EVOLUTION OF A SPECIES' RANGE

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Abstract.—Gene flow from the center of a species' range can stymie adaptation at the periphery and prevent the range from expanding outward. We study this process using simple models that track both demography and the evolution of a quantitative trait in a population that is continuously distributed in space. Stabilizing selection acts on the trait and favors an optimum phenotype that changes linearly across the habitat. One of three outcomes is possible: the species will become extinct, expand to fill all of the available habitat, or be confined to a limited range in which it is sufficiently adapted to allow population growth. When the environment changes rapidly in space, increased migration inhibits local adaptation and so decreases the species' total population size. Gene flow can cause enough maladaptation that the peripheral half of a species' range acts as a demographic sink. The trait's genetic variance has little effect on species persistence or the size of the range when gene flow is sufficiently strong to keep population densities far below the carrying capacity throughout the range, but it can increase the range width and population size of an abundant species. Under some conditions, a small parameter change can dramatically shift the balance between gene flow and local adaptation, allowing a species with a limited range to suddenly expand to fill all the available habitat.

A familiar experience when traveling across a continent is to see a widely distributed species decline in abundance until it disappears from the local community. Such range boundaries often coincide with discontinuities in the habitat, for example, with a mountain range or the ocean's edge. But in other cases the boundaries lie at seemingly arbitrary points along continuous gradients of environmental factors such as temperature and moisture. Such boundaries confront us with a mystery: What sets the geographical limits on a species' range? From an ecological perspective, the (tautological) answer is that the species reaches the limits of its niche. When the density of a key predator becomes too high or the concentration of a limiting nutrient too low, the birthrate falls below the death rate, and the population is no longer able to sustain itself.

But from an evolutionary perspective, there is a deeper mystery. Why do the populations at the range margin not adapt to their local conditions and then spread outward? One broad category of explanations is that the species has reached an intrinsic limit in its evolutionary capacity. Most palm trees, for example, seem constrained from evolving a tolerance for hard frosts. In genetic

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terms, the range limit in such cases is determined by an evolutionary constraint: the species simply lacks the appropriate mutations to adapt to greater environmental extremes. However, although there must ultimately be physical limits to the niche, this explanation conflicts with the ready response of so many traits to artificial selection.

The focus of this article is on a second type of explanation. One expects that peripheral populations receive gene flow from the center of the species' range. These immigrant genes will typically be adapted to the conditions at the range center and could inhibit adaptation at the periphery. Peripheral populations are thus trapped by gene flow into acting as demographic sinks, preventing the range from expanding outward. Mayr (1963) suggested that gene flow from large, central populations might limit adaptation at the periphery and so halt range extension. The basic concepts behind this suggestion have been supported by both empirical and theoretical studies (Hoffman and Blows 1994). Work on several species has shown that gene flow in a patchy habitat can keep local populations in a maladapted state (e.g., Camin and Ehrlich 1958; McNeilly 1968; Antonovics 1976; Endler 1977; Stearns and Sage 1980; Macnair 1981; Dhondt et al. 1990; Blondel et al. 1992; Riechert 1993; Dias 1996). Likewise, models of demographic sources and sinks have shown that asymmetrical gene flow can inhibit local adaptation (Holt and Gaines 1992; Kawecki 1995; Holt and Gomulkiewicz 1997).

Here we study the possibility that range limits are determined by a balance between adaptation and gene flow using models that describe both the evolution and demography of a species distributed in space. The models consider a quantitative trait that experiences different selection pressures in different parts of the range. The kinds of questions we have are, When will gene flow limit a species' range? What is the range boundary expected to look like in these circumstances?

The first theoretical studies of the interplay between migration and population persistence were purely demographic models (e.g., Skellam 1951; Okubo 1980). A major result from that work was that a population cannot persist in a suitable habitat patch if individuals disperse too rapidly into neighboring regions that are unsuitable. The first quantitative genetic models to examine adaptation under spatially varying patterns of selection in continuous populations assumed that population size is constant in time and space. Felsenstein (1977) found that when the optimal value for a quantitative trait varies linearly in space, the trait's mean evolves to the local ecological optimum at all points. Although migration introduces alleles adapted to other environments into each local population, the effects of gene flow cancel when population densities are equal everywhere because the number of introduced alleles that decrease the trait equals the number of alleles that increase the trait.

This outcome no longer holds when population sizes vary in space. In an earlier work (García-Ramos and Kirkpatrick 1997), the evolution of a cline was studied when population densities are fixed in time but decrease in space from the range center to the periphery. The changes in population density produce a net flux of genes toward the periphery. This gene flow establishes a migration-selection balance that can cause substantial maladaptation in peripheral popula-

tions under biologically plausible conditions. A model that includes both evolutionary and demographic change was introduced by Pease et al. (1989). They considered a quantitative trait under a clinal pattern of selection that changes in time and allowed a local population's growth rate to be determined by how closely its trait mean matches the ecological optimum in that spot. They showed that environmental changes in time must be sufficiently small if the species is to avoid extinction.

Here we build on this foundation by exploring how interactions between gene flow and local selection pressures can constrain the geographical range of a species. The models track evolutionary and demographic changes in a population distributed continuously in space. Variation in the environment generates patterns of selection that change in space but that are constant in time. A quantitative trait evolves under the influences of selection and gene flow. All points in the environment are habitable: there is no extrinsic limit to how far the species can expand in space. Populations that are well adapted to their local environment increase toward the carrying capacity, whereas those whose trait values lie far from the local ecological optimum decline. Models developed below will show how and when the feedback between adaptation, gene flow, and population growth can limit the spread of a species.

<div align="center">MODELS</div>

We will begin by describing the evolution of a quantitative character in a population that inhabits an environment that changes in space. The trait's evolution is found to depend on the densities of individuals at different points in the range, which leads us to consider how the trait and population densities change jointly. We first study this question by introducing a very simple model that caricatures the problem by reducing the trait and population density to a single variable. We then go on to consider a more detailed model that accounts explicitly for both demography and evolution.

Our models assume that the species is distributed continuously in space in a linear habitat. (The results also apply to a two-dimensional range if environmental change occurs only along a single dimension.) Following birth, individuals disperse randomly. The variance in distance between parent and offspring, along the relevant axis, is denoted σ^2; in one dimension, σ is the root-mean square distance between the birthplaces of a female and her offspring. Selection acts on a normally distributed quantitative trait. We assume that the mean of the trait responds to directional selection at a rate that is proportional to the selection intensity, an assumption that is quite robust to the genetics underlying the trait (Turelli and Barton 1994). The trait's additive genetic variance is denoted G. Local population sizes are taken to be sufficiently large that random genetic drift is negligible.

These assumptions lead to a partial differential equation that describes the rates of change in the trait mean $\bar{z}$ at each location x:

$$\frac{\partial \bar{z}}{\partial t} = \frac{\sigma^2}{2} \frac{\partial^2 \bar{z}}{\partial x^2} + \sigma^2 \frac{\partial \ln(n)}{\partial x} \frac{\partial \bar{z}}{\partial x} + G \frac{\partial \bar{r}}{\partial \bar{z}}, \tag{1}$$

where n is the population density (Pease et al. 1989); n and $\bar{z}$ are understood to be functions of x. Here $\bar{r}$ denotes the intrinsic rate of increase for a local population, averaged over all its phenotypes. Because selection is assumed to be density and frequency independent, the rate of change in the density of any phenotype can be written as the sum of a component that declines with density but is independent of the phenotype and a component that depends on the phenotype but not density; $\bar{r}$ is the mean of the latter. Equation (1) can be derived either from the underlying continuous processes or as the limit of a discrete-time stepping-stone model (see Nagylaki 1975; Okubo 1980). In the latter case, $\bar{r}$ corresponds to $\ln(\bar{\bar{W}})$. Equation (1) holds even when G, σ^2, and fitnesses are not constant in space or time.

   This result shows that three factors influence evolution of the trait's mean. The first term on the right-hand side of equation (1) represents the diffusion of genes that results from random dispersal: migration tends to increase the trait mean in a locality, for example, if the surrounding localities have higher means. The second term, which also involves migration, accounts for asymmetrical gene flow caused by changes in density over space: gene flow from more abundant populations will increase $\bar{z}$, for example, if the trait mean is higher in those regions (i.e., if $\partial \bar{z}/\partial x > 0$ and $\partial \ln(n)/\partial x > 0$, or $\partial \bar{z}/\partial x < 0$ and $\partial \ln(n)/\partial x < 0$). The effect of asymmetrical gene flow depends on $\ln(n)$, because only relative density matters: multiplying $n(x)$ by a constant factor would make no difference. The last term reflects the force of directional selection favoring the ecologically optimal value for z in each locality. Notice that while the rate of evolution caused by selection (the last term) depends on the amount of genetic variation available, the impact of gene flow (the first two terms) does not. We will see later that this fact has important implications for how the genetic variance affects evolution of the range.

   Although equation (1) holds quite generally, we will make a series of additional assumptions to make analysis tractable. At each locality x there is a single value of the trait, $\theta(x)$, that maximizes survival and reproduction. This optimum changes as a linear function of space: $\theta(x) = bx$. The parameter b measures the steepness of the environmental gradient, that is, how rapidly the optimum changes as one moves across the range. Lifetime fitness is lower for individuals whose phenotypes deviate farther from the optimum. Specifically, the intrinsic rate of increase for individuals with phenotype z is

$$r(z) = r_{\max} - \frac{(\theta(x) - z)^2}{2V_s}. \tag{2}$$

Here $r_{\max}$ is the intrinsic rate of increase for optimally adapted individuals, and V_s measures the strength of stabilizing selection toward the optimum $\theta(x)$, with larger values corresponding to weaker selection. (This fitness function produces the same rate of evolution as a Gaussian fitness function with variance V_s in a discrete-time model.) Under these assumptions, the last term on the right-hand side of equation (1) becomes $G(bx - \bar{z})/V_s$, where $\bar{z}(x)$ is the trait mean at point x.

We will initially assume that b, V_s, and G are constant across the range. Although this condition will certainly never be met exactly in nature, it may often be a plausible approximation. Moreover, since we know little about the factors that determine genetic variance or selection strength in nature, there is no straightforward alternative to this simple assumption. Assuming a constant genetic variance is consistent with an additive polygenic model, provided that a large number of genes contribute and selection is weak (Slatkin 1978; Barton and Turelli 1989). Because we will work with dimensionless ratios, this assumption does not restrict the range of the scaled parameters we use. We return later to the situation in which these parameters vary in space.

Equation (1) shows that evolution of the trait is affected by variation in population density across the range: populations can only track their local optima if density is the same everywhere. Conversely, population density will generally depend on how well a population is adapted to its local environment. This brings us to consider models that account for the feedback between evolution and demography. We look first at a simplified model in which changes in population density and the trait are subsumed into a single equation, then study a model that accounts separately for evolution and demography.

A Simplified Model of Demography

Here we consider a model in which simultaneous changes in adaptation and demography are collapsed down to a single equation. This greatly simplifies the analysis and allows us to see the qualitative outcome of interest: when gene flow constrains a species' geographical range.

Suppose that equilibrium population density at each point is an increasing function of that local population's mean fitness:

$$n(x) = ke^{\bar{r}\gamma}. \tag{3}$$

The parameter γ measures the intensity of population regulation, with $\gamma = 0$ corresponding to soft selection and a large value of γ implying that the population size is very sensitive to mean fitness. Equation (3) holds if each individual's absolute fitness decreases with increasing population size according to a power law, as $n^{-1/\gamma}$ (see Barton 1986 for a derivation in the analogous discrete-time case). This is a simplification of the actual population dynamics: the density at equilibrium depends on migration as well as on mean fitness, and the power law implies that absolute fitness grows without limit as density approaches 0. Nevertheless, this simple model is attractive because it may capture the qualitative feedback between adaptation and population growth and because it leads to analytic solutions. Note that if fitness approaches some upper bound at low density, rather than increasing indefinitely, then the sensitivity of adaptation to gene flow will be greater than implied by the model of equation (3). Thus, this model gives a conservative picture of the potential for gene flow to inhibit adaptation and prevent the range from expanding.

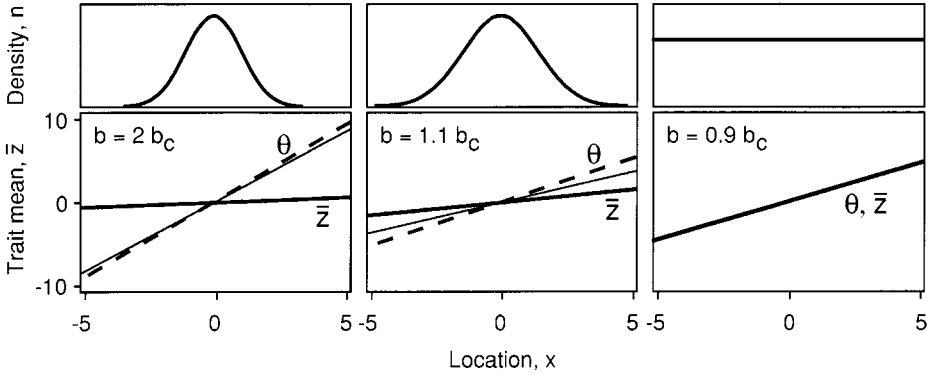We find the rate of change in the trait mean by calculating $\bar{r}$ from equation

FIG. 1.—Examples of solutions to the simple model of equation (4) for three different values of the environmental gradient, b. The thick dashed line shows the optimum for the trait, $\theta = bx$; this is always an equilibrium, for which density is constant at $n = k$. The thick solid line shows the alternative stable solution for $\bar{z}$, given by equation (5), which exists when $b > b_c$. The thin line shows the unstable solution for $\bar{z}$, which lies between the two stable states. When $b < b_c$, the stable equilibrium is with perfect adaptation ($z = \theta$), and the population is at carrying capacity ($n = k$) everywhere (*right-hand panel*). Distance is measured in units $\sigma\sqrt{V_s/4G}$ and the trait in units of $\sqrt{V_s/\gamma}$. The maximum density is $n(0) = k\exp(r_{max} - I_s/2)$.

(2). Substituting that result and equation (3) into equation (1) gives

$$\frac{\partial\bar{z}}{\partial t} = \frac{\sigma^2}{2}\frac{\partial^2\bar{z}}{\partial x^2} + \frac{(bx - \bar{z})}{V_s}\left[G - \sigma^2\gamma\frac{\partial\bar{z}}{\partial x}\left(b - \frac{\partial\bar{z}}{\partial x}\right)\right]. \tag{4}$$

Equation (4) shows that an equilibrium occurs when the species fills the habitat with equal density (in which case, $\partial^2\bar{z}/\partial x^2 = 0$), and each local population evolves to its ecological optimum (so that $\bar{z}(x) = bx$). On an infinite range, this equilibrium is stable to small perturbations regardless of the strength of density regulation (i.e., the size of γ) or the steepness of the environmental gradient (the size of b). However, this analysis may not apply on a finite range or with a nonlinear environmental gradient (see the appendix).

   If the gradient is steep enough, however, equation (4) shows that there is another equilibrium in which the species is confined to a limited area. In this event, there is a linear cline in the trait mean:

$$\bar{z}(x) = \frac{b}{2}[1 - \sqrt{1 - (b_c/b)^2}]x, \tag{5}$$

where $b_c^2 = 4G/(\sigma^2\gamma)$. Examples of this equilibrium are shown in figure 1.

   For this equilibrium to exist, equation (5) shows that we must have $b > b_c$. That is, the change in optimum must be sufficiently rapid, and the population must be sensitive to mean fitness. It is interesting that this criterion is independent of the strength of selection, V_s. The threshold can be expressed as $(b_c\sigma/$

$\sqrt{G}) = \sqrt{2/\gamma}$, which relates the change in optimum over one dispersal range $(b_c\sigma)$ measured in genetic standard deviations $(\sqrt{G})$ to the strength of density-dependent regulation $(\sqrt{2/\gamma})$.

What of the distribution of density across the range? Substituting equation (5) and the expression for $\bar{r}$ into equation (3) shows that $n(x)$ is proportional to a Gaussian distribution. Thus, the range boundary is ''soft'' in the sense that the population density never actually reaches 0 as one moves farther from the range center but rather approaches 0 asymptotically. We can measure the range's extent R by the region that encloses, say, 95% of the total population. Since $n(x)$ has a Gaussian form, this criterion corresponds to 2 SD on either side of the range center. (Alternatively, if one prefers to define the range as some other number s of standard deviations, the following result can simply be multiplied by $s/2$.) A calculation shows that the range's width is

$$R = \frac{8 \sqrt{V_s}}{\sqrt{\gamma} [1 + \sqrt{1 - (b_c/b)^2}]}. \tag{6}$$

This equilibrium is neutrally stable whenever it exists (see the appendix). A disturbance will shift the positions of the range and the cline but not affect their shapes. This behavior is inevitable: the optimum changes at the same rate everywhere, and so there is nothing that favors the center of the range appearing at any particular point along the environmental gradient. (There is another solution in which the minus sign preceding the radical in eq. [5] is replaced by a plus sign, but it is always unstable.)

This simplified model has yielded an important qualitative conclusion: if the environmental gradient is steep enough, then the species' range can collapse to a limited region within which local populations are sufficiently adapted to support population growth. If, on the other hand, the gradient is not too extreme, then the species will expand throughout the habitat and become perfectly adapted everywhere.

Joint Changes in Population Size and the Trait

We now go on to see how the species' range evolves when the trait and population size are free to vary independently. Assume that density regulation follows the standard Lotka-Volterra dynamics: a population of optimally adapted individuals increases at the rate $r_{max} n(1 - n/K)$, where K is the equilibrium density that they would reach. The partial differential equation describing changes in population density is then

$$\frac{\partial n}{\partial t} = \frac{\sigma^2}{2} \frac{\partial^2 n}{\partial x^2} + n\bar{r}(\bar{z}, n), \tag{7}$$

where

$$\bar{r}(\bar{z}, n) = r_{max}\left(1 - \frac{n}{K}\right) - \frac{(\theta(x) - \bar{z})^2}{2V_s} - \frac{I_s}{2},$$

where $I_s = P/V_s$ is a natural measure of the intensity of stabilizing selection, P is the phenotypic variance, and again n and $\bar{z}$ are understood to be functions of the spatial location x. Equation (7) is similar to a result derived by Pease et al. (1989), the major difference being that ours includes density-dependent limits to population growth.

The first term in equation (7) results from random dispersal, which causes a net flux of individuals from high-density regions into low. The factors governing demography are revealed by the three terms that make up the mean fitness at location x, $\bar{r}(\bar{z}, n)$. The first is the density-dependent component of population growth. The second results from the decline in fitness caused by the deviation of a population's trait mean from the local ecological optimum. The final term results from the fitness load caused by phenotypic variation around the trait mean.

Equation (7) implies a useful fact about any equilibrium: regions where the density distribution is concave upward represent demographic sinks where local populations tend to increase as a result of immigration. This conclusion follows because in these regions the first term on the right of equation (7) is positive, and so the second term, which represents the net contribution to changes in density made by local population dynamics, must be negative. Conversely, parts of the range where the density distribution is convex upward are source regions from which there is a net flux of individuals outward. This conclusion does not just apply to the specific model for population growth given by the equation for $\bar{r}(\bar{z}, n)$, but rather is general to any model that includes random movement of individuals.

Equations (1) and (7) give a joint description of how the trait cline and population densities change in time and space. To analyze them, it is helpful first to rescale the variables. By doing so, we can substantially reduce the number of independent parameters and also gain some insight into the processes. Begin by rescaling r and K:

$$r* = r_{max} - I_s/2, \quad K* = \left(1 - \frac{I_s}{2r}\right)K. \tag{8a}$$

Equation (7) is simplified when written in terms of $r*$ and $K*$ as the last term is absorbed into the second. We will assume that $r* > 0$, which implies that an optimally adapted population (i.e., with $\bar{z} = \theta$) will persist in the absence of migration. Next, rescale time by the intrinsic rate of increase, space by the dispersal rate, density by the carrying capacity, and the trait by the strength of stabilizing selection:

$$T = r*t, \quad X = \frac{\sqrt{2r*}}{\sigma}x$$

and $\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad$ (8b)

$$N = n/K*, \quad Z = \bar{z}/\sqrt{r*V_s}.$$

Equations (1) and (7) can now be rewritten in terms of nondimensional parameters and variables:

$$\frac{\partial Z}{\partial T} = \frac{\partial^2 Z}{\partial X^2} + 2\frac{\partial Z}{\partial X}\frac{\partial \ln(N)}{\partial X} + A(BX - Z),\tag{9}$$

and

$$\frac{\partial N}{\partial T} = \frac{\partial^2 N}{\partial X^2} + N(1 - N) - \frac{1}{2}N(BX - Z)^2.\tag{10}$$

The dividend of the rescaling is that the number of independent parameters has now been reduced from six to two. The new parameters are

$$A = \frac{G}{2V_s r^*} = \frac{h^2 I_s}{2r^*},\tag{11a}$$

and

$$B = \frac{b\sigma}{r^* \sqrt{2V_s}},\tag{11b}$$

where $h^2 = G/P$ is the trait's heritability, and again $I_s = P/V_s$. Thus, the model apparently has just two degrees of freedom: all situations can be described in terms of only A and B. The compound parameter A can be interpreted as the genetic potential for adaptation to the local ecological optimum. The compound parameter B is proportional to the speed with which ecological conditions change as one crosses the range, b, and to the dispersal rate, σ. More precisely, A is the ratio between the loss of mean fitness due to genetic variation around the optimum ($G/[2V_S]$) and the intrinsic rate of increase (r^*); B^2 is the ratio between the mean loss of fitness due to dispersal to places with a different optimum ($\sigma^2 b^2/[2V_S]$) and r^{*2}.

What are the equilibria for the species' range and the cline in the trait? Inspection of the equations shows that two equilibria always exist. As in the simple one-variable model developed earlier, equilibrium is reached when the population density is at carrying capacity, $N(X) = K^*$, and adaptation is perfect, $Z(X) = BX$, everywhere. A second equilibrium occurs when the population is extinct, with $N(X) = 0$ everywhere. The question then becomes whether there are other equilibria in which the species persists, but its range is limited by gene flow. Although we have not been able to find exact solutions for a limited range, progress has been made using analytic approximations and numerical methods.

Evolution of the Range and Cline: Approximations

An approximation for the equilibrium is made possible by considering situations in which population density is far below the carrying capacity ($N \ll 1$). Then density dependence is weak, and the term $N(1 - N)$ in equation (10) can be approximated by N. Considering the situation as X grows large yields an ap-

proximation for the equilibrium:

$$Z(X) \approx AX/\sqrt{2}, \tag{12}$$

$$N(X) \approx N(0)\exp(-CX^2/2), \tag{13}$$

where

$$C = (\sqrt{2}\,B - A)/2. \tag{14}$$

Substituting equation (13) into equation (7) and solving at $X = 0$ gives the species' maximum equilibrium density as $N(0) \approx 1 - C$. Thus, the distribution of densities across the range depends only on a single dimensionless parameter, and this distribution is proportional to a Gaussian distribution with variance $1/C$ and maximum density $1 - C$. As with the one-variable model, the solution is neutrally stable with respect to shifts in space: the center of the range can come to rest at any point along the environmental gradient.

The steepness of the trait cline depends only on A. Rescaling equation (12) to the original units, we find that the cline's slope is $\sqrt{PI_s h^2}/\sigma$. Thus, when this approximation holds, the cline is not affected by the steepness of the environmental gradient. That is because this approximation represents a high-migration limit: gene flow is sufficiently powerful to keep population densities far from the carrying capacity throughout the range. In this situation, the cline's slope is so far from that of the optimum that the cline is quite insensitive to what the optimum is. On the other hand, the cline's slope is affected by the amount of genetic variation (h^2) and the intensity of stabilizing selection (I_s), both of which decrease the discrepancy between the cline and the optimum, and by the mean dispersal distance (σ), which increases the discrepancy. These conclusions generalize from our Lotka-Volterra assumption to any form of population regulation in which population size has little effect on the per capita growth rate when densities are low.

A species faces extinction if conditions change too rapidly as one moves across the habitat. For the species to persist, $N(0)$ must be positive, which implies extinction if B exceeds the threshold value $B_U = (A + 2)/\sqrt{2}$. The result is easier to visualize in the original units if we express the environmental gradient b as the change in the optimum, measured in units of phenotypic standard deviations, per change in distance, measured in units of dispersal:

$$b* \equiv \frac{\sigma}{\sqrt{P}}\,b. \tag{15}$$

In these terms, the upper limit for the environmental gradient that will still allow the species to persist is

$$b_U^* \approx \frac{4r_{max} - (2 - h^2)I_s}{2\sqrt{I_s}}. \tag{16}$$

This shows that a species can persist in a stronger gradient when the maximum growth rate (r_{max}) and heritability (h^2) are large and the intensity of stabilizing selection (I_s) is small.

The width of the range can also be calculated at this high-migration limit. The boundary is soft, as in the simpler one-variable model. Because there are no absolute range boundaries, we again measure the range's width R as the region enclosing 95% of the population. The Gaussian approximation for the density distribution of equation (13) implies that the width is $4/\sqrt{C}$, or, in terms of the original units,

$$R \approx \frac{4\sigma^4 \sqrt{P}}{(b\sigma \sqrt{I_s} - h^2 I_s \sqrt{P}/2)^{1/2}}. \tag{17}$$

We noted earlier that regions where the equilibrium density distribution is concave upward are demographic sinks in which local populations tend to increase as a result of immigration. Inflection points in the density distribution occur 1 SD to the left and right of the range center. This means that on this definition, only the middle half of the species' range is demographically self-supporting. One can also consider the region in which adaptation is sufficient that the population would increase from low density: from equation (13), this has width $2/\sqrt{C}$.

Using equations (16) and (17), one can show that the range has positive width when the environmental gradient b is just steep enough to cause extinction. Extinction apparently does not occur as the result of the range width shrinking to 0. Rather, the population growth rate falls below 0 over the entire range.

How does the migration rate affect the species at the high-migration limit? Linearizing R around the critical value of σ that leads to extinction shows that in general (i.e., when $4r^* > h^2 I_s$) the range broadens as migration increases. But increasing migration also causes decreased adaptation across the range and depresses the maximum density everywhere. By integrating equation (13), we find that the total population size is $n_T \approx K^* (1 - C) \sqrt{2\pi/C}$, which is a decreasing function of C. Since C increases with σ, we conclude that the equilibrium population size declines as the migration rate goes up.

A species meets a very different fate if the environmental gradient is too shallow: its range will expand without limit. For the solution of equation (13) to exist, B must be greater than a critical lower threshold value $B_L = A/\sqrt{2}$. This implies that the environmental gradient b must be at least $b_L = G/2\sigma\sqrt{V_s}$, or the range will expand without limit. In terms of the rescaled b, an approximation for the lower limit of the environmental gradient that will still constrain the range is

$$b_L^* \approx \frac{1}{2} h^2 \sqrt{I_s}. \tag{18}$$

Thus, the gradient needed to stop range expansion increases as the intensity of selection and the heritability go up. This result is sensible, as both factors tend to favor adaptation to local conditions and therefore make it more difficult for
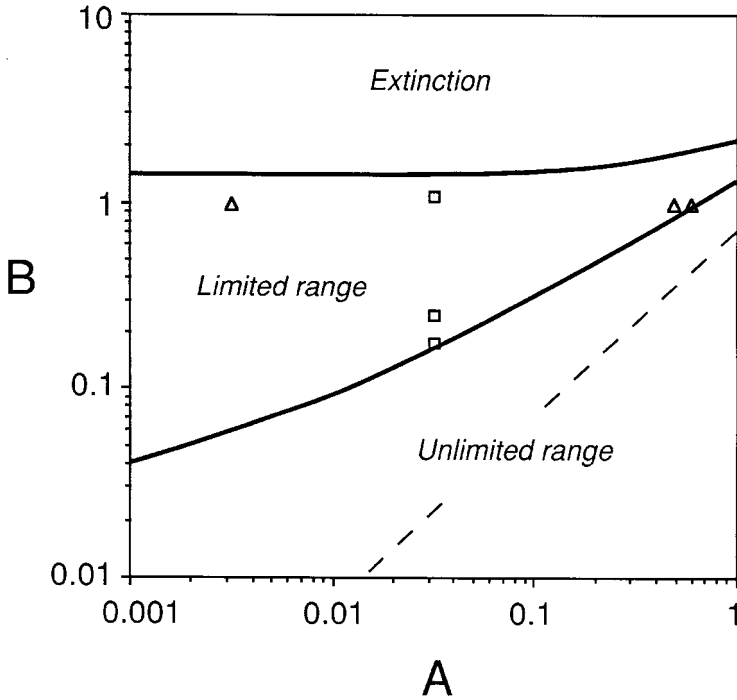
Fig. 2.—Parameter combinations that lead to extinction, saturation (i.e., range expansion without limit), and a finite range for the two-variable model of equations (1) and (7). Boundaries between the regions (*solid curves*) were determined by simulation. The dashed curve shows the analytic approximations B_L for the lower bound of the limited range region; the approximation for the upper bound (B_U) is indistinguishable from the simulation results. Triangles show the parameter combinations illustrated in figure 3; squares, those in figure 4.

gene flow to constrain the range. Comparing equations (16) and (18) shows that the amount of genetic variation present in local populations plays a more important role in constraining the expansion of a wide-ranging species than in preventing extinction of a locally restricted species.

Evolution of the Range and Cline: Simulations

These approximations give us some insights regarding the equilibrium for the species range and trait cline. But several interesting questions have not yet been addressed: When will these equilibria be stable? How rapidly are they approached? A second set of issues involves the accuracy of the approximations. They are expected to do best when population densities are low everywhere. We would like, however, to understand how the range and cline behave under all conditions. These questions were answered by iterating equations (9) and (10) forward in time by computer using the finite difference method.

Figure 2 shows the conditions that result in extinction, a limited range, and an unlimited range. The approximation for the boundary between extinction and
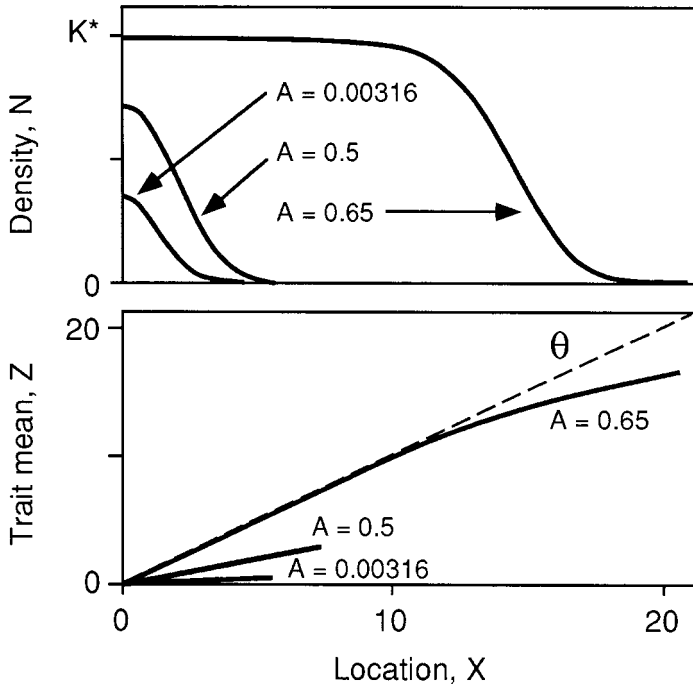
Fig. 3.—Effects of the compound parameter A (roughly speaking, a measure of the potential for local adaptation) on the equilibrium population density and trait mean for $B = 1$. The range and cline are symmetrical, and only the right-hand half of each are shown. As A increases, the range expands and the cline more closely approaches the environmental optimum, θ.

persistence, equation (16), is very accurate: this is because that approximation assumes that density is very low, which is the case when the species is on the verge of extinction. With $A = 0$ (i.e., with no genetic variation and hence no local adaptation), it is easy to show that $B_U = \sqrt{2}$; this corresponds to equation (16) with $h^2 = 0$. The upper limit for B that allows population persistence is very insensitive to A over a wide range of values: $B_U \approx \sqrt{2}$ for $A < 0.1$ (fig. 2). Thus, the amount of genetic variation available for adaptation within local populations (which affects A but not B) has only a weak effect on the species' survival in this model. Range expansion is inhibited by gene flow in a spatially varying environment, and this deleterious effect is independent of the local genetic variance. The approximation for the critical value of B that prevents the range from expanding without limit, equation (18), is less accurate. The error presumably results from the effects of density-dependent population regulation, which are neglected by the approximation but become important when populations approach the carrying capacity.

Examples of equilibria for the range and cline are shown in figures 3 and 4. The distributions of population densities across the range fall into a single fam-
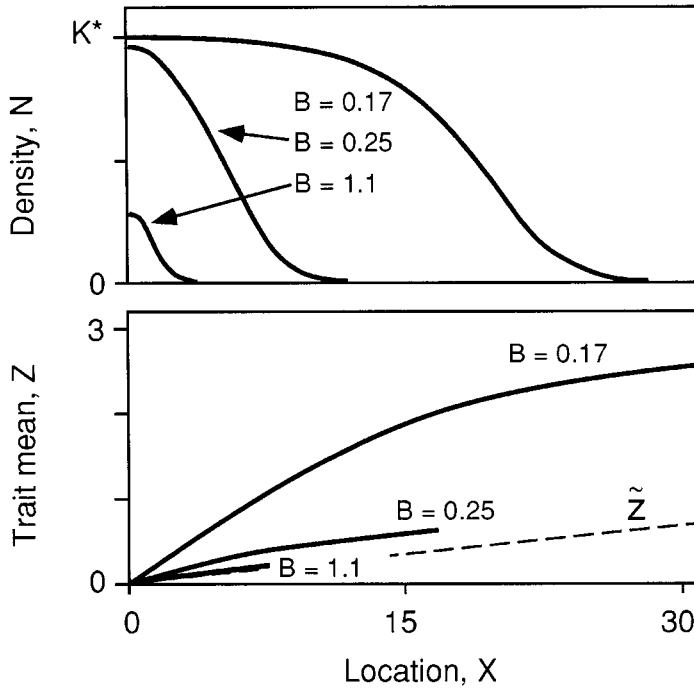
FIG. 4.—Effects of the compound parameter B (roughly speaking, a measure of the rate that the environment changes in space) on the equilibrium population density and trait mean for $A = 0.0316$. When B is sufficiently large that population density is far from the carrying capacity, the trait cline is close to the analytic approximation (given by eq. [13]) shown by the dashed line labeled $\tilde{z}$. With smaller values of B, the cline approaches the environmental gradient near the range center but still has a slope of approximately $\tilde{z}$ in the range periphery.

ily of curves, as anticipated from equation (13). When the environmental gradient is sufficiently steep that population density is low throughout the range, the density distribution is nearly Gaussian and the cline nearly linear throughout the range. The analytic approximations for the range width and the cline's slope do reasonably well in this situation, generally within 10% accuracy, but the expressions for the maximum density and total population size are less accurate. This situation holds unless parameters are very close to the critical values that allow the range to expand without limit. In that case, populations at the range center approach the carrying capacity and the density distribution across the range becomes platykurtotic. The cline is no longer linear: near the range center, the trait equilibrates close to the environmental optimum, while far out in the periphery the cline's slope approaches the high-migration limit of equation (12).

The core of the range acts as a demographic source and the periphery as a sink in our models. Figure 5 shows $\bar{r}$, the mean intrinsic rate of increase for local populations, across the range. Two situations are illustrated, when the range is small and when it is large. The points in space at which $\bar{r}$ switches from posi-
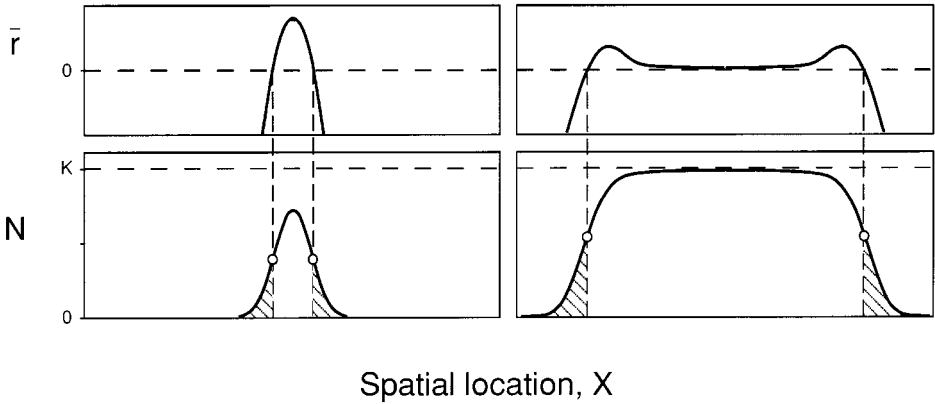
FIG. 5.—Local population growth rates, $\bar{r}$, for a restricted and a widespread species (calculated from eq. [7]). The boundaries between source ($\bar{r} > 0$) and sink ($\bar{r} < 0$) populations coincide with the inflection points of $N(X)$ (marked by circles in the lower panels). Source populations make up a smaller fraction of the total range in restricted species than in widespread species.

tive to negative, indicating the transition from source to sink, coincide with the inflection points of $N(X)$. Referring back to figures 3 and 4 shows that maladaptation caused by gene flow occurs in source populations as well as in sinks. The fraction of the range that acts as a source changes with the size of the range. About half of the range is a sink when densities are low everywhere. This fraction declines as the size of the range increases.

Simulation results suggest there is a unique stable equilibrium for the shapes of the density distribution and cline. When parameters fall in the intermediate range shown in figure 2, both extinction ($N = 0$ everywhere) and saturation ($N = 1$ everywhere) are unstable, and the same density distribution and cline are reached from a variety of initial conditions. When the environmental gradient is sufficiently steep, the population goes to extinction. When the migration rate and environmental gradient are sufficiently small, the density grows toward the carrying capacity everywhere. From at least certain initial conditions, the periphery of a well-adapted population expands outward in a traveling wave. The dynamics of N are qualitatively similar to those described by Fisher (1937) for the spread of an advantageous gene in a population of constant density. As expected, in the interior of the range the trait cline is very close to the optimum, while far in front of the wave the cline's slope is well approximated by equation (12).

The balance between adaptation and gene flow can be drastically shifted by small changes in the parameters. When the range is barely confined by gene flow, a small increase in A or decrease in B can cause it to suddenly expand without limit. Figure 6 shows an example of the relations among B, the range width, and the total population size. When the species is near extinction, the range width and population size vary nearly linearly with B. As the earlier ana-
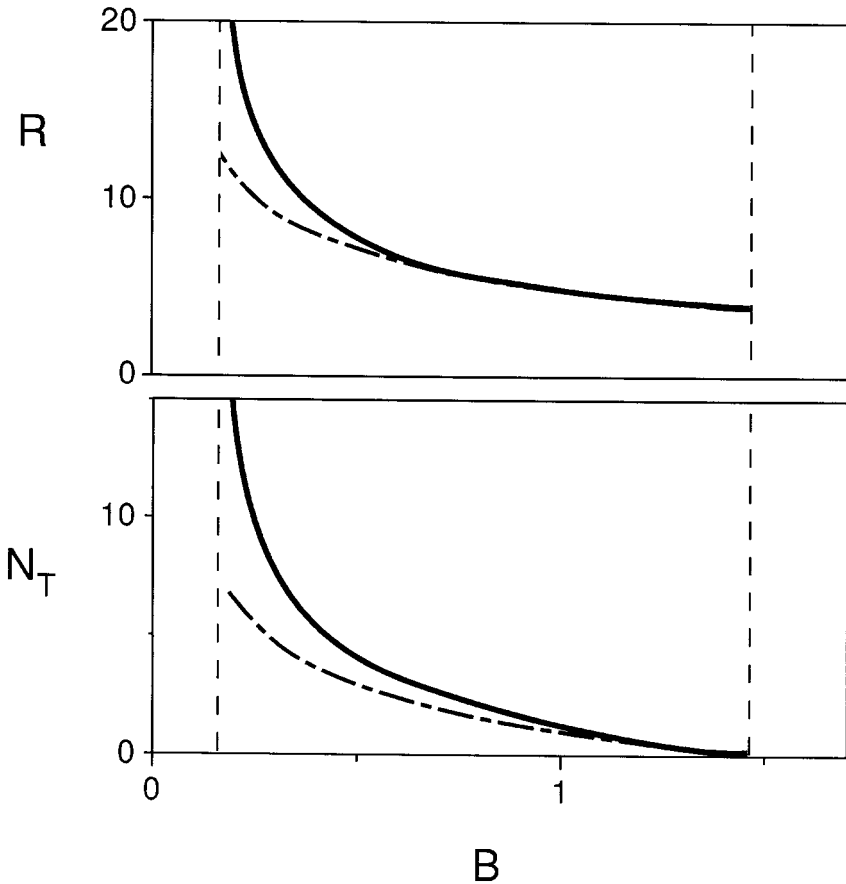
FIG. 6.—The range width R and total population size N_T as a function of B for $A =$ 0.0316. The curves were determined from the equilibrium density distributions found by simulation. Range width is in units of $\sigma/\sqrt{2(r_{max} - I_s/2)}$ and population size in units of $\sigma K\sqrt{2r_{max} - I_s}/2r$. Dashed vertical lines indicate values of B at which an unlimited range (*left*) and extinction (*right*) occur; dot-dashed curves show the analytic approximations.

lytic results showed, the range width remains positive as the population approaches extinction. But as the environmental gradient decreases toward the threshold that allows the range to expand without limit, the equilibrium population size shoots up rapidly. This observation suggests a possible mechanism for explosive range expansions that are sometimes observed in nature.

When gene flow confines the species' range, how rapidly is the equilibrium approached? The speed of approach can be quantified by the dominant eigenvalue. Table 1 shows the eigenvalues, determined by simulation, for various combinations of A and B. A smaller (more negative) eigenvalue indicates that the equilibrium is approached rapidly. The basic pattern seen in the table is that the equilibrium is approached slowly when the parameters are near the critical values that lead to extinction or to indefinite range expansion.

TABLE 1

Dominant Eigenvalue for the Limited Range Equilibrium

B	.001	.00316	.01	.0316	.1	.316
1.0	−.291	−.292	−.295	−.305	−.335	−.380
.562	−.57	−.56	−.542	−.489	−.297	. . .
.316	−.258	−.251	−.231	−.173	. . .	. . .
.178	−.0937	−.0876	−.0683	. . .	. . .	. . .
.1	−.030	−.0236	. . .	. . .	. . .	. . .

A major simplifying assumption that allowed us to find approximate solutions is that the model's parameters are constant across the range. But the model (i.e., eqq. [1] and [6]) is valid even when the parameters change in space. We therefore carried out a series of simulations in which the parameters were allowed to vary smoothly across the range. Two conclusions that were obtained earlier seem to apply also to this more general case. First, so long as parameters stay positive and finite, the range boundary is soft. Diffusion is a sufficiently powerful force that population densities at the range boundary approach 0 only asymptotically. Second, if there is a limited range at equilibrium and if the parameters cease changing beyond a certain point in the range periphery, then the cline's slope asymptotically approaches the high-migration approximation of equation (12).

DISCUSSION

Dispersal has antagonistic effects on a species' distribution: although it favors colonization, it also causes gene flow that frustrates local adaptation. The deleterious effects of gene flow may often be most severe in the periphery of a widespread species' range. Random dispersal causes a net flow of genes from regions of high density to low and therefore hampers adaptation in the periphery. Our models show that this effect can be strong enough to prevent the expansion of a species' range into suitable habitat. When the conditions are appropriate, a balance is struck between gene flow and local adaptation that confines the species to a limited range.

This outcome apparently has not been found in earlier models. Pease et al. (1989) developed a model for joint changes in population density and a quantitative trait that differs from ours in three main respects. In their model, there is no density dependence, the environment changes in time, and the maximum possible intrinsic rate of increase changes in space. When the rate of change in time is set to 0, their results show that the population will either shrink to extinction or grow without limit, depending on the parameters. This behavior is consistent with results from the purely demographic model of Gurney and Nisbet (1975). The key difference in our model that makes the limited-range equilibrium possible is the addition of density-dependent population regulation. Because popula-

tions growing in environments that are relatively constant in time must eventually encounter density-dependent limits, we expect some natural populations to show the limited-range equilibrium seen in our model.

The tendency for gene flow from better-adapted, and hence more abundant, regions to swamp local adaptation elsewhere may be ameliorated by phenotypic plasticity (such that the same genotype can adapt to different environments) and by any increase in genetic variation caused by the admixture (see Grant and Grant 1994). To the extent that gene flow imposes some constraint on adaptation, however, our conclusions remain qualitatively the same. Empirical studies reviewed in the introduction show that gene flow does prevent local adaptation in at least some populations, and so plasticity and increased genetic variation apparently cannot always offset the maladaptive effects of gene flow.

We need to know something about parameter values in natural populations to evaluate the biological relevance of our results. There appear to be no species for which all the data needed to estimate the compound parameters A and B are available. A sense for the ranges of values that they might take can, however, be gained from data on the individual parameters that comprise A and B. Pianka (1988, table 7.2) reviews data on maximal rates of increase for organisms ranging from bacteria to mammals and reports values ranging from ~0.1 to >8 when time is measured in generations. Studies of stabilizing selection in natural populations reviewed by Endler (1986) give estimates for I_s (equivalent to Endler's j) that range from 0 to 2, and Turelli (1984) suggests that values on the order of 0.1 may be typical. (It is easy to extend the model to multiple traits; then I_s simply increases with the square root of the number of traits.) Mousseau and Roff's (1987) compilation of heritabilities shows examples spanning almost the entire possible range from 0 to 1; the mean for morphological traits is near 0.5. The standardized environmental gradient, b^*, is the most poorly known of the numbers that we need. Indirect information on three bird species reviewed elsewhere (García-Ramos and Kirkpatrick 1997) suggests that b^* might take on values of at least 0.25.

Together, these data suggest that in natural populations A might range from near 0 to something >1, while B might range from near 0 to something >2. Although these estimates are crude, they do suggest that the full range of outcomes, from extinction to saturation of all available habitat, are biologically plausible consequences of the forces considered in our models. A variety of other explanations have been also suggested as factors that limit species' ranges (Hoffmann and Parsons 1991, chap. 8). Distinguishing between these possibilities is, of course, an empirical task (Hoffmann and Blows 1994). Observations that would support the gene flow mechanism discussed here include persistent directional selection on heritable traits in marginal populations (García-Ramos and Kirkpatrick 1997). This effect, caused by gene flow from the range center that keeps peripheral populations away from their local ecological optima (figs. 1, 3, and 4), could be revealed by direct measurement of selection or by rapid evolution following experimental interruption of gene flow.

The models give several conclusions about mechanisms that regulate species' abundance and distribution that may be useful in conservation and management.

When extinction occurs because the environmental gradient is too steep, the range's width does not shrink to zero. Rather, local populations decline over a region of finite size. This suggests that a substantial geographical range does not necessarily indicate that the species is at low risk of extinction. Second, the genetic variance has little effect on population persistence. If the species is able to colonize a region along the environmental gradient where it is well adapted, range expansion is not much affected by the amount of genetic variation available locally for adaptation. (The picture will be quite different, of course, if the environment is changing in time or if limits to dispersal require that the species adapt in its current location if it is to persist.)

Factors that do exert important controls over a rare population's fate are those involved in the dimensionless parameter B: the steepness of the environmental gradient, the maximum rate of increase, the dispersal rate, and the intensity of stabilizing selection. One interesting implication is that the species' range can actually contract as the dispersal rate increases. This effect, caused by the evolutionary consequences of gene flow, runs counter to the simple intuition that the increasing dispersal favors colonization and therefore might cause the range to expand. A second implication is that extinction can result if the environmental gradient becomes steeper, even if the species remains perfectly adapted to the habitat at the range center.

Maladaptation caused by gene flow forces peripheral populations into the role of demographic sinks. These regions of the range are maintained by migration from better-adapted populations toward the range center. The situation for peripheral populations is ironic, since without migration the peripheral populations would adapt to the local conditions and become self-sustaining. As much as one half of the total range can be a sink (fig. 5). The fraction is greatest when the ecological gradient is steep enough to depress densities well below the carrying capacity throughout the range. Thus, the closer a species is to extinction, the smaller is the fraction of its total range that functions as a demographic source.

The range of an abundant species can be extremely sensitive to the parameters that appear in our models. In some situations, a small change in the environment or even the species itself will cause a population breakout. This occurs when the force of adaptation in the range periphery becomes stronger than that of gene flow, allowing the range to expand dramatically. Factors that can trigger a breakout include ecological changes that weaken the environmental gradient and increases in the maximum intrinsic rate of increase or the genetic variance.

A consistent outcome from these models is that the range boundaries are soft: population density declines asymptotically to 0 rather than actually vanishing at a defined point in space. Ranges of real species truly do have limits, of course, which leads to the question of how the models can be reconciled with nature. The models may reasonably describe some species once we have corrected for the effects of very low population densities. A variety of effects (e.g., demographic stochasticity, or the need to find a mate) make persistence impossible below a certain density. Truncating the model's density distribution at this threshold may give a reasonable prediction in this situation.

An alternative explanation for species with hard range boundaries is that they

do not meet fundamental assumptions of our models. Perhaps the two most biologically plausible possibilities involve the assumptions regarding mortality and dispersal. A range can have a hard boundary if the mortality rate becomes infinite at some point in space. Some species of terrestrial plants may have no chance of survival when exposed to salt water, for example, and so a hard boundary can be produced at the sea's edge. Our models do not show this outcome because the mortality rate remains finite with the fitness function of equation (2). Changes in the dispersal model can also lead to hard range boundaries. We assumed random dispersal. Some forms of active habitat choice, on the other hand, can produce a hard range boundary; a terrestrial animal that actively avoids water can also establish a hard range boundary at the sea's edge.

We have considered here a species distributed over a continuous habitat in which the ecological optimum for a single trait changes at a constant rate as one moves across the range. Our results do suggest, however, what to expect when the environmental gradient is not constant. A case of interest is when the gradient is benign in a core area but steepens toward the edge of the range. If the core area is much wider than the dispersal distance σ, the trait is expected to approach perfect adaptation and population densities to approach the carrying capacity in that region. When the rate of change in the optimum increases to approximately b^*, gene flow makes local adaptation impossible. Local population densities will then decline from that point outward in a soft range boundary. When ecological changes across the range generate clines in more than one trait, we expect qualitatively similar patterns to those seen in these models. But because gene flow will generate maladaptation in each trait, the critical migration rates needed to cause extinction and to prevent the range from expanding indefinitely will be smaller.

The assumption of habitat continuity is a plausible representation for some species, such as marine organisms living along a coast, but clearly does not apply to others, such as birds inhabiting an archipelago. It would be interesting to extend the analysis to a ''metapopulation,'' in which adaptation would be impeded by local extinctions and recolonization, as well as by gene flow (see Barton and Whitlock 1996; Dias 1996).

Other extensions to our models can be suggested. We have assumed that population densities are sufficiently large everywhere that genetic drift can be ignored. When densities drop to the point that genetic drift becomes important, both the trait mean and the genetic variance will be affected. Drift will certainly be a factor in the periphery when the range boundary is soft. Intuitively, one expects that drift will make local adaptation even more difficult there and so further inhibit range expansion.

Demography will also be affected by random events. In our models, a species is guaranteed to persist if the parameters are appropriate, regardless of the initial state of the population. If a species is introduced in a region to which it is poorly adapted, it will establish itself by adapting and by spreading to a region where it has high fitness. During this period, however, it may go through a phase in which its total population size is very small. Gomulkiewicz and Holt (1995) de-

veloped a model for the demography and evolution of a single population responding to a novel environment. They assumed there is a minimum population size that allows the species to persist and determined the initial conditions and levels of genetic variation that do and do not lead to extinction. An extension of our models might incorporate a similar threshold by setting a minimum density needed for population growth or by including an explicit model of demographic stochasticity. We anticipate that this addition might have two kinds of effects on the conclusions: it could limit the range of initial conditions that would allow the species to persist, and it could inhibit further range expansion at the periphery of a species near equilibrium. Together, the effects of low density on demography and genetic drift suggest that the conditions for persistence found in our models will be necessary but not sufficient for species in nature.

This article focuses on detailed models in which gene flow acts as a mechanism that limits the geographical range of a species. These models are far from a complete study of how a range evolves: alternative scenarios can be imagined in which gene flow constrains the range, and there are other mechanisms that do not involve gene flow at all (Hoffman and Blows 1994). We hope that despite these limitations our models will stimulate further work on the evolutionary dimension of species' ranges. Ecologists have a long-standing interest in the patterns of geographical ranges (Brown et al. 1996; Gaston 1996). We would hope ultimately to have an understanding of evolutionary mechanisms that underlie these patterns.

APPENDIX

STABILITY OF THE ONE-VARIABLE MODEL

This appendix establishes the stability of the two equilibria for equation (4) that are discussed in the text. Consider first the case in which $\bar{z} = bx$ and population density is equal everywhere. The feedback from variations in density caused by a small perturbation in the trait, ϵ, is proportional to ϵ^2 and is negligible compared with linear terms. Thus, this solution is always stable in an infinite range. This argument may not apply over a finite range, however, where edge effects may produce a substantial perturbation to the solution $\bar{z} = bx$, so that terms of order ϵ^2 become important. Simulations (which assume no flow across the boundary, $\partial \bar{z}/\partial x = 0$) show that for $b > b_c$ and $\bar{z} = bx$ initially, adaptation collapses from the boundaries. The same arguments apply to the two-variable model of equations (9) and (10). There, the solution $Z = BX$, $N = 1$, is stable on an infinite range, but simulations show that it is unstable on a finite range when the alternative solution exists.

Now consider solution (5). Linearizing shows that it is stable whenever it exists. Let $\bar{z} = y + \kappa x$:

$$\frac{\partial y}{\partial t} = \frac{\sigma^2}{2}\frac{\partial^2 y}{\partial x^2} - \alpha x \frac{G}{V_s}\frac{\partial y}{\partial x}, \tag{A1}$$

where $\alpha = 4(b - \kappa)(2\kappa - b)/b_c^2$. Since $b/2 < \kappa < b$, α is always positive.

If a perturbation $y_0(x)$ is introduced at $t = 0$, it grows as

$$y(x, t) = \int_{-\infty}^{\infty} y_0(\chi)\frac{e^{\alpha Gt/V_s}}{\sqrt{2\pi\sigma^2 v}}\exp\left[-\frac{(x - \chi e^{\alpha Gt/V_s})^2}{2\sigma^2 v}\right]d\chi, \tag{A2}$$

where $v = (e^{2\alpha Gt/V_s} - 1)/(2\alpha G/V_s)$. The perturbation eventually leads to a shift in position of the cline but no change in its form:

$$y(x, \infty) = \int_{-\infty}^{\infty} y_0(\chi)\sqrt{\frac{\alpha G}{\pi V_s\sigma^2}}\exp\left(-\frac{\alpha G\chi^2}{V_s\sigma^2}\right)d\chi. \tag{A3}$$

Thus, the system is neutrally stable. Perturbations will move the bubble of adaptation up or down the environmental gradient, but a new equilibrium will be reached at which the shapes of the density distribution and the cline are unchanged.

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Associate Editor: Robert D. Holt