

255   (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 ($\widehat{N}_i$) is g_i/d_i

260   when $g_i>0$. If the density independent growth rate of species i is negative, then $\widehat{N}_i=0$.

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

265　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 expresses how the impact of species 2 on species 1 saturates when either species 1 or species 2 are at high densities see Table 2 for a full list of terms.

270　　　　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 equation 4a describes the cost that blue mussels incur from predation. The term q_1 describes

275　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

280　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"

285 term in Equation 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

290

A location will be a part of species 1's establishment niche if species 1 can

increase in numbers when it is rare and the other species is at its equilibrium

density when alone (denoted $\widehat{N}_2$). From equation 4, this requires:

295      $$g_1 + \frac{c_1 \widehat{N}_2}{1 + c_1 b_2 \widehat{N}_2} - \frac{q_1 \widehat{N}_2}{1 + q_1 a_2 \widehat{N}_2} > 0. \ (5)$$

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

300 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 numbers when

rare (inequality 5 holds when $g_1 = 0$). The second possibility is range contraction.

305   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

310   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

315   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

320   equilibrium density of species 2 ($\widehat{N}_2$) and the ability of species 1 to increase in numbers 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 $\widehat{N}_2$; (2) increasing

325   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

330   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

335   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

340   denote by I_1, I_2 respectively). Isoclines for species 1 can take on four distinct shapes

(Figure 2 a-d; See Appendix 1 for details). When the interaction has no effect on

species 1, I_1 is a vertical line (Figure 2 a). When species 1 benefits from the

interaction, I_1 starts at $N_1 = g_1/d_1$, then increases monotonically as N_1 increases

(Figure 2 b). When the interaction harms species 1, I_1 can take on one of two shapes.

345   When the following inequality is true:

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

I_1 decreases monotonically as N_1 increases (Figure 2 c). When inequality 6 is false

(Figure 2 d), I_1 increases, reaches a local maximum (Arditi and Ginzburg 1989;

Huisman and De Boer 1997). See appendix S1 for the derivation of Equation 6. I_2 can

350   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

355   would disappear (Figure 3 a). 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

360   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

365   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

370 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

375 phase portrait. We can meet these criteria when both species are mutualists (Figure 3 a). 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 (Figure 3 b,c).

When the focal species is harmed by biotic interactions ($c_1=0$, $q_1>0$), our

380 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 establish when species 2 is a predator, an amensalist, or a competitor (Figure 3 d, e, f). Oro et al. (2006) provide a concrete example of a system where this could occur in a predator-prey system. Nesting colonies of

385 Audouins 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 Andouin'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 (Figure 2

390   c), 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

395   (Figure 3 i). 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 (Figure 3 g, 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

400   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

405   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 $(\widehat{N}_1, 0)$

is stable. These conditions can be met when I_1 has a local maximum when species 2

is an amensalist, predator or competitor (Figure 3 d, e, f). When I_1 decreases

410   monotonically, they can only be met when species 2 is a competitor (Figure 3 i).

Changing between predation, amensalism and competition typically changes

whether I_2 is increasing, flat or decreasing (Figure 3 d, e, 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) are 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 isn't 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 Figure 4 a) and changes interactions from harmful to beneficial (dotted line Figure 4 b). A stress gradient can produce range limits in benign environments (Figure 4 c). However, it can produce many other types of range limits, including range limits in harsh environments Figure 4 d. Expansion of a species' range limit into harsh environments Figure 4 e 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 non-focal species $(\widehat{N}_2)$ decreases with x. This detail is enough to make the impact of the non-focal species on the focal species $(f_1(N_1 \rightarrow 0, \widehat{N}_2))$ curve substantially (Figure 5 a). In the portion of x where species 2 is harmful, much of this curvature arises because the impact of the non-focal species saturates when $\widehat{N}_2$ is large. In the portion of the environmental gradient where the non-focal species is beneficial, its impact switches from highly beneficial to negligible. This is the result of the joint influence of 2 processes. The non-focal species is becoming more beneficial, while the density of the non-focal species is $\widehat{N}_2$ is declining towards 0.

Because the impact of the non-focal 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 $f_1(N_1 \rightarrow 0, \widehat{N}_2)$ Figure 5 b. In some cases, the boundaries look like those described above. For example, in Figure 5 c the focal species can only establish in the most benign environments (small values of x; grey background). Other potential range limits are much more complex. In Figure 5 d competition keeps the non-focal 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 Figure 5 e, but in

455   addition the distribution of the focal species expands into harsher

environments because of facilitation from the non-focal species. In Figure 5 f

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

460   complex because it may be able to persist in environments where it cannot

establish. Such areas are denoted by the dashed lines in Figures 5 c-f.

Discussion

Ecologists seek to anticipate when biotic interactions affect the presence of

465   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'

470   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

475   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

480   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 (Figure 4). Though community ecologists have long recognized the value in investigating the ability of species to increase in

485   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).

490   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, commensal or prey. Similarly, the focal species' ability to increase in numbers when rare is comparably affected when it interacts with a predator, amensalist or competitor; all make life

495   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

500 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 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

505 identify a species' establishment niche in multispecies communities. See Chesson

(2000) 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

510 persistence niche is identical to its establishment niche when species 2 is 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

515 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

520 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).

525   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

530   persistence niche at large spatial scales. On the 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

535   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

540   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

545   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

550   general model of biotic interactions, and we assumed that biotic interactions happen

at a small scale relative to the environmental gradient of interest (Eqations 4a and

4b). We have represented the effects of the environment by studying the growth

rate when rare of species in the absence of biotic interactions, the carrying

capacities of species, and by recognizing that the consequences of species

555   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

560   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

565   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 were 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 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 (Figure 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.

590   **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

595   on a species. So, for example, (+ -) indicates an interaction from which species 1

benefits and species 2 is harmed (i.e. predation).

Fig. 2 An illustration of the four qualitatively different isoclines produced by our

model for species 1. (a) The isocline for interactions with no effect on species 1 i.e.

Amensalism (0 -), or commensalism (0 +). (b) The isocline for interactions that

600   benefit species 1. (c) The isocline for interactions that inflict limited harm on species

D) The isocline with a local maximum from interactions that harm species 1.

Fig. 3 Phase portraits where species 1 cannot increase in numbers when rare. These

illustrations include I_1 (light green), I_2 (dark brown), the change in population

605   density (grey 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

610   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

615   species 1 to persist in the competition case (i).

Fig. 4 An analysis of range limits that can emerge from the stress gradient hypothesis. Panel (a) represents a gradient where environments to the left are

620   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 grey 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

625   interactions switch from harmful to beneficial (Panel b, dashed line). This mechanism can affect a species' distribution by altering its establishment niche (EN). This happens when biotic interactions switch equation 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.

630   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

635   indicated with a horizontal "}".

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

640   the density of species 2 changes linearly with x the impact of species 2 curves

(dashed line; $f_1\left(N_1 \rightarrow 0, \widehat{N}_2\right)$). As a result, $f_1\left(N_1 \rightarrow 0, \widehat{N}_2\right)$ may cross g_1 (black

line) several times b). Each of these crossings represents a boundary of the

establishment niche of the focal species. Panels c-f shows how this can produce

dramatic differences in environments where the focal species can establish (grey

645   shading), relative to the boundary of its fundamental niche (dark grey line). The

black solid line to 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 the panels c-f is

650   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,

655   all other parameter values were set to 0.001.

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
$\widehat{N}_i$	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)

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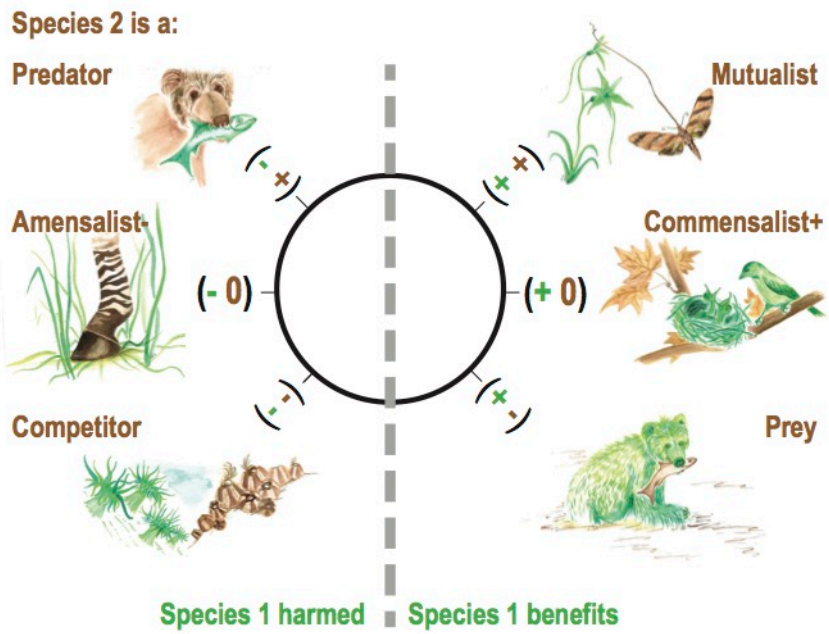
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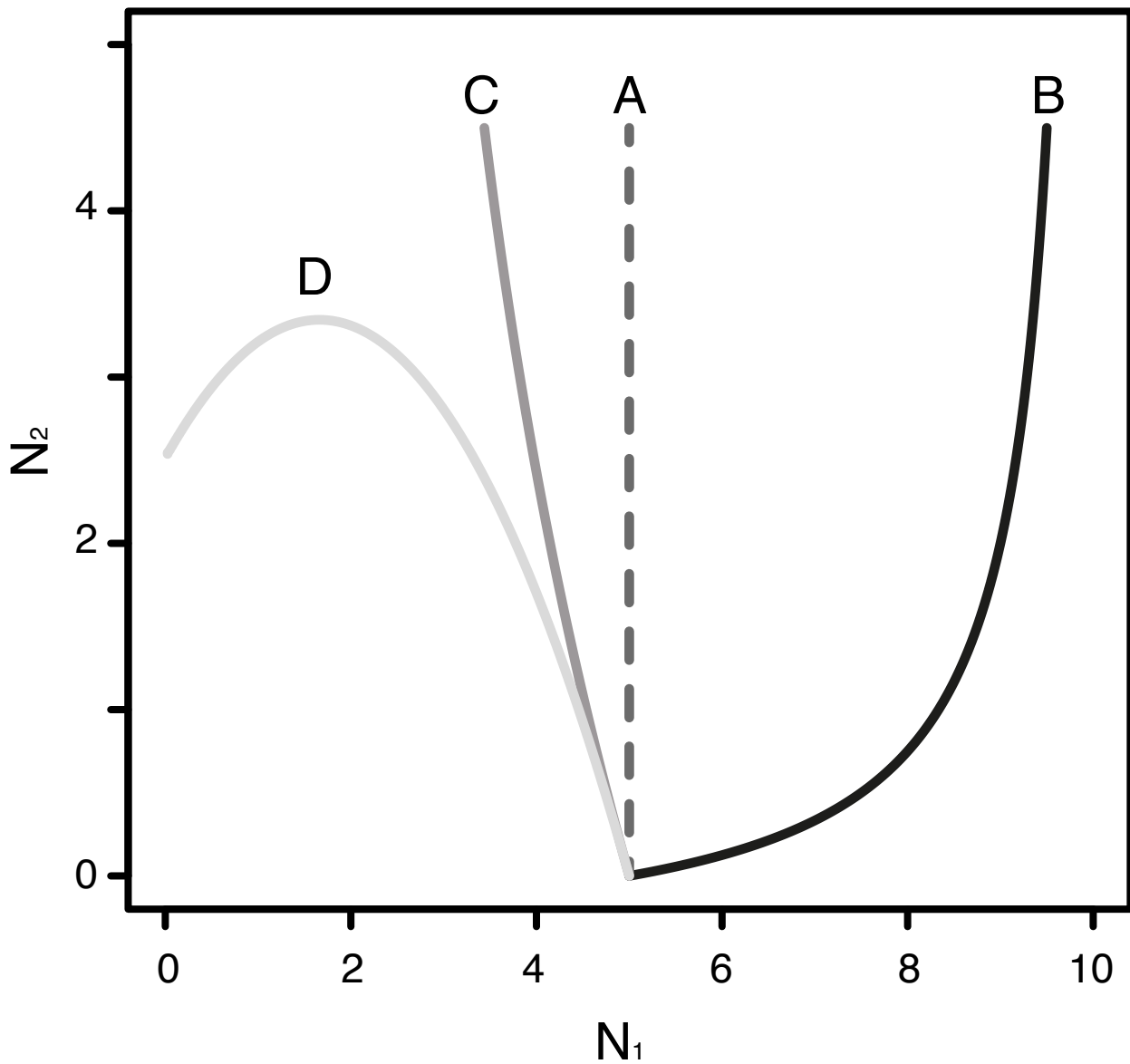   Naturalist 170:297--304

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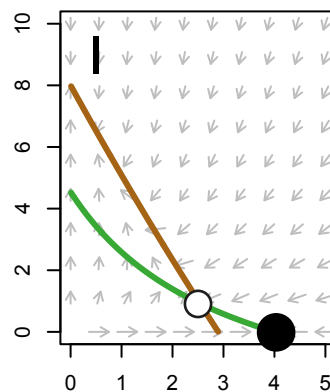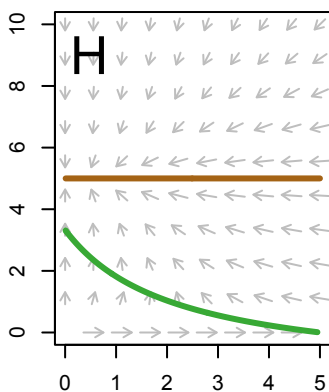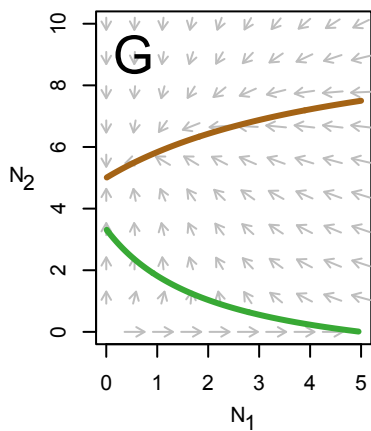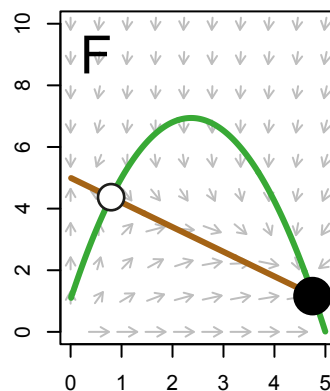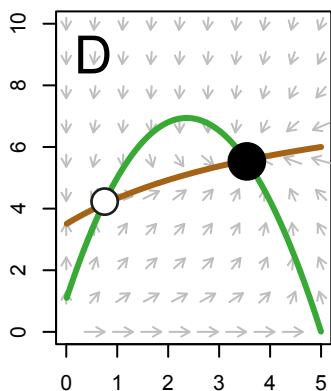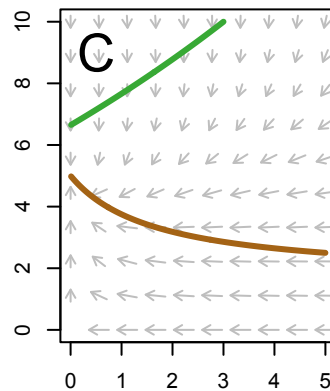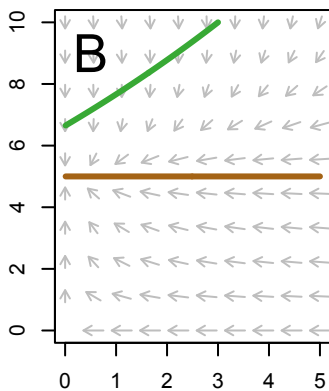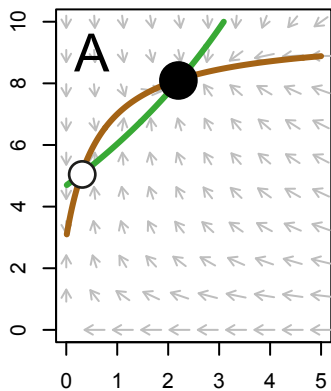   798

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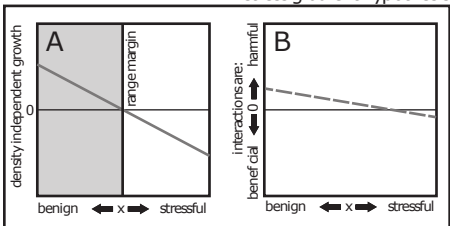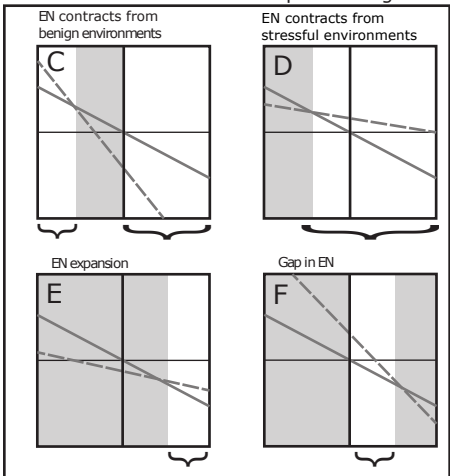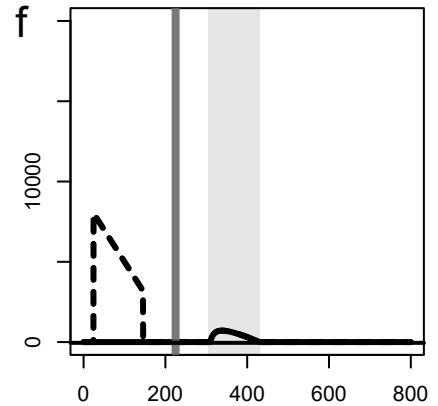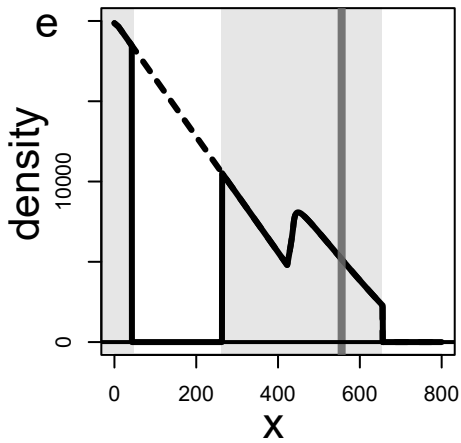
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Species 2 is a:

Predator

Amensalist-

Competitor

Mutualist

Commensalist+

Prey

(- +)

(- 0)

(- -)
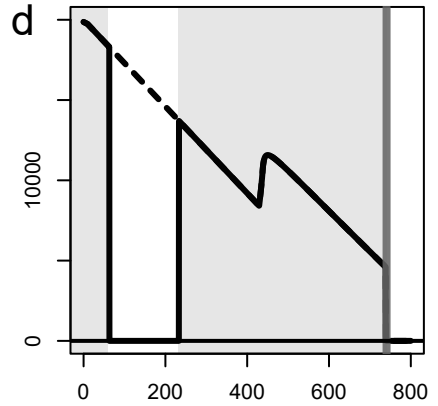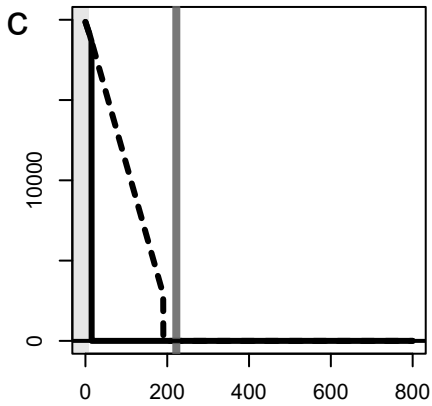
(+ +)

(+ 0)

(+ -)

Species 1 harmed ┆ Species 1 benefits
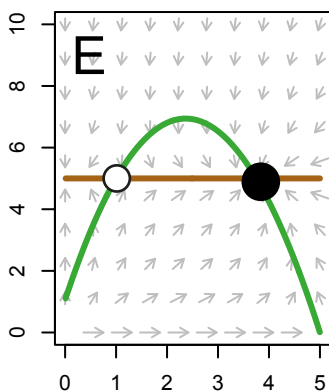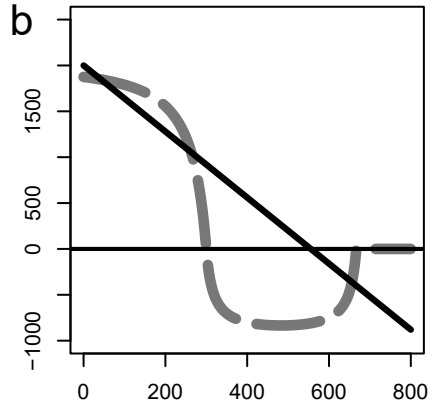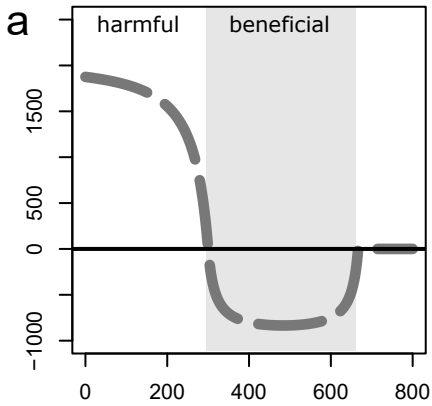
stress gradient hypothesis

possible range limits

Online Appendix 1: phase portraits

analysis of isoclines

The isocline of species 1 (I_1), can be found by setting equation 4a equal to zero, after setting irrelevant parameters to zero. I_1 can take on several shapes, as a result it is useful to distinguish shapes that arize when species 2 has no effect on species 1, species 2 harms species 1 and species 2 benefits species 1.

Neutral interactions

When species 2 has no effect on species 1 the isocline for species 1 can be found by setting $q_1 = c_1 = 0$ in equation 4a, giving an isocline of:

$$N_1 = \frac{g_1}{d_1} \tag{S.1}$$

This is as a vertical line figure 2 A.

Harmful interactions

So long as we restrict ourselves to positive population densities $(N_1, N_2 > 0)$, I_1 can have two shapes when species 1 is harmed by species 2. I_1 will either be a strictly

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decreasing function figure 2 C or a function that increases initially, reaches a local maximum then decreases figure 2 D. In this subsection we explain how these two shapes emerge and how to distinguish them. To find I_1 take equation 4a, set $c_1 = 0$ then solve for $dN_1/dt = 0$ giving:

$$I_1 : N_2 = -\frac{(g_1 - d_1 N_1)(e_1 q_1 N_1 + 1)}{q_1(a_2(g_1 - d_1 N_1) - 1)} \tag{S.2}$$

To determine the shape of I_1 predicted by S.2, we first note that this function is a ratio of two polynomials. This type of function known as a rational function can be plotted using information on its asymptotes, and intercepts (Forbes et al., 1989).

To find the N_2 intercept set $N_1 = 0$. equation S.2 reduces to:

$$N_2^{intercept} = -\frac{g_1}{q_1(a_2 g_1 - 1)}. \tag{S.3}$$

Equation S.2 includes two N_1 intercepts, which can be found by identifying values which make the numerator of equation S.2 equal to 0. The first intercept can be found by solving $g_1 - d_1 N_1$ giving:

$$N_1^{intercept_1} = \frac{g_1}{d_1} \tag{S.4}$$

in this section we are concerned with cases where harm inflicted by species 2 eliminates species 1. As a result we need only consider cases where $N_1^{intercept_1} > 0$

2

(i.e. species 1 could be present in the absence of species 2).

The second intercept can be found by solving $e_1 q_1 N_1 + 1 = 0$ giving:

$$N_1^{intercept_2} = \frac{-1}{e_1 q_1} \tag{S.5}$$

We have already assumed that $e_1, q_1 > 0$, as a result $N_1^{intercept_2}$ is always less than zero.

Equation S.2 has a single, vertical asymptote when species 1 is harmed by species 2 (i.e. when $q_1 > 0$). This can be found by finding values where the denominator of S.2 is equal to 0. By re-arranging we obtain:

$$Vertical\,Asymptote : N_1 = \frac{a_2 g_1 - 1}{d_1 a_2} \tag{S.6}$$

To understand the shapes of I_1, it is important to note that the vertical asymptote always has an opposite sign as the $N_2^{intercept}$. This is because the vertical asymptote is the same sign as $a_2 g_1 - 1$ (we have assumed that d_1 and a_2 are never negative), while $N_2^{intercept}$ will be the opposite sign as $a_2 g_1 - 1$ (q_1, a_2 and g_1 are presumed to be non-negative).

Next, we check for diagonal asymptotes (Forbes et al., 1989). To do this we first expand the numerator and denominator of equation S.2 giving:

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$$I_1 : N_2 = -\frac{\overbrace{-d_1 e_1 q_1 N_1^2}^{\text{largest power}} +g_1 e_1 q_1 N_1 - d_1 N_1 + g_1}{\underbrace{-q_1 a_2 d_1 N_1}_{\text{largest power}} +q_1 a_2 g_1 - q_1} \tag{S.7}$$

In the numerator the largest power of N_1 is N_1^2 while in the denominator the largest power of N_1 is N_1^1. Such a rational function has a diagonal asymptote (Forbes et al., 1989). The slope of this asymptote can be found by comparing the leading coefficients associated with the largest power in the numerator and denominator:

$$N_2 = -\frac{-d_1 e_1 q_1 N_1^2}{-q_1 a_2 d_1 N_1} \tag{S.8}$$

simplifying this gives:

$$N_2 = -\frac{e_1 N_1}{a_2}, \tag{S.9}$$

equation S.9 indicates that the slope of the diagonal asymptote is $-e_1/a_2$. Since $e_1, a_2 \geq 0$, the slope is never positive.

As we move from small values of N_1 to larger values, the intercepts always occur in the same order because $N_1^{intercept_2} < 0$, $N_2^{intercept}$ occurs at 0, while $N_1^{intercept_1} > 0$. This observation is illustrated in figure S.1 where $N_1^{intercept_2}$ is a triangle, $N_2^{intercept}$ is a square and $N_1^{intercept_1}$ is a circle.
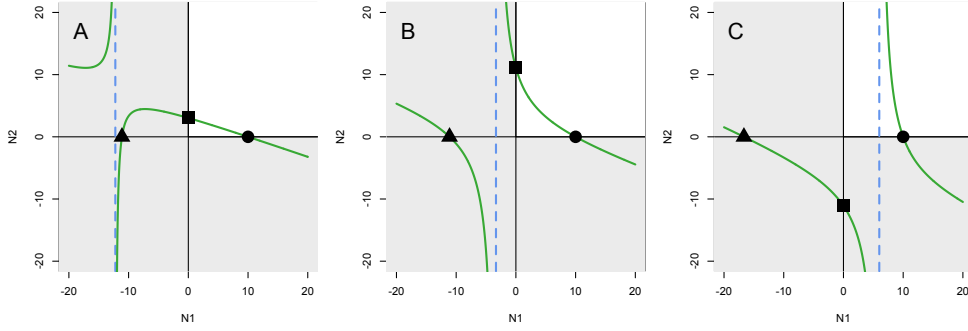
Figure S.1: Ilustrations of three qualitatively different shapes possible for I_1 (green), including the vertical asymptote (blue dotted line), $N_1^{intercept_2}$ (triangle), $N_2^{intercept}$ (square) and $N_1^{intercept_1}$ (circle). The positive quadrants of each plot (i.e. the portions where $N_1, N_2 > 0$) are white. Portions in grey represent other quadrants, and hence population densities we would not observe in nature.

We can distinguish three qualitatively different shapes for I_1 based on the position of the vertical asymptote. In case A, the asymptote occurs at a lower N_1 value than any of the intercepts (figure S.1 A). Since the vertical asymptote is less than

55 0 ($N_1 < 0$), the $N_2^{intercept}$ is positive ($N_2 > 0$). So, starting slightly the right of the vertical asymptote, I_1 starts at negative infinity, moves through $N_1^{intercept_2}$, then $N_2^{intercept}$, down through $N_1^{intercept_1}$ and approaches its diagonal asymptote as N_1 becomes large. In case B, the asymptote occurs between $N_1^{intercept_2}$ and $N_2^{intercept}$ (figure S.1 B). Here again, $N_2^{intercept} > 0$, because the vertical asymptote is less than

60 0. To the right of the vertical asymptote I_1 begins at positive infinity, then moves down through $N_2^{intercept}$, $N_1^{intercept_1}$ then approaches its diagonal asymptote as N_1 gets large. In case C, the vertical asymptote occurs between $N_2^{intercept}$ and $N_1^{intercept_1}$. Here $N_2^{intercept}$ is less than zero because the vertical asymptote is greater than zero. As a result, starting from to the right of the vertical asymptote, I_1 decreases, crosses

65 $N_1^{intercept_1}$, then approaches the diagonal asymptote as N_1 gets large.

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In each of the cases listed above, the portion of I_1 to the left of the vertical asymptote has no direct effect on the population dynamics. In cases A and B, this branch only occurs for values of $N_1 < 0$. In case C this branch never reaches feasible population densities where $N_1, N_2 > 0$. Starting at $N_1 = -\infty$, the branch is close to its diagonal asymptote, moves through $N_1^{intercept_2}$ (at this point $N_1 < 0$), I_1 then moves through $N_2^{intercept}$ (at this point $N_2 < 0$), I_1 then approaches negative infinity as it nears the vertical asymptote.

Does I_1 have local maxima?

In the previous section we described the behavior of I_1 in coarse terms. We did not determine if it has local turning points (maxima or minima), which could lead to an isocline with a local maximum, which in turn alters population dynamics. To investigate this later question we consider the derivative of I_1 (i.e. equation S.2) with respect to N_1:

$$\frac{dI_1}{dN_1} = -\frac{e_1 d_1^2 a_2 N_1^2 q_1 - 2e_1 d_1 a_2 g_1 N_1 q_1 + 2e_1 d_1 N_1 q_1 + e_1 a_2 g_1^2 q_1 - e_1 g_1 q_1 + d_1}{q_1(-d_1 a_2 N_1 + a_2 g_1 - 1)^2}.$$

(S.10)

For there to be a local maximum somewhere on I_1, $\frac{dI_1}{dN_1}$ must be equal to zero. $\frac{dI_1}{dN_1} = 0$ occurs when the numerator of equation S.12 is equal to zero. The numerator of equation S.12 can be expressed as a quadratic equation (i.e. it can be expressed

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as $\alpha N_1^2 + \beta BN_1 + \kappa$, where α, β, and κ are constants). Quadratic equations have no more than two solutions. As a result I_1 has no more than two turning points.

We can break I_1 into a branch to the left to its asymptote and a branch to the right of its asymptote. It is impossible for one such branch to have two turning points. If one branch did, then there would need to be an inflection point between the two turning points. This would imply that there was a location where the d^2I_1/d^2N_1. However the second derivative of I_1 is:

$$\frac{d^2I_1}{d^2N_1} = -\frac{2d_1(e_1q_1(1 - a_1g_1) + d_1a_2)}{q_1(a_2(g_1 - d_1N_1) - 1)^3}, \tag{S.11}$$

and since no value of N_1 makes the numerator equal to zero, there are no inflection points.

I_1 can have a local maximum in the positive quadrant in the case illustrated in figure S.1 A. In this case, the right branch of I_1 starts at $-\infty$ reaches a single minimum then decreases as it approaches its diagonal asymptote (figure S.2 A). To determine if this maximum occurs in the positive quadrant, determine if $dI_1/dN_1 > 0$ when I_1 crosses into this quadrant by substituting $N_1 = 0$ into equation S.12, giving:

$$\frac{dI_1}{dN_1} = -\frac{e_1a_2g_1^2q_1 - e_1g_1q_1 + d_1}{q_1(a_2g_1 - 1)^2}. \tag{S.12}$$

This expression will be positive when $e_1a_2g_1^2q_1 - e_1g_1q_1 + d_1$, which can be re-arranged to obtain:
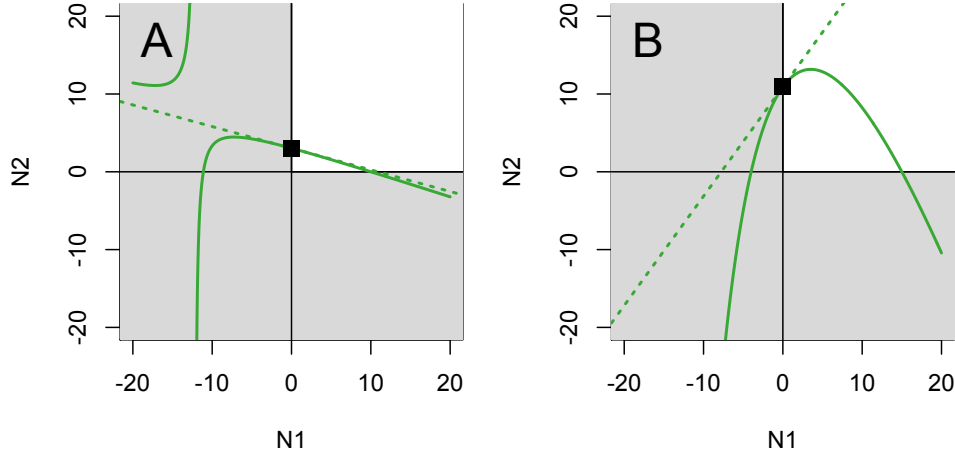
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Figure S.2: The relationship between the shape of I_1 (green solid line) in the positive quadrant (white portions of the chart) and its derivative (the green dotted line) at its N_2 intercept (square). In A)

$$e_1 g_1 q_1 (1 - a_2 g_1) > d_1 \qquad \text{(S.13)}$$

If inequality S.13 is true, I_1 has a local maximum in the positive quadrant figure S.2 B. If inequality S.13 is fase, I_1 decreases monotonically in the positive quadrant (figure S.2 A). Inequality S.13 is simply the reverse of inequality 6 in the main text.

We can also use inequality S.13 to test for local maxima in the other two cases illustrated in (figure S.1 B and C). In both cases, each branch of I_1 is strictly decreasing (implying both that $dI_1/dt < 0$ at $N_1 = 0$ and that I_1 has no local maxima). We know that each branch is strictly decreasing because each branch starts at $+\infty$ and finishes at $-\infty$ (figure S.1 B and C). This is only possible if each branch has zero turning points. If a single branch had a single turning point, it could not go

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from $+\infty$ to $-\infty$. We have already established that a single branch has no more than one turning point.

If we ignore a_2, inequality S.13 is easy to interpret, e_1, q_1 and g_1 all increase the left-hand side of this expression making an isocline with a local maximum more likely; high values of e_1 indicate that the harm species 2 inflicts on species 1 saturates when the density of species 1 is high. High values of g_1 indicate a high density independent growth rate for species 1; while high values of q_1 indicate that species 2 can dramatically harm species 1. High values of d_1 indicate strong density dependence for species 1, this makes an isocline with a local maximum less likely. High values of a_2 indicate that the the harm species 2 inflicts on species 1 saturates at high densities of species 2. Increasing $a_2 > 0$ makes a isocline with a local maximum likely. When $a_2 > 0$, increasing g_1 can make it either easier or harder to get a local maximum, depending on the size of g_1 versus g_1^2. Large values of g_1 make $e_1 g_1 q_1 (1 - a_2 g_1)$ negative, eliminating the maximum.

Interactions that benefit species 1

When biotic interactions benefit species 1, the isocline for species 1 can be found by taking equation 4a, setting $q_1 = 0$ then solving for $dN_1/dt = 0$ and re-arranging, giving:

$$N_2 = -\frac{(c_1 h_2 N_1 + 1)(g_1 - d_1 N_1)}{c_1(b_2(g_1 - d_1 N_1) + 1)} \tag{S.14}$$

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The N_2 intercept of equation S.14 is:

$$I_1(N_1 = 0) : -\frac{g_1}{c_1(b_2 g_1 + 1)}. \tag{S.15}$$

Equation S.14 has two N_1 intercepts given by:

$$N_1 = -\frac{1}{c_1 h_2}, \tag{S.16}$$

which is always negative and:

$$N_1 = \frac{g_1}{d_1} \tag{S.17}$$

which is negative when species 1 cannot persist in the absence of species 2.

Equation S.14 approaches a vertical asymptote, so long as $b_2 > 0, d_1 > 0$. This asymptote is given by:

$$N_1 = \frac{g_1 + 1/b_2}{d_1}, \tag{S.18}$$

Note that this asymptote is equal to equation S.17 plus a positive constant. As such, the vertical asymptote is to the right of this intercept on a phase portrait.

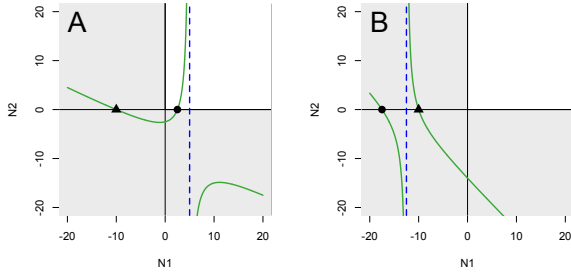Equation S.14 also has a slant asymptote with a slope of $-h_2/b_2$. This asymptote

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Figure S.3: Graphs of potential shapes for I_1.

always has a negative slope.

For I_1 to cross into the positive quadrant, the vertical asymptote must be to right of both N_1 intercepts (figure S.3 A). In this case the left most branch of I_1 starts at $N_2 = +\infty$ decreases, crosses the left most N_1 intercept, arrives at a turning point, crosses the right most intercept and increases towards $N_2 = +\infty$. This branch of I_1 can only reach the positive quadrant after crossing through the right most asymptote. As a result I_1 is increasing in the positive quadrant, or entirely absent from this quadrant. The right branch of I_1 does not reach the positive quadrant.

It is mathematically possible for the vertical asymptote to occur between the two N_1 intercepts (figure S.3). In this case the left and right branches of I_1 start at $N_2 = +\infty$ and decrease towards $N_2 = -\infty$. For this scenario to occur, both N_1 intercepts must be negative. Neither branch crosses into the positive quadrant. No other shapes occur because the vertical asymptote must be to the right of at least one of the intercepts.

Parameter values

Table S1. List of parameter values used in Figure 3 organized by panel.

	A	B	C	D	E	F	G	H	I
g_1	-9.50	-6.00	-9.50	5.00	5.00	5.00	5.00	5.00	4.00
g_2	5.00	3.00	5.00	5.00	3.50	5.00	5.00	5.00	8.00
c_1	2.00	2.00	2.00	0.00	0.00	0.00	0.00	0.00	0.00
c_2	0.00	10.00	0.00	0.00	1.00	0.00	0.00	1.00	0.00
q_1	0.00	0.00	0.00	5.00	5.00	5.00	5.00	5.00	2.00
q_2	0.00	0.00	2.00	0.00	0.00	0.80	0.00	0.00	3.00
b_1	0.20	0.15	0.20	0.20	0.20	0.20	0.20	0.20	0.20
b_2	0.03	0.06	0.03	0.03	0.03	0.03	0.03	0.03	0.03
h_2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
h_1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
f_1	0.00	0.00	0.30	0.00	0.00	0.00	0.00	0.00	0.01
f_2	0.00	0.00	0.00	0.01	0.01	0.01	0.14	0.14	0.14
e_1	0.00	0.00	0.00	1.00	1.00	1.00	0.00	0.00	0.00
e_2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
d_1	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
d_2	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

Online Appendix 2: the relationship between invasion and phase portraits

On a phase portrait, we can check if species 1 can increase in numhers when rare by examining the N_2 axis, which represents conditions where species 1 is rare enough to be essentially absent. Along the N_2 axis $I_2 = \hat{N}_2$ (the equilibrium density of species 2 in the absence of species 1), while the point where I_1 crosses the N_2 axis is the boundary between densities of species 2 where species 1 increases in numbers when rare $dN_1/dt > 0$, and densities at which species 1 decreases in numbers when rare $dN_1/dt < 0$.

When species 1 benefits from species 2, a value of I_1 above $\hat{N}_2$ indicates that when species 1 is rare, the benefit it obtains from species 2 is too low for species 1 to increase in numbers when rare. As a result species 1 cannot invade. A value of I_1 below $\hat{N}_2$ indicates that species 1 could increase in numbers, even if species 2 were less dense than $\hat{N}_2$. Thus, when species 1 benefits and I_1 is above I_2 at the N_2 axis, species 1 cannot invade. When I_1 is below I_2, species 1 can invade.

When species 1 is harmed by species 2, a value of I_1 above I_2 on the N_2 axis indicates that when species 1 is rare, it could resist extinction even if it were harmed by more individuals of species 2 than would be present at equilibrium ($dN_1/dt = 0$ at a point where $N_2 > \hat{N}_2$). Conversely, a value of I_1 below I_2 on the N_2 axis indicates that when species 1 is rare it could not resist extinction even if it were harmed by fewer individuals of species 2 than would be present at equilibrium ($dN_1/dt = 0$ at a

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point where $N_2 > \hat{N}_2$). Thus, when species 1 is harmed by species 2 and I_1 is above I_2 at the N_2 axis, species 1 can invade. When I_1 is below I_2, species 1 cannot invade.

References

Forbes, S., Morton, M., and Rae, H., 1989. Skills in Mathematics, volume 2. Forbes, Morton and Rae.

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