

# Species' Range: Adaptation in Space and Time

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**ABSTRACT:** Populations living in a spatially and temporally changing environment can adapt to the changing optimum and/or migrate toward favorable habitats. Here we extend previous analyses with a static optimum to allow the environment to vary in time as well as in space. The model follows both population dynamics and the trait mean under stabilizing selection, and the outcomes can be understood by comparing the loads due to genetic variance, dispersal, and temporal change. With fixed genetic variance, we obtain two regimes: (1) adaptation that is uniform along the environmental gradient and that responds to the moving optimum as expected for panmictic populations and when the spatial gradient is sufficiently steep, and (2) a population with limited range that adapts more slowly than the environmental optimum changes in both time and space; the population therefore becomes locally extinct and migrates toward suitable habitat. We also use a population-genetic model with many loci to allow genetic variance to evolve, and we show that the only solution now has uniform adaptation.

**Keywords:** adaptation, gradient, moving optimum, extinction, load, cline.

## Introduction

While many boundaries to species ranges are caused by sharp changes in the environment or are driven by interaction with other species (Gaston 2003; Bridle and Vines 2007), there is oftentimes no apparent reason for the sharp spatial limits that are commonly observed. Some species survive remarkably well when transferred outside their range (Prince and Carter 1985). More often, though, species need to extend their niche via adaption in one or several traits (table 2.1 in Gaston 2003). There is currently only a limited understanding of why such adaptation fails even when the environment changes smoothly in space. Haldane (1956) suggested that the sharp boundary may be a result of maladaptive gene flow from central populations, preventing adaptation in less dense marginal populations. This is a likely explanation for limits to adap-

tation due to highly asymmetrical gene flow when density changes sharply for extrinsic reasons (as in the mainland-island model of Kawecki et al. 1997). The second classic argument for limits to a species range is that genetic variance is insufficient to allow niche extension (see Antonovics 1976). Two questions follow from this argument: how can we quantify such limits, and what constrains genetic variance in the first place?

Existing studies predicting response to a temporally changing optimum in structured populations are rather limited. Most notably, Pease et al. (1989) analyzed evolution where the optimum changed in time and space, as described by a bivariate Gaussian fitness (in time and space), assuming no density dependence and that genetic variance is small and constant. Later, Case and Taper (2000) allowed for species interactions in an extension of Kirkpatrick and Barton's (1997) model; they briefly assessed the response of species range to a sudden change in environment. More is known about the response of a single, unstructured population: for a Gaussian-distributed trait, the lag of trait mean behind the optimum is proportional to the speed of movement of the optimum divided by genetic variance and the strength of stabilizing selection (Charlesworth 1993; Lande and Shannon 1996; Bürger 1999; Waxman and Peck 1999).

The additive genetic variance determines the rate of evolution of quantitative traits. Thus, it is crucial to understand how such variance is maintained and how it changes under selection. Observed genetic variance is substantially higher than we would expect from a simple mutation-selection balance (see Turelli 1988; Johnson and Barton 2005). The variance can increase due to a range of factors, namely frequency-dependent selection, heterozygote advantage, diversifying selection, and temporal fluctuations in the optimum. In a single population, additive genetic variance maintained by mutation-selection balance,  $\hat{V}_G$ , reflects the product of genomic mutation rate ( $U = 2n\mu$ ) and the width of stabilizing selection,  $V_S$ ; for multiple loosely linked loci and rare alleles,  $\hat{V}_{G,HC} \approx 2UV_S$  (Turelli 1984). However, unless stabilizing selection  $\gamma_i = -V_P/(2V_S)$  is very weak (see Kingsolver et al. 2001

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and “Discussion”), an unrealistically high mutation rate per locus or a high number of loci of small effect is required to maintain the variance that we observe (with heritability  $h^2 = 0.4$ , we require  $U = 1/10 V_p/V_s$ ).

High levels of genetic variance can be readily maintained in a spatially heterogeneous environment. For a single locus, Slatkin (1975) and Nagylaki (1976) showed that a cline will develop if the environment changes over a scale that is large relative to the ratio of dispersal over the square root of intensity of selection per gene,  $\sigma/s^{1/2}$ . It also follows that adaptation to a pocket or a marginal habitat of different environment that is small in terms of  $\sigma/s^{1/2}$  is prevented (for a real world example, see Lenormand et al. 1999). Hedrick (2006) gives a nice review of current studies of adaptation to spatially varying environments; Bridle et al. (2008) discuss studies on both spatial and temporal adaptation.

Theoretically, if genetic variance of a quantitative trait can freely evolve in response to spatially variable selection, it should at any particular location increase with the extent of migration across the environmental gradient and the width of stabilizing selection (Barton 2001). Therefore, the ability to adapt to temporal change can be significantly higher in species that are living in a spatially variable environment. Because migration may be several orders of magnitude higher than mutation, it may significantly increase local genetic variance even when spatial variability is low. It is less clear under what conditions and by how much genetic variance increases when the environment changes in time; we return to this matter in “Discussion.”

It has been shown by Kirkpatrick and Barton (1997) that low genetic variance combined with high gene flow can prevent adaptation to a stable environment when the optimum varies smoothly in space. Conversely, when genetic variance is unconstrained, there is no direct limit to species range (Barton 2001). Kirkpatrick and Barton’s (1997) study jointly follows population dynamics and the evolution of trait mean due to adaptation to a static spatial gradient. They find two classes of solutions at equilibrium: uniform adaptation when the trait mean matches the optimum perfectly on the whole range, and the solution, where the gradient in trait mean is shallower than the gradient in environmental optimum, such that maladaptation increases away from the center and leads to a limited range. Limited adaptation arises as the environmental gradient steepens relative to genetic variance. Both solutions are stable when the available habitat is infinite, but if an expanding population reaches the margins of the suitable habitat, adaptation collapses from the margins toward a state of limited adaptation, where the gradient in trait mean is shallower than the environmental gradient (Kirkpatrick and Barton 1997). Barton (2001) extended the model by allowing the genetic variance to evolve. With

this, the population could always adapt to the environmental gradient by increasing its variance, and there is no equilibrium with a limited range. However, population density steadily decreases with increasing variation around the optimum, and eventually, as the gradient steepens, the population becomes extinct over the whole range.

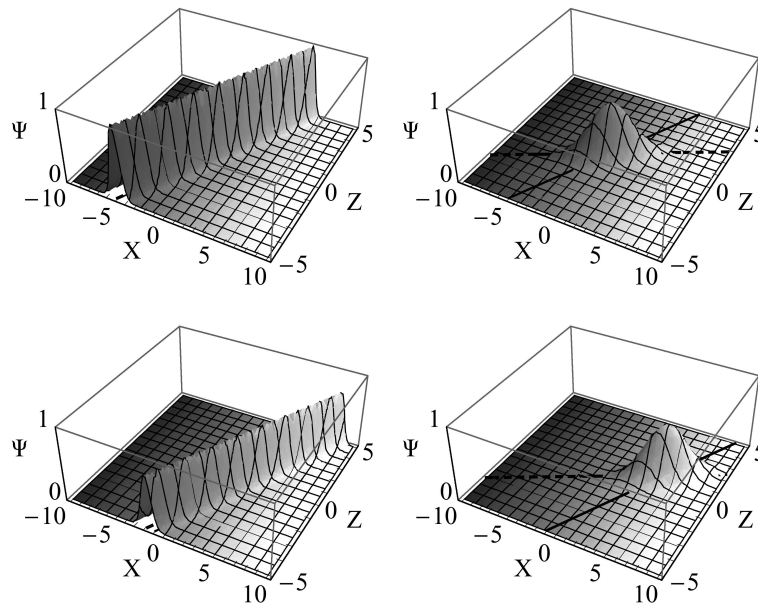
Here we extend the models described in the previous paragraph to allow the environmental optimum to vary in both time and space. Via continuity with the static case, we would expect that when genetic variance is fixed, there would still be two solutions, either with uniform adaptation or with adaptation over only a limited range. When the optimum changes in time, we suppose the population would track the changing optimum through both adaptation and migration (unless the environment changes too fast in either space or time, leading to extinction). In relation to the static case, we are interested in whether, when the environment also varies in time, the gradient in trait mean changes (thereby leading to a change in the size of the species range), and whether there is any change to the critical spatial gradient (above which limited adaptation occurs). Subsequently, we address the evolution of genetic variance with a population genetic model, assuming that the quantitative trait under selection is determined by  $n_i$  loci with approximately additive effects and under weak selection. With this, genetic variance can increase with migration across the spatial gradient. We address whether the genetic variance now also increases with the rate at which the optimum changes in time and how temporal change in the optimum affects the species’ range.

#### *Adaptation to a Linear Environmental Gradient Moving in Time: Phenotypic Model*

Following Pease et al. (1989), the change of the mean phenotype  $z$  can be written as

$$\frac{\partial \bar{z}}{\partial t} = \frac{\sigma^2}{2} \frac{\partial^2 \bar{z}}{\partial x^2} + \sigma^2 \frac{\partial \ln(n)}{\partial x} \frac{\partial \bar{z}}{\partial x} + V_A \frac{\partial \bar{r}}{\partial \bar{z}}. \quad (1)$$

This equation describes the effects of migration and selection on a population with density  $n$  and with quantitative trait ( $z$ ) under selection. The first term represents migration, approximated by diffusion with variance  $\sigma^2$ . The second term describes gene flow from populations that vary in population density  $n$ . The third term describes the effect of selection on a normally distributed character  $z$  with additive genetic variance  $V_A$  (Fisher 1930; Lande 1976;  $\bar{r}$  is the mean [Malthusian] fitness, which is equal to  $\bar{r}$  in continuous time and  $\sim \log(\bar{W})$  in discrete time):  $\partial \bar{z} / \partial t = h^2 V_p \partial \bar{r} / \partial \bar{z} = V_A \partial \bar{r} / \partial \bar{z}$ ; here,  $V_A$  is additive genetic variance,  $V_p$  is the phe-



**Figure 1:** Distribution of phenotypes ( $\Psi$ ) for the logarithmic model with a spatially and temporally varying environment: left, uniform adaptation; right, limited range. Distance  $X$  is scaled relative to the standard deviation of dispersal distance, trait  $Z$  is scaled relative to the strength of selection, and time  $T$  is scaled relative to the rate of return to equilibrium; see equation (4). The top row shows the equilibrium density when the optimum is stable in time ( $k^* = 0$ ); the bottom row shows the density when the optimum is changing at speed  $k^* = 0.2$  at time  $T = 20$ . Notice the decrease in density for uniform adaptation, where the lag behind the optimum is about  $a^* = 1$ . The environmental optimum is shown by the solid line; the dashed line depicts the trait mean. Other parameters, measuring genetic and dispersal load, are kept the same throughout this figure:  $A = 1/4$  and  $B = 1$ .

notypic variance, and  $h^2$  is the narrow-sense heritability ( $h^2 \equiv V_A/V_P$ ).

We assume that there is an optimal value  $\theta(x, t)$  for the trait  $z(x, t)$  that is changing at steady and independent rates through space ( $x$ ) and time ( $t$ ):

$$\theta(x, t) = bx - kt, \quad (2)$$

where  $b$  is the gradient of optimum in space and  $k$  is the rate of change of the optimum in time. The habitat is one-dimensional, and the position on it is denoted by  $x$ .

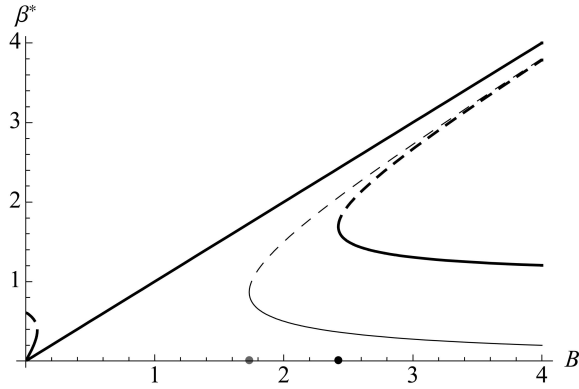
Following Kirkpatrick and Barton (1997), one would naturally start with a simple population regulation, where population density just reflects mean fitness, because this readily leads to exact results. In appendix A, we explain how models with joint regulation converge to the equilibrium solution of this simple model.

It is more realistic to assume that there is a joint regulation of trait mean (eq. [1]) and population density (Kirkpatrick and Barton 1997). The population grows locally at rate  $\bar{r}$ , and migration is approximated by diffusion with variance  $\sigma^2$ :

$$\frac{\partial n}{\partial t} = \frac{\sigma^2}{2} \frac{\partial^2 n}{\partial x^2} + \bar{r}n. \quad (3)$$

The average fitness gives the intrinsic rate of increase of the population,  $\bar{r}(n, \bar{z})$ . Fitness  $r(n, z)$  and the intrinsic rate of increase depend on both the population density (ecological component,  $r_e$ ) and adaptation in the trait (genetic component,  $r_g$ ):  $r = r_e(n) + r_g(z)$ ,  $\bar{r} = r_e(n) + \bar{r}_g(\bar{z})$ . The genetic component of fitness declines with the distance of the trait from the optimum:  $r_g \equiv -(z - \theta(x, t))^2/(2V_S)$ ,  $\bar{r}_g \equiv -(z - \theta(x, t))^2/(2V_S) - V_P/(2V_S)$  (the last term arises as the phenotypic variance  $V_P \equiv \overline{(z - \bar{z})^2} = \bar{z}^2 - \bar{z}^2 = \overline{(z - \theta)^2} - (\bar{z} - \theta)^2$  for any  $\theta$ ). The variable  $V_S$  is the variance of stabilizing selection around the optimum; the strength of stabilizing selection is  $1/V_S$ .

We assess both a “logarithmic model” of density dependence, where fitness is very high for low densities ( $n \ll K$ ):  $r_e = -1/\gamma \log(n/K)$ , and a “logistic model,” where the environmental growth rate is defined as  $r_e = r_m[1 - (n/K)]$ ,  $K$  reflects the carrying capacity of the environment,  $\gamma$  is the intensity of density-dependent regulation, and  $r_m$  gives the maximum growth rate. The logarithmic density dependence converges to “simple”



**Figure 2:** Equilibrium values of scaled gradient in trait mean,  $\beta^*$ , for logarithmic growth rate (thick lines) and simple regulation (thin lines), as functions of the scaled environmental gradient,  $B$ .  $B^2$  is the load due to dispersal across the gradient, when time is scaled relative to the rate of return to equilibrium. The solution with  $\beta^* = B$  always exists, and the solution with limited adaptation ( $\beta^* < B$ ) exists when the spatial gradient is steeper than the critical gradient  $B_c$  (dots on  $B$ -axis; see also fig. 3). The thick line shows the solution for joint regulation with logarithmic density dependence,  $2B^2\phi^2(1-\phi) = A^2(1-\phi) + A\phi$ ,  $\beta^* = B\phi$ . The equilibrium value for imperfect adaptation under joint regulation tends to the one with simple regulation as  $A \rightarrow 0$ . When population density is just given by mean fitness, as under simple regulation, the gradient in trait mean for limited adaptation is  $\beta^* = B/2[1 \pm (1 - 2A/B^2)^{1/2}]$  (thin line). Equilibrium gradients in trait mean that are always unstable (both below and above equilibrium,  $\beta^* = B$ ) are shown as dashed lines. The dots illustrate the critical gradients  $B_c$  for both simple and logarithmic regulation (see fig. 3).

regulation (app. A) near equilibrium ( $n \rightarrow K$ ), and as such it allows an exact solution. The logistic model has a more realistic growth rate at low density, which, in contrast to the logarithmic model, leads to a threshold of rates of change in space and time where the population becomes extinct.

It is useful to reduce the number of parameters by re-scaling time, distance, and trait. Following Kirkpatrick and Barton (1997), we therefore introduce

$$\begin{aligned} T &= r^* t, \\ X &= x \sqrt{\frac{2r^*}{\sigma^2}}, \\ Z &= \frac{z}{\sqrt{r^* V_s}}. \end{aligned} \quad (4)$$

Time is scaled to the strength of density dependence, defined as  $r^* \equiv -n \, d\bar{r}/dn|_{n=\hat{n}_m}$  (Kirkpatrick and Barton 1997), where  $\hat{n}_m$  is the density at carrying capacity (i.e., when the trait mean matches the optimum). For the logarithmic model,  $r^* = 1/\gamma$ .

We thus have three parameters,  $A$ ,  $B$ , and  $k^*$ :

$$\begin{aligned} A &= \frac{V_A}{r^* V_s}, \\ B &= \frac{b\sigma}{r^* \sqrt{2V_s}}, \\ k^* &= \frac{k}{\sqrt{r^* V_s}}. \end{aligned} \quad (5)$$

The new parameters  $A$ ,  $B$ , and  $k^*$  describe three kinds of “load,” that is, the decrease of mean fitness due to the standing genetic variance, the spatial gradient, and the temporal change in the optimum. When time is scaled relative to the rate of return to the equilibrium ( $r^*$ ),  $A/2$  is the standing genetic load due to variance around the optimum,  $B^2$  is the load due to dispersal across the spatial gradient, and  $k^{*2}/2$  is the load due to temporal change in the optimum over the characteristic time  $\Delta t = 1/r^*$ . The load components are defined as the expected loss of the mean Malthusian fitness ( $\bar{r}$ ) due to any of the above given factors.

In addition, we scale the population density so that it is equal to 1 when the trait mean matches the gradient:  $N = n/K^*$  (in the logarithmic model,  $K^* = K \exp[-\gamma V_p/(2V_s)] = K \exp[-A/(2h^2)]$ ; in the logistic model,  $K^* = K r^*/r_m = K[1 - A/(A + 2h^2)]$ ).

For joint regulation of trait mean and population density, we obtain (from eqq. [1] and [3]):

$$\frac{\partial \bar{Z}}{\partial T} = \frac{\partial^2 \bar{Z}}{\partial X^2} + \frac{2}{N} \frac{\partial N}{\partial X} \frac{\partial \bar{Z}}{\partial X} - A(\bar{Z} - BX + k^* T), \quad (6)$$

$$\frac{\partial N}{\partial T} = \frac{\partial^2 N}{\partial X^2} + \bar{R} N, \quad (7)$$

where the environmental optimum is now  $\theta^* = BX - k^* T$ . The scaled growth rate  $\bar{R} = \bar{r}/r^*$  is, for the logarithmic model,

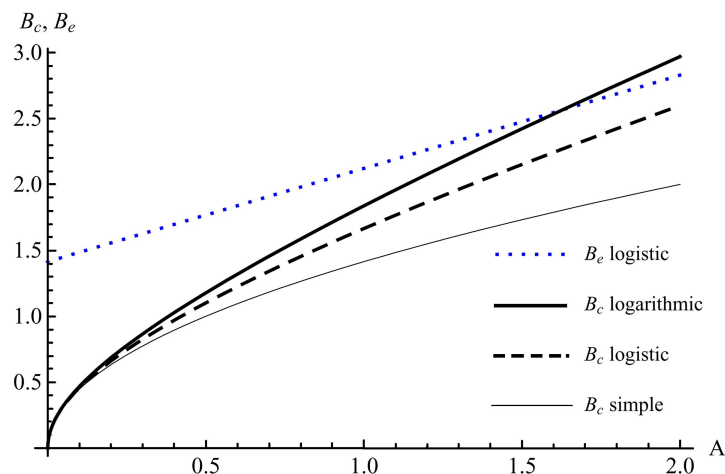
$$\bar{R} = -\log(N) - \frac{1}{2}(\bar{Z} - BX + k^* T)^2, \quad (8)$$

and, for the logistic model,

$$\bar{R} = 1 - N - \frac{1}{2}(\bar{Z} - BX + k^* T)^2. \quad (9)$$

For the static case ( $k^* = 0$ ), these equations correspond to equations (8), (9) and below in Barton (2001).

We search for an equilibrium solution in the form of a traveling wave, where  $U = X - c^* T$  transforms the spatial



**Figure 3:** A solution on a limited range exists only for steep gradients,  $B > B_c$ : black thick, dashed, and thin lines show the critical gradient,  $B_c$ , for logarithmic, logistic, and simple regulation, respectively. A critical gradient for simple regulation,  $B_c = (2A)^{1/2}$  (solid line), is also the approximation for the joint regulation for small values of  $A$ .  $A/2$  is the load due to standing genetic variance when time is scaled relative to the rate of return to equilibrium. The exact formula for the logarithmic model is  $B_c = 1/4[20A + (1 + 8A)^{3/2} - 1 + 8A^2]^{1/2}$ , and from the approximation for a logistic model (using a Gaussian density at equilibrium  $2B^2\phi^2(1 - \phi) = A^2/2(1 - \phi) + A\phi(1 - a^2/2)$ ) we obtain  $B_c \approx 1/4[20A + 2(1 + 4A^2)^{3/2} - 2 + 4A^2]^{1/2}$  for small values of  $k$ . In the simple and logarithmic models, the critical gradient does not depend on the rate at which the optimum changes in time, and the dependence is weak for the logistic model. The blue dotted line is the estimated extinction gradient for logistic growth rate and imperfect adaptation,  $B_e = (2 + A)/2^{1/2}$ ; hence, the area between the dotted and dashed lines delimitates the region where a solution with limited range exists for the logistic model. In the logarithmic model, density  $N \rightarrow 0$  as  $B \rightarrow \infty$ , so the extinction gradient depends on the (arbitrary) choice of density,  $N_e$ , which would be deemed as subcritical. Extinction gradients are discussed in the text and in figure 6. Note that the solid lines for  $B_c$  in the figure are the same as in Barton (2001), but the dashed line for the logistic model differs because here we do not assume that  $B$  is large when estimating  $B_c$ .

coordinate with the distance traveled over time  $T$ , and the speed of the traveling wave is  $c^*$ . Now the scaled lag of trait mean behind the optimum is a function of a single variable,  $U$ :  $\bar{Z} - \theta^* = f(U) + a^*$ , where  $a^*$  measures the lag load (Maynard Smith 1968) at the center of the range (or anywhere for a uniform solution). The logarithmic model now gives an exact solution with the population density of the form  $N = n_1^* e^{-U^2 \zeta^*/2}$ ; for the logistic model, we get only an approximate solution using  $N \approx n_1^*(1 - U^2 \zeta^*/2)$  in equation (7). Just as when the environmental gradient is fixed in time (Kirkpatrick and Barton 1997), we find two classes of solutions: uniform adaptation along the environmental gradient and, when the loss of fitness due to dispersal across the spatial gradient is sufficiently large ( $B > B_c$ ), a limited adaptation, where density declines away from the center. Both solutions with uniform and limited adaptation can be described jointly by the following formulas, which are exact for the logarithmic model but are only approximations for the logistic case. Later we discuss the cases of uniform and limited adaptation in detail.

At equilibrium, the lag load caused by the temporally changing optimum, relative to  $r^*$ , is  $1/2 a^{*2}$ , and  $a^* = k^*/[A + (2B^2/A)\phi(1 - \phi)]$ . Here,  $\phi \equiv \beta^*/B$  describes the

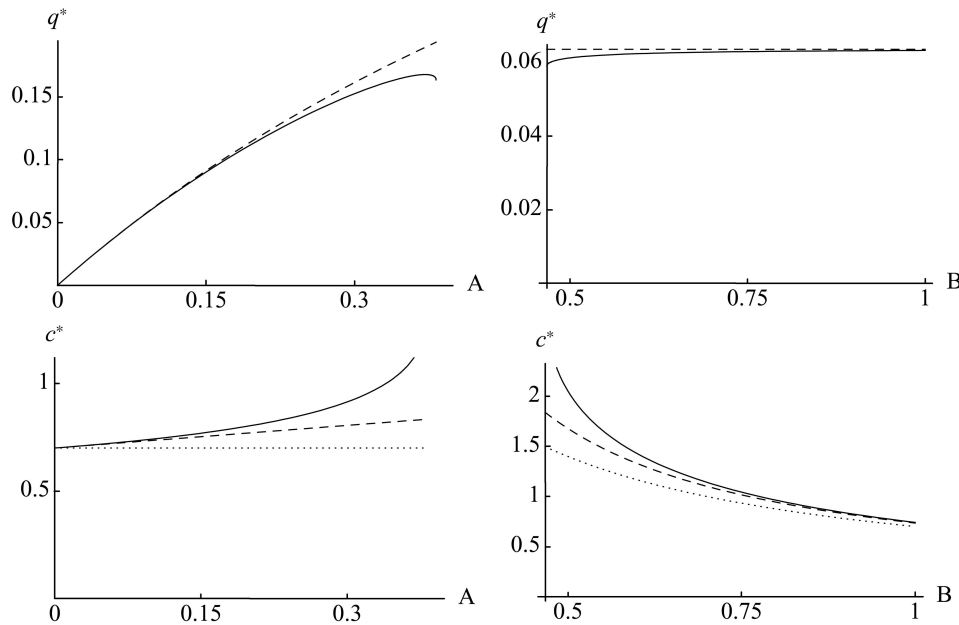
degree of adaptation in the gradient of trait mean, which stays the same (or close to) that found in the static model. The trait mean  $\bar{Z} = \beta^*X - q^*T + a^*$  adapts at a rate  $q^* = k^* - c^*(B - \beta^*)$ .

For limited adaptation, the range shifts at a rate  $c^* = 2a^*B\phi/A$  for  $\phi \neq 1$ . When the gradients match ( $\phi = 1$ ), the solution is uniform with respect to  $U$ ; the range extends along the whole gradient and for any point density,  $c^* = k^*/B$ . The rate of adaptation then simplifies to  $q^* = a^*A$ .

Whereas the above formulas apply to both the logarithmic model (exactly) and the logistic one (as an approximation), the equilibrium population density differs: for the logarithmic model, the density is  $N = e^{-\zeta^* - a^{*2}/2 - U^2 \zeta^*/2}$ ; for the logistic model, the density is  $N \approx (1 - \zeta^* - a^{*2}/2)e^{-U^2 \zeta^*/2}$ . Here,  $\zeta^* = A(1 - \phi)/2\phi$  is the inverse of the variance in population density along the scaled space  $U$ :  $1/\zeta^{*1/2}$  is a measure of the width of the species range.

#### Uniform Adaptation

The formulas above simplify considerably when adaptation is uniform (see fig. 1, left), so that spatial gradients



**Figure 4:** Scaled rate of adaptation,  $q^*$ , and the speed of a traveling wave,  $c^*$ , for the solution with limited range  $\beta^* < B$ . The solid line is the exact solution for logarithmic growth rate, whereas the dashed line is an approximation. The scaled rate of adaptation is approximately  $q^* \approx k^*A/(1+A)$ . The scaled lag of trait mean behind the optimum at equilibrium is  $a^* = q^*/A$ ; hence,  $a^* \approx k^*/(1+A)$  (not shown). With uniform adaptation, the trait mean tracks the optimum, matching its rates of change in both space  $\beta^* = B$  and time  $q^* = k^* = 0.7$ , and the scaled lag is  $a^* = k^*/A$  (not shown). The scaled rate at which the point (e.g., the center of) population density moves through space is  $c^* \approx k^*/B(1+A/2B^2)$ . The dotted line depicts the solution for uniform adaptation, where any point moves at speed  $c^* = k^*/B$ .  $B$  measures the load due to dispersal across the gradient;  $A$  measures the load due to standing genetic variance. For the left column,  $B = 1$ ; for the right column,  $A = 0.1$ .

in the trait mean and the environment are equal ( $\beta^* = B$ ). The rate of adaptation in trait mean matches the rate of a temporal change of the environment,  $q^* = k^*$ . The scaled trait mean,  $\bar{Z}$ , lags behind the optimum by  $a^*$ , leading to a load of  $1/2 a^{*2}$ . The scaled lag of the trait mean behind the optimum increases linearly with the scaled rate of temporal change:  $a^* = k^*/A$ . In the original units, we recover  $a = kV_S/V_A$ ; this is the same for unstructured populations (Lande and Shannon 1996).

The population density for uniform adaptation is  $\hat{N} = e^{-1/2 k^{*2}/A^2}$  for the logarithmic model and  $\hat{N} = 1 - 1/2 k^{*2}/A^2$  for the logistic model. When genetic variance is fixed, uniform adaptation is possible on arbitrarily steep spatial gradients: in principle, the only limitation comes from phenotypic load (with logistic growth rate,  $V_P/(2V_S)$  must be greater than the maximum growth rate,  $r_m$ ). However, in fact, the uniform adaptation is prone to collapse when the spatial gradient is steep,  $B > B_o$ , as we discuss later.

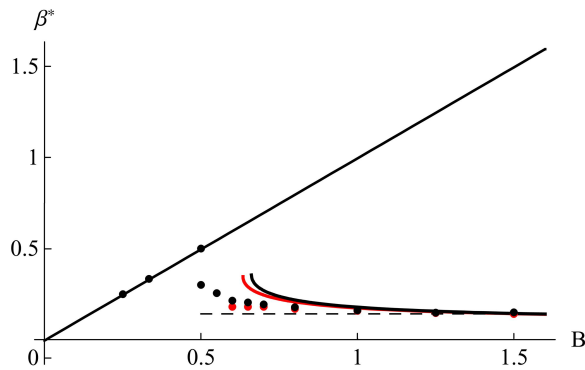
When the cost  $k^{*2}$  due to the optimum changing in time is large relative to the genetic load scaled by the strength of density dependence  $A$ , a uniformly adapted population fails to survive. Under the logistic regulation, the population becomes extinct when the cost due to temporal

change in the optimum is greater than  $k_e^* \approx 2^{1/2}A$ . Logarithmic regulation is likely to be less relevant to extinction thresholds because the growth rate increases without bound as the density approaches 0.

When we scale the population density  $n = N/K^*$  back to the original units, we uncover the trade-off between the phenotypic load  $V_A/(2h^2V_S)$  and the lag load  $a^{*2}r^*/2$ , which decreases with the additive genetic variance  $V_A$ . When adaptation is uniform, the genetic component of fitness and the population density is highest when  $V_A = (2k^{*2}h^2V_S^2)^{1/3}$ , as predicted for an unstructured population by Lande and Shannon (1996). The rate of temporal change, which leads to extinction in the logistic model, is in the original units  $k_e = (2r^*/V_S)^{1/2}h^2V_P$ , which is in agreement with the result for an unstructured population (see eq. [11] in Lynch and Lande 1993).

#### Limited Adaptation

Whereas uniform adaptation confirms the earlier predictions for panmictic populations, this is not the case when adaptation is limited ( $\phi = \beta^*/B < 1$ ); see the right-hand side of figure 1. This solution emerges when the spatial gradient,  $B$ , is sufficiently steep relative to the scaled genetic



**Figure 5:** As the optimum moves in time, the equilibrium gradient in trait mean,  $\beta^*$ , stays close to that found in the static case if the population can persist. The equilibrium values with logistic regulation in a static environment ( $k = 0$ ) are shown in black; solutions for the scaled rate of temporal change of  $k^* = 0.5$  are shown in red. Lines refer to analytic results, and dots refer to numerical solutions. The dashed line depicts the prediction for steep gradients:  $\beta^* = A/2^{1/2}$ . In a static environment (black), the uniform solution (with  $\beta^* = B$ ) always exists, the solution with limited adaptation ( $\beta^* < B$ ) exists when the spatial gradient  $B$  is steeper than the critical gradient  $B_c \approx 0.66$  (see figs. 2 and 3), and both are locally stable on the infinite range. In numerical solutions (dots), however, the adaptation collapses from the margins whenever the solution with limited adaptation exists (and even for slightly shallower spatial gradients,  $B$ : the gradient in trait mean,  $\beta^*$ , is concave rather than constant, as assumed in the depicted analytical approximation). Note that, when gradient is too steep ( $B > B_c$ ), a population with limited adaptation cannot persist ( $B_c \approx [(A + 2)/(2)]^{1/2} \doteq 1.56$  for  $k^* = 0$  decreases to  $B_c \doteq 1.52$  for  $k^* = 0.5$ ; see text). A uniformly adapted population cannot adapt to a temporal change faster than  $k_c^* \approx 2^{1/2}A \doteq 0.28$ . Parameters:  $A = 1/5$ ,  $k^* = 0$  (black), and  $k^* = 0.5$  (red). The numerical solutions are run on a spatial lattice with spacing  $\delta X = 1/16$  and the time step is  $\delta T = \delta X^2/4$  (so that consistently, with the scaled model, migration is  $m = 2\delta T/\delta X^2 = 1/2$ ), and there is no migration over the margins (reflective boundary conditions).

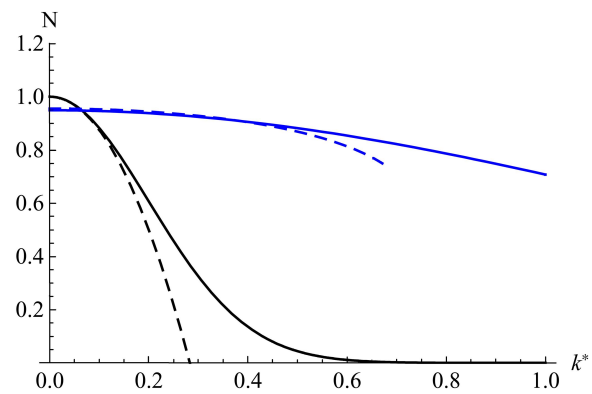
variance,  $A: B > B_c(A)$ . Now, as the gradient in trait mean is much shallower than the environmental gradient, the population density decreases away from the center, leading to a limited species range. As the optimum changes in time, the trait mean adapts more slowly than the environment changes ( $q^* < k^*$ ), and the species range shifts as the population moves toward the habitat to which it was previously adapted.

With logarithmic regulation, the gradient in trait mean,  $\beta^*$ , is independent of the speed of movement of the optimum,  $k^*$ . The gradient in trait mean  $\beta^*$  stays shallower than the environmental gradient  $B$  following a cubic equation for  $\phi \equiv \beta^*/B$ :  $2B^2\phi^2(1 - \phi) = A^2(1 - \phi) + A\phi$  (see fig. 2). It follows that a solution with limited range exists when  $B > B_c = 1/4[20A + 8A^2 + (1 + 8A)^{3/2} - 1]^{1/2}$ , which, for small  $A$ , occurs approximately when  $B > (2A)^{1/2}$  or  $V_A < 1/4 \gamma \sigma^2 b^2$  in the original units (see fig. 3). Note that this approximate formula is the same as the exact result for the

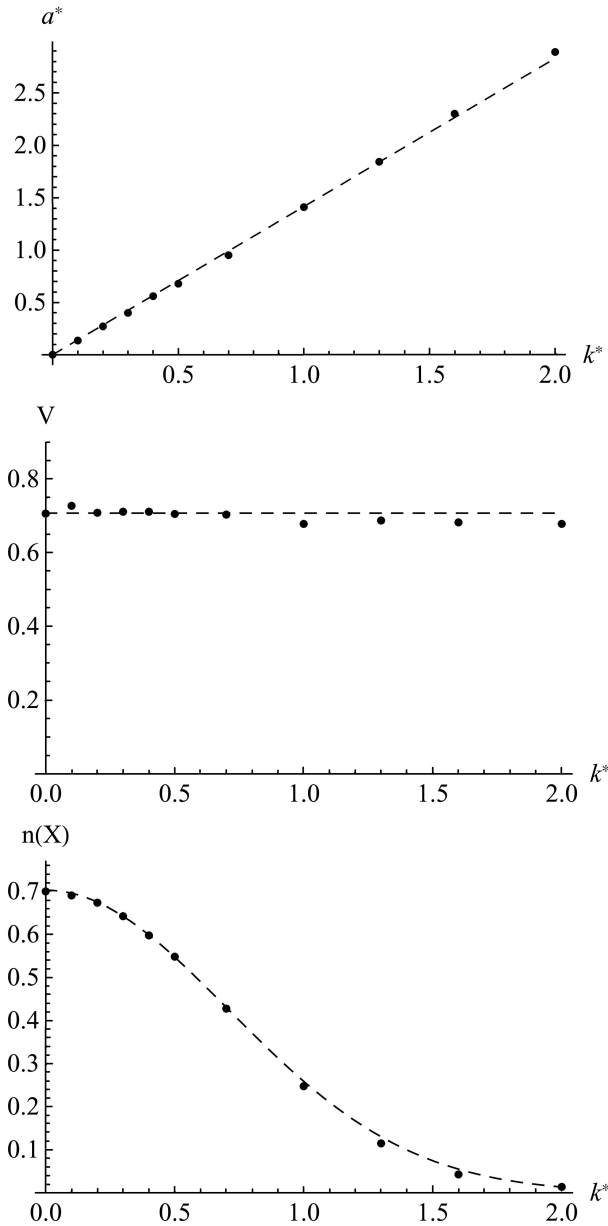
gradient in trait mean under simple population regulation (eq. [A2]). In contrast to the simple and logarithmic regulations, the approximation for the logistic model shows a weak dependence on the rate of temporal change, although the deviation is smaller than can be detected numerically (see fig. 5). It is worth noting that, although overall density declines with increased rate or cost of temporal change ( $k, k^*$ ), this does not directly reduce the width of species range: for example, two standard deviations of  $N(X)$  is  $2/\xi^{*1/2}$ , where  $\xi^* = A(1 - \phi)/(2\phi)$  and the degree of adaptation,  $\phi$ , is independent of  $k^*$ .

The rate of adaptation increases with the standing genetic load ( $A$ ):  $q^* = k^*A^2/[A^2 + 2B^2\phi(1 - \phi)] \approx k^*A/(1 + A)$  (approximately for small  $A$ ; see fig. 4, *top left*). Unexpectedly, the rate of adaptation hardly depends on the effective gradient  $B$  (fig. 4, *top right*). The scaled lag of trait mean behind the optimum is simply  $a^* = q^*/A$ . The population is centered at  $X = c^*T$ , and the rate at which the population moves in space is  $c^* = 2B\phi k^*/[A^2 + 2B^2\phi(1 - \phi)] \approx k^*/B[1 + A/(2B^2)]$ , which increases as the standing genetic load ( $A$ ) increases and decreases as the effective gradient  $B$  gets steeper (fig. 4, *bottom row*).

Assuming that favorable habitat is available, the decline in density is now much less sensitive to  $k^*$  than it was when adaptation was uniform. In contrast, the degree of maladaptation increases quite quickly with the dispersal load,  $B^2$ . The critical rate of change of environment in space (and time) when the population with logistic regulation becomes extinct is given by  $B_c \approx (A + 2)/2^{1/2} -$



**Figure 6:** Population density for the uniform population (where  $\beta^* = B$ ) decreases as fast as the optimum moves:  $N = e^{-1/2 k^* 2/A^2}$  for the logarithmic model (solid black line), and ( $N = 1 - 1/2 k^* 2/A^2$ ) for the logistic model (dashed black line,  $k_c^* \approx 2^{1/2}A$ ). As the cost of temporal change, measured by  $k^*$ , increases, local population density becomes higher for a population adapted to a limited range (where  $\beta^* < B$ , blue lines), because the population can slide along the environmental gradient. The cost of temporal change ( $k^*$ ) when local population density becomes higher for the population with limited adaptation than for the uniform one increases with  $A$  (not shown). Parameters:  $A = 1/5$ ,  $B = 0.7$ .



**Figure 7:** Simulations (dots) and predictions (dashed lines) for the two-allele model with logarithmic regulation match well. At the top, the lag of the trait mean behind the optimum matches the analytical solution shown by the dashed line  $a^* = k^*/V$ , where  $V = 2^{1/2}B$  (in the original units,  $a = kV_S/V_A$ ). In the middle, genetic variance stays close to prediction for a fixed gradient,  $V = 2^{1/2}B$  (rescaling back to the original units,  $V_A = \sigma b V_S^{1/2}$ ). At the bottom, population density at equilibrium is  $n = Ke^{-1/2 A|f^2 + k^{*2}/A^2}$ . The dots show results of a stepping-stone model on a spatial lattice with range  $(-X_m, X_m)$  and spacing  $\delta X$ . In the scaled model, the time step must be  $\delta T = \sigma^2/2 = m\delta X^2/2$ , where  $m \leq 1/2$  is the migration rate. Parameters:  $B = 1/2$ , number of loci  $n_l = 20$ ,  $\delta X = 1/2$ ,  $m = 1/2$ ,  $X_m = 50$ ,  $K = 1$ , and  $h^2 = 1$  (note that we display the density  $n(x)$  in the original units). Cline shapes and more details of the equilibrium solution are shown in figures 8 and 9.

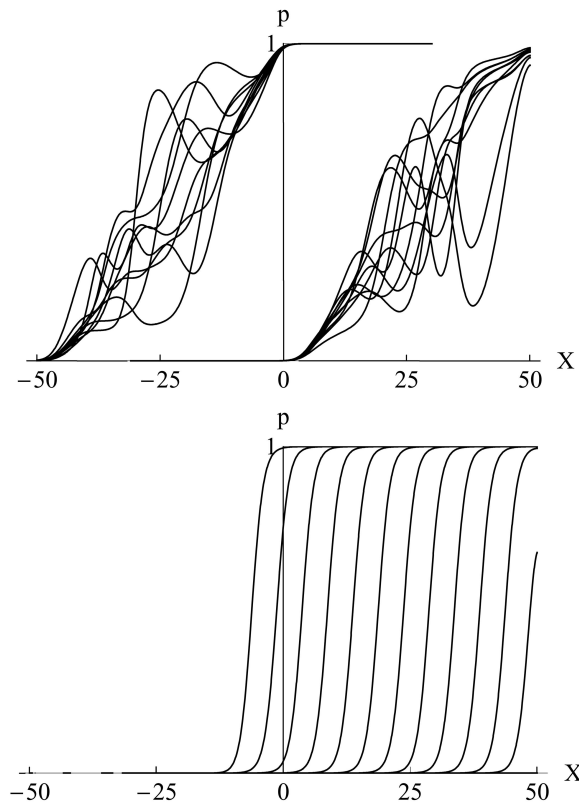
$k^{*2}/(2^{1/2}4)(1 - A + 3/4 A^2) + O(k^{*3}) + k^{*2}O(A^3)$  (where  $O(x^i)$  refers to terms of the “order of”  $x^i$  for  $i \geq y$ ). In terms of the original units, we recover  $b_e \sigma/V_S^{1/2} \approx 2r_m + V_p/V_S(h^2 - 1) - 1/4 k^2[r_m - V_p/V_S(1/2 + h^2)]$ . The extinction gradient increases with the genetic load  $Ar^*/2 = h^2 V_p/(2V_S)$  both because of the static term and because the decrease due to temporal change (last term) becomes smaller. Note that, for the static case ( $k = 0$ ), this formula corrects a typographical error in Kirkpatrick and Barton (1997; eq. [A5]), as their scaling uses genetic load  $A$  rather than  $A/2$  (as stated in their eq. [11a]; this was mentioned earlier by Case and Taper 2000).

#### Transition: The Critical Gradient

The critical rate (gradient) of change of the optimum in space, above which uniform adaptation may collapse, does not change significantly with the rate at which the optimum moves in time, and it depends only on standing genetic variance. For both models of density dependence that we assessed, the critical gradient is close to  $B_c = (2A)^{1/2}$  (see fig. 3), as shown previously for a static optimum by Kirkpatrick and Barton (1997) and Barton (2001). In the original units, limited adaptation emerges approximately when the change in spatial optimum over one dispersal range,  $b\sigma$ , relative to the standard deviation of genetic variance,  $V_A^{1/2}$ , is larger than twice the square root of the strength of density dependence:  $b\sigma/(h^2 V_p)^{1/2} > 2r^{*1/2}$ .

Both uniform adaptation and limited-range solutions are locally stable on an infinite range (see app. B); however, as the spatial gradient steepens above the critical gradient  $B_c$ , uniform adaptation becomes increasingly prone to collapse toward the limited adaptation due to perturbations of the uniform solution. Such a collapse is triggered by the imposed reflective boundary conditions at the margins of the available habitat: this effect can be important in nature when there is a rigid boundary to the habitat (e.g., a river), so that dispersal—and hence, maladaptive gene flow—is reduced at the margin. Density of a population adjacent to the boundary then increases, increased gene flow to the neighboring population (closer to the center of the range) leads to a drop in a density there, and, eventually, the whole population collapses to the regime with limited adaptation (see Kirkpatrick and Barton 1997; Polechová and Barton 2005). When the cost of temporal change ( $k^*$ ) is large, limited adaptation may constitute the only way a population can survive: this is because the lag of trait mean behind the optimum is actually smaller, because populations with limited adaptation move faster through space (see figs. 4, 6).





**Figure 8:** Illustration of the shape of allele frequencies ( $p$ ) at time  $T = 5$  (top) and  $T = 70$  (bottom). At equilibrium, the cline shape is  $\hat{p}(X) = 1/(1 + e^{-4/W(X+c^*T)})$ , where the scaled cline width is  $W = 4(n_i/A_m)^{1/2}$  and the clines move across the space  $X$  at a speed  $c^* = k^*/B$ . The allelic effect is scaled as  $\alpha = \alpha^* = BX_m/n_i$ , and the maximum scaled variance is  $A_m = 1/2 \alpha^2 n_i/(r^* V_s)$ . Fixing  $\alpha^*$  and  $A_m$ , and taking a higher number of loci than can fix in the static case,  $n_i > BX_m/\alpha^*$ , does not lead to a higher number of diversified loci (and thus higher variance). Parameters are as they are in figure 7;  $k^* = 0.3$ .

#### *Adaptation to a Linear Environmental Gradient Moving in Time: Population Genetic Model*

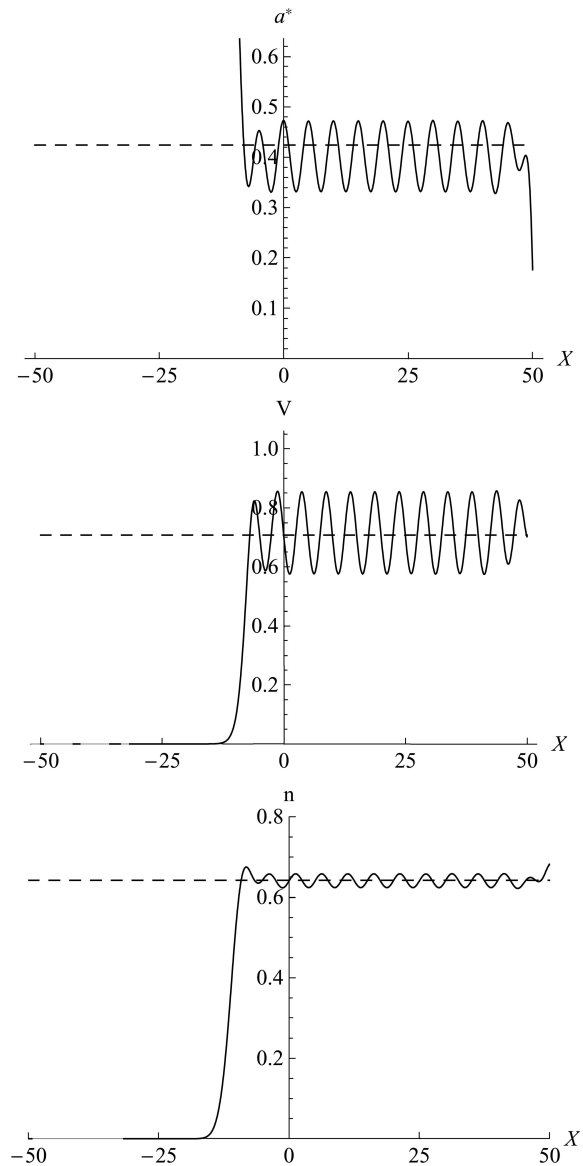
In order to relax the assumption of fixed genetic variance, we need a model with explicit determination of a trait; for comparison with the phenotypic model above, the trait distribution should be (close to) a Gaussian. We chose a two-allele model (Barton 2001) where the trait under selection is determined by  $n_i$  independent biallelic diploid loci of additive effect (with frequencies  $q_i$  and  $p_i$  and effects  $-\alpha_i/2$  and  $\alpha_i/2$ ). The trait mean is  $\bar{z} = \sum_{i=1}^{n_i} \alpha_i(p_i - q_i)$ , and variance at linkage equilibrium is  $V_A = 2 \sum_{i=1}^{n_i} \alpha_i^2 p_i q_i$ .

The cline shape in a static environment ( $k = 0$ ) has been derived by Barton (1999, 2001), with the assumption that clines have the same form and are distributed in space so that the trait mean matches the gradient. Substituting in equation (1) with  $\bar{r}$  for the logarithmic model as defined

below, equation (3) gives the rate of change of allele frequency:

$$\frac{\partial p_i}{\partial t} = \frac{\sigma^2}{2} \frac{\partial^2 p_i}{\partial x^2} + \sigma^2 \frac{\partial \log(n)}{\partial x} \frac{\partial p_i}{\partial x} + \frac{\alpha^2}{2V_s} p_i q_i (p_i - q_i - 2\delta) - \mu(p_i - q_i), \quad (10)$$

where  $\delta \equiv (\bar{z} - \theta)/\alpha$ ,  $\mu$  is the mutation rate (which is



**Figure 9:** Scaled lag of the trait mean behind the optimum,  $a^*$ , scaled variance  $V$ , and the population density  $n(X)$  vary periodically as the optimum is matched by a finite number of loci. Parameters are as they are in figure 7;  $k^* = 0.3$ ,  $T = 70$ .

**Table 1:** Variables and parameters, original units

Variable	Parameter
$z$	Phenotypic trait
$x$	Spatial axis
$t$	Time
$n(x, t)$	Population density
$\bar{z}(x, t)$	Trait mean
$\psi(z, x, t)$	Phenotypic density
$\theta(x, t)$	Ecological optimum, $\theta = bx - kt$
$b$	Spatial gradient
$\phi$	Degree of adaptation, $\phi \equiv \beta/b$
$\sigma$	Standard deviation of dispersal distance
$k$	Rate of temporal change
$V_p$	Phenotypic variance
$V_A$	Additive genetic variance
$h^2$	Heritability, $h^2 \equiv V_A/V_p$
$V_S$	Variance of fitness due to stabilizing selection; strength of stabilizing selection is $1/(2V_S)$
$K$	Measure of carrying capacity
$\beta$	Spatial gradient in trait mean ( $\bar{z} = \beta x$ )
$a$	Lag of the trait mean behind the optimum
$q$	Rate of adaptation in trait mean
$c$	Speed of traveling wave through space $x$
$u$	Transposed space, $u = x - ct$
$\zeta$	Inverse of variance of population density $n$ along spatial axis $x$
$r(z, x, t)$	Fitness of phenotype $z$ at location $x$ and time $t$ ; defined below equation (3)
$r_e(x, t)$	Ecological component of fitness (density dependent)
$r_g(z, x, t)$	Genetic component of fitness, given by adaptation of the trait $z$ to the optimum $\theta$
$\bar{r}(x, t)$	Fitness of mean phenotype $\bar{z}$ at location $x$ and time $t$
$\bar{r}_g(z, x, t)$	Genetic component of mean fitness, given by adaptation of the trait mean $\bar{z}$ to the optimum $\theta$
$r^*$	Rate of return to equilibrium
$\gamma$	Intensity of density dependence (with simple and logarithmic regulation)
$r_m$	Maximum growth rate in the logistic model
$n_l$	Number of loci
$\gamma_m$	Mutation rate
$\alpha_i$	Allelic effect at locus $i$
$p_i, q_i$	Allele frequency at locus $i$

assumed to be symmetric), and  $\alpha_i = \alpha$ . Note that now the genetic variance changes with allele frequency, so we get an extra term  $(p_i - q_i)/2V_S$  arising from  $\partial \bar{r}/\partial \bar{z}$ .

For the static case, Barton (2001) showed that at the spatially uniform equilibrium with no mutation, allele frequency (centered at  $x = 0$ ) has a form  $\hat{p}[x] = 1/\{1 + \exp[-(4/w)x]\}$  (we set  $\alpha_i = \alpha$ ) where the width of the cline is  $w = 4(\sigma^2 V_S/\alpha^2)^{1/2}$ . The variance contribution due to one locus is  $V_{G, n_l=1} = 2\alpha(\sigma^2 V_S)^{1/2}$ , obtained by integrating the variance formula over space, with  $p \rightarrow \hat{p}(x)$ . To match the spatially variable optimum  $\theta$ , the additive genetic variance at equilibrium is  $\hat{V}_A = b(\sigma^2 V_S)^{1/2}$ , since there must be  $b/(2\alpha)$  clines per unit distance (as each cline shifts the trait mean by  $2\alpha$ ); the genetic variance is maintained by the dispersal across the gradient, and it is independent as to the number of loci. In the scaled model (see app. C), we get  $V \equiv V_A/(r^* V_S) = 2^{1/2} B$ .

As the optimum changes in time, allele frequencies will

need to move in space. We are again looking for a traveling-wave solution where the allele frequency,  $p(x, t) = p(u)$ , is solely a function of a new variable  $u = x - ct$  (and  $\partial/\partial x = d/du$ ,  $\partial/\partial t = -c d/du$ ):

$$-c \frac{dp_i}{du} = \frac{\sigma^2}{2} \frac{d^2 p_i}{du^2} + \sigma^2 \frac{d \log(n)}{du} \frac{dp_i}{du} + \frac{\alpha_i^2}{2V_S} p_i q_i (p_i - q_i - 2\delta) - \mu(p_i - q_i), \quad (11)$$

and where the allele frequency (which was, at time  $t = 0$ , centered on  $u = 0$ ) has a form  $p(u) = 1/\{1 + \exp[-(4/w)u]\}$ . Then,  $dp/du = (4/w)pq$  and  $d^2 p/du^2 = (4/w)^2 pq(p - q)$ , so with no mutation there is a spatially uniform solution for a given  $\delta = (\bar{z} - bx + kt)/\alpha$ , where  $w = 4(\sigma^2 V_S/\alpha^2)^{1/2}$  and  $c/\delta = w\alpha^2/(4V_S)$ .

The cline shape stays the same as it is in the static case:

**Table 2:** Variables and parameters, scaled

Variable	Parameter
$Z$	Phenotypic trait, $Z \equiv z/(r^* V_S)^{1/2}$
$X$	Spatial axis, $X \equiv x(2r^*/\sigma^2)^{1/2}$
$T$	Time, $T \equiv r^* t$
$N(X, T)$	Population density, $N = n/K^*$
$\bar{Z}(X, T)$	Trait mean
$\Psi(Z, X, T)$	Phenotypic density
$\theta^*(X, T)$	Ecological optimum, $\theta^* = BX - k^* T$
$B$	Spatial gradient, $B = b\sigma/[r^*(2V_S)^{1/2}]$ ; dispersal load, relative to the rate of return to equilibrium, $r^*$ , is $B^2$
$\phi$	Degree of adaptation, $\phi = \beta^*/B$
$k^*$	Rate of temporal change, $k^* = k/(r^* V_S)^{1/2}$ ; the load, relative to $r^*$ , is $k^*/2$
$A$	Additive genetic variance, $A = V_A/(r^* V_S)$ ; standing (genetic) load, relative to $r^*$ , is $A/2$
$K^*$	Measure of carrying capacity
$\beta^*$	Spatial gradient in trait mean ( $\bar{Z} = \beta^* X$ )
$a^*$	Lag of the trait mean behind the optimum, $a^* = a/(r^* V_S)^{1/2}$ ; lag load, relative to $r^*$ , is $a^*/2$
$q^*$	Rate of adaptation in trait mean, $q^* = q/(r^* V_S)^{1/2}$
$c^*$	Speed of traveling wave, $c^* = c[(2/(r^* \sigma^2))]^{1/2}$
$U$	Transposed space, $U = X - c^* T$
$\zeta^*$	Inverse of variance of population density $N$ along spatial axis $X$ , $\zeta^* = \zeta \sigma^2/(2r^*)$
$R(Z, X, T)$	Fitness of phenotype $Z$ at location $X$ and time $T$
$\bar{R}(\bar{Z}, X, T)$	Fitness of mean phenotype $\bar{Z}$ at location $X$ and time $T$ ; equations (8) and (9)

as the optimum changes in time, the clines uniformly shift in space at a rate  $c$ . We find the solution only with uniform adaptation, where the rate of change in the trait mean matches the change in the optimum ( $q = k$ ). Hence, we must have  $c = k/b$ , and the lag of trait mean behind the optimum is  $a = k V_S^{1/2}/(b\sigma)$ . The number of clines required to match the optimum at any particular time stays the same as in the static case at  $b/(2\alpha)$ , and hence the resulting variance stays at  $\hat{V}_G = b(\sigma^2 V_S)^{1/2}$  (without mutation and under linkage equilibrium); as in the static case (Barton 2001), it is independent of allelic effect or numbers of genes. The lag of the trait mean is therefore  $a = kV_S/\hat{V}_G$ , in agreement with the prediction for the phenotypic model.

We test the robustness of the predictions by numerically iterating the two-allele model, following joint evolution of clines (and hence that of mean and variance) and population density, as described by equations (C1) and (7). All clines evolve independently, and so there is no linkage disequilibrium. Initially, the population has no spatial adaptation: allele frequencies at time 0 are uniform in space and almost fixed at 0 or 1, with uniform distribution of deviations ranging from 0 to 0.01. Over time (see fig. 8), allele frequencies diversify across the range to match the optimum (fig. 9).

The population evolves to be uniformly adapted, with the gradient in trait mean matching the optimum and lagging behind by  $a^* = k^*/A$  ( $a = kV_S/V_A$  in the original units), matching the predictions for the phenotypic model (see top rows of figs. 7, 9). Scaled genetic variance  $V$  stays

very close to the prediction (above),  $V = 2^{1/2}B$  (figs. 7, 9, *middle rows*). Because genetic variance does not increase above the static equilibrium when the optimum changes faster in time, population density decreases toward 0 when the loss of fitness due to temporal change is too large relative to the standing genetic variance (fig. 7). The variance does not increase above the static equilibrium even when we add mutation to the model. The rate of decrease of population density obviously quantitatively differs between the logistic and the logarithmic models; for the logistic model, population density declines faster with  $k^*$ , leading to extinction at  $k^* \geq 2^{1/2}A = 2B$ .

## Discussion

When the environment varies in both time and space, how fast do population traits evolve and how does the species range change in size and position? In panmictic populations, it is predicted that the rate of adaptation matches the rate of change in time and the trait mean lags behind the optimum by a constant delay (Charlesworth 1993; Lande and Shannon 1996; Bürger 1999; Waxman and Peck 1999). These predictions agree with those of our spatial model when the adaptation is uniform in space. If this is not the case, and if gradient in trait mean is shallower than the environmental gradient, then the rate of adaptation is considerably slower (see fig. 4) and the population moves to the habitat optimum to which it was previously adapted. If this was not available, then the population would become extinct. Perhaps surprisingly, the extent to

which the population trait mean matches the spatial gradient is the same as it is in the static case (Kirkpatrick and Barton 1997). Only when variance can evolve freely is the adaptation always uniform. Interestingly, the variance is the same as when it is maintained by dispersal across the spatial gradient in the static case (Barton 2001).

Whether a population can adapt to an unlimited range depends on the dimensionless parameters  $A$  and  $B$ , and its ability to respond to change through time depends on the scaled parameter  $k^*$ . These three parameters can be thought of as three kinds of genetic loads, each scaled relative to the strength of density dependence,  $r^*$ . The equation  $A/2$  is the standing genetic load due to genetic variance around the optimum,  $B^2$  is the loss of fitness when an optimally adapted population shifts by one dispersal range, and, similarly,  $k^{*2}/2$  is the loss of fitness when an optimally adapted population shifts over the characteristic time  $1/r^*$ . All loads are relative to the rate of return to the equilibrium,  $r^*$ : the absolute costs are  $Ar^*/2$ ,  $B^2r^{*2}$ , and  $k^{*2}r^*/2$ . The corresponding scalings of trait, space, and time are introduced in equations (4) and (5); all parameters are listed in tables 1 and 2.

#### Parameters in Nature

What are plausible values for the parameters  $A$ ,  $B$ ,  $k^*$ , and  $r^*$ ? First, consider  $A$ , a measure of the load due to genetic variance around the optimum. Since Lande and Arnold (1983) renewed interest in the quantitative genetics of wild populations, there have been hundreds of studies of the strength of stabilizing selection and additive genetic variation in nature. The observed distribution (Kingsolver et al. 2001) of the standardized quadratic selection gradient,  $\gamma_p$ , is wide and fairly symmetrical on the continuum of stabilizing ( $\gamma_i < 0$ ) to disruptive selection ( $\gamma_i > 0$ ), with the median (tilde) for stabilizing selection  $-\tilde{\gamma}_{i,-} = \tilde{V}_p/(2V_S) \doteq 0.1$ , but ranging from 1.5 to 0. This corresponds to  $V_S/V_E = 5/(1 - h^2)$  rather than  $V_S/V_E = 20$ , which used to be the common assumed value (see Lande 1975; Johnson and Barton 2005). If we take heritability  $h^2 = 1/2$  (which implies that  $V_A = V_E + V_R$ , where the components of  $V_R$  are all nonadditive components of genetic variance), the median of  $A = V_p h^2 / (r^* V_S)$  per measured trait is  $A \doteq 0.1$  for  $r^* \doteq 1$  and, mostly,  $A < 2$ .

Burt (1995, 2000) reviewed evidence on the additive genetic variance for fitness and made an interesting argument concerning (in our notation) the scaled dispersal load,  $B^2$ . He pointed out that the total dispersal load can be estimated from transplant experiments in which individuals are moved from their native location or are fertilized by pollen from elsewhere. This dispersal load must be balanced against the increase in relative mean fitness due to selection, which equals the standardized additive

variance in fitness ( $\Delta \bar{W}/\bar{W} = h^2 \text{Var}(W)/\bar{W}^2 = V_W$ ). Now suppose that we can identify a principal component (of measured traits) that explains most of the variance in the reproductive success due to dispersal across the spatial gradient. Then,  $B$  can be related to the combined genetic load ( $A$ ) for this component. By dispersal of a distance  $\sigma$ , fitness decreases by  $B^2 r^{*2}$ . The decrease in fitness due to dispersal and mutation is at equilibrium, balanced by a corresponding increase via additive variance in fitness,  $V_W$ ; if we ignore mutation,  $V_W = B^2 r^{*2}$  (where  $W$  is the fitness in discrete time, and  $\Delta \bar{W}/\bar{W} \approx \Delta \log(\bar{W}) \approx \Delta \bar{r}$ ). Burt (1995, 2000) reviewed a few estimates for the total dispersal load and reported a median of  $B^2 \doteq 0.02/r^{*2}$  and, mostly,  $B^2 \leq 0.1/r^{*2}$ .

How fast might environmental optima change through time? In reality, change may occur over all timescales, rather than as a simple linear change as assumed here. However, fast changes will average out, and slow changes will have a negligible effect; we are concerned with changes that occur over the joint evolutionary and ecological timescale. The load from a perfectly adapted population, due to a changing optimum over characteristic time  $1/r^*$ , is  $k^2/(2r^{*2}V_S) = k^{*2}r^*/2$ . We can get an estimate of a load due to a temporally changing environment from the speed of advance of the range due to temporal change in the environment. This speed (in terms of dispersal ranges, as  $c^* = c/\sigma(2/r^*)^{1/2}$ ), at which a point population density moves in space, is  $c^* \approx k^*/B$  when  $\beta^* \rightarrow B$  or  $A \ll 2B^2$ . We give an example of one well-studied, fast-advancing species: the butterfly *Hesperia comma* is advancing at a rate of  $c \doteq 0.63$  km per generation due to rising temperature (Thomas et al. 2001), while its expected dispersal distance is  $\sigma \doteq 0.1$  km (as measured by Hill et al. 1996 for the first nine generations). Approximately, the load due to a temporally changing optimum is  $k^{*2}r^*/2 \approx (c/\sigma)^2 B^2$  at equilibrium; using the medians for  $B$  and  $r^*$ , we get an estimate of  $k^*$  of about 2.7 (this is an overestimate, because the range will expand faster than would follow from a model with diffusive migration as a result of occasional long-distance dispersal, and  $\sigma$  is necessarily going to be an underestimate to some extent, because migrants a long distance away will not be measured and dispersal may increase during expansion). Perhaps as a better approach, the load due to the temporal change in the optimum could be estimated directly by comparing reproductive success between progeny of a current and a significantly older generation (e.g., studying organisms with a long dormancy, using seeds or diapausing invertebrates as in Decaestecker et al. [2007]).

Finally, the characteristic time is given by the inverse of the strength of density dependence,  $1/r^*$ , where  $r^*$  is the rate of return toward the equilibrium at carrying capacity  $\hat{n}_m$ :  $r^* = -\partial/\partial n \partial n/\partial t|_{n=\hat{n}_m} = -n \partial \bar{r}/\partial n|_{n=\hat{n}_m}$ .

From Sæther et al. (2005), we see that values of  $D \equiv -\partial \log(\lambda^{\Delta t})/\partial \log(n)|_{n=\hat{n}_m}$ , where  $\lambda^{\Delta t}$  is the growth rate per generation, lie mostly between 0 and 2.5. In appendix D, we show that  $D$  is approximately equivalent to  $r^*$ , and thus, the median for  $r^*$  is around 1. Also, for logistic growth, the intrinsic growth rate  $\bar{r}$  gives the upper bound for  $r^*$ : Grosholz's (1996) study provides  $\bar{r}$  for some invasive species: the range of  $r = 10^{-1}$  to 10, with a median of  $\bar{r} \leq r^*$  again around 1 (see also Case and Taper 2000). The importance of strength of density dependence for limits to species range and behavior at the margins has also been discussed in a recent article by Filin et al. (2008).

The above rough overview gives the estimates for the measure of standing genetic load,  $A$ , at  $\tilde{A} \doteq 0.1$  (generally,  $<2$ ). The known (few) estimates of total dispersal load give  $\tilde{B}$  at  $0.02^{1/2} \doteq 0.15$  (generally,  $<0.3$ ). From the anecdotal butterfly example, we see that some populations can respond to strong selection due to a temporally changing optimum,  $k^2/2$ ; the indirectly estimated value should be taken with caution, perhaps on the order of 1. In the examples above, all loads are given relative to the characteristic time  $1/r^*$ . The strength of density dependence,  $r^*$ , is mostly  $<2.5$ , and above it is set to around 1. We return to the ways of relating a standing genetic load to the (total) dispersal and/or temporal loads in the next section. Ideally, we would like to get all three loads and the rate of return to the equilibrium,  $r^*$ , estimated for one species, as they may well be correlated. We have not found such data, however, and the above paragraphs are intended to give insights into plausible ranges and possible estimation methods as well as to illustrate the meaning of the load parameters.

#### *Limitations, Predictions, and Nature*

Out of an infinite number of possible scenarios one could think of, we chose a particular simple model of uncorrelated temporal and spatial change and assessed adaptation in a single additive trait. The population dynamics are simple (e.g., no Allee effect) and deterministic, although genetic drift could have a qualitative effect on the results regarding species range (see Butlin et al. 2003; Alleaume-Benharira et al. 2006); certainly, drift would further limit adaptation at low densities at the edge of the species range. Large asymmetries in carrying capacity can also impede adaptation deterministically in the subpopulation, with little contribution to the total reproduction (see Kawecki et al. 1997). Another obvious extension is to include the age structure of the population (see Charlesworth 1980); the spatial gradient can be thought of as "blurred" with the standard deviation as a function of the change in the environment over the average generation

time,  $k\Delta t$ , which would lead to an increase in variance due to the temporal change in the optimum.

We find it surprising that, when the environmental optimum moves in time, genetic variance does not increase from the value maintained by dispersal across the spatial gradient. An optimum changing smoothly over sufficiently long time periods (relative to the width of the fitness function) can lead to a significant increase in variance when recombination is high (Bürger and Lynch 1995; Kondrashov and Yampolsky 1996; Bürger 1999, 2000; Waxman and Peck 1999). According to Bürger's theoretical predictions based on dynamics of underlying cumulants of the genotypic distribution, genetic variance should increase with the lag behind the optimum multiplied by the skewness of the distribution. However, as the equations do not form a closed system, it is unclear how skewness increases as the optimum moves in time. (Both the lag and the skewness decrease with the variance.) We see no increase in variance; the distribution remains Gaussian, with skewness of 0.

Although we can think of genetic variance as being constrained due to interactions with other traits, we do not explicitly model interactions. It is well known that covariance between traits can pose a significant constraint on the response to selection on the trait mean (see Antonovics 1976; Grant and Grant 1995; Etterson and Shaw 2001), and it also influences the variance: if variance of a correlated trait decreases, for example, due to stabilizing selection, so then would the variance of our focal trait (see Pearson 1903; Lande and Arnold 1983; eq. [11]). Our model also does not include genotype-by-environment interactions, which can readily extend the range of favorable habitat (Nussey et al. 2005). Perhaps more importantly, the population genetic model for an additive trait follows only allele frequencies, and not genotypes. Therefore, these results only apply with linkage equilibrium, under weak selection. Sensitivity of our results toward specific scenarios, which violate our assumptions, can be numerically and experimentally tested.

A recent preliminary study by Bridle et al. (2009) reveals results that are reasonably consistent with some of the predictions of Kirkpatrick and Barton (1997), but as far as we are aware, no study provides the data needed to test any of the predictions above. What could be done in principle? The total dispersal load ( $B^2$ ) could be measured directly by making transplants between different places and finding the decrease in fitness with transplant distance, measured relative to the standard deviation of dispersal distance. Similarly, the load due to change through time ( $k^2/2$ ) could in principle be measured by comparing the fitnesses of individuals from the present population with the fitnesses of those in the past (e.g., using diapausing individuals from sediment caves, as in Decaestecker et al.

2007). For all loads, the time should be scaled relative to the rate of return to equilibrium,  $1/r^*$ . The load due to additive genetic variance in specific traits ( $A/2$ ) can be measured by comparing the fitnesses of those at the population mean with the fitnesses of those that are some standard deviations from the mean; heritability would also need to be measured. However, unlike the other two loads, we do need to know about the traits: what matters is the loss of fitness with variance along a particular axis in trait space, defined by the change in mean through time and along the transect. However, finding this axis is a not a trivial task in the real world. If we know the trait axis, then we can readily measure the load due to genetic variance along the axis. If we do not know the trait axis, then we could measure the excess variance in fitness between clones of the parents and their offspring as a function of distance between the parents. Replicates of parents can be ideally obtained from an organism capable of both asexual and sexual reproduction; however, in principle, one could

also reintroduce inbred lines. If the traits involved were additive, this would give us the total standing genetic load directly. Obtaining the load parameters allows us to assess the key predictions of the model; most obviously, we can ask whether there is evidence for a critical gradient,  $B_c$ , above which uniform adaptation tends to collapse.

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## APPENDIX A

### Simple Regulation

With simple regulation, we assume that local population density grows with the average fitness  $\bar{r}(\bar{z})$ :

$$n = Ke^{\gamma \bar{r}}, \quad (\text{A1})$$

where  $K$  reflects the carrying capacity and  $1/\gamma$  is the intensity of density-dependent regulation. This is a simplification of the real population dynamics, because we omit the effect of dispersal. However, it has the advantages of being readily solvable and that the logarithmic model converges to it near equilibrium. Neglecting migration, at equilibrium of the logarithmic model we have  $\bar{r} = r_c + \bar{r}_g = 0$ , and hence, using the formula for the logarithmic model  $r_c = r_\theta - 1/\gamma \log(n/K)$ , we recover  $n = Ke^{\gamma(r_\theta + \bar{r}_g)}$ , as for simple regulation. (In the main text,  $r_\theta$  gives the growth rate when the mean phenotype is perfectly adapted; in the logarithmic model  $n = K$ , it is set to 0.)

With simple regulation, the genetic component of fitness

$$r(z) = r_\theta - \frac{(z - \theta(x, t))^2}{2V_s}, \quad (\text{A2})$$

is a function of the adaptation of phenotype  $z$  at position  $x$  at time  $t$ , and the average fitness  $\bar{r}(\bar{z})$  determines the size of population (eq. [A1]):

$$\bar{r}(\bar{z}) = r_\theta - \frac{(\bar{z}(x) - \theta(x, t))^2}{2V_s} - \frac{V_p(x)}{2V_s}. \quad (\text{A3})$$

It follows from the above equations that, just as for a fixed environmental gradient (Kirkpatrick and Barton 1997; eq. [1]), the mean phenotype changes as

$$\frac{\partial \bar{z}}{\partial t} = \frac{\sigma^2}{2} \frac{\partial^2 \bar{z}}{\partial x^2} + \frac{-\bar{z} + bx - kt}{V_s} \left[ V_\lambda - \sigma^2 \gamma \frac{\partial \bar{z}}{\partial x} \left( b - \frac{\partial \bar{z}}{\partial x} \right) \right]. \quad (\text{A4})$$

We can immediately see a solution where the population adapts as the optimum moves: the trait mean is  $\bar{z} = bx -$

$kt + a$ , lagging behind the optimum by  $a = kV_s/V_A$ . If there is no variance in the trait ( $V_A = 0$ ), a solution exists only for an optimum fixed in time,  $k = 0$ . Population density is uniform in space, at  $n = K \exp \{ \gamma [r_\theta - V_p/(2V_s) - k^2 V_s/(2V_A^2)] \}$ . High genetic variance allows the population to maintain its trait mean closer to the changing optimum, but the population growth rate also decreases with phenotypic variance (by  $V_p/(2V_s)$ ), and so there is an optimal variance when a population has the highest density:  $V_A = (2k^2 h^2 V_s^2)^{1/3}$ , as predicted by Lande and Shannon (1996) for a panmictic population.

We continue with detailed discussion of the solutions after rescaling the model, following equations (4) and (5). The scaled growth rate is then

$$\bar{R} = \frac{\bar{r}}{r^*} = \frac{r_\theta}{r^*} - \frac{1}{2}(\bar{Z} - BX + k^*T)^2 - \frac{A}{2h^2}. \quad (\text{A5})$$

Now, the rescaled trait mean changes as follows:

$$\frac{\partial \bar{Z}}{\partial T} = \frac{\partial^2 \bar{Z}}{\partial X^2} + (BX - k^*T - \bar{Z}) \left[ A - 2 \frac{\partial \bar{Z}}{\partial X} \left( B - \frac{\partial \bar{Z}}{\partial X} \right) \right]. \quad (\text{A6})$$

As in the case of the environmental gradient fixed in time (Kirkpatrick and Barton 1997), we get two locally stable equilibrium solutions for the trait mean  $\bar{Z} = \beta^*X - q^*T + a^*$ : one with uniform adaptation, where the gradient in trait mean matches the environmental gradient,  $\beta^* = B$  (and hence, the range is unlimited), and another where adaptation is constrained by genetic variance, the gradient in trait mean is shallower than the environmental gradient ( $\beta^* < B$ ), and species' range is limited. With simple regulation, however, adaptation to temporal change occurs only for the uniform solution. (This is not the case for joint regulation, as assessed later.) As the optimum changes over time, the trait mean changes at the same rate as the optimum ( $q^* = k^*$ ) and lags behind the optimum uniformly by  $a^* = k^*/A$ . Population density is uniform at  $n = \exp(\bar{R}) = \exp[r_\theta - 1/2(k^{*2}/A^2 + A/h^2)]$ , where  $r_\theta \equiv r_\theta/r^*$ .

In the second solution, the population is adapted on a limited range and the gradient in trait mean  $\beta^* = \beta_-^* = B/2[1 - (1 - 2A/B^2)^{1/2}]$  is shallower than the environmental gradient (see fig. 2, *thin lines*). Such a solution exists only if the environment changes sufficiently sharply relative to the genetic variance,  $B > (2A)^{1/2}$  (see fig. 3, *thin curve*). The population density is highest where the line  $\bar{Z} = \beta^*X + a^*$  intersects the trait optimum (on the infinite range, the shift  $a^*$  of the trait mean is arbitrary), and population density  $n = \exp[r_\theta - 1/2[(B - \beta^*)^2 X^2 + A/h^2]]$  declines as a Gaussian from the center of the range, with variance given by the difference between gradient in trait mean and environmental gradient,  $1/(B - \beta^*)$ . As the optimum changes in time, the trait mean stays constant:  $q^* = 0$ . Thus, locally, the population becomes extinct: the population density (given by the simple regulation) simply tracks the changing optimum in space, moving at speed  $c^* = k^*/(B - \beta^*)$ , as long as there is a suitable habitat available.

On an infinite (spatial) range, both abovementioned solutions (with  $\beta^* = \beta_-^*$  and  $\beta^* = B$ ) are locally stable whenever they exist ( $B > (2A)^{1/2}$ ). The third, unstable solution,  $\beta_+^* = B/2[1 + (1 - 2A/B^2)^{1/2}]$  (see fig. 2, *dashed line*), determines the global stability. If the space is effectively infinite and the initial gradient in trait mean,  $\beta_0^*$ , is above the unstable solution with intermediate gradient,  $\beta_+^*$ , the population always evolves toward uniform adaptation. Conversely, if  $\beta_0^* < \beta_+^*$ , the trait mean evolves toward the solution with the shallow gradient in trait mean,  $\beta_-^* = B/2[1 - (1 - 2A/B^2)^{1/2}]$ , and the range is limited at equilibrium. Note that, as  $B$  steepens,  $\beta_+^* \rightarrow B$ , so that uniformly adapted solutions can be disturbed by smaller perturbations and  $B$  collapses to the solution with limited range, with  $\beta^* = \beta_-^*$ . The gradients and, hence, the stability are independent of the rate at which the optimum moves in time. When available habitat is limited and there is no gene flow over the margins, however, adaptation collapses from the margins toward the trait mean with the shallow gradient,  $\beta_-^*$ , whenever a solution with limited adaptation exists (see "Simple Regulation" in app. B; no gene flow over the margins is represented by either reflecting or absorbing boundary conditions, when in the first case, migrants intending to migrate over the margins move back to the range, and in the second case, they die). This corresponds to similar results for local stability under a static environmental gradient (see table 17.1 and the appendix in Kirkpatrick and Barton 1997).

## APPENDIX B

## Stability

*Simple Regulation*

With simple regulation, we need to follow only the evolution of the trait mean,  $\bar{Z}$  (eq. [A6]). We introduce a perturbation to the equilibrium solution for trait mean, obtaining  $\bar{Z}_\varepsilon = \beta^*X - q^*T + a^* + \varepsilon(X, T)$ . Equilibrium with uniform adaptation has  $\beta^* = B$ ,  $a^* = k^*/A$ , and  $q^* = k^*$ , and substituting  $\bar{Z}_\varepsilon$  into equation (A6) leads to

$$\frac{\partial \varepsilon}{\partial T} = \frac{\partial^2 \varepsilon}{\partial X^2} - A\varepsilon + O(\varepsilon^2).$$

As for the static environment (Kirkpatrick and Barton 1997), the uniform adaptation is locally stable, as perturbation always decreases over time, without migration, at a rate  $-\lambda = A$ . Perturbation around limited adaptation, where  $\beta^* = B/2[1 \pm (1 - 2A/B^2)^{1/2}]$  and  $q^* = 0$  ( $a^*$  is arbitrary, set to 0), grows at a rate

$$\frac{\partial \varepsilon}{\partial T} = \frac{\partial^2 \varepsilon}{\partial X^2} + 2X(B - \beta^*)(2\beta^* - B) \frac{\partial \varepsilon}{\partial X} + O(\varepsilon^2) = \frac{\partial^2 \varepsilon}{\partial X^2} + 2X \frac{\partial \varepsilon}{\partial X} (A - B\beta_c^*) + O(\varepsilon^2),$$

where  $\beta_c^*$  is the complementary solution for adaptation on limited range ( $\beta_+^*$  for  $\beta_-^*$ , and vice versa). Because the central position of such a population is arbitrary, we can set the central location and the perturbation  $\varepsilon(0, T)$  to 0 without further loss of generality. For the gradient to change, the perturbation  $\varepsilon$  has to grow away from the origin, so  $X \partial \varepsilon / \partial X$  would be  $>0$ . Such perturbation changes at a rate  $2(A - B\beta_c^*)$ , which is always negative for the solution with shallower gradient,  $\beta_-^* = B/2[1 - (1 - 2A/B^2)^{1/2}]$ ; thus, this solution is always locally stable. The converse holds for the locally unstable steeper solution. Global stability has been assessed numerically: the unstable solution  $\beta_+^* = B/2[1 + (1 - 2A/B^2)^{1/2}]$  acts as a repeller, and the gradient in trait mean evolves toward perfect adaptation if the initial gradient  $\beta_0$  in trait mean is greater than  $\beta_+^*$  and toward the solution with shallow gradient if  $\beta_0$  is smaller than  $\beta_+^*$ . The equilibrium gradient in trait mean is independent of the rate the optimum changes in time,  $k^*$ , as is the stability.

*Joint Regulation: Stability for  $k = 0$ , Logarithmic Model*

Under joint regulation, we follow both the evolution of the trait mean (eq. [6]) and the dynamics of the population density (eq. [7]). For uniform adaptation, around equilibrium at  $k = 0$  we have  $\beta^* = B + \varepsilon(X, T)$  and  $N = 1 + \nu(X, T)$ . Linearizing gives

$$\begin{aligned} \frac{\partial \varepsilon}{\partial T} &= \frac{\partial^2 \varepsilon}{\partial X^2} + 2B \frac{\partial \nu}{\partial X} - A\varepsilon + O(\nu^2) + O(\varepsilon\nu), \\ \frac{\partial \nu}{\partial T} &= \frac{\partial^2 \nu}{\partial X^2} - \nu - \frac{1}{2}\varepsilon^2 + O(\nu^2). \end{aligned}$$

Hence, without migration, the perturbation changes at rates  $\lambda_1 = -A$  and  $\lambda_2 = -1$ . The effect of the term  $2B \partial \nu / \partial X$  on the rate of growth of the perturbation is of order  $O(\varepsilon^2)$  (from  $\partial \nu / \partial T$ ), and hence it can be omitted for any  $A \neq 1$ ,  $|\lambda_1| \neq |\lambda_2| \neq 0$ . The fixed point is a stable node unless  $A$  is exactly 1; the solution with perfect adaptation is always locally stable on the infinite range.

For adaptation on limited range, around equilibrium we have (for  $k^* = 0$ )  $\beta^* = B\phi + \varepsilon(X, T)$  and  $N = e^{-\xi^* - X^2 \xi^{*/2}} + \nu(X, T)$ . Linearizing gives



$$\frac{\partial \varepsilon}{\partial T} = \frac{\partial^2 \varepsilon}{\partial X^2} - \frac{\partial \varepsilon}{\partial X} X \frac{\zeta^*}{2} + 2B\phi \left( \frac{\partial \nu}{\partial X} + \nu X \zeta^* e^{\zeta^* + X^2 \zeta^*/2} \right) - A\varepsilon + O(\nu^2) + O(\varepsilon \nu),$$

$$\frac{\partial \nu}{\partial T} = \frac{\partial^2 \nu}{\partial X^2} - \nu \left( 1 - \zeta^* + X^2 \frac{\zeta^*}{2} \right) - \varepsilon XB(1 - \phi) + O(\varepsilon^2) + O(\nu^2).$$

Under joint regulation, obtaining eigenvalues for a nonuniform solution appears to be intractable even for  $k^* = 0$ , so we assess the stability numerically and by using a discrete lattice with a stepping-stone migration (not shown). Also, we know that the stability of the equilibrium is sensitive to behavior on the boundaries, which is easier to address in a stepping-stone model.

## APPENDIX C

### Two-Allele Model

#### Scaling

To scale the two-allele model, we define  $A_m \equiv v_{\max}/(r^* V_s)$ , where  $v_{\max} = 1/2 \alpha^2 n_1$ . Equation (10) then becomes

$$\frac{\partial p_i}{\partial T} = \frac{\partial^2 p_i}{\partial X^2} + 2 \frac{\partial \log(n)}{\partial X} \frac{\partial p_i}{\partial X} + \frac{A_m}{n_1} p_i q_i (p_i - q_i - 2\delta^*) - \frac{\gamma_m}{2n_1} (p_i - q_i), \quad (C1)$$

where  $\delta^* = (\bar{Z} - BX)(n_1/2A_m)^{1/2}$  and  $\bar{Z} = z/(r^* V_s)^{1/2} = (2A_m/n_1)^{1/2} \sum_{i=1}^{n_1} p_i - q_i$ , and scaled genetic variance is  $V = V_A/(r^* V_s) = 4A_m/n_1 \sum_{i=1}^{n_1} p_i q_i$ . Hence, the scaled average effect of gene substitution is  $\alpha_* = (2A_m/n_1)^{1/2}$ . The last term is mutation rate scaled by the intensity of density-dependent selection,  $r^*$ :  $\gamma_m \equiv U/r^*$ , where  $U = 2n_1\mu$  is the genomic mutation rate. (The scaling is the same as in Barton [2001], apart from the fact that here,  $V$  is not scaled directly relative to the maximum variance possible, and hence it is consistent with  $\bar{Z}$  and maintains the same scale as the parameter describing decrease of population density due to genetic variance,  $A$ .) When the solution is uniform, the second term vanishes; thus, if we are interested in the accuracy of our predictions for the uniform solution, we can drop the term  $2\partial \log(n)/\partial X \partial p/\partial X$ . Including this term only leads to temporarily increased fluctuations, because the clines take longer to settle.

#### Iterating the Two-Allele Model on a Lattice, with Discrete Time

We follow the population density in the original units in an attempt to match the continuous equation  $\partial n/\partial T = (\partial^2 n/\partial X^2) + \bar{R}n$  with a stepping-stone model. After selection, the population density is

$$n_w(X, T') = n(X, T)(1 + \delta T \bar{R}), \quad (C2)$$

where the growth rate is either logarithmic,

$$\bar{R} = r_0 - \left[ \log\left(\frac{n}{K}\right) - \frac{(\bar{Z} - BX + k^* T)^2}{2} - \frac{V}{2h^2} \right], \quad (C3)$$

or logistic,

$$\bar{R} = \frac{r_m}{r^*} \left( 1 - \frac{n}{K} \right) - \left[ \frac{(\bar{Z} - BX + k^* T)^2}{2} - \frac{V}{2h^2} \right]. \quad (C4)$$

Migration is after selection,

$$n(X, T + \delta T) = n_w(X, T') + \frac{m}{2}(n_w(X + \delta X, T') + n_w(X - \delta X, T') - 2n_w(X, T')), \quad (C5)$$

which is an accurate description of the continuous model to the order of  $O(\delta T)^2$ . The carrying capacity is set to  $K = 1$ , and heritability is  $h^2 = 1$ ; for the logistic model,  $r_m/r^* = 1$ .

After selection, the allele frequencies are

$$p_{i,w}(X, T') = p_i(X, T) + \frac{\delta T}{n_1}(A_m p_i(X, T) q_i(X, T)(p_i(X, T) - q_i(X, T) - 2\delta^*) - \frac{\gamma_m}{2}(p_i(X, T) - q_i(X, T))), \quad (C6)$$

and, after migration, they are

$$p_i(X, T + \delta T) = p_{i,w}(X, T') + \frac{m}{2}(p_{i,w}(X + \delta X, T') + p_{i,w}(X - \delta X, T') - 2p_{i,w}(X, T')). \quad (C7)$$

We use a stepping-stone model on a spatial lattice with spacing  $\delta X$  and time step  $\delta T$ , where the migration rate  $m \leq 1/2$  is scaled according to the spacing,  $m = 2\delta T/\delta X^2$ . In relation to the continuous model, variance in dispersal is approximately  $\sigma^2 \approx m\delta X^2$ , and in the scaled continuous model, it is  $\sigma^2/2 = \delta T$ . Throughout this study, Mathematica (Wolfram Research) was used to obtain numerical solutions and to manipulate some formulas.

## APPENDIX D

### The Characteristic Time

The characteristic time, which measures how long it takes the population to return to equilibrium, is given by the inverse of the strength of density dependence  $1/r^*$ , where  $r^*$  is the rate of return toward the equilibrium at carrying capacity,  $\hat{n}_m$ :  $r^* = -\partial/\partial n \partial n/\partial t|_{n=\hat{n}_m} = -n \partial \bar{r}/\partial n|_{n=\hat{n}_m}$  (Kirkpatrick and Barton 1997). Lande et al. (2002) and Sæther et al. (2005) studied this measure in detail and gave estimates both relative to a year,  $\gamma_d \equiv -\partial \log(\lambda)/\partial \log(n)|_{n=\hat{n}_m}$ , and as change per generation,  $D \equiv \Delta t \gamma_d = -\partial \log(\lambda^{\Delta t})/\partial \log(n)|_{n=\hat{n}_m}$  (where  $\Delta t$  is generation time). Their growth rate per generation is  $\lambda^{\Delta t}$ ; therefore, after  $t$  generations, population density is  $n(t) = n_0 \lambda^{\Delta t t}$ . Throughout this article, “time” indicates generations: with simple regulation (and ignoring mutation), we have  $n(t) = n_0 e^{\bar{r}t}$ . Between the continuous and the discrete times,  $\bar{r} \sim \log(\lambda^{\Delta t})$ , and the measures of  $r^*$  and  $D$  are approximately equivalent. From Sæther et al. (2005), we see that values of  $D$  lie mostly between 0 and 2.5. We include another estimate from Krüger et al. (2002), where continuous-time approximation to their discrete-time autoregressive model directly gives the estimate for  $r^*$  for the logarithmic model, with mean strength of density dependence  $\bar{r}^* = -(\overline{1 + \beta_1}) \doteq 1$ . The overall median for  $r^*$  is thus around 1.

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