

Appendix from I. Filin et al., “The Relation of Density Regulation to Habitat Specialization, Evolution of a Species’ Range, and the Dynamics of Biological Invasions” (Am. Nat., vol. 172, no. 2, p. 233)

Supplemental Derivations for the Two Models Described in the Main Text

Derivation of the Dynamics Equations of the Ronce-Kirkpatrick and Kirkpatrick-Barton Models

In the Ronce-Kirkpatrick (2001) model, the fitness of an individual of phenotype z in habitat i is $r_0(1 - n_i/K) - \gamma(z - z_{\text{opt},i})^2/2$, where $z_{\text{opt},i}$ is the habitat-specific phenotypic optimum and n_i the population density in habitat i , K is the carrying capacity, r_0 is the intrinsic growth rate (fitness at low density) of the optimum phenotype, and γ is the strength of stabilizing selection. Given the mean phenotypes \bar{z}_i and the phenotypic variance σ_p^2 and genetic variance σ_g^2 (the variances being constant and the same in both habitats), a population with its mean phenotype at the habitat-specific optimum has a realized growth rate of $r' = r_0 - \gamma\sigma_p^2/2$. Time is rescaled using this growth rate ($T = r't$). Assuming the theta-logistic form of density dependence, population densities are also rescaled using the carrying capacity, growth rates, and θ : $N_i = (n_i/K) \times (r_0/r')^{1/\theta}$. The mean phenotypes are expressed as normalized deviations from the habitat optima ($Y_i = |\bar{z}_i - z_{\text{opt},i}|/\sigma_g$). The per capita rate of immigration between the two habitats is m (assumed to be symmetrical; there is no habitat selection, and the two habitats are assumed to be equal in area). We scale m against the realized growth rate r' . The dimensionless parameters of equations (1) and (2) are (i) $\Gamma = \sigma_g^2\gamma/r'$, the standardized intensity of selection; (ii) $H = (z_{\text{opt},2} - z_{\text{opt},1})/\sigma_g$, the rescaled difference in phenotypic optima; and (iii) $M = m/r'$.

In the Kirkpatrick-Barton model, the original dynamic equations are given by

$$\frac{\partial n}{\partial t} = D \frac{\partial^2 n}{\partial x^2} + n \left[r_0 \left(1 - \frac{n}{K} \right) - \frac{\gamma\sigma_p^2}{2} - \frac{\gamma}{2} (\bar{z} - z_{\text{opt}})^2 \right],$$

$$\frac{\partial \bar{z}}{\partial t} = D \frac{\partial^2 \bar{z}}{\partial x^2} + 2D \frac{\partial \ln(n)}{\partial x} \times \frac{\partial \bar{z}}{\partial x} - \gamma\sigma_g^2 (\bar{z} - z_{\text{opt}}),$$

where D is the diffusion coefficient representing the rate of random dispersal across space, z_{opt} (a function of x) replaces $z_{\text{opt},i}$ as the spatially varying optimum phenotype, and all other parameters are as described above for the Ronce-Kirkpatrick model. Equations (4) are obtained by rescaling the variables as follows: $T = r't$, $N_i = n_i r_0 / (K r')$ (or for the theta-logistic model, $N_i = (n_i / K) \times (r_0 / r')^{1/\theta}$), $\bar{Z} = \bar{z} \times (\gamma / r')^{1/2}$, and $X = x \times (r' / D)^{1/2}$. (Note that the rescaling of the mean phenotype is different in the Kirkpatrick and Barton model compared with the Ronce-Kirkpatrick model.) Finally, the dimensionless parameter A , the genetic potential for adaptation, is given by $A = \gamma\sigma_g^2 / r'$; that is, it is identical to Γ of the Ronce-Kirkpatrick model. (Note the factor 2 typographical error in the definition of A in the original article of Kirkpatrick and Barton [1997], which is corrected by Case and Taper [2000]. In the original nomenclature of Kirkpatrick and Barton [1997], $\gamma = 1/V_s$, $r' = r^*$, and $\sigma_g^2 = G$).

Dynamics Equations under the Gaussian Approximation

Substituting a Gaussian spatial density profile, $N(X) = N_0 \exp(-\kappa X^2/2)$, into the density dependence relationship $U(N)$ results in $U[N(X)] = U[N_0 \exp(-\kappa X^2/2)]$. This last expression can be expanded using a second-order Taylor expansion in X around $X = 0$:

$$U[N(X)] \approx U(N_0) + \left(\frac{dU}{dN}\right)_{N=N_0} \times \left(\frac{dN}{dX}\right)_{X=0} \times X + \left(\frac{dU}{dN}\right)_{N=N_0} \times \left(\frac{d^2N}{dX^2}\right)_{X=0} \times \frac{X^2}{2} + \left(\frac{d^2U}{dN^2}\right)_{N=N_0} \times \left[\left(\frac{dN}{dX}\right)_{X=0}\right]^2 \times \frac{X^2}{2}.$$

The first derivative of $N(X)$, $(dN/dX)_{X=0}$, is 0, and the second is $(d^2N/dX^2)_{X=0} = -\kappa N_0$. Therefore, $U[N(X)] \approx U(N_0) - N_0 \times (dU/dN)_{N=N_0} \times \kappa X^2/2$, which is equal to $U[N(X)] \approx U(N_0) + (\phi\kappa/2) \times X^2$, where ϕ is defined as $-N_0(dU/dN)_{N=N_0}$.

Substituting the expressions for $N(x)$ and $U[N(x)]$ and a linear environmental gradient, $Z_{\text{opt}} = B \times X$, in equations (4) results in the following expressions:

$$\frac{\partial N_0}{\partial T} - \frac{N_0}{2} X^2 \times \frac{\partial \kappa}{\partial T} = \left[\kappa^2 X^2 - \kappa + U_0(N_0) + \frac{\phi(N_0) \times \kappa}{2} X^2 - \frac{1}{2} (\bar{Z} - BX)^2 \right] \times N_0, \quad (\text{A1})$$

$$\frac{\partial \bar{Z}}{\partial T} = \frac{\partial^2 \bar{Z}}{\partial X^2} - 2\kappa X \times \frac{\partial \bar{Z}}{\partial X} - A(\bar{Z} - BX). \quad (\text{A2})$$

An equilibrium solution of equation (A2) (i.e., $\partial \bar{Z}/\partial T = 0$) is a linear mean phenotype cline, $\bar{Z}(X) = \beta_{\text{eq}} \times X$, where

$$\beta_{\text{eq}} = \frac{A}{A + 2\kappa} \times B. \quad (\text{A3})$$

Additionally, substituting $\bar{Z} = \beta \times X$ in equation (A2) results in the following dynamical equation for β :

$$\frac{\partial \beta}{\partial T} = -2\kappa \times \beta - A(\beta - B). \quad (\text{A4})$$

Finally, when $\bar{Z} = \beta \times X$ is substituted into equation (A1), one obtains two equations: one for the dynamics of N_0 (based on the free terms), the other for the dynamics of κ (based on the X^2 terms):

$$\frac{1}{N_0} \frac{\partial N_0}{\partial T} \equiv \frac{\partial \ln N_0}{\partial T} = U(N_0) - \kappa, \quad (\text{A5})$$

$$\frac{\partial \kappa}{\partial T} = -\phi(N_0) \times \kappa - 2\kappa^2 + (\beta - B)^2. \quad (\text{A6})$$

Equation (A6) is equation (5) analyzed in the main text for the dynamics of range limitation.

Treatment of Theta-Logistic Density Regulation under the Gaussian Approximation

Substituting equation (A3) in equation (A6) and solving for the equilibrium range limitation give

$$\left(\frac{2\kappa_{\text{eq}}}{A + 2\kappa_{\text{eq}}}\right)^2 \times B^2 - 2\kappa_{\text{eq}}^2 - \phi_{\text{eq}}\kappa_{\text{eq}} = 0. \quad (\text{A7})$$

The term ϕ_{eq} refers to the equilibrium strength of density regulation, which is derived using the theta-logistic form of U and is given by

$$\phi_{\text{eq}} = \theta \times (N_0)_{\text{eq}}^\theta, \quad (\text{A8})$$

and the equilibrium version of equation (A5) gives

$$(N_0)_{\text{eq}}^\theta = 1 - \kappa_{\text{eq}}. \quad (\text{A9})$$

The final result is equation (8): $\phi_{\text{eq}} = \theta \times (1 - \kappa_{\text{eq}})$.

Given this expression for ϕ_{eq} , equation (A7) becomes

$$\left(\frac{2\kappa_{\text{eq}}}{A + 2\kappa_{\text{eq}}} \right)^2 \times B^2 - 2\kappa_{\text{eq}}^2 - \theta \times \kappa_{\text{eq}}(1 - \kappa_{\text{eq}}) = 0. \quad (\text{A10})$$

One possible solution is always $\kappa_{\text{eq}} = 0$, that is, an unlimited-range equilibrium. A limited-range equilibrium is also possible when equation (A10) has a positive root; that is, $\kappa_{\text{eq}} > 0$. First, if the limited-range solution obeys $\kappa_{\text{eq}} > 1$, then on the basis of equation (A5), this is a solution of an exponentially decaying population, which results in global extinction. Hence, the extinction threshold B_{U} can be found by substituting $\kappa_{\text{eq}} = 1$ in equation (A10) and solving for B . The solution is $B_{\text{U}} = (A + 2)/2^{1/2}$, regardless of the value of θ , that is, regardless of the specific theta-logistic form of density regulation. Second, the limited-range threshold, B_{L} , can also be found using equation (A10). For unregulated dynamics, the third term on the left-hand side vanishes. Then, a positive solution, $\kappa_{\text{eq}} > 0$, exists if B exceeds $A/2^{1/2}$. Therefore, for unregulated dynamics, $B_{\text{L}} = A/2^{1/2}$.

For density-regulated dynamics, the situation is a bit more complex. First, observe that a limited-range equilibrium must obey $\kappa_{\text{eq}} < 1$; otherwise, we obtain global extinction. Therefore, the third term on the left-hand side of equation (A10) (i.e., the density regulation term) is always negative. Consequently, for any combination of A and B that allow a limited-range equilibrium, κ_{eq} in the density-regulated case is always smaller than that for the unregulated case, and this difference increases with θ . Additionally, combinations of A and B that supported a limited-range equilibrium in the unregulated case might have no positive solution, $\kappa_{\text{eq}} > 0$, in the density-dependent case, thus pushing B_{L} upward as indeed observed in the numerical results (fig. 3). Second, whenever a positive solution of equation (A10) exists within the interval $[0, 1]$, there are two such solutions within this interval. However, only the higher value of κ_{eq} is a stable solution. Third, in the limit $A \ll 2\kappa \ll 1$, we find that the limited-range threshold can be approximated by $B_{\text{L}}^2 = 4\theta A$, which also demonstrates how the limited-range threshold becomes higher as θ increases.

Straightforward solution of equation (A10) fails to provide a good approximation to the numerically obtained curves of B_{L} (fig. 3). This is because the Gaussian approximation is eventually only an approximation. Specifically, the Gaussian approximation considers a linear mean phenotype cline. However, because in a limited-range equilibrium the dynamics at the range center is density dependent while at the periphery it is largely density independent, the slope of the mean phenotype cline will tend toward different equilibrium values in either center or periphery. This creates a curvature of the mean phenotype cline, which feeds back into the equation for the slope (first term on the right-hand side in eq. [A2]). Similarly, the dynamics of range limitation, κ , will change from center to periphery. Nonetheless, the Gaussian approximation captures well the qualitative dependence of the dynamics on the form of density regulation.

Explanations of Numerical Procedures for the Continuous Gradient

The numerical procedures used in this article are similar to those previously described by Kirkpatrick and Barton (1997), Case and Taper (2000), and García-Ramos and Rodríguez (2002). The finite difference method was used to solve equations (4), with a linear environmental gradient and theta-logistic density dependence. Numerical results were verified for the unregulated case by comparing them with the analytical solution. The limited-range threshold curves (fig. 3) were found by sampling the A - B parameter space in a uniform manner: A from 0.05 to 1 at increments of 0.02, and B from 0.05 to $3/2^{1/2}$ at increments of 0.04. Cases of limited range were determined as having a final range limitation value of $\kappa > 0.0005$ at the final simulation time ($T = 100$). The parameter κ was estimated by fitting a quadratic polynomial around $X = 0$ at the final time. The curves themselves (fig. 3) are quadratic polynomial fits of the actual contours that separate cases of limited and unlimited range in the A - B parameter space for each value of θ . Numerical work and figure preparation were done using MATLAB 6.5 and 7 (MathWorks, Natick, MA).

Transforming Fowler’s R into Estimates of θ

Fowler’s (1988) R represents the relative density (relative to the carrying capacity K) at which population growth (i.e., dN/dt) is maximal. Given the theta-logistic model, one obtains $dN/dt = N(1 - N^\theta)$, which has a maximum at $N^* = 1/(1 + \theta)^{1/\theta}$. Because the dimensionless density N is already scaled relative to the carrying capacity, we obtain $R = 1/(1 + \theta)^{1/\theta}$, or, alternatively, $\ln R = -1/\theta \times \ln(1 + \theta)$, which can be solved for θ numerically.