Notes and Comments Species' Borders and Dispersal Barriers

Emma E. Goldberg^{*} and Russell Lande[†]

Division of Biological Sciences, University of California, San Diego, La Jolla, California 92903

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ABSTRACT: Range limits of species are determined by combined effects of physical, historical, ecological, and evolutionary forces. We consider a subset of these factors by using spatial models of competition, hybridization, and local adaptation to examine the effects of partial dispersal barriers on the locations of borders between similar species. Prompted by results from population genetic models and biogeographic observations, we investigate the conditions under which species' borders are attracted to regions of reduced dispersal. For borders maintained by competition or hybridization, we find that dispersal barriers can attract borders whose positions would otherwise be either neutrally stable or moving across space. Borders affected strongly by local adaptation and gene flow, however, are repelled from dispersal barriers. These models illustrate how particular biotic and abiotic factors may combine to limit species' ranges, and they help to elucidate mechanisms by which range limits of many species may coincide.

Keywords: biogeography, cline, range limit, species interactions.

The locations of species' range limits are determined by a wide array of physical, historical, and biotic factors. Among these, competition, hybridization, and local adaptation may be quite important in shaping the borders between closely related or ecologically similar species. Here we modify existing theoretical models to illustrate how these processes can interact with spatial structure—in the form of a partial barrier to dispersal—to affect the locations of borders between species. The situations we consider therefore encompass a variety of population dynamic and geographic scenarios. Our focus is on understanding

[†] E-mail: rlande@biomail.ucsd.edu.

the relative locations of the range limits of various species (e.g., whether many range limits tend to occur in the same location) rather than identifying factors causing range limits of particular species. The approach we use connects results from theoretical population genetics with population dynamic models and biogeographic observations.

A feature of the environment that entirely prevents individual dispersal can obviously limit the range of a species. Environmental features that only partially reduce dispersal may slow rates of range expansion, but they are not expected by themselves to impose range limits. Such partial or "porous" (Rapoport 1982) barriers to dispersal may, however, interact with other ecological or evolutionary factors to induce range limits. Partial barriers may be imposed by, for example, sudden changes in currents or topography, a limited passageway like a strait or an isthmus, or a relatively narrow habitat feature such as a river.

Range limits of groups of species are often observed to align with one another (e.g., Horn and Allen 1978; Pielou 1979; Baker et al. 1998; Roy et al. 1998; Hughes et al. 2003; Swenson and Howard 2005). At the largest spatial scales, this is driven by geologic processes such as glaciation and plate tectonics (Pielou 1979; Cox and Moore 2005) and has led to the designation of faunal and floristic realms (Wallace 1876; Takhtajan 1986; Cox 2001). At smaller spatial scales, co-occurrence of species' range limits to form biotic provinces may be driven more by contemporary physical conditions (Pielou 1979; Halffter 1987; Gaylord and Gaines 2000; Unmack 2001; Morrone 2006). Species interactions, particularly hybridization, can cause borders between species (Key 1981; Hewitt 1988) and have also been suggested as driving range limit alignment (forming "suture zones," in which hybrid zones of many species pairs coincide [Remington 1968; Swenson and Howard 2005]). Here we consider some of these mechanisms to examine how species interactions may combine with abiotic conditions to cause co-occurrence of range limits.

In addition to such biogeographic observations, this investigation is prompted by an analogy with results from population genetics. Bazykin (1969) and Barton (1979*a*) showed that selection against heterozygotes can produce

^{*} E-mail: goldberg@biomail.ucsd.edu.

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a geographic cline in allele frequency, or a "tension zone" (Key 1968; Barton and Hewitt 1985), which moves toward a region of reduced individual dispersal. Such a cline is analogous to the border between the ranges of hybridizing species when hybrids have reduced fitness. This suggests that a border between hybridizing species will be attracted to a region of reduced dispersal, and we investigate this situation.

We use models of intra- and interspecific competition and mating to examine the effect of a partial barrier to dispersal on the position of the border between species. We find that borders maintained purely by competition or those maintained primarily by hybridization tend to move toward (be "attracted" to) dispersal barriers.

We also employ a model by Case and Taper (2000) to examine the situation in which two species experience stabilizing selection toward an optimum phenotype that varies over space because of an underlying environmental gradient. Dispersal decreases the degree of local adaptation for each species, and we show that the border between such species is "repelled" from a dispersal barrier because it diminishes detrimental gene flow. Finally, we discuss the influences of asymmetric species differences and temporal changes in dispersal barriers on biogeographic patterns.

Models

Much work has been done on population genetic models of clines in allele frequencies, and the intuition and logic of this area are relevant to the population dynamic models we use below. We therefore begin by discussing previous cline models.

Spatial models of allele frequencies (e.g., Haldane 1948; Bazykin 1969; Slatkin 1973, 1975, 1978; Nagylaki 1975, 1976, 1978; Barton 1979*a*, 1979*b*) typically assume constant population size across space and treat dispersal as diffusive and independent of space. A stable cline can be maintained by selection against heterozygotes (Bazykin 1969; Slatkin 1973; Barton 1979a) or by a balance between migration and spatially varying selective pressure (Slatkin 1973; Nagylaki 1975, 1976, 1978). For clines maintained by reduced heterozygote fitness (underdominance), regions of lower dispersal or lower population density tend to attract clines that would otherwise have a neutrally stable position or to stop clines that would otherwise be moving because of unequal fitnesses of the two homozygotes (Bazykin 1969; Barton 1979a). Such regions may accumulate multiple underdominant clines (Bazykin 1969; Slatkin 1975; Barton 1979b), thereby reducing gene flow and contributing to reproductive isolation between incipient species (Bazykin 1969; Barton 1979b; Walsh 1982).

The above models of allele frequencies do not, however, include population dynamics: population size at each lo-

cation is assumed to be fixed rather than determined by growth rates, dispersal, and species interactions. In the following three models, we investigate the impact of a dispersal barrier on the border between two species, and we therefore require models that explicitly include population dynamics. We use the term "border" to describe a limited region of sympatry in which the abundances of the two species decline to 0 in opposite directions. A border may be broad (if the region of sympatry is large) or narrow (if there is little sympatry), and its "position" is the location where the lines depicting abundance of the two species cross.

The results of the studies by Bazykin (1969) and Barton (1979*a*) suggest that, for two species forming hybrids with reduced fitness, the position of the border between the species may be attracted to a barrier to dispersal, and we investigate this possibility in model 2 below. In model 1, we examine a similar situation: for two species with greater interspecific than intraspecific competition, individuals of the rarer species will be less successful, causing competitive exclusion and possible formation of a stable spatial border between them. In model 3, we allow phenotypes to evolve in response to competition and environmental conditions. For each model, we illustrate the effects of a partial barrier to dispersal on the position of the border between the species.

The models below are based on standard diffusive Lotka-Volterra models describing competition between two similar species, but we make time and space discrete rather than continuous to simplify the treatment of hybridization and selection and to facilitate numerical analysis. We therefore assume that each species has nonoverlapping generations and that movement of individuals is only to neighboring spatial units or "demes" (Kimura and Weiss 1964). The models are straightforward modifications of previous work, so we only describe them briefly in the text and summarize them in the appendix. We consider only one-dimensional space and two species, but the methods are easily extended. Initially, we consider species with symmetric ecological interactions such that, in homogeneous space, a border with a stable shape but neutrally stable spatial position can form between the species. We also discuss results of asymmetric differences between species, which can produce a traveling border in the absence of a barrier to dispersal.

In Bazykin's (1969) model with continuous space, a dispersal barrier is defined by a sharp impediment to dispersal or a region in which the diffusion coefficient (describing the variance of individual dispersal distance per generation) is reduced. In discrete space with nearest-neighbor dispersal, the diffusion coefficient is replaced by the probability that an individual will disperse to a neighboring deme, and so we reduce this probability at or within



Figure 1: Model 1. A border between species, occurring when interspecific competition is stronger than intraspecific competition, is attracted to a partial dispersal barrier. *A*, A border with a stable shape but neutrally stable spatial position (without a barrier) is attracted to the center of a region of reduced dispersal. Solid lines indicate the population size of one species, and dashed lines show that of the other species. Light gray lines (border at x = 50) give the equilibrium without a dispersal barrier; black lines (border at x = 65) show the equilibrium after a dispersal barrier (*gray rectangle*) is imposed. The medium gray lines (border at x = 58) show an intermediate state with motion (*arrow*) left to right. Parameter values are identical for each species: $R_i = 0.1$, $K_i = 10$, $\alpha_{ij} = 1.1$, $\delta = 0.2$, c = 0.5, $\beta = 0$. See appendix for definitions. *B*, A border that is otherwise a traveling wave is attracted to the edge of a region of reduced dispersal. The arrow indicates the direction of movement. Darkening shades of gray show snapshots at four times, and black lines indicate the equilibrium position (border at x = 75). Parameter values are the same as in *A* except for $\alpha_{12} = 1.05$ and c = 0.1.

the dispersal barrier (more details in the appendix). Model 3 includes a dispersal barrier and an environmental gradient as distinct factors. This separates the concepts of individual movement, which may be impeded by barriers in the form of abrupt changes in habitat type (e.g., a river) or topography (e.g., a cliff) or other extrinsic factors (e.g., crosswinds or currents), from individual fitness, which is affected by the degree of adaptation to a smooth environmental gradient (e.g., continuous changes in temperature or elevation).

We consider two initial conditions in determining the effect of a dispersal barrier on the shape and location of the border between species: beginning with a few individuals of each species at opposite ends of the available space and beginning with the border formed in the absence of the barrier. For the parameter values used in the figures, the results from these two initial conditions are identical, so we show only the second. However, when the region of sympatry around the border does not extend into the barrier, the barrier does not affect the position of the border. We address implications of this scenario in the discussion.

Model 1: Strong Interspecific Competition

First, we consider a model of competition between two species in one-dimensional space. At each location in space, competition within and between species follows Lotka-Volterra dynamics, and individuals can disperse to adjacent locations in space (see the appendix for details). Competition is spatially homogeneous (all model parameters are constant across space). The possible outcomes are analogous to, but somewhat more complicated than, the three possible nonspatial outcomes (e.g., Roughgarden 1979). First, if both species coexist stably in the nonspatial model, they coexist everywhere in space. Second, if one species always excludes the other in the nonspatial model, it will exclude the other everywhere in space, though there may be a transient border between them in the form of a traveling wave. Third, if in the nonspatial model the surviving species is determined by the initial abundances, a border with a stable shape will form when initial abundances are not too asymmetric in number or space (Case et al. 2005). This third situation occurs when interspecific competition is stronger than intraspecific competition; such strong interspecific competition is observed in natural systems, though less commonly than the reverse (Connell 1983; Fowler 1986; Goldberg and Barton 1992). In this third situation, when the species are symmetric (have identical parameter values), the border's location will be neutrally stable, with an arbitrary position determined only by the initial conditions. When the species are asymmetric, the border will be a traveling wave. (Related models in which population growth rates or carrying capacities differ



Figure 2: Model 2. Hybridization between species (with inviable hybrids) allows a border to form even when interspecific competition is not stronger than intraspecific competition, and this border is attracted to a partial dispersal barrier. The border does not become centered in the barrier, as it did in figure 1*A*, because the region of sympatry is narrow compared with the width of the barrier. Figure components are the same as in figure 1*A* (the final position of the border is x = 61), and parameter values are the same except for $\beta = 0.01$ and $\alpha_{ij} = 0.75$.

between species and across space have shown other more complex conditions under which a stable border between the species may form [Bull and Possingham 1995; García-Ramos et al. 2000; Case et al. 2005].)

A partial barrier to dispersal can attract the borders formed in model 1, which would otherwise be neutrally stable or a traveling wave. Figure 1A shows the border formed by strong interspecific competition, and it also shows that this border moves toward a region in space where individual dispersal is reduced, ultimately centering itself in the dispersal barrier. Figure 1B shows a traveling wave border driven by unequal competitive strengths that is stopped by a region of reduced dispersal. Although the species on the right is a weaker competitor, it sends more individuals into the region of sympatry than does the species on the left, which is affected by the dispersal barrier, and so the position of the border is stabilized.

Model 2: Competition and Hybridization

Model 1 shows that species' borders can be attracted to a region of reduced dispersal, but it applies only when interspecific competition is stronger than intraspecific competition. Adding interspecific hybridization to the previous model, however, allows a stable border to form in homogeneous space even when intraspecific competition is greater, and we show that this also results in borders being attracted to barriers.

We assume that hybrids are inviable to limit the models

to situations with two clear species. This limitation is restrictive but not unreasonable: such hybridization occurs between closely related species in laboratory studies (Dobzhansky 1951; Coyne and Orr 1989) and nature (Arnold 1997), and it may be more common that is realized because hybrid phenotypes are not seen. In addition to situations where embryos are inviable, our formulation is also appropriate whenever individual mating success is reduced by the presence of members of the other species, such as if an abundance of heterospecifics makes mate identification or courtship inefficient.

In the model, the chance of an individual of the first species mating with a conspecific is greater in demes where the first species is more common than the second and vice versa (details in the appendix). Fitnesses of the species are therefore frequency dependent, and a border with a stable shape and neutrally stable position may exist between the species, even when it would not under competition alone (Ribeiro and Spielman 1986; Case et al. 2005). This is true for any amount of hybridization (Goldberg and Lande 2006); the more hybridization, the smaller the region of sympatry.

Figure 2 shows this border, and it also shows that the border is attracted to a partial barrier to dispersal. In this instance, the border is not centered in the barrier, as it was in figure 1*A*, because the width of the region of sympatry is narrower than that of the barrier. The species on the right retreats because it sends fewer individuals toward the border than does the species on the left; when the region of sympatry is entirely within the barrier, this migration differential is not present, and the border stops moving.

Model 3: Competition and Local Adaptation

Finally, we include genetics in the model, allowing adaptation in a single quantitative character to an underlying environmental gradient (details in Case and Taper 2000, with a summary in the appendix). This character affects competition, with stronger competition between individuals of more similar phenotypes; because the phenotype distribution of each species at each location is assumed to be Gaussian, the average intraspecific competition. Because the optimum phenotype varies across space, gene flow inhibits local adaptation and thus reduces the fitness of each species. The combination of competition and gene flow can create a stable border between the species (Case and Taper 2000).

The presence of a barrier to dispersal reduces gene flow, thus allowing better adaptation (fig. 3) and increasing fitness. The species that the barrier affects more (the species on the right in all our figures) benefits more, thus ex-



Figure 3: Model 3. A partial barrier to dispersal will repel, to some extent, a border maintained by local adaptation. In the species shown by the dashed lines, local adaptation improves in the region of reduced dispersal, in which the mean phenotype evolves closer to the optimum (*B*), and the population size therefore increases in that region, pushing the border to the left (*A*). Figure components in *A* are the same as in figures 1*A* and 2; the border's final position is x = 35. Mean phenotypes are plotted in *B*, and the optimum phenotype is shown by the dotted line. Parameter values are $r_i = 0.1$, $K_i = 10$, $\sigma_z^2 = 1$, $\sigma_u^2 = 25$, $\sigma_s^2 = 300$, $h^2 = 0.5$, $\theta(x) = 0.1x$, $\delta = 0.2$, c = 0.5, and $\beta = 0$; see appendix for definitions.

panding its range (pushing the border to the left in fig. 3*A*). (If the barrier in figure 3 extended just past the center of the border [e.g., if the barrier were from x = 45 to x = 65], the border would also be pushed to the left.) The dispersal barrier therefore repels the border to some extent. This repulsion stops when the region of sympatry is mostly outside the barrier. These results hold for any combination of parameter values under which a stable border forms in the absence of a barrier (see Case and Taper 2000).

When hybridization is included, as in model 2, the direction of movement of the border is determined by the balance between the forces of hybridization and local adaptation. With appreciable hybridization and a strong barrier, the border moves toward the barrier; when the environmental gradient is relatively steep, the border moves away from the barrier (results not shown).

Discussion

Range limits of species are determined by combinations of physical, ecological, evolutionary, and historical factors. Among these, we investigated how dispersal barriers, competition, hybridization, and local adaptation determine the spatial position of species' borders. With strong interspecific competition (model 1) or with matings between species with inviable hybrids even when interspecific competition is weak (model 2), we found that the border between two species often will be attracted to a region of reduced dispersal. In these two situations, a balance between dispersal and the reduced fitness of the rarer species maintains a border with a stable shape between the species. When part of the sympatric area falls in a region of reduced dispersal, the dispersal asymmetry at the edge of the barrier will give an advantage to the species that has a larger population size just outside the barrier than inside, thus pushing the border into the barrier (figs. 1A, 2). For a barrier that is narrow compared with the region of sympatry, pushing from the two edges of the barrier will center the border within the region of reduced dispersal (fig. 1A). For a wider barrier, the border will be attracted only part way into the barrier, stopping when the sympatric area is mostly inside the barrier (fig. 2). At this point, asymmetric dispersal no longer aids the advancing species because there is essentially no population size difference across the edge of the barrier.

With local adaptation to a smooth environmental gradient, the border between the species will be repelled by a dispersal barrier (fig. 3*A*). In this case, asymmetric gene flow across the edge of the barrier is more detrimental to the species with a greater population size just outside the barrier than inside. This result contrasts with the effect of an ecotone, which attracts species' borders (Case and Taper 2000; Goldberg and Lande 2006). A narrow region across which the environment changes rapidly may therefore either attract a border, if this change affects the optimum phenotype but does not reduce individual dispersal, or repel a border, if this change impedes dispersal but does not affect the optimum phenotype. Some narrow regions of rapid environmental change may affect both the optimum phenotype and dispersal, making it difficult to predict whether they will attract or repel species' borders.

The model results that we describe concerning attraction or repulsion of species' borders from dispersal barriers occur for any size or strength of barrier, though stronger barriers cause more rapid changes in species' borders. However, for a border with a neutrally stable position in the absence of a dispersal barrier, the imposition of a barrier outside the area of sympatry will not attract or repel the border, although it may still trap a traveling border. Species pairs with wider areas of sympatry at their borders can be affected by barriers in more locations and may therefore be more likely to have borders that coincide with other species pairs.

We show one example of how biotic and abiotic factors may combine to limit species ranges. When one species would likely exclude a weaker competitor in homogeneous space, the presence of a partial dispersal barrier can allow them to coexist stably (fig. 1B). Thus, while neither competition nor the region of reduced dispersal would alone impose a stable range limit, the interaction of these two factors can create a border between the species with a stable shape and location. This effect of a partial dispersal barrier stopping the advance of a species is consistent with previous work showing that patchy spatial structure can interact with an Allee effect to limit the range of a species (Keitt et al. 2001). In our model, however, the negative growth rate at the edge of the advancing species' range results from the greater local abundance of the competitor rather than being an intrinsic feature of the population.

Real physical barriers change over time because of changing geologic or climatic conditions. A barrier that increases in size would have an increasing effect on nearby borders, and one that disappears would leave any borders it had affected as neutrally stable in their new positions. A barrier that moves slowly across space could carry or push borders with it, thus perhaps collecting borders between many pairs of species. Even if the barrier then vanished, this could leave many range limits co-occurring.

Real species pairs are not likely to interact in a perfectly symmetrical way. We illustrate one possible result for asymmetry in competitive ability (fig. 1*B*), and here we briefly summarize results of other asymmetries between the species, which are easily incorporated in the models. In the absence of local adaptation (models 1, 2), if one of the species has a higher dispersal rate or a higher carrying capacity or is a stronger competitor, it will have an advantage. Asymmetries in intrinsic growth rates are somewhat more complicated: when the border is maintained by hybridization (model 2), the species with the higher growth rate has the advantage, but when the border is maintained by strong interspecific competition (model 1), the species with the higher intrinsic growth rate is at a disadvantage because it declines more rapidly when in the minority. When the asymmetry is large relative to the strength of the barrier, the species with the advantage will expand its range, forcing its competitor to retreat and eventually excluding it from the available space. When the barrier is relatively strong, it can stop the advance. With local adaptation to an environmental gradient (model 3), the species with the higher carrying capacity, higher intrinsic growth rate, lower dispersal rate, or higher heritability will have the advantage. This species will expand its range through a weak barrier, but the other species will still maintain itself near the edge of available space since it is not disadvantaged there by gene flow. An advancing border can be repelled by a strong barrier. These outcomes suggest a variety of possible mechanisms by which biotic exchange may be asymmetric (Vermeij 1991).

Application of our results to empirical data on species ranges could help elucidate the importance of partial barriers to dispersal, species interactions, and local adaptation in setting range limits. Model 2 predicts that borders between closely related hybridizing species will be more clustered in space than will borders between other species pairs and that these clusters of borders will coincide with regions of reduced dispersal. When a smooth environmental gradient extends over a much larger scale than the sympatric regions of species' borders, model 3 predicts that clustering of species' borders will be more pronounced when the slope of this gradient is small (or 0) than when it is large. In models 1 and 2, broader borders are more likely to overlap dispersal barriers and become centered in them, facilitating the alignment of borders between multiple pairs of species. Additional tests may be possible using data on changes in species' borders over time. For example, borders are predicted to move in concert with slowmoving barriers, and borders are predicted to move faster toward (models 1, 2) or away from (model 3) stronger barriers, stopping when the barrier's edge does not fall in the region of sympatry. The increasing availability of databases on species ranges will aid searches for the above patterns predicted by these models. While the observation of any of these patterns in a particular system would not rule out all alternative hypotheses, it would strongly suggest that the interaction of dispersal barriers with competition (model 1), hybridization (model 2), or local adaptation (model 3) drives range limits, and the relevance of these processes could then be assessed more directly with tests in the field.

Our results illustrate how population dynamic and genetic forces can interact with partial barriers to dispersal, affecting the spatial distribution of borders between similar species. They thus emphasize that our understanding of species' range limits and biogeographic patterns will be more complete when ecological, evolutionary, and physical forces are considered together.

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APPENDIX

Model Details

In models 1–3, we use a discretized version of the diffusive Lotka-Volterra competition model. In each time step (generation), population size at each location is altered first by competition, then (in model 2 and optionally in model 3) by hybridization, and then by dispersal.

Let $n_i(x)$ denote the population size of species *i* at location (or deme) *x*. Population size is also a function of time, but we outline here only changes within a single time step, and so we omit the time argument to keep the notation simpler. Let R_i be the intrinsic growth rate and K_i be the carrying capacity of species *i*, which we assume are constants across space and time. The competition coefficient α_{ij} is the effect of species *j* on species *i*. The degree of hybridization is determined by the value of β , which is the amount of consideration given to a heterospecific individual, relative to a conspecific individual, when choosing a mate. The actual amount of interspecific matings depends on the abundances of the two species (see eq. [A2]).

The probability that an individual disperses to the adjacent deme to the left is $\delta_{-}(x)$, and the probability of dispersal to the right is $\delta_{+}(x)$. In the limit of infinitesimal units of time and space, these dispersal probabilities can be related to the diffusion coefficient and transport velocity (e.g., Nagylaki 1976; Shigesada and Kawasaki 1997, p. 57). We consider only barriers in which dispersal is reduced by a constant fraction *c* in a block of demes. Therefore, for demes well away from the barrier, $\delta_{-}(x) = \delta_{+}(x) \equiv$ δ ; within the barrier, $\delta_{-}(x) = \delta_{+}(x) = c\delta$; for the deme to the left of the barrier, $\delta_{-}(x) = \delta, \delta_{+}(x) = c\delta$; and for the deme to the right of the barrier, $\delta_{-}(x) = c\delta, \delta_{+}(x) = \delta$. The edges of space are reflecting.

For models 1 and 2, in one time step, the new population size of species i at location x due to competition is

$$n_i^*(x) = n_i(x) \left[1 + R_i \left(1 - \frac{n_i(x) - \alpha_{ij} n_j(x)}{K_i} \right) \right],$$
 (A1)

the population size after hybridization is

$$n_i^{**}(x) = \frac{(n_i^*(x))^2}{n_i^*(x) + \beta n_i^*(x)},$$
 (A2)

and finally, the population size after dispersal is

$$n_i^{***}(x) = [1 - \delta_{-}(x) - \delta_{+}(x)]n_i^{**}(x) + \delta_{+}(x - 1)n_i^{**}(x - 1) + \delta_{-}(x + 1)n_i^{**}(x + 1).$$
(A3)

For the next generation, $n_i^{***}(x)$ becomes $n_i(x)$ in equation (A1).

In model 3, the evolution of a quantitative trait is affected by stabilizing selection toward an optimum value that varies over space, by competition with con- and heterospecifics (stronger for more similar phenotypes, independent of species identity), and by gene flow. The derivation of this model is fairly complicated, so we refer the reader to the study by Case and Taper (2000) for the original derivation and the study by Goldberg and Lande (2006) for the discretized version and incorporation of hybridization. Here, we define the parameter values only qualitatively to assist with interpretation of figure 3: $\theta(x)$ is the optimum phenotype, r is the intrinsic growth rate (in continuous time), σ_{μ} is the width of the Gaussian resource utilization function, σ_z^2 is the variance of the Gaussian phenotypic distribution of each species at each location, σ_s^2 is the variance of the Gaussian stabilizing selection function, and h^2 is the heritability.

Literature Cited

- Arnold, M. J. 1997. Natural hybridization and evolution. Oxford University Press, Oxford.
- Baker, W. J., M. J. E. Coode, J. Dransfield, S. Dransfield, M. M. Harley, P. Hoffmann, and R. J. Johns. 1998. Patterns of distribution of Malesian vascular plants. Pages 243–258 *in* R. Hall and J. D. Holloway, eds. Biogeography and geological evolution of SE Asia. Backhuys, Leiden.
- Barton, N. H. 1979a. The dynamics of hybrid zones. Heredity 43: 341-359.
- ——. 1979b. Gene flow past a cline. Heredity 43:333–339.
- Barton, N. H., and G. M. Hewitt. 1985. Analysis of hybrid zones. Annual Review of Ecology and Systematics 16:113–148.
- Bazykin, A. D. 1969. Hypothetical mechanism of speciation. Evolution 23:685–687.
- Bull, C. M., and H. Possingham. 1995. A model to explain ecological parapatry. American Naturalist 145:935–947.
- Case, T. J., and M. L. Taper. 2000. Interspecific competition, environmental gradients, gene flow, and the coevolution of species' borders. American Naturalist 155:583–605.
- Case, T. J., R. D. Holt, M. A. McPeek, and T. H. Keitt. 2005. The community context of species' borders: ecological and evolutionary perspectives. Oikos 108:28–46.

- Connell, J. H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. American Naturalist 122:661–696.
- Cox, C. B. 2001. The biogeographic regions reconsidered. Journal of Biogeography 28:511–523.
- Cox, C. B., and P. D. Moore. 2005. Biogeography: an ecological and evolutionary approach. 7th ed. Blackwell, Oxford.
- Coyne, J. A., and H. A. Orr. 1989. Patterns of speciation in *Drosophila*. Evolution 43:362–381.
- Dobzhansky, T. 1951. Genetics and the origin of species. Columbia University Press, New York.
- Fowler, N. 1986. The role of competition in plant communities in arid and semiarid regions. Annual Review of Ecology and Systematics 17:89–110.
- García-Ramos, G., F. Sánchez-Garduño, and P. F. Maini. 2000. Dispersal can sharpen parapatric boundaries on a spatially varying environment. Ecology 83:749–760.
- Gaylord, B., and S. D. Gaines. 2000. Temperature or transport? range limits in marine species mediated solely by flow. American Naturalist 155:769–789.
- Goldberg, D. E., and A. M. Barton. 1992. Patterns and consequences of interspecific competition in natural communities: a review of field experiments with plants. American Naturalist 139:771–801.
- Goldberg, E. E., and R. Lande. 2006. Ecological and reproductive character displacement on an environmental gradient. Evolution 7:1344–1357.
- Haldane, J. B. S. 1948. The theory of a cline. Journal of Genetics 48: 277–284.
- Halffter, G. 1987. Biogeography of the montane entomofauna of Mexico and Central America. Annual Review of Entomology 32: 95–114.
- Hewitt, G. M. 1988. Hybrid zones: natural laboratories for evolutionary studies. Trends in Ecology & Evolution 3:158–167.
- Horn, M. H., and L. G. Allen. 1978. A distributional analysis of California coastal marine fishes. Journal of Biogeography 5:23–42.
- Hughes, J. B., P. D. Round, and D. S. Woodruff. 2003. The Indochinese-Sundaic faunal transition at the Isthmus of Kra: an analysis of resident forest bird species distributions. Journal of Biogeography 30:569–580.
- Keitt, T. H., M. A. Lewis, and R. D. Holt. 2001. Allee effects, invasion pinning, and species' borders. American Naturalist 157:203–216.
- Key, K. H. L. 1968. The concept of stasipatric speciation. Systematic Zoology 17:14–22.
- ———. 1981. Species, parapatry, and the morabine grasshoppers. Systematic Zoology 30:425–458.
- Kimura, M., and G. H. Weiss. 1964. The stepping stone model of population structure and the decrease of genetic correlation with distance. Genetics 49:561–576.

- Morrone, J. J. 2006. Biogeographic areas and transition zones of Latin America and the Caribbean islands based on panbiogeographic and cladistic analyses of the entomofauna. Annual Review of Entomology 51:467–494.
- Nagylaki, T. 1975. Conditions for the existence of clines. Genetics 80:595–615.
- ———. 1976. Clines with variable migration. Genetics 83:867–886.
- ——. 1978. Clines with asymmetric migration. Genetics 88:813– 827.
- Pielou, E. C. 1979. Biogeography. Wiley, New York.
- Rapoport, E. H. 1982. Areography: geographic strategies of species. Pergamon, Elmsford, NY.
- Remington, C. L. 1968. Suture-zones of hybrid interaction between recently joined biotas. Evolutionary Biology 2:321–428.
- Ribeiro, J. M. C., and A. Spielman. 1986. The satyr effect: a model predicting parapatry and species extinction. American Naturalist 128:513–528.
- Roughgarden, J. 1979. Theory of population genetics and evolutionary ecology: an introduction. Macmillan, New York.
- Roy, K., D. Jablonski, J. W. Valentine, and G. Rosenberg. 1998. Marine latitudinal diversity gradients: tests of causal hypotheses. Proceedings of the National Academy of Sciences of the USA 95:3699– 3702.
- Shigesada, N., and K. Kawasaki. 1997. Biological invasions: theory and practice. Oxford University Press, Oxford.
- Slatkin, M. 1973. Gene flow and selection in a cline. Genetics 75: 733–756.
- ———. 1975. Gene flow and selection in a two-locus system. Genetics 81:787–802.
- . 1978. Spatial patterns in distributions of polygenic characters. Journal of Theoretical Biology 70:213–228.
- Swenson, N. G., and D. J. Howard. 2005. Clustering of contact zones, hybrid zones, and phylogeographic breaks in North America. American Naturalist 166:581–591.
- Takhtajan, A. 1986. Floristic regions of the world. University of California Press, Berkeley.
- Unmack, P. J. 2001. Biogeography of Australian freshwater fishes. Journal of Biogeography 28:1053–1089.
- Vermeij, G. 1991. When biotas meet: understanding biotic interchange. Science 253:1099–1104.
- Wallace, A. R. 1876. The geographic distribution of animals. Harper, New York.
- Walsh, J. B. 1982. Rate of accumulation of reproductive isolation by chromosome rearrangements. American Naturalist 120:510–532.

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