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The community context of species' borders: ecological and evolutionary perspectives

Ted J. Case, Robert D. Holt, Mark A. McPeek and Timothy H. Keitt

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Species distributional limits may coincide with hard dispersal barriers or physiological thresholds along environmental gradients, but they may also be influenced by species interactions. We explore a number of models of interspecific interactions that lead to (sometimes abrupt) distribution limits in the presence and absence of environmental gradients. We find that gradients in competitive ability can lead to spatial segregation of competitors into distinct ranges, but that spatial movement tends to broaden the region of sympatry between the two species, and that Allee effects tend to sharpen these boundaries. We generalize these simple models to include metapopulation dynamics and other types of interactions including predator–prey and host-parasite interactions. We derive conditions for range limits in each case. We also consider models that include coevolution and gene flow and find that character displacement along environmental gradients can lead to stable parapatric distributions. We conclude that it is essential to consider coevolved species interactions as a potential mechanism limiting species distributions, particularly when barriers to dispersal are weak and environmental gradients are gradual.

T. J. Case, Dept of Biology, Univ. of California at San Diego, La Jolla, CA 92093-0116, USA (case@biomail.ucsd.edu). – R. D. Holt, Dept of Zoology, Univ. of Florida, Gainesville, FL 32611, USA. – M. A. McPeek, Dept of Biological Sciences, Dartmouth College, Hanover, NH 03755, USA. – T. H. Keitt, Integrative Biology, Univ. of Texas, Austin, TX 78712, USA.

A common observation about life is that species have geographical distributions that are more or less spatially confined. Biogeography attempts to make sense of these distributional patterns by studying both present day environmental and ecological factors determining fitness and populational persistence, and the historical origins and subsequent movements of individuals. One obvious feature that prevents species from spreading uniformly over space is the existence of physical barriers to dispersal. The association between broad scale biogeographic provinces and major barriers to dispersal, (e.g. oceans for terrestrial forms, or strong cross currents for ocean forms with pelagic larval dispersal, Gaylord and Gaines 2000) is a persistent reminder of the role of barriers in determining community composition. The fact that South Africa has a fauna that is different from, say, Argentina, depends on the important role of barriers in preventing colonization of species. The common observation that introduced species can sometimes thrive in foreign terrain, once transported there, indicates that present day distributions are not determined solely by environmental conditions, but that barriers to dispersal, both past and present, are responsible for some degree of the regional and global patterning of the biota.

Over time, however, even hard barriers to dispersal may be breached. Oceanic volcanic islands (e.g. Hawaii, the Galapagos, or the Canary Islands) that have never been connected to another region are eventually colonized by a wide range of terrestrial species. Furthermore, given the ability of populations to adapt to local

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conditions by natural selection, it is not immediately obvious why some hard barriers to dispersal could not eventually be breached. A mountain range may form a barrier to dispersal for a lowland species. However, populations at elevations at the base of the mountain may adapt to survive there. What prevents a sequence of such episodes of local adaptation from eventually allowing the populations to march across the mountain? One explanation is that there may not be sufficient genetic variation in the population for natural selection, given the intensity of selection. As shown by Holt and Gomulkiewicz (1997), adaptation in marginal populations requires the availability of genetic variation simply for population persistence in the absence of immigration. Sometimes such variation will be absent (Bradshaw 1991). It is hard to imagine that sufficient genetic variation exists to allow a mouse to evolve to both live in the ocean and then to colonize the next continent on the other side. A barrier to dispersal is one that must be defined in terms of the existing genetic variability of the focal species, the severity of the selection gradient over space, and the time scale in question.

Another reason that local adaptation may fail to advance the spatial spread of a population is because it is opposed by net gene flow from a more populous distributional center where different genotypes may be favored. Theoretical studies suggest that this antagonism between local adaptation and the detrimental effects of gene flow can produce a stable limited geographic range even in the absence of any barriers to dispersal (Kirkpatrick and Barton 1997, Case and Taper 2000, Antonovics et al. 2001, but see Barton 2001 and Gomulkiewicz et al. 1999 for analyses of the countervailing positive effect of gene flow upon local adaptation via the infusion of genetic variation). If the environment varies smoothly and gradually over space, and dispersal coefficients are not too high (which would cause high gene flow), and given adequate genetic variation, these models predict that a species range could eventually expand across space. As we discuss further below, however, the capacity for unlimited spread is greatly diminished in the presence of interspecific interactions.

In this paper, we review and synthesize the ways that biotic interactions may produce stable range limits. We focus on situations where the species boundary is stable or quasi-stable but not associated with obvious barriers to dispersal. This restriction on "stable" is important because the geographic ranges of species with low movement rates and slow population growth may not yet be at equilibrium with respect to past climate change and continuing habitat alteration. Fossil records over the late Pleistocene and Holocene for tree and mammal species show slow spatial dynamics as they respond to glacial cycles (Davis 1986, Graham 1986, Woods and Davis 1989, Gear and Huntley 1991, Martin and Fairbanks 1999). Recent human modifications to the landscape and the transport of organisms allows unique mixing of faunas that may not have existed even just a century ago. For instance, Nowak (1971) cataloged 28 examples of recent range expansions of plants and animals primarily in Europe. In a majority of cases, the range expansion could be attributed to some human-caused alteration of the landscape creating new habitat or avenues for dispersal. Finally, habitat loss through human alteration has caused many species' ranges to retract to selected corners of their former range where human impacts have been less (Lomolino and Channell 1995). A study of these present day ranges, in the absence of historical information about their former extents would provide a misleading and biased impression of the role of climate, interspecific interactions, and evolutionary dynamics in determining range limits.

Nonevolutionary models

Two competitors

Range limits with an environmental gradient

Interspecific competition has the capacity to produce abrupt range limits in either homogeneous or heterogeneous space, although by different scenarios. Roughgarden (1979) was one of the first to model range limits in the context of the Lotka–Volterra competition equations. The carrying capacity of the two competitors was assumed to vary inversely over one-dimensional space x; competitor A's carrying capacity $K_A(x)$ monotonically declines going from left to right, while competitor B's carrying capacity monotonically increases over the same range. In the absence of the other competitor, each species' equilibrium density over space would follow its K curve. Movements were not explicitly considered and interspecific competition coefficients (a) were assumed to be constants independent of spatial position or population density. Even if interspecific competition is less than intraspecific competition, one species can competitively exclude its competitor in some portion of space where it has a sufficiently higher carrying capacity, giving rise to more or less sharp range limits depending on the magnitude of the interspecific effects and the steepness of the K gradients.

As a simple example, assume that two Lotka–Volterra competitors have equal competition coefficients and that their carrying capacities vary in opposite directions along a gradient. Coexistence at any point along the gradient requires that $1/\alpha > K_1(x)/\ K_2(x) > \alpha$, where α is the competition coefficient, and $K_i(x)$ is the carrying capacity of competitor i at gradient position x. For illustrative purposes, assume that $\alpha \leq 1$, and that the two competitors are specialized to opposite ends of the gradient, with linear but opposite relations of spatial position to carrying capacity, as follows:

$K_1(x) = K' - gx$, and $K_2(x) = gx$, for $0 \le x \le K'/g$. The gradient has length K'/g, and in the absence of competition each species can occupy the entire gradient. If both species are present, competition can restrict each species' range size, with a zone of overlap in the middle of the gradient. After substitution into the expression for coexistence, the width W of the overlap zone is $W = (K'/g)\,(1-\alpha)/(1+\alpha)$. Competition shrinks the range edge of, say, species 1, from K'/g to $K'/(g(1+\alpha))$. Competition coefficients near unity imply a narrow overlap zone, and a range limit for species 1 that is strongly displaced from the limit observed in the absence of competition.

More mechanistic models of exploitative competition explicitly include the dynamics of resources. In stable environments and without interference, for a single limiting resource, the single winning competitor is the one that can persist at the lowest level of the shared resource, denoted R* (Tilman 1982). This measure of competitive dominance integrates many different aspects of a species' biology. Given two competing species, along a gradient there can be abrupt shifts in dominance leading to sharply defined parapatric distributions for several distinct mechanistic reasons. For instance, the two species' relative rankings with respect to their abilities to acquire the resource may change along the gradient. Or, alternatively, their relative capacities for converting acquired resource into offspring could shift. Finally, their relative abilities to escape density-independent mortality factors in the environment (e.g. severe abiotic conditions or generalist predators) may vary along the gradient. To show that competition produces a species border does provide a useful explanation at one level – we know that removing the competitor would permit a range expansion for the remaining species – but does not fully explain the border, because there can be a wealth of underlying mechanistic explanations for the shift in dominance along the gradient.

None of the models sketched above explicitly included movements across space and how they might affect the ranges and zones of overlap. Within the context of continuous time and space, interactions and random-walk type movements can be combined in a reaction-diffusion model.

$$\frac{\partial N_i(x,t)}{\partial t} = D_i \frac{\partial^2 N_i(x,t)}{\partial x^2} + f_i(x, N_i, \ldots, N_n) \qquad (1)$$

The first term on the right governs movement, and the second term gives the local population dynamics. Extension to an additional spatial dimension y is accomplished by adding a term: $D_i \partial^2 N_i / \partial y^2$. An example based on two-species Lotka–Volterra competition is

$$\frac{\partial N_i(x,t)}{\partial t} = D_i \frac{\partial^2 N_i(x,t)}{\partial x^2} + \frac{r_i N_i(x,t)}{K_i(x)} \times [K_i(x) - N_i(x,t) - \alpha_{ij} N_j(x,t)] - d_i N_i(x,t) \qquad (2)$$

Here, D_i is the diffusion coefficient and d_i is density-independent mortality. Compared to nonspatial models, one effect of movements here is to increase the zone of sympatry between the species, because marginal sink populations that would otherwise become extinct if closed to movements, are sustained by immigration from adjacent populations with higher growth rates. Another feature of Eq. 1, which is general for any function $f(x, N_i, N_j)$, is that we can solve for the spatial steady state equilibrium by setting the left-hand side equal to zero and then solving the resulting second-order differential equation, with attention to the initial conditions and the boundary conditions specifying the movement behavior at spatial edges. While the solution of this problem can be difficult, we can gain some insights immediately upon inspection. Imagine we have a spatial equilibrium $N_i^*(x)$, then it must fulfill the following condition,

$$D_i \frac{\partial^2 N_i^*(x,t)}{\partial x^2} = -f_i(x, N_i^*, \ldots, N_n^*) \qquad (3)$$

Hence, places where the equilibrium density curve over space are concave upward (i.e. the term on the left is positive), are also areas that are net demographic "sinks" at equilibrium (i.e. have a negative local growth rate $f_i(x, N_i^*, \ldots, N_n^*)$). Similarly, population "sources" exist where the density curve over space is convex downward at equilibrium (Lande et al. 1989), which must be balanced by a positive growth rate. However, we caution that in the context of a density-dependent demographic model, "source" and "sink" are relative terms. A sink area is not necessarily one that is incapable of supporting a viable population, rather it is one where for realized equilibrium population densities, the local growth rate is negative. This equilibrium includes density-dependence; the net effect of dispersal for these places is to push population size above local carrying capacity, so that local growth rates are negative. Watkinson and Sutherland (1995) call such sites "pseudosinks". At lower densities, these pseudosinks could become sources. However, note that this simple relationship between curvature and demography may be lost for more complicated movement behavior.

Now we explore the specific behavior of Eq. 2 under different assumptions on the parameters. If two species are similar enough ecologically to experience strong interspecific competition, one might also expect them to respond similarly to the abiotic environment, and thus their K's should positively covary across space (not negatively covary as assumed in the Roughgarden model). Figure 1 shows such an example. Range limits can still be rather abrupt if one species' K increases across space at a faster rate than the other. MacLean and Holt (1979) describe one plausible example of this pattern for geckos on St. Croix.

The replacement of species B by species A along the spatial gradient depends on an interaction between the environmental gradient and competition. Both species benefit from left to right along space, but A is favored more than B and thus eventually outcompetes it. This general pattern has long been recognized by biologists (Tansley 1917). For example, Darwin (1859), speaking from a northern hemisphere perspective, wrote:

> "When we travel southward and see a species decreasing in numbers, we may feel sure that the cause lies quite as much in other species being favored, as in this one being hurt. So it is when we travel northward, but in a somewhat lesser degree, for the number of species of all kinds, and therefore of competitors, decreases northwards; hence in going northward, or in ascending a mountain, we far oftener meet with stunted forms, due to the directly injurious action of climate, than we do in proceeding southwards..."

In Darwin's view, stable range limits were the ultimate evolutionary response to an interaction between biotic and abiotic factors (Repasky 1991) and the relative importance of each varied latitudinally, with biotic factors being more important at lower latitudes. This conjecture of Darwin's has been more recently invoked by Dobzhansky (1950) and MacArthur (1972), although there are actually few studies that quantify the causes of northern and southern range limits and thus allow one to tally the results (but see Kaufman 1998). Loehle (1998) concluded that most boreal trees can grow in more moderate climates beyond their southern range limits. He also noted that within tree species, there was a trade-off between high growth rates and freezing tolerance. He speculated that the trees' southern limits were set by competitors with higher growth rates, but that the evolution of higher growth rates in boreal trees which would make them more competitive, was restrained because of this fitness trade-off. Gross and Price (2000) studied the winter range limits of the yellow-browed leaf warbler (*Phylloscopus humei*), a small insectivorous bird of broadleaf forests in India. They found that the northern limit coincided with the disappearance of arthropod food due to leaf loss associated with cold temperatures. The southern limit was associated with high food levels but increasing numbers of a competitor, *P. trochiloides*, which was 40% heavier in body mass and occupied the same habitats and foraging sites. Other potential competitors are present in the north, but they segregate into different habitats.

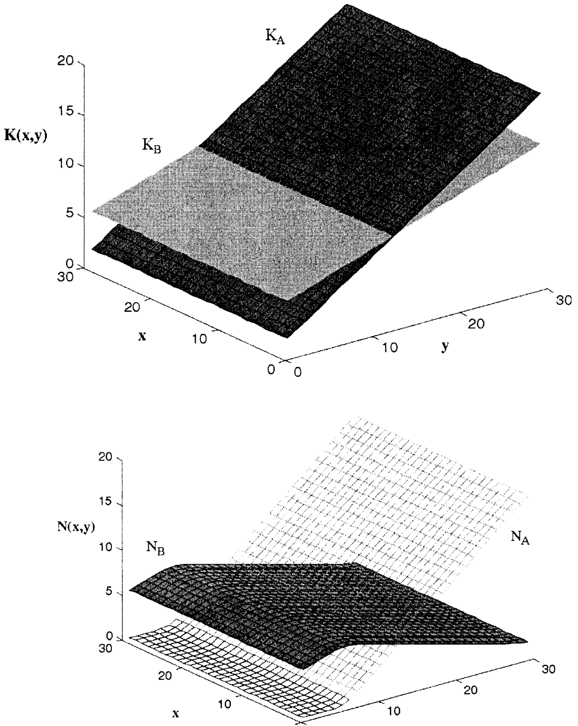

Fig. 1. Two Lotka-Volterra competitors competing over two-dimensional space. Interspecific competition $\alpha_{AB} = \alpha_{BA} = 0.7$. The top panel shows their K's over space and the bottom panel shows the resulting equilibrium population sizes. Movements are governed by a diffusion process, as in Eq. 2 with $D_A = D_B = 0.03$. $r_A = r_B = 0.5$, $d = 0$.

Range limits over homogeneous space

Another way that range limits may emerge in competition is when space is homogeneous, i.e. all of the model's parameters are invariant over space, but interspecific effects are stronger than intraspecific effects, i.e. $\alpha > 1$. For the non-spatial version of Eq. 2 there are two domains of attraction: species A at its single species equilibrium density (and no species B); or species B at its single species equilibrium density (and no species A). The interior equilibrium, if it exists, is unstable; which of the two domains is reached depends upon initial conditions. For the spatial model, however, other outcomes are possible. Figure 2 is again based on Eq. 2 (both species have the same r's, K's, and D's). Species A begins in one corner of space and species B begins in the opposite corner. The two species' populations grow and expand across space until they contact somewhere in the middle and then settle into a stable parapatric distribution with sharp range borders. For diffusion coefficients sufficiently low (as for the case shown), this equilibrium is stable, as Levin (1974) has shown for a two-patch model and Yodzis (1978) for continuous space. If diffusion coefficients are too high, or if one species has too large a numerical headstart, the system collapses to a homogeneous equilibrium with only one species. When both species coexist, the location of the range transition is sensitive to initial conditions. If one species begins with a larger population size than the other, or if one

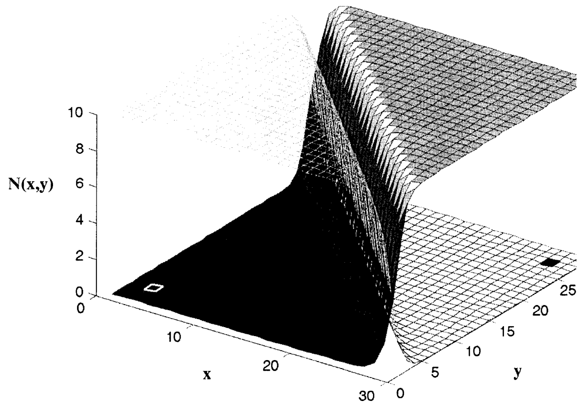

Fig. 2. The equilibrium spatial distribution (given the initial conditions) for two competitors competing over two-dimensional homogeneous space. Interspecific competition $\alpha_{AB} = \alpha_{BA} = 1.5$. Movements over space are governed by a diffusion process, as in Eq. 2 but for two spatial dimensions with $D_A = D_B = 0.03$. $r_A = r_B = 0.5$, $d = 0$). The species began in the shaded corners of space.

species begins closer to the center of space than the other, then that species will have a larger range at equilibrium. The strength of the ecological interaction needed to maintain a parapatric boundary is reduced if the boundary coincides with a region of lower carrying capacity (Bull and Possingham 1995) because reduced numbers lead to less total movement across that zone. Also the width of the overlap zone declines (all else being equal) with increasing α.

Such an explanation for range limits has been invoked to explain the elevational ranges of chipmunks in the southwestern US (Heller and Gates 1971). There are two other possible outcomes dependent upon parameters and initial conditions. One or the other species may entirely swallow the other; or, there can be a complicated patchwork over space where species A and B form a mosaic. For homogeneous space, the latter situation only arises for initial conditions that also form such a patchwork. Strong competitive interactions may produce alternative community states for multi-species pools (Gilpin and Case 1976, Gilpin 1994). Over homogeneous space, if D is sufficiently low, these alternative multi-species domains can replace each other as discrete and sharp blocks in a manner like that envisioned by Clements (1936). The importance of biotic interactions in creating a "coevolved" biogeographic province that repels invaders has been much debated. This notion appears in the writings of early biogeographers (Wallace 1876); it also crops up in the paleontological literature (Boucot 1978, Benton 1987, Vermeij 1991, Jablonski and Sepkoski 1996) and has been a perennial element of community ecology and invasion biology (Case 1990, Levine and D'Antonio 1999). As an example, consider Wallace's line, which separates those Indonesian islands formerly connected with the Malay peninsula during the last glacial maxima, from those formerly connected with the Australian/New Guinea region. Not too surprisingly the terrestrial mammals on either side of the line, which runs between Bali and Lombok, show strong affinities to Asia on the west and Australia on the east. Since land mammals are relatively poor overwater dispersers, these alternative communities may simply reflect insufficient time for the missing species to colonize. However, when we look at land birds, where dispersal powers are greater, the difference between Bali and Lombok is also notable (Mayr 1944), particularly when relative abundance of species is taken into account. On the other hand, for terrestrial reptiles Wallace's line is practically non-existent in terms of separating alternative community compositions, and one sees more of a gradual mingling of faunas across the Indonesian region (Darlington 1957). Does this mean that the two types of bird communities are alternative stable states, each repelling colonization of forms from the other fauna? If so, why isn't this happening with reptiles and other taxa? Answers to these questions are lacking.

The anoles of the Greater Antilles provide a striking example where nearby islands have drastically different faunas at the species level but the communities are very similar in their ecological and morphological patterns. The remarkable feature of this radiation is that only particular combinations of body size, perch type, and climate-space are realized, and these same "ecomorphs" are filled by unrelated forms on the different islands (Williams 1983, Losos et al. 1998). Using phylogenetic reconstructions based on DNA, Losos et al. (1998) found that the sequence of evolution of the various ecomorphs was probably different between islands, which makes the similarity of their end states even more remarkable. Interspecific competition is intense between island anoles (Losos 1994) and may drive these adaptive radiations. Presumably, the ancestors of these species dispersed among islands. The current communities are thus likely resisting occasional bouts of colonization and so may represent alternative stable states structured under a common motif.

Allee effects

If the local growth function $f_i(N_i, \ldots, N_n)$ is negative at low population sizes N_i, and only becomes positive at still higher levels, say at $N_i = C$, the population experiences an Allee effect. A cubic form for f(N) could have this feature. It can be shown that for continuous time reaction-diffusion equations over homogeneous space the presence of such an Allee effect is that the population will advance with a constant asymptotic velocity if $C <$ a critical threshold (which is K/2 for the cubic) and contract at constant asymptotic speed at higher C (Fife 1979, Lewis and Kareiva 1993, Keitt et al. 2001). By simply discretizing space into spatial cells Δx, even for small Δx, a new behavior can happen. For species i and spatial cell x, Eq. 1 becomes

$$\frac{dN_{i,x}}{dt} = m_i(N_{i,x-\Delta x} - 2N_{i,x} + N_{i,x+\Delta x}) + f_i(N_{i,x}, \ldots, N_{n,x}) \tag{4}$$

where m is the discrete analog of the diffusion coefficient. As Δx goes to zero, Eq. 4 approaches Eq. 1. (A biological rationale for discretizing space is that it provides one way to represent environmental patchiness; the assumption is that each patch is separated from its neighbors by a region of unsuitable habitat avoided entirely by the species during migration, e.g. rivers bisecting the habitat). For discrete space, a population following Eq. 4 may neither advance nor retreat but remain stationary. Spread (or retreat) can be renewed, however, by increasing (or decreasing) r, m, or K by a sufficient amount. If there is a decreasing productivity gradient affecting K(x), a species introduced into the high K region might be able to initially advance but the speed of advance will slow as it invades lower K areas and eventually spread may stop altogether giving a stable species border (Keitt et al. 2001). The example shown in Fig. 3 for $\Delta x = 1$ and a spatial gradient of length 40 illustrates how abrupt such a range limit can be by this process. If Δx is decreased, say to 0.5, in this example, this population would be able to spread over the entire space.

If a species with a limited range set by Allee effects is also a dominant competitor, then its own range limit may enforce a stable range limit on competitors that lack Allee effects. The range limits in this case would have different causes among subordinate and dominant competitors. Subordinates would be restricted from expansion by competitive exclusion, while the dominant species will be restricted by its own Allee effect. Moreover, Allee effects in general should greatly enhance the likelihood of parapatric boundaries in the model of competitive gradients discussed above. Sexual reproduction can often lead to Allee effects because mate location is made increasingly difficult at lower population densities and low frequencies if similar potentially cross-mating species are involved.

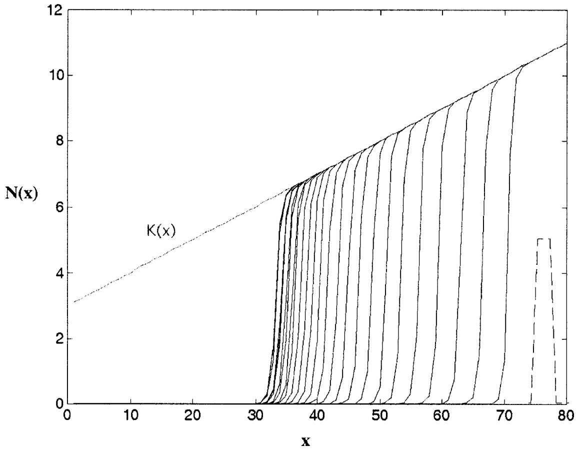

Fig. 3. An example of a species range set by Allee effects in discrete space with a linear gradient in K. The model is Eq. 4 (the discrete space analog to Eq. 1. $\Delta x = 1$; local population growth is described by the cubic equation $f(N) = ((N-3)/10)(1.5)\,N(1-N/K(x))$, and $K(x) = 3 + 0.1x$. The initial abundance is shown by the dashed curve. The final curve of N(x) on the left is the steady state distribution. If Δx is decreased, say from 1 to 0.5, in this example, this population would begin to spread and eventually cover the entire space. $D = 0.1$.

Interspecific hybridization and parapatric boundaries

Reproductive interference is an oft neglected interspecific interaction, which implicitly involves an Allee effect. Gorman et al (1971) and Gorman and Boos (1972) studied the patchy distribution of two introduced anole species on Trinidad and observed the rapid displacement of one species (*Anolis aeneus*) by another (*A. trinitatis*) in some enclaves. The two species freely hybridized and the hybrids were sterile. When modeled this situation produces a strong priority effect. For example, if a confined area contained 90% species A and 10% species B, and assuming random mating and equivalent birth and survival rates in each species, the next generation would contain 81% A, 18% hybrids and 1% B. If all hybrids were sterile, then in each succeeding generation, species B, which was initially rarer, would grow progressively rarer still. These arguments can be expanded to include explicit spatial movements by a slight modification of Eq. 2. Set $\alpha = 1$ so that intraspecific and interspecific competition are identical. Next, to include the effects of reproductive interference from interspecific hybridization make the intrinsic growth rate $r_i(N_i, N_j)$, decline as the frequency of the other species j increases in the local population. This can be modeled as

$$r_i(N_i, N_j) = \mathrm{rmax}_i \left[1 - \left(\frac{N_j(x,t)}{N_i(x,t) + N_j(x,t)}\right)^p\right] \tag{5}$$

The maximum growth rate for each species, rmax_i, is assumed here to be constant over space. The shape of the decline in r_i is controlled by a single parameter, p. If p is 1, then r_i declines linearly with increases in the frequency of species j. This would be the case if mating was at random between the two forms and all hybrid zygotes were inviable. Higher values of p describe greater degrees of premating isolation. For example if $p = 2$, and with both species equally common, the proportion of interspecific matings by species i would be 0.25 instead of 0.5. Except for the density dependence here, this model is similar to a models of Bazykin (1969) for the spatial evolution of chromosomal polymorphisms that have heterozygote underdominance.

In the nonspatial version of this model only one species prevails. The winner is determined in a complicated way by the magnitude of any initial frequency

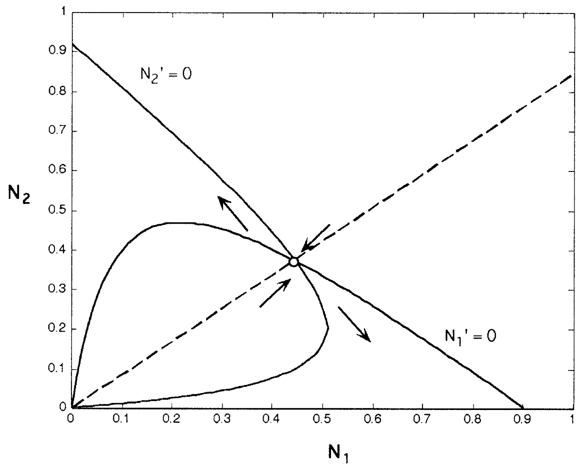

Fig. 4. The zero-isoclines for a non-spatial situation where two ecologically similar species have mutual reproductive interference through interspecific hybridization. This is Eq. 2 without the diffusion term and with r's given by Eq. 5 as $rmax_1 = 1$, $rmax_2 = 1.2$, $K_1 = K_2 = 1$, $d_1 = d_2 = 0.1$, $\alpha_{12} = \alpha_{21} = 1$, $p = 1$. The interior equilibrium point is unstable. The dashed line shows the separatrix. If initial densities fall to the right of the separatrix, then species 1 displaces species 2 but if initial densities fall to the left, the reverse happens.

advantage and the relative rmax's of the two species. Figure 4 shows an example of the zero-isoclines for this highly frequency dependent system when both species have the same D, K, and d, but slightly different rmax. As for standard Lotka–Volterra competition, the interior equilibrium point is unstable and the two boundary single-species equilibria are each locally stable.

Consider the spatial model with diffusive movements (using Eq. 2 and expression 5 as the function f) if the two species are initially allopatric and then spread to meet somewhere in the middle, they can reach a stable parapatric distribution, if the movement constant D is sufficiently low, even if one species has a numerical headstart and/or a higher rmax. This is reminiscent of the situation when $\alpha > 1$. The maximum values of D that will still allow this parapatric result and prevent the advantaged species from completely overrunning the other depends on the degree of the advantage. Fig. 5 (top) shows an example of the expansion of two species from opposite sides of one-dimensional space.

The final positions shown are at steady state where the two species form a very narrow stable zone of spatial overlap. Since the local population growth term also includes some density-independent mortality d, species A in allopatry reaches a higher equilibrium population size than does species B. As for the $\alpha > 0$ case, in the Lotka-Volterra model, the position of the range borders depends on the initial conditions and the other parameters. In this example, if the diffusion coefficient D is increased sufficiently, then species 1 with the higher rmax will ultimately drive out species 2 everywhere. While this example was based on $p = 1$, a similar result occurs for much higher values of p. The bottom panel shows the range pattern emerging from a patchy set of initial abundances, as might be expected for a pair of introduced species with multiple introduction foci, like the two anoles in Trinidad studied by Gorman et al (1971). These initial conditions give rise to a stable and patchy distribution of the two species. Again, however, if D is increased for both species, species A will close in on the enclaves of species B and displace it everywhere.

Two competitors in a metapopulation

Many natural environments are patchy and experience varying degrees of disturbance. In such landscapes, colonization may permit a species to persist despite recurrent episodes of local extinction (Hanski 1998). The companion paper by Holt et al. (this issue; Lennon et al. 1997, Holt and Keitt 2000) argues that metapopulation dynamics can generate range limits via three distinct causal mechanisms along environmental gradients: a decline in habitat availability, an increase in extinction rates, and a decrease in colonization rates. Since competition between species can influence colonization and extinction probabilities, it can provide a causal basis for range limits.

Metapopulation dynamics are often at rather local scales, whereas geographical ranges are often circumscribed at much larger scales, along gradients which vastly exceed the spatial scale of individual dispersal. As in the models for direct competition along gradients sketched above (Roughgarden 1979), it is useful to make the parameters of metapopulation models into functions of spatial position, and then characterize patterns of zonation (e.g. zones of dominance by a single species, or coexistence) and species borders along gradients. Consider for instance the metapopulation competition model of Nee et al. (1997). This model describes an interaction between a dominant competitor (which occupies a fraction p of landscape patches), and an inferior competitor (occupying a fraction q of patches). Since by assumption no patches are jointly occupied, the dynamics of occupied patches can be described by the equation pair

$$dp/dt = c_A\, p\, (h - p) - e_A\, p \quad \text{(dominant species)} \qquad (6)$$

$$dq/dt = c_B\, q(h - q - p) - e_B\, q - c_A\, p\, q \quad \text{(subordinate species).} \qquad (7)$$

The first equation is a standard metapopulation model (Hanski 1998) and assumes that a fraction h of the landscape is suitable for either species, and that the dominant species is not affected at all by the inferior species. The second equation incorporates two distinct effects the dominant has on the inferior species: patches occupied by the superior species cannot be colonized by the inferior species (reducing its colonization rate) and patches with the inferior species can be invaded by the

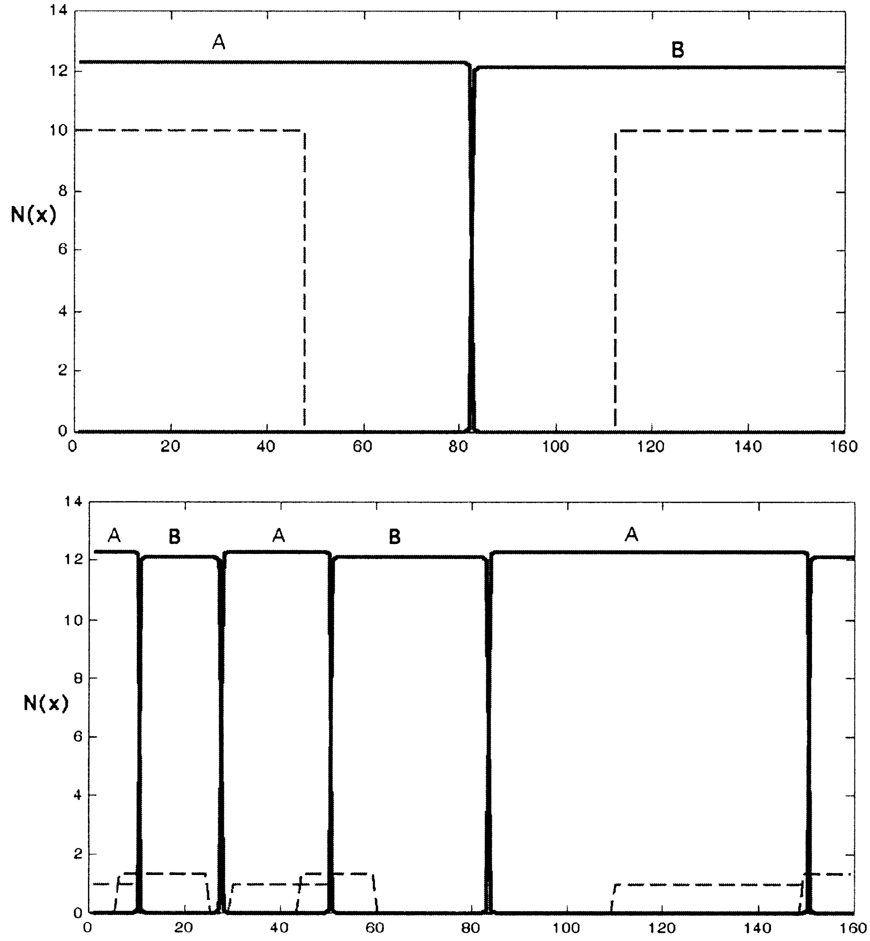

Fig. 5. Interspecific hybridization can produce stable parapatric boundaries with diffusive movements. Two outcomes of the model of Eq. 2 and Eq. 5. Both top and bottom panels are identical except for initial conditions. Space is one-dimensional and the initial densities of the two species are shown as dashed curves. The final steady state distributions are shown as solid lines. Parameters are: $p = 1$, $K(x) = 12.83$, $rmax_1 = 0.6$, $rmax_2 = 0.5$, $d = 0.0034$, $D_i = D_j = 0.0003$, $\alpha_{ij} = \alpha_{ji} = 1$. In this example, if D for both species is increased to 0.03, then species 1 with the higher rmax will ultimately drive out species 2 everywhere for the same initial conditions.

superior species, which then supplants the inferior species (in effect, increasing its extinction rate). The model assumes that the time-scale of replacement is short relative to other dynamical processes in the system, so we can ignore transient phases when patches are occupied by each species.

The equilibrium occupancy of the dominant competitor is $p^* = h - e_A/c_A$, and of the subordinate species is $q^* = e_A(c_A + c_B)/\ (c_A\ c_B) - (e_B/c_B) - (h\ c_A/c_B)$ (Nee et al. 1997). For the inferior species to coexist with the superior competitor, it is necessary that the former have either a higher colonization rate, or a lower basic extinction rate. Coexistence occurs (if it does) because one species is superior at competing within-patches, and the other is superior at occupying and holding empty space. We assume this necessary condition for coexistence holds.

Any of the parameters in this model could in principle vary as a function of position along a large scale environmental gradient. After substitution into the expressions for equilibrial occupancy we can find the position of a given species' border by setting its occupancy to zero. Manipulating the resulting expressions leads to several intuitive conclusions:

i) Nee et al. (1997) note that habitat destruction can increase the abundance of an inferior competitor. In like manner, if the availability of the habitat required by both species diminishes along a spatial gradient, only the superior competitor may be present when habitat is frequent; with declining h, the frequency of the dominant competitor declines, until at some h, the inferior competitor appears (this defines its border); as h continues to decline, the dominant species declines further, and the inferior species increases in occupancy until, at some low h, the dominant competitor disappears entirely. Still further decreases in h depress the occupancy of the subordinate species. Competitors inferior at directly competing for space may thus have geographical ranges restricted to regions where their preferred habitat is relatively sparse.

ii) Similar patterns of zonation can occur with a gradient of increasing extinction rates, which is uniformly experienced by both species (e.g. localized catastrophic disturbances). The subordinate competitor suffers directly from increased extinction rates, but indirectly benefits because of reduced occupancy of patches by the superior competitor (recall that the subordinate has a higher colonization rate into empty patches). Along a gradient in increasing extinction, the inferior competitor occupies a zone of higher overall extinction rates because the indirect positive effect of extinction freeing up space from the dominant species exceeds the negative direct interspecific effect.

iii) Likewise, if we assume that both species have equal colonization rates, and the inferior competitor enjoys a lower extinction rate, then along a gradient in declining colonization rates (for both species) a species border for the inferior competitor will arise when the colonization rate is sufficiently reduced.

In all cases, the direct response of both species to the environmental gradient may be the same, but as for the reaction–diffusion systems considered earlier, the competitive interaction reverses the impact of the spatially-varying factor upon the range limit of the inferior species.

Specialist predator–prey and host–parasite systems

The theme of indirect versus direct effects in determining causes of range limits along gradients is broadly applicable. Consider for example the factors which define the range limit of a specialist predator dependent upon a single prey species (or in like manner, a parasite specialized to a single host species). It is clear that if dispersal is limited, the distribution of the specialist predator will be nested within the distribution of its required prey (Holt et al. 1999), but a more refined understanding of the range position requires a dynamical model. We assume again that dynamics at the scale of local landscapes adequately match the assumption of metapopulation models. The model we consider is adapted from Holt (1997). Patches can be in one of four states: unsuitable (with a frequency $1-h$), state 0 (empty), state 1 (prey present alone); state 2 (prey present with the predator). For simplicity, we assume that the predator in a patch only goes extinct when the prey there goes extinct, and that predators can only colonize patches already occupied by prey. Moreover, we assume that prey colonization only occurs from patches with the prey alone. This assumption is reasonable if the predator greatly reduces local prey abundance, causing a dramatic reduction in prey numbers in patches with the predator. With these assumptions, the two-species metapopulation model is as follows:

$$\frac{dp_1}{dt} = c_{01}p_1(h - p_1 - p_2) - c_{12}p_1p_2 - e_{10}p_1 \qquad (8)$$

$$\frac{dp_2}{dt} = c_{12}p_1p_2 - e_{20}p_2 \qquad (9)$$

where h is the fraction of patches suitable for colonization by the prey species (and hence the predator), p_i is the fraction of patches in state i, c_{ij} is the rate of colonization from state i to state j, and e_{ij} is the rate of extinction from state i to state j. Now make all these parameters and variables functions of position along a gradient, x. The predator will be present at points along the gradient within the prey distribution where:

$$h(x) > \frac{e_{10}(x)}{c_{01}(x)} + \frac{e_{20}(x)}{c_{12}(x)} \qquad (10)$$

(Holt 1997). The condition for the prey to be present is $h(x) > e_{10}(x)/c_{01}(x)$. Thus, this inequality reveals that the predator has more stringent requirements for persistence than does its prey, and so will have a nested distribution along the gradient, contained within the range of its prey. The inequality makes explicit the importance of dynamic processes affecting prey occupancy (other than predation) which indirectly constrain the predator's distribution.

The predator's distributional range limit will occur when the above expression is an equality. A species' border for a specialist predator species can arise because of the predator's own direct response in colonization and extinction rates along the gradient. Alternatively, the predator may have spatially invariant colonization and extinction rates, but indirectly have its range limited because there is a gradient in availability of habitats suitable for its prey, or in the colonization rate of its prey, or in the extinction rate of its prey (in the absence of the predator). A comprehensive explanation of a specialist predator species' border needs to consider both direct and indirect effects of position along the gradient.

In the above model, the prey species has range limits set by its own autecological requirements, rather than by the predator. If dispersal rates are very low, it would appear to be difficult for a monophagous predator to generate a stable species border in its solitary species of prey. The reason for this is simply that if a monophagous predator causes a range limit in its prey, then by assumption the prey is excluded by predation just beyond the range limit, but if so, the predator itself should starve and go locally extinct. Later-arriving prey could then freely invade, and hence the range limit would not be stable! More generally, prey limits can be set by predation, via two distinct mechanisms: 1) specialist predator 'spillover' effects, and 2) generalist predators sustained by alternative prey (apparent competition).

If one explicitly accounts for dispersal along the gradient by the predator, spillover effects can lead to a limited range for the prey, maintained by the specialist predator. Holt (1979) suggested that a specialist natural enemy could enforce a range limit in its prey, if predator dispersal rates were high, and if the prey had sharp spatial gradients in production. Hochberg and Ives (1999) extended this idea using a host–parasitoid model, and demonstrated that a specialist parasitoid could enforce a geographical range limit in its prey (and hence in itself). The conditions that favored this outcome were as follows: i) the parasitoid must have high attacks rates, permitting moderate parasitoid numbers to limit the host to well below local carrying capacity; ii) there must be gradients in host production, indirectly producing "hot spots" of parasitoid production; iii) the parasitoid must have high dispersal rates, permitting these hot spots to indirectly sustain parasitoid populations at sites where the host is nearly or entirely eliminated.

One interesting effect revealed by their model (and conjectured in Holt 1979) is that a parasitoid can lead to the absence of a host in regions where host populations would be most abundant in the absence of the parasitoid. The reason is that high host productivity tends to induce strongly unstable population dynamics in host-parasitoid systems, tending to eliminate both hosts and parasitoids (an example of the "paradox of enrichment"). Because of these instabilities, the species border in regions of high productivity is rather unstable, with eruptions of both species from more stable, persistent regions. The species borders for both host and parasitoid in the productive region are fluctuating bands of unstable populations at sites that are colonized by hosts, which then grow and thrive until the parasitoids arrive and set up locally highly unstable dynamics, leading to extinction for both species. Hassell (2000, chapter 7) reviews such models and shows sample illustrations of some the resulting intricate spatial patterns.

As Hochberg and Ives (1999) note, these results depend upon substantial parasitoid dispersal, and the spatial scales over which such dispersal is likely to occur would seem to be more likely to pertain to patterns of local habitat patchiness (Hastings et al. 1997) than to the determination of geographical range limits. However, if there are sharp spatial gradients in environmental conditions, parasitoid or predator dispersal could further sharpen the species border of a host or prey species.

Generalist predators and prey range limits

Polyphagous predators can of course stably eliminate particular prey species from local communities, and are quite likely to generate stable range limits in prey species, particularly when different species are differentially productive or vulnerable to predation across a gradient. The likelihood of this occurring depends upon the availability of alternative prey, which are sufficiently productive to sustain the predator, and hence the existence of apparent competition between alternative prey (Holt 1977, Holt and Lawton 1994). A simple model with this feature is to assume logistic prey growth for each of two prey species, and a predator with a standard linear functional and numerical response to each prey, as follows (Holt 1984):

$$dR_i/dt = r_iR_i(1 - R_i/K_i) - a_iR_iP \qquad \text{for } i = 1, 2 \tag{11}$$

$$dP/dt = P(a_1b_1R_1 + a_2b_2R_2 - d), \tag{12}$$

where a_i is the predator attack rate upon prey i, and b_i measures the benefit enjoyed by the predator from those attacks. The quantity d is predator density independent mortality. For simplicity, assume that the prey feeds in an even-handed manner such that both attack rates equal a, and both prey benefits are b. Define $\Delta = 1 - d/abK$. The quantity Δ measures the fractional reduction of prey at equilibrium below carrying capacity due to the predator (Holt 1984). For the two prey species to coexist, the prey with lower intrinsic growth rate (say prey 2) must satisfy the inequality $r_2/r_1 > \Delta$.

As an illustrative example, assume that prey 1 has a linear decline in its intrinsic growth rate along the gradient, given by $r_1 = r' - gx$, and prey species 2 has an opposite pattern, with $r_2 = gx$ (for $0 < x < r'/g$). The length of the gradient is r'/g, and this is the range of each prey species when it is alone with the predator. Given that both prey species are present, the width of the overlap zone between the two prey is

$$w = \frac{r'}{g}\frac{(1 - \Delta)}{(1 + \Delta)} \tag{13}$$

an expression that parallels the one we found for directly competing species (with Δ substituting for α). One immediately sees that the more effective the predator is at limiting prey well below carrying capacity (i.e. Δ near one), the narrower the zone of overlap between the prey. Strong shared predation can thus readily generate distributional boundaries for alternative prey along gradients. Presumably, the inclusion of diffusive movement terms to this model would simply smear out these zones.

Settle and Wilson (1990) describe an example of a range limit that has seemingly emerged in leafhoppers in southern California due to shared parasitism. In this and other examples, there is often a strong asymmetry in the indirect interaction (Chaneton and Bonsall 2000). In a geographical context, such asymmetries can lead to one species having a range limit set by a natural enemy, without there being a reciprocal effect on the other species. Parasites are often relatively benign in their impact upon one host species, and severely debilitating in others. For instance, the parasitic worm *Pneumostrongylus* is carried by the white-tailed deer, with little demographic impact, but is fatal to caribou. Because caribou herds wander widely during foraging, they are likely to encounter browse with the intermediate host (a gastropod), and thus become infected, if white-tailed deer are present anywhere in a broad region. Embree (1979) argues that this indirect interaction via shared parasitism may explain the southern geographical limit of caribou in eastern Canada, where they are roughly parapatric with white-tailed deer.

The small shrub, *Happlopappus squarrosus*, increases in abundance from coast to mountains in southern California. While still in the flowers, its seeds suffer substantial predation by insects, both generalists and specialists. The abundance of adult shrubs tracks geographic variation in the impact of these predators and experimental removals of these predators leads to substantial recruitment, particularly in the low-abundance coastal sites (Louda 1982).

Mutualism

Obligate mutualisms or commensalisms could readily give rise to sharp species borders. Rather than present another model, we sketch an example that shows the effect, albeit at a local scale. Old beaver ponds in boreal regions take a very long time to revert to forest. Terwilliger and Pastor (1999) suggest that this reflects a complex web of interspecific interactions, including mutualisms. The dominant tree at their study site is black spruce (*Picea mariana*), which is an ecomycorrhizal species requiring specific fungi in its root system to grow effectively. These fungi cannot withstand long-term submergence and so are likely to be absent when the beaver pond is abandoned and begins to revert to a meadow. Terwilliger and Pastor experimentally demonstrate that spruce seedlings do poorly in beaver meadow soils. So, at this local spatial scale, the distribution of spruce is constrained because of the absence of an obligate mutualist. But the plot thickens: why is the mutualist absent? The long lag in succession makes it improbable that wind dispersal is responsible for establishment of ecomycchorizal fungi on meadows. Terwilliger and Pastor suggest that instead a mammal, the red-backed vole (*Clethrionomys gupperi*) carries the spores, picking them up by eating mushrooms, and depositing them in its feces. Inoculating beaver meadow soil with fecal material from the vole did introduce the ecomycorrhizal fungi and facilitated spruce survival and growth. The red-backed vole in turn does not wander onto the meadows because of competitive interactions with another rodent, the meadow vole (*Microtus pennsylvanicus*), which in turn does not enter the forest. At a local scale, a short-term distributional limit in the tree thus arises from cascading mutualisms, in the context of a competitive interaction.

Similar effects must surely arise whenever species are obligate mutualists. For instance, a given species of yucca requires a given species of yucca moth for successful reproduction. It is likely that a climate envelope describes the range of abiotic conditions that the moth can successfully tolerate. Even if the yucca can survive as individuals at sites with conditions outside that climate envelope, self-sustaining populations cannot persist in the absence of the moth. Abiotic constraints on the distribution of the moth should automatically generate a range limit in the yucca. Although this scenario seems very plausible, we are unaware of any detailed study of the phenomenon.

Comparable patterns may arise in the very numerous mutualisms which are not so species-specific. For instance, many plant species require mammals for dispersal, either via fruit ingestion, or by adhesion to skin or fur, but the dependence is not tightly specific to a particular species of dispersal agent. In a metapopulation context, any factor that reduces the efficacy of colonization can generate a range limit (Holt and Keitt 2000). Gradients in mammal abundance due to, e.g. food availability, could thus indirectly lead to range limits for these plant species in regions where overall mammal abundance is reduced.

Models that include coevolution and gene flow

Competition

Why doesn't local adaptation in populations at the range boundary allow the continual expansion of the range over evolutionary time? One explanation is that these marginal populations lack the requisite genetic variability to improve fitness. Usually this does not appear to be the case. For example, Jenkins and Hoffmann (1999) found that the southern limit of *Drosophila serrata* was determined in eastern Australia by the fly's ability to withstand cold stress but southern populations had heritable variation in this character. The interesting observation that when species experience decline, many persist in the periphery of their historical geographic range, but not the core (Brooks 2000, Channell and Lomolino 2000), suggests these populations may retain adaptive potential. Haldane (1956) suggested that continued local adaptation at the margin would be countered by detrimental effects of gene flow from the population's more populous interior, with the result that a stable range limit could evolve even in the absence of any physical barriers to dispersal. Kirkpatrick and Barton (1997) modeled this situation using a quantitative character subject to stabilizing selection for an optimum temperature that varied geographically. They found stable limited ranges as one of several possible results. The addition of interacting species can enhance this effect (Case and Taper 2000). The effect of gene flow upon local adaptation can at times be positive, because migration permits an infusion of genetic variation, thereby facilitating selection (Gomulkiewicz et al. 1999, Barton 2001). There is still much that can be done in this framework to explore the coevolution of quantitative traits in different species and its effect on range limits; hence we review the structure of the model explored in Case and Taper (2000) and present some new results.

The local growth rate of a population of species i with mean phenotype at spatial position x is

$$\frac{dN_i(x,t)}{dt} = N_i(x,t)\bar{w}_i(\bar{z}_i,x,t) \tag{14}$$

where $\bar{w}_i(\bar{z}_i,x,t)$ denotes the intrinsic growth rate of species i's population averaged over all its phenotypes (see expression 16 below; for simplicity, the dependence upon the mean is shown, though in general the average growth rate depends upon the full phenotypic distribution). Each phenotype z in species i at position x has an intrinsic rate of growth $w_i(z,x,t)$ from selection that depends upon population density N_i and phenotypic frequency distribution p(z) in all species. A quantitative phenotypic character, z, influences the strength of competition between phenotypes intra- and interspecifically through a function $\alpha(z,z')$. Additionally, the physical environment selects for some optimum phenotype $\theta(x)$ at spatial position x. For the case of two competing species i and j, the Malthusian fitness of phenotype z in species i at time t is

$$\begin{aligned} w_i(z,x,t) = r(x) &- \frac{r(x)N_i(x,t)}{K(x)}\int_{-\infty}^{\infty}\alpha(z,z')p_i(z',x,t)dz' \\ &- \frac{r(x)N_j(x,t)}{K(x)}\int_{-\infty}^{\infty}\alpha(z,z')p_j(z',x,t)dz' \\ &- \frac{(\theta(x) - z(x,t))^2}{2V_s} \end{aligned} \tag{15}$$

The first integral, which is the convolution of species i's phenotypic distribution with the competition function $\alpha(z,z')$, gives the total amount of intraspecific competition on phenotype z (once multiplied by the current population density of species i at time t, N_i). The second integral gives the total amount of interspecific competition from all phenotypes within species j on phenotype z in species i. The competition function α, provides a force for diversifying selection. It is modeled as a Gaussian function of phenotypic separation, $z-z'$ with variance V_α. Finally, the last term represents the stabilizing selection on z around the optimum phenotype θ at position x, as a quadratic function with variance V_s. Note that this final term provides a density-independent source of selection. This term represents a fitness penalty for deviation from the optimum phenotype for the local physical environment. Thus a homogeneous population at position x, comprised solely of the optimum phenotype $\theta(x)$, would have carrying capacity K(x), but other phenotypes would have equilibrium densities less than K(x). The smaller V_s, the more severely nonoptimal phenotypes are penalized as they depart from $\theta(x)$. Also note that r(x) and K(x) are thought to be independent of phenotype but potentially varying across space.

To track the changes in population size of species i using Eq. 14 requires an expression for mean fitness at point x, which is

$$\bar{w}_i(x,t) = \int_{-\infty}^{\infty} w_i(z,x,t)p_i(z,x,t)dz \tag{16}$$

The effects of local selection on mean phenotype is

$$\frac{d\bar{z}_i(t)}{dt}(\text{local}) = h^2\left[\int_{-\infty}^{\infty} zp_i(z,t)w_i(z,t) - \bar{w}_i(t)\bar{z}_i(t)dz\right] \tag{17}$$

The heritability h^2 is assumed to be constant, which can result under weak selection, if a mutation-selection balance occurs, and the phenotypic distribution remains approximately Gaussian with constant variance V_P (Lande 1976). Because the model also includes frequency dependence generated by competition in this model, an equilibrium phenotypic variance is also expected due to a balance between diversifying selection (from competition) and balancing selection (Bulmer 1980, chapter 10). A more tenuous assumption is that V_P is constant over space despite strong differences in population size and gene flow. By linking Eq. 2, Eq. 16 and Eq. 17, Case and Taper (2000) were able to evaluate the resulting double integrals and provide closed-form expressions for dN_i/dt and $d\bar{z}_i/dt$.

Movements and gene flow were handled by a diffusion process. For continuous space and time, the change in numbers of species i at point x, in one-dimensional space, due to movement and local population growth is then:

$$\frac{\partial N_i(x,t)}{\partial t} = D\frac{\partial^2 N_i(x,t)}{\partial x^2} + N_i\bar{w}_i(x,f_i(\bar{z}_i,x,t)) \tag{18}$$

where D is the diffusion parameter (or dispersal coefficient). D is assumed to be equal for both species and spatially and density-independent. Individual movements also change the mean phenotype at position x due to gene flow, so the total change in mean phenotype is the sum of changes from diffusive mixing and local evolution, as follows

$$\begin{aligned} \frac{\partial\bar{z}_i(x,t)}{\partial t} &= D\frac{\partial^2\bar{z}_i(x,t)}{\partial x^2} + 2D\frac{\partial\ln(N_i(x,t))}{\partial x}\frac{\partial\bar{z}_i(x,t)}{\partial x} \\ &\quad + \frac{\partial\bar{z}_i(x,t)}{\partial t}(\text{local}) \end{aligned} \tag{19}$$

The coupled partial differential Eq. 18 and 19 provide the model. (Extensions to two-dimensional space are simple.) In Eq. 19, the third term describes local selection, in the absence of movement and gene flow (i.e. Eq. 17); the first term describes the impact of simple movement; and, the second term describes how spatial variation in local abundance alters the expected effect of movement upon phenoypic values. The net change in phenotype at a given locality thus reflects the interplay of local selection and gene flow (Kirkpatrick and Barton 1997, Case and Taper 2000).

The retarding effect of gene flow on local adaptation, thus potentially causing a range limit, is influenced by the product of the diffusion coefficient D and the steepness of the environmental gradient through the slope of θ(x). If this product is sufficiently high and heritability sufficiently low, even a single species can have a stable range limit. Naturally, if parameters are such that either species alone has a limited range, then for two competing species, each will have a limited range in allopatry. What is more interesting is how the two species populations behave in situations where either alone would have an unlimited range. Case and Taper (2000) found that stable range limits were produced for lower values of this product when species also potentially compete. Empirical estimates for r, h^2, D, and the slope of the environmental gradient did not usually seem consistent with an evolutionarily stable limited range for the single-species case, although interspecific interactions (and presumably other biotic interactions as well) considerably relax the requirements on these parameters.

In two-competitor models, the mutual range limits are associated with character displacement (generalizing in a spatial context prior studies of local character displacement, such as Slatkin 1980 and Taper and Case 1985, 1992). The co-occurrence of the two species in sympatry induces a character displacement in z, which in turn, initially allows local coexistence. As spatial overlap between the two species increases so does the departure of each species, induced by the character displacement, from the optimum phenotype θ(x). This, in turn, leads to a reduction in population density in part from interspecific competition and in part from the departure of each species from θ(x) from character displacement. In this way, the local evolution of character displacement interacts with asymmetric gene flow caused by reduced abundance in sympatry to produce a stable range boundary in each species. At the evolutionary equilibrium, a portion of each species' range is allopatric and a portion is in sympatry (examples are shown in Case and Taper 2000).

If the physical environment has particularly rapid changes over some parts of space, nearby positions will have very different optimum phenotypes. The same amount of gene flow becomes more disruptive to local adaptation because immigrants from nearby populations have phenotypes less suitable to the local optima. This slows down and may even stop range expansion leading to stable borders. An example is shown in the top panel of Fig. 6 for a single species case. This species was initialized in the center of space and evolves mean phenotypes to match the regions of space where the θ(x) has a shallow slope. However, for the parameters here, the sharp ecotone on the left can not be surmounted by local adaptation. Note the severe departure of mean phenotype in this region from the optimum curve, due to gene flow from populations with smaller z to the right. In the bottom panel, the K(x) curve, which was uniformly flat in the top panel, is modified to provide a biogeographic filter (by reduced numbers) at position x = 25 to the right of the θ(x) kink in θ(x). The consequence of this is a partial relaxation of the retarding effect of gene flow for populations to the left of x = 25, and the consequent evolutionary ability to now expand to the left.

What at first glance would seem like an impediment to range expansion, a zone of sharply lower carrying capacity K, actually facilitates a ultimate range expansion as we saw in Fig. 6 and does not lead to coincident range termini in this model. Figure 7 shows an optimum curve with two regions that have particularly rapid slopes: one on the left and another on the right. This leads to two alternative coevolutionary outcomes, and in both the range termini are fixed onto the zone of rapid transition in θ(x), either the left zone or the right zone.

The range boundaries for two species, like those shown in Fig. 7, arise from the interaction of interspecific competition with the environmental gradient. If species 2, for example, is removed, then for these parameters, species 1 is capable of evolving a mean phenotype that allows it to evolve to cover the entire spatial gradient, ultimately "hugging" the optima over its entire spatial range (similarly for species 2, if species 1 is removed). If the kinks in the environmental gradient θ(x) are smoothed out, both species will also be able to expand their regions of sympatry with an accompanying character-displacement.

The predication that range boundaries will be associated with sharp abiotic environmental gradients (but not necessarily with decreases in productivity) provides a sharp distinction for future testing. Boone and Krohn (2000) analyzed the range limits of bird species in Maine and found that for forest specialists their borders were spatially coincident with rapid transitions in vegetation.

Future directions with spatial coevolution

A somewhat paradoxical conclusion from this model is that the ultimate geographic spread of an invading species may be inversely related to its dispersal rate. This result only arises if continued spread of an invader over

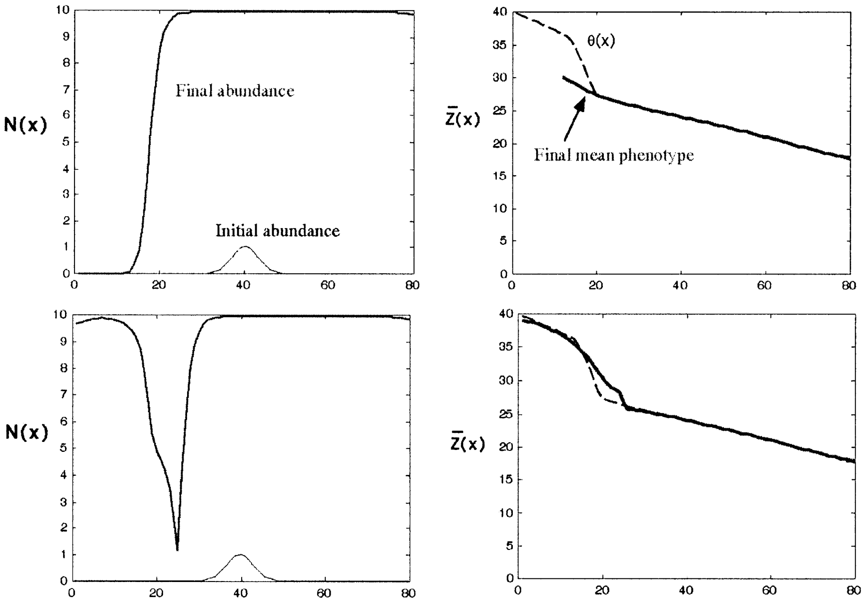

Fig. 6. Top. The equilibrium distribution of population size (left) and the evolved mean phenotype z (right) over space x in a one-species case where the optimal phenotype θ(x) based on stabilizing selection (dashed curve) varies in a nonlinear way. The initial conditions for N(x) were Gaussian and initial mean phenotype for these populations began at θ(x). In the top pair of figures, the carrying capacity curve is flat across space at K(x) = 10. In the bottom pair of subfigures K(x) has a sharp drop to 20% of its former level at spatial position 25. $V_S = 36$, $h^2 = 0.2$, $D = 0.1$, $V_\alpha = 36$, $V_P = 2$, $r(x) = 1$.

new terrain requires continuing adaptation to local environments. Many invaders, on the other hand, may be able to spread by avoiding local adaptation and instead finding human-modified habitats to which they are pre-adapted, such as urban/suburban settings or particular agricultural crops. In these cases, rapid spread is achieved by long-distance dispersal, which allows individuals to "hop" over less suitable habitats that would require local adaptation. An interesting example is provided by Niemel and Spence (1991, 1999), who describe the invasion dynamics of a carabid beetle (*Pterostichus melanarius*) in Canada. The beetle does

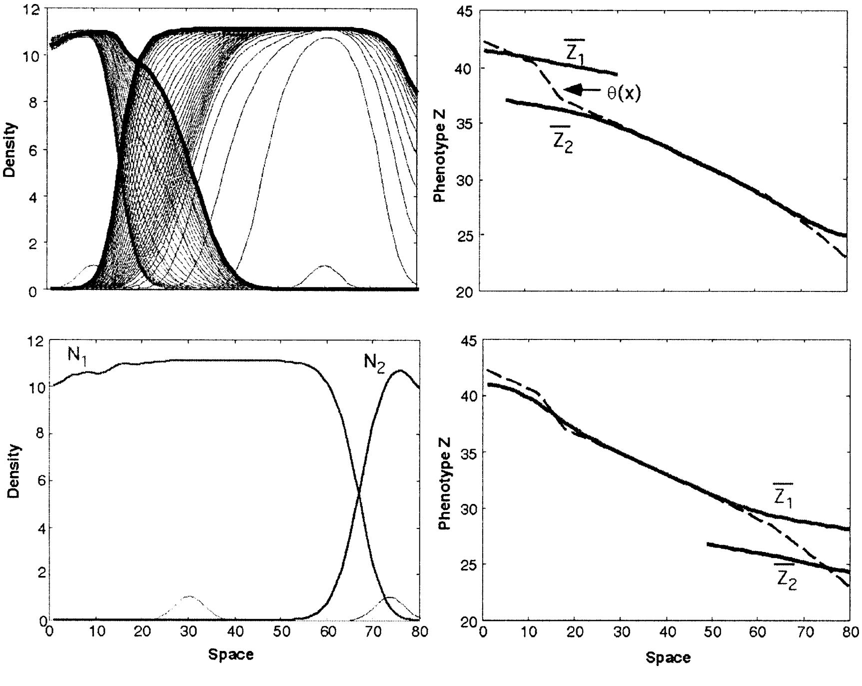

Fig. 7. The effect of nonlinear θ(x) on the coevolution of character displacement and geographic ranges for two species. There are two zones of rapid transition in θ(x), shown by the dashed line, one on the left and one on the extreme right. Each species' density (left panels) was initialized with Gaussian distributions (maximum density of 1) at the spatial positions shown. The top and bottom panel pairs are identical except for the initial conditions. Density curves (on the top-left) are drawn every 40 time units. The right-hand figure shows the resulting equilibrium mean phenotype for both species over space. The two different initializations reach two different spatial equilibria, but in each the transition zone between the two species coincides roughly with the center of the θ(x) kink. Each species if alone would evolve to cover the entire space. Other parameters: $V_s = 36$, $h_2 = 0.2$, $D = 0.1$, $V_\alpha = 3$, $V_P = 2$, $r(x) = 0.2$, $K(x) = 10$.

very well in urban areas, and spreads among spatially distant urban environments largely via long-winged individuals who are capable of dispersing over large distances. Such movement patterns are not adequately described by a pure diffusion process (Holmes et al. 1994). To predict possible consequences of invaders in a fragmented landscape, and to model more realistically the effect of climate change on range shifts and local evolution, and extinction along continuous environmental gradients, the above model must be generalized to include a wider array of dispersal behavior and a biased directionality to movement to produce habitat selection. It would also be important to consider stochasticity. Demographic stochasticity is likely to lead to local extinctions, genetic drift, and loss of genetic variation, which should impede adaptive evolution at range margins. Environmental stochasticity can have a variety of effects. Holt et al. (2004) have recently shown that temporal correlated variation that is moderate in magnitude can actually facilitate adaptive variation in marginal populations, by providing 'windows of opportunity' for selection to enhance local adaptation.

The consideration of the effects of individual movements on gene flow is also grossly incomplete in the present models. As individuals move, the genetic and phenotypic variances may also change. Dispersal alone should increase the local genetic variation, but it is not so clear how genetic variances are simultaneously affected by drift and effective population size, dispersal, stabilizing selection, and diversifying selection. If peripheral populations tend to be small and isolated, and if this leads to reduced genetic variance, then local adaptation at the range boundary will be reduced if migration is not too strong (Gomulkiewicz et al. 1999). This could reduce the capability of peripheral populations to respond adaptively to selection, compared to those in the interior.

Most organisms will probably not choose movement directions at random, but rather be guided by habitat selection that provides a better match between phenotype and spatial position. A framework for modeling habitat choice in continuous time is provided by Shigesada et al (1979), Pease et al. (1989) and Holmes et al. (1994). If individuals have a movement bias that tends to bring them into areas to which they are already preadapted, then the disruptive effects of gene flow will be mitigated to some extent. The same level of dispersal will not be as damaging to local adaptation compared to random movements. Similarly, phenotypic plasticity that allows the same phenotype to adjust to local environmental conditions in an adaptive manner will tend to mitigate the disruptive effect of gene flow.

The spatial coevolution models discussed above created a framework for exploring the interaction between gene flow, local adaptation through stabilizing selection to the physical environment, and local adaptation through diversifying selection to the biotic environment created by competition. Several authors (Hochberg and Ives 1999, Hochberg and Holt 2002, Nuismer and Kirkpatrick 2003) have explored similar issues in predator–prey and host–pathogen interactions. One issue which complicates matters in interesting ways in host-parasite and predator–prey coevolution is that at times, dispersal can have a strong positive effect on local genetic variation (Gomulkiewicz et al. 1999, Barton 2001), which can substantially reverse the expected negative effect of gene flow upon local adaptation. In predator–prey and host–pathogen systems, this can permit the species which disperses at the greater rate to develop local adaptation more effectively (Gandon et al. 1996, Hochberg and van Baalen 1998).

Range limits in the context of entire communities

In most of this paper, we have been concerned with interspecific interactions among very small numbers of strongly interacting species (2 to 3). We conclude by discussing some issues that arise when considering range limits in the context of entire communities, including many weakly interacting species.

Studies of distributional patterns of assemblages along environmental gradients suggest that range limits in many species do not obviously arise from pairwise interactions (Whittaker and Niering 1965, Terborgh 1971, Whittaker 1975). The importance of individualistic determinants of range limits is also suggested by paleoecological studies of historical shifts in ranges and community composition, which reveal that species ranges often respond idiosyncratically to climate change (Davis 1986, Graham 1986, Coope 1987). However, experimental studies of local populations and communities usually demonstrate the existence and importance of strong interspecific interactions such as predation and competition in determining local community membership, and relative abundances of community members. Moreover, some paleoecological studies do suggest patterns of concordant responses by entire communities to climate change (Boucot 1978). Concordant responses imply that entire suites of range limits shift roughly synchronously, over some spatial scale. How does one reconcile the presence of strong local interactions, with individualistic responses by species to environmental gradients over broader spatial scales? When might one expect to observe concordant versus individualistic responses in range limits?

First, consider a community in which species in a given trophic level are to a reasonable approximation non-interactive. The geographical ranges of a given species should in this case just reflect the fundamental niche of that species (its basic abiotic and resource requirements), mapped onto the array of available environmental states, and constrained further by barriers to dispersal. Concordant changes in species' range limits following an environmental change requires that the following hold: 1) the edges of species' fundamental niches in abstract niche space must cluster; 2) species niches must remain relatively constant in the face of environmental change (i.e. "niche conservatism", Holt and Gaines 1992); 3) barriers to dispersal must be experienced similarly by most species. It seems unlikely in general that all of these will hold. This may help explain the general pattern of individualistic responses by species, while leaving room for some clear cases of concordant range responses.

In a multispecies context, interspecific interactions will often lead to a great deal of indeterminacy (Bender et al. 1984, Yodzis 1988) in the net effect of any change upon species' abundances. Close analyses of local communities usually reveal that most species are locked into a complex web of interactions, including both a few strong and numerous weak interactions. However, interaction strengths among co-occurring species within a community often do not reflect the importance of a particular key species in preventing the invasion of missing species into the system. The abundances of species among local assemblages where a key species does and does not occur are influenced by a complicated web of interactions involving both direct and indirect effects of species interactions both within and between assemblages (McPeek 1990a, Werner and McPeek 1994). For example, some fish species are key species in aquatic systems because predation by them is strong enough to drive some prey locally extinct, but these same key fish species have only weak direct effects on prey that coexist with them (McPeek 1990a, 1998, Werner and McPeek 1994). Moreover, fish can have an indirect positive effect on the prey with which they coexist, because some of the other prey species they exclude are also voracious predators of the fishes' coexisting prey (i.e. many invertebrate predators) (Werner and McPeek 1994). These invertebrate predators excluded by fish predation are relegated to fishless waters and coexist with (and feed upon) these prey species that are excluded from fish lakes. In each of these communities (water bodies with fish or invertebrates respectively as the top predators) the top predator (1) imparts strong negative direct effects on species in the other community that results in the exclusion of those species, (2) imparts weak negative direct effects on prey that can coexist with that top predator, and (3) imparts strong positive indirect effects on these same coexisting prey because it is excluding species via the direct effects in 1.

Just as changes in species composition will result from adding or losing a key species in a local community, the borders of prey species ranges may be strongly influenced by the changes in community structure that are caused by crossing the border of a key species' range. The borders of species that depend on the presence of a key species for their persistence in a community should be nearly coincident with the borders of that same key species. We know of no experimentally verified examples where species ranges are terminated because of the loss of a key species. However, one of the systems studied by one of us provides much circumstantial evidence that suggests this as the cause for range limits in a number of species. In eastern North America, species of *Enallagma* damselflies (Odonata: Coenagrionidae) segregate between water bodies that have fish as the top predators and large dragonflies as top predators (Johnson and Crowley 1980, Pierce et al. 1985, McPeek 1990a, 1998). The large dragonflies are also themselves relegated to fishless waters by fish predation (Crowder and Cooper 1982, Werner and McPeek 1994). Each *Enallagma* species coexists with only one of these two predators because each is differentially vulnerable to fish and dragonfly predators; those that are more active and use swimming to evade attacking predators coexist with the large dragonflies, and those that are less active and remain motionless when predators are near coexist with fish (Pierce et al. 1985, McPeek 1990b).

The possible effects of key species on prey distributional limits are evident in the distributions of those *Enallagma* species that coexist with fish. The 38 North American *Enallagma* species fall into two primary clades (McPeek and Brown 2000). One clade with 18 species has its center of diversity in New England (hereafter the "northern" clade), but three of these species are found only in the western half of the continent, and six species have distributions that stretch across the continent (Westfall and May 1996). In contrast, the other clade with 20 species has its center of diversity in the southeastern USA, and the ranges of all but one species are restricted to the eastern half of the continent (i.e. the area from the Gulf of Mexico north to southern Canada, and Texas to the Dakotas). (The one species in this clade that is now found outside this area, *E. basidens*, has greatly expanded its range outside of this area only since the 1930's (Westfall and May 1996).) The area of the continent covered by this second "southern" clade (excluding the current range of *E. basidens*) is very similar to the area inhabited by the sunfishes in the genus *Lepomis*, and the *Lepomis* are typically the most abundant littoral feeding fishes (in biomass and numbers) in lakes in this area of North America (Hayne and Ball 1956, Werner and Hall 1988).

Two lines of evidence suggest that the range boundaries of these southern-clade *Enallagma* species may be set by facilitation by their key species, the *Lepomis*. First, clade-level differences exist in phenotypic traits that make species better at avoiding dragonfly predation. Species in the southern clade are very poor swimmers, whereas species in the other clade are strong swimmers, although they rarely swim when attacked by predators (McPeek 2000). Second, the species that are found coexisting only with large dragonflies in eastern North America are common in lakes with fish in western North America (R. Garrison, D. Paulson, L. Ramsay, pers. comm.). Perhaps the fish species in western North America are less effective littoral predators and thus reduce the abundances of large, active dragonfly predators (and the *Enallagma* species that are found only in fishless waters in the east) to a much lesser degree than *Lepomis* are capable of doing in eastern North American waters. Consequently, the ranges of the species that are less able to cope with dragonfly predation (i.e. the southern clade species) are limited in their geographic distributions to only areas of the continent where *Lepomis* species occur. Clearly, these are only conjectures that must be experimentally tested. However, this proposed mechanism does illustrate how direct and indirect effects emanating from a few key species can limit the distributions of species in complex food webs. Replacement or loss of the key species may diminish or remove the strong, positive indirect effect of the key species on its coexisting prey, and thus limit the ranges of many of those prey.

Conclusions

The geographical range of a species should often reflect both the abiotic environment, the ensemble of species with which it interacts, and its own capacity to respond via natural selection to those interactions. When a species interacts with a complex ensemble of other species (competitors, predators, mutualists, etc.), variation in the abundance or traits of any of those species could conceivably lead to a range limit. One might expect that suites of interlocked demographic and evolutionary responses, rich in potential for nonlinear feedbacks, could generate a great deal of indeterminacy in the spatial responses of single species and entire communities to abiotic environmental gradients. Indeed, the microcosm experiments of Davis et al. (1999) reveal that interactions can indeed lead to sharp deviations in range limits from those expected from individual climatic tolerances alone.

Given the potential complexity of multispecies interactions and evolutionary responses, it is surprising that range limits are predictable at all. Yet empirical studies (Parmesan et al., this issue) reveal a substantial amount of predictability in studies of range limits. This makes sense, if the life of a species is governed principally by interactions with the physical environment, and/or a few key species (e.g. congeneric competitors, as in Gross and Price 2000). The theoretical studies we have explored here help sharpen our expectations about how strong interspecific interactions can mold range limits over both ecological and evolutionary time scales. The degree to which insights from these simple pairwise models pertain to species' ranges emerging in complex multispecies communities is an open and challenging question.

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