Supplementary material to:

Chapter 15: Analyzing Continuous Stochastic Models – Diffusion in Time and Space

From:

A Biologist's Guide to Mathematical Modeling in Ecology and Evolution

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Supplementary Material 15.1: The expected trait value of a trait when mutations are limiting

In section 15.2.3, we described a diffusion model for the long-term evolutionary dynamics of a trait when mutations are limiting. In this model, the probability density function, $\phi(x,t|x_0,t_0)$, describes the probability that the resident trait lies within a small region around x at time t. According to Definition P3.9, the expected trait value of this probability density function is:

$$\bar{x} = \int_{-\infty}^{+\infty} x \, \phi(x,t|x_0,t_0) \, \mathrm{d}x. \tag{S15.1.1}$$

Remember that the population is assumed to be fixed for a particular trait value at every point in time, and equation (S15.1.1) describes what this trait value is expected to be. The rate of change of the expected trait value is found by differentiating with respect to time:

$$\frac{\mathrm{d}\bar{x}}{\mathrm{d}t} = \int x \frac{\partial \phi(x,t|x_0,t_0)}{\partial t} \mathrm{d}x. \tag{S15.1.2}$$

We can then substitute the forward Kolmogorov equation into (S15.1.2) for $\partial \phi / \partial t$ and, after some simplification (Problem S15.1), obtain

$$\frac{\mathrm{d}\bar{x}}{\mathrm{d}t} = \int \mu(x) \, \phi(x,t|x_0,t_0) \, \mathrm{d}x. \tag{S15.1.3}$$

Equation (S15.1.3) reveals that the rate of change of the expected trait value at time t is given by the drift parameter, $\mu(x)$, averaged over the probability density function describing the state of the system at time t, $\phi(x,t|x_0,t_0)$. This makes sense – the drift parameter tells us the expected rate of change in the trait value *given that the population is currently at trait value x*. Thus, to find the expected rate of change for the trait we would average the drift rate over all possible current values of the trait.

Further progress can be made if we assume that the probability distribution $\phi(x,t|x_0,t_0)$ at time t is very tightly centered around its expected value. Assuming that the drift parameter, $\mu(x)$, is very nearly constant at $\mu(\bar{x})$ across this tightly centered distribution, equation (S15.1.3) can be approximated as $\mathrm{d}\bar{x}/\mathrm{d}t \approx \mu(\bar{x}) \int \phi(x,t|x_0,t_0)\,\mathrm{d}x$, which equals $\mu(\bar{x})$ (using the fact that a probability distribution integrates to one, Rule P3.12).

In summary, the expected value of the phenotype changes at a rate $\mathrm{d}\bar{x}/\mathrm{d}t \approx \mu(\bar{x})$ under the assumptions that (i) mutations are limiting so that the population rarely contains more than one allele, (ii) mutations do not cause large jumps in the trait value, and (iii) the probability density function describing the possible trait values at any point in time is tightly centered around the mean. The expected trait value within a population remains at $\bar{x}^*$ if it starts at $\bar{x}^*$ when $\mu(\bar{x})\big|_{\bar{x}=\bar{x}^*} = 0$. This is a stochastic analog to the first derivative condition for an ESS (see Recipe 12.2).

Supplementary Material 15.2: Deriving the expected waiting time until absorption in a diffusion model

Here we derive the waiting time to absorption in state *b* for a diffusion model with two absorbing states, a lower one at *a* and an upper one at *b*. The derivation depends on the backward Kolmogorov equation (15.11) and follows the method described in the Appendix of Kimura and Ohta (1971). If $u(b,t|x_0,t_0)$ is the probability of reaching an absorbing state, *b*, from initial position x_0 over a time interval $\tau = t - t_0$, then the rate at which absorption at *b* occurs is measured by $\frac{\partial u}{\partial \tau}$. The probability density function, $f_b(\tau)$, describing the probability of absorption at state *b* in an interval of time, $d\tau$, around τ will be proportional to $\frac{\partial u}{\partial \tau}$:

$$f_b(\tau) = \frac{\frac{\partial u}{\partial \tau}}{\int\limits_{\tau=0}^{\infty} \frac{\partial u}{\partial \tau}\,\mathrm{d}\tau}. \tag{S15.2.1}$$

The denominator ensures that the total probability, integrated over the probability density function, is one and it equals:

$$\begin{aligned}\int\limits_{\tau=0}^{\infty} \frac{\partial u}{\partial \tau}\,\mathrm{d}\tau &= u(b,\infty|x_0,t_0) - u(b,t_0|x_0,t_0)\\ &= u(b,\infty|x_0,t_0) - 0\\ &= u(b|x_0)\end{aligned} \tag{S15.2.2}$$

where $u(b|x_0)$ is the probability of ultimately becoming absorbed in state *b* from a non-absorbed state x_0.

Using (S15.2.1), the mean time until hitting *b* is defined as (Definition P3.9):

$$\bar{t}_b(x_0) = \frac{\int\limits_{\tau=0}^{\infty} \tau \frac{\partial u}{\partial \tau}\,\mathrm{d}\tau}{u(b|x_0)}. \tag{S15.2.3}$$

Next, we use the backward Kolmogorov equation (15.11) for $u(b,t|x_0,t_0)$ to obtain a differential equation that is satisfied by the numerator of (S15.2.3), $\int\limits_{\tau=0}^{\infty} \tau \frac{\partial u}{\partial \tau}\,\mathrm{d}\tau$, which we will call T_b. First, let's rewrite the backward Kolmogorov equation (15.11) in terms of the time interval, τ, using the fact that $\frac{\partial u}{\partial t_0} = \frac{\partial u}{\partial \tau}\frac{\partial \tau}{\partial t_0} = -\frac{\partial u}{\partial \tau}$ (because $\tau = t - t_0$, $\frac{\partial \tau}{\partial t_0} = -1$):

$$-\frac{\partial u(b,t|x_0,t_0)}{\partial \tau} = -\mu(x_0)\frac{\partial u(b,t|x_0,t_0)}{\partial x_0} - \frac{1}{2}\sigma^2(x_0)\frac{\partial^2 u(b,t|x_0,t_0)}{\partial x_0^2}$$

Taking the derivative of both sides with respect to τ, multiplying both sides by τ, integrating with respect to τ, and exchanging the order of integration with respect to τ and the derivatives with respect to x_0, leaves us with:

$$\begin{aligned}\int\limits_{\tau=0}^{\infty} \tau \frac{\partial^2 u}{\partial \tau^2}\,\mathrm{d}\tau &= \mu(x_0)\frac{\partial\left(\int\limits_{\tau=0}^{\infty} \tau \frac{\partial u}{\partial \tau}\,\mathrm{d}\tau\right)}{\partial x_0} + \frac{1}{2}\sigma^2(x_0)\frac{\partial^2\left(\int\limits_{\tau=0}^{\infty} \tau \frac{\partial u}{\partial \tau}\,\mathrm{d}\tau\right)}{\partial x_0^2}. \\ &= \mu(x_0)\frac{dT_b}{dx_0} + \frac{1}{2}\sigma^2(x_0)\frac{d^2 T_b}{dx_0^2}\end{aligned} \tag{S15.2.4}$$

The goal of these manipulations is to get a differential equation that can be solved for T_b. We're already there on the right hand-side. Integrating by parts (Rule A2.29), we can also rewrite the left-hand side:

$$\int\limits_{\tau=0}^{\infty} \tau \frac{\partial^2 u}{\partial \tau^2}\,\mathrm{d}\tau = \left(\Big|_{\tau=0}^{\infty} \tau \frac{\partial u}{\partial \tau}\right) - \int\limits_{\tau=0}^{\infty} \frac{\partial u}{\partial \tau}\,\mathrm{d}\tau. \tag{S15.2.5}$$

The term in parenthesis measures the contribution to the mean fixation time at time zero and after an infinite amount of time has passed, both of which we take to be zero. Replacing the last term in (S15.2.5) with (S15.2.2), we are left with the ordinary differential equation:

$$-u(b|x_0) = \mu(x_0)\,\frac{\mathrm{d}T_b}{\mathrm{d}x_0} + \frac{1}{2}\sigma^2(x_0)\,\frac{\mathrm{d}^2T_b}{\mathrm{d}x_0^2}. \tag{S15.2.6}$$

Equation (S15.2.6) can be solved to get equation (15.40) as follows.

Defining a new variable, $w(x_0) \equiv \frac{dT_b}{dx_0}$, equation (S15.2.6) can be rewritten as a linear differential equation, $-u(b|x_0) = \mu(x_0)\,w(x_0) + \frac{1}{2}\sigma^2(x_0)\,\frac{\mathrm{d}w}{\mathrm{d}x_0}$, whose solution is (Box 6.2):

$$w(x_0) = e^{-A(x_0)}\,\big(B(x_0) + c_2\big), \tag{S15.2.7}$$

where

$$B(y) = \int \frac{-2u(b|y)}{e^{-A(y)}\sigma^2(y)}\,\mathrm{d}y. \tag{S15.2.8}$$

Replacing $w(x_0)$ with $\frac{dT_b}{dx_0}$ and solving via a separation of variables we get:

$$T_b = \int e^{-A(x_0)}\,\big(B(x_0) + c_2\big)\,\mathrm{d}x_0 + c_3. \tag{S15.2.9}$$

Dividing by $u(b|x_0)$ gives the average time to absorption in state *b* (see equation (S15.2.3)):

$$\bar{t}_b(x_0) = \frac{T_b}{u(b|x_0)} = \frac{\int e^{-A(x_0)}\,\big(B(x_0) + c_2\big)\,\mathrm{d}x_0 + c_3}{u(b|x_0)}, \tag{S15.2.10}$$

If we start in the absorbed state $x_0 = b$, the expected time to absorption is zero. Consequently, c_3 must equal $-\left(\int e^{-A(x_0)}\left(B(x_0)+c_2\right)\mathrm{d}x_0\right)_{x_0=b}$. Making this substitution, we can rewrite (S15.2.10) as a definite integral:

$$\bar{t}_b(x_0)=\frac{-\int\limits_{z=x_0}^{b} e^{-A(z)}\left(B(z)+c_2\right)\mathrm{d}z}{u(b|x_0)} =\frac{-\int\limits_{z=x_0}^{b} e^{-A(z)}\left(\left(\int \frac{-2u(b|y)}{e^{-A(y)}\sigma^2(y)}\,\mathrm{d}y\right)_{y=z}+c_2\right)\mathrm{d}z}{u(b|x_0)}. \tag{S15.2.11}$$

A key step in what follows is exchanging the order of integration in equation (S15.2.11). To do so, we first convert the inner integral into a definite integral by subtracting and adding the constant $B(a)$:

$$\bar{t}_b(x_0)=\frac{-\int\limits_{z=x_0}^{b} e^{-A(z)}\left(\left(\int\limits_{y=a}^{z} \frac{-2u(b|y)}{e^{-A(y)}\sigma^2(y)}\,\mathrm{d}y\right)+B(a)+c_2\right)\mathrm{d}z}{u(b|x_0)}. \tag{S15.2.12}$$

We can then define a new constant as $C_2 = B(a) + c_2$, which we can factor out of the integral:

$$\bar{t}_b(x_0)=\frac{-\int\limits_{z=x_0}^{b} e^{-A(z)}\left(\int\limits_{y=a}^{z} \frac{-2u(b|y)}{e^{-A(y)}\sigma^2(y)}\,\mathrm{d}y\right)\mathrm{d}z-C_2\int\limits_{z=x_0}^{b} e^{-A(z)}\,\mathrm{d}z}{u(b|x_0)}. \tag{S15.2.13}$$

Next, consider the limit as we start near the other absorbed state, $x_0 = a$. The probability of fixation in the denominator goes to zero in this limit, but the time to absorption should remain finite as long as the system is not absorbed. This suggests that the numerator of (S15.2.12) must also go to zero as x_0 goes to a. This allows us to solve for C_2:

$$C_2 = -\frac{\int\limits_{z=a}^{b} e^{-A(z)} \left(\int\limits_{y=a}^{z} \frac{-2u(b|y)}{e^{-A(y)}\sigma^2(y)} \mathrm{d}y \right) \mathrm{d}z}{\int\limits_{z=a}^{b} e^{-A(z)} \mathrm{d}z}. \tag{S15.2.13}$$

Making this substitution, the average time until absorption becomes:

$$\bar{t}_b(x_0) = \frac{-\int\limits_{z=x_0}^{b} e^{-A(z)} \left(\int\limits_{y=a}^{z} \frac{-2u(b|y)}{e^{-A(y)}\sigma^2(y)} \mathrm{d}y \right) \mathrm{d}z + \int\limits_{z=a}^{b} e^{-A(z)} \left(\int\limits_{y=a}^{z} \frac{-2u(b|y)}{e^{-A(y)}\sigma^2(y)} \mathrm{d}y \right) \mathrm{d}z \frac{\int\limits_{z=x_0}^{b} e^{-A(z)} \mathrm{d}z}{\int\limits_{z=a}^{b} e^{-A(z)} \mathrm{d}z}}{u(b|x_0)}. \tag{S15.2.14}$$

Exchanging the order of integration (making sure to integrate over the entire region as described in introductory calculus textbooks), we get:

$$\begin{aligned} \bar{t}_b(x_0) = &-\frac{1}{u(b|x_0)} \int\limits_{y=a}^{x_0} \frac{-2u(b|y)}{e^{-A(y)}\sigma^2(y)} \left(\int\limits_{z=x_0}^{b} e^{-A(z)}\, \mathrm{d}z \right) \mathrm{d}y \\ &-\frac{1}{u(b|x_0)} \int\limits_{y=x_0}^{b} \frac{-2u(b|y)}{e^{-A(y)}\sigma^2(y)} \left(\int\limits_{z=y}^{b} e^{-A(z)}\, \mathrm{d}z \right) \mathrm{d}y \\ &+\frac{1}{u(b|x_0)} \int\limits_{y=a}^{b} \frac{-2u(b|y)}{e^{-A(y)}\sigma^2(y)} \left(\int\limits_{z=y}^{b} e^{-A(z)}\, \mathrm{d}z \right) \mathrm{d}y \, \frac{\int\limits_{z=x_0}^{b} e^{-A(z)} \mathrm{d}z}{\int\limits_{z=a}^{b} e^{-A(z)} \mathrm{d}z} \end{aligned}. \tag{S15.2.15}$$

Using the definition $S(x) = \int e^{-A(x)}\, dx$,

$$
\begin{aligned}
\bar{t}_b(x_0) = &-\frac{1}{u(b|x_0)} \int_{y=a}^{x_0} \frac{-2u(b|y)}{e^{-A(y)}\sigma^2(y)} \left(S(b)-S(x_0)\right) \mathrm{d}y \\
&-\frac{1}{u(b|x_0)} \int_{y=x_0}^{b} \frac{-2u(b|y)}{e^{-A(y)}\sigma^2(y)} \left(S(b)-S(y)\right) \mathrm{d}y \\
&+\frac{1}{u(b|x_0)} \int_{y=a}^{b} \frac{-2u(b|y)}{e^{-A(y)}\sigma^2(y)} \left(S(b)-S(y)\right) \mathrm{d}y \ \frac{\left(S(b)-S(x_0)\right)}{\left(S(b)-S(a)\right)}
\end{aligned}
\quad . \qquad \text{(S15.2.16)}
$$

Bringing the constant –2 out of the integrals and using equation (15.36a) for the probability that absorption in state *b* does not occur:

$$
1-u(b\,|\,x_0) = \frac{S(b)-S(x_0)}{S(b)-S(a)},
$$

the average time until absorption in state *b* becomes:

$$
\begin{aligned}
\bar{t}_b(x_0) = &\ 2\left(S(b)-S(a)\right)\frac{1-u(b|x_0)}{u(b|x_0)} \int_{y=a}^{x_0} \frac{u(b|y)}{e^{-A(y)}\sigma^2(y)} \mathrm{d}y \\
&+2\left(S(b)-S(a)\right)\frac{1}{u(b|x_0)} \int_{y=x_0}^{b} \frac{u(b|y)\left(1-u(b|y)\right)}{e^{-A(y)}\sigma^2(y)} \mathrm{d}y \\
&-2\left(S(b)-S(a)\right)\frac{1-u(b|x_0)}{u(b|x_0)} \int_{y=a}^{b} \frac{u(b|y)\left(1-u(b|y)\right)}{e^{-A(y)}\sigma^2(y)} \mathrm{d}y
\end{aligned}
\qquad \text{(S15.2.17)}
$$

Finally, we can break apart the integral on the last line into the sum of integrals from *a* to x_0 and from x_0 to *b*, and then factor together the integrals involving the same range to get:

$$
\bar{t}_b(x_0) = 2\left(S(b)-S(a)\right)\frac{1-u(b|x_0)}{u(b|x_0)} \int_{y=a}^{x_0} \frac{u(b|y)^2}{e^{-A(y)}\sigma^2(y)} \mathrm{d}y + 2\left(S(b)-S(a)\right) \int_{y=x_0}^{b} \frac{u(b|y)\left(1-u(b|y)\right)}{e^{-A(y)}\sigma^2(y)} \mathrm{d}y \,. \qquad \text{(S15.2.18)}
$$

At last, we have arrived at equation (15.40) for the average time until absorption in state *b*. Equation (15.41) follows by symmetry or can be derived by the carrying out the above steps focusing on those cases that ultimately become absorbed in state *a*.

Supplementary Material 15.3: Modeling populations in space using the diffusion equation

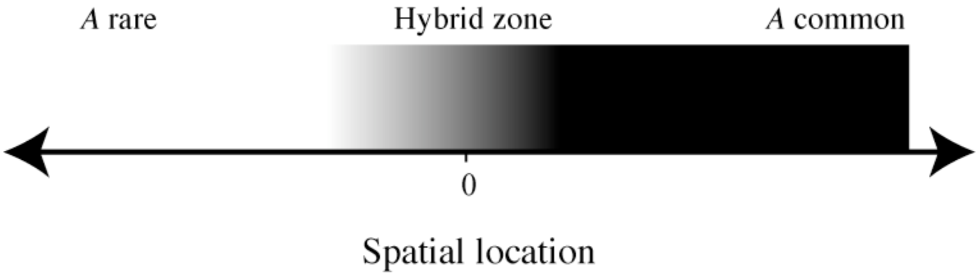
In this section we illustrate how diffusion models that are used to describe the deterministic dynamics of entire populations in a spatial setting can be extended to allow for evolutionary change as well.

Example: The shape of a hybrid zone

This model describes a "hybrid zone, " which is a region in space where two types of individuals meet and produce less fit hybrids. The two types are distributed over space along one-dimension, and we explore how the frequency of each type varies across the hybrid zone. In the simplest scenario the two types of individuals have equally high fitness, but they produce less fit hybrid offspring. For historical reasons (e.g., past isolation or past environmental differences), one type predominates on the left and the other type predominates on the right (Figure S15.3.1).

Bazykin (1969) considered this scenario and asked what would happen in the zone of contact. To answer this question, he used a model of individual dispersal akin to Brownian motion with $\mu(x) = 0$ and $\sigma^2(x) = \sigma^2$, assuming that descendants disperse to a location that is normally distributed with variance σ^2 per unit time. Although these rules governed the stochastic movement of each individual within the population, the model was interpreted as describing the deterministic dynamics of the entire population. In addition, he considered a deterministic diploid model of underdominance, where the fitnesses of the two parental types (AA and aa) were one and the fitness of the hybrids (Aa) was $1 - s$.

Figure S15.3.1: Variation across a hybrid zone. Type *A* is initially rare on the far left of the linear spatial array and common on the far right. Where type *A* and *a* meet, a "hybrid zone" or "contact zone" forms.



To construct a model for these processes, we need to merge a diffusion model for the dispersal of individuals with a deterministic model for evolutionary change in allele frequencies. We do this in a general manner below in Sup. Mat. 15.4. Assuming a constant population size over space and symmetric dispersal, the change in frequency of allele *A* at location *x*, *p*(*x,t*), is:

$$\frac{\partial p}{\partial t}=\frac{\sigma^2}{2}\frac{\partial^2 p}{\partial x^2}-s\,p\,(1-p)\,(1-2p). \tag{S15.3.1}$$

Equation (S15.3.1) has two components: the first due to the diffusive process of dispersal (without drift) and the second due to selection (see Problem 3.20).

Of particular interest is the stationary distribution of (S15.3.1), describing how the allele frequency depends on the location when the processes of dispersal and selection reach a balance. Setting $\frac{\partial p}{\partial t}=0$ in (S15.3.1) and rearranging, the shape of the hybrid zone at this stationary distribution must satisfy the differential equation:

$$\frac{\mathrm{d}^2 p}{\mathrm{d}x^2}=\frac{2\,s\,p\,(1-p)\,(1-2p)}{\sigma^2}. \tag{S15.3.2}$$

To solve equation (S15.3.2), we can use some biological insight. We might expect the change in allele frequency over space to be proportional to how often the two types meet; that is, $\mathrm{d}p/\mathrm{d}x=c\;p\,(1-p)$ where *c* is some proportionality constant. We might expect this proportionality constant to depend on the strength of selection and the amount of dispersal, but in what way? Taking this guess and differentiating both sides with respect to *x*, we get

$\mathrm{d}^2p/\mathrm{d}x^2 = c(1-2p)(\mathrm{d}p/\mathrm{d}x) = c^2 p\,(1-p)(1-2p)$. Comparing this guess to equation (S15.3.2), we find that it does the trick as long as the proportionality constant, c, is $\sqrt{2s/\sigma^2}$, so that

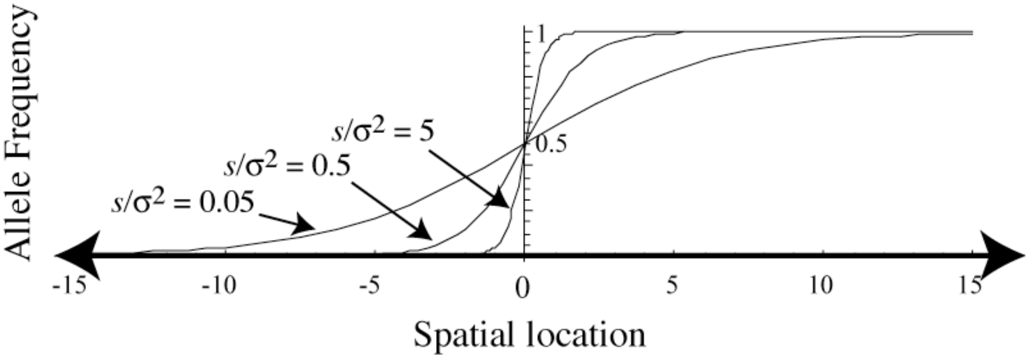
$$\frac{\mathrm{d}p}{\mathrm{d}x} = \sqrt{\frac{2s}{\sigma^2}}\, p\,(1-p). \tag{S15.3.3}$$

We could next solve for p using a separation of variables, but it is more insightful to draw a connection between equation (S15.3.3) and previous models. Equation (S15.3.3) is the very same equation as the differential equation (3.5c) describing logistic population growth with $r = \sqrt{\frac{2s}{\sigma^2}}$ and $K = 1$, although it is now space, x, that varies rather than time. Assuming that allele A is initially absent on the left (as x goes to $-\infty$) and fixed on the right (as x goes to $+\infty$), the solution will be logistic in shape and rise from 0 to 1. Where this rise occurs (the center of the hybrid zone) is arbitrary and depends on the initial conditions (i.e., where the two types first meet). If we let $x = 0$ represent the point where the allele frequency is 1/2, then using the general solution (6.14a) of the logistic, the stationary distribution of the hybrid zone is:

$$p(x) = \frac{e^{\sqrt{\frac{2s}{\sigma^2}}\,x}}{1 + e^{\sqrt{\frac{2s}{\sigma^2}}\,x}} \tag{S15.3.4}$$

Figure S15.3.2 illustrates the shape of the hybrid zone for various dispersal rates and selection coefficients against hybrids. The hybrid zone is sharp if selection against the hybrids is strong (s large) or if dispersal rates are low (σ^2 small).

Figure S15.3.2: Allele frequency across a hybrid zone. Assuming a Brownian motion model with dispersal rates measured by the diffusion coefficient σ^2 and with the degree of selection against hybrids measured by *s*, a stationary distribution of the allele frequency forms over space that is logistic in shape. The spatial scale is determined by the units of σ^2 (e.g., kilometers if σ^2 is measured in units of km^2). Steeper hybrid zones form if selection is stronger and/or if the average dispersal distance is lower, with the maximum slope of the hybrid zone depending on s/σ^2.



This model maintains hybrids indefinitely in the same spatial location, even though hybrids are least fit. In reality, fitness differences among the homozygotes and random genetic drift due to finite population size will cause the hybrid zone to shift over time. On the other hand, variation in population density over space can cause the hybrid zone to become “stuck” in regions of low population density, stabilizing the hybrid zone for longer periods of time. These processes have been analyzed by Barton (1979). The many implications of hybrid zone models to biogeographical patterns and speciation are reviewed by Barton and Hewitt (1985; 1989).

Supplementary Material 15.4: Deriving spatial models of natural selection

Here we show how to develop a relatively general model incorporating both spatial movement of individuals and selection. We start with a fairly general model of dispersal, which allows for the possibility of long-distance dispersal. We then apply a diffusion approximation, assuming that changes in location are small, which allows us to justify equation (S15.3.1). For simplicity we assume that movement is through haploid gametes (e.g., pollen) rather than diploid individuals.

We start by counting the number, $n_i(x,t)$, of gametes of type *i* (allele *A* or *a*) at location *x* and time *t*. The number of gametes at location *x* after dispersal is given by the number of gametes that migrate to location *x* from all possible other locations:

$$\int \kappa(\delta)\, n_i(x-\delta,t)\, \mathrm{d}\delta,$$

where δ is the change in location and $\kappa(\delta)$ is the probability density function describing the chance of a gamete moving by an amount δ. $\kappa(\delta)$ is sometimes called a *dispersal kernel*. The change in the number of gamete type *i* at location *x* resulting from dispersal is thus:

$$\begin{aligned}\Delta n_i(x,t) &= \left(\int \kappa(\delta)\, n_i(x-\delta,t)\, \mathrm{d}\delta\right) - n_i(x,t)\\ &= \left(\int \kappa(\delta)\, n_i(x-\delta,t)\, \mathrm{d}\delta\right) - \left(\int \kappa(\delta)\, n_i(x,t)\, \mathrm{d}\delta\right).\\ &= \int \kappa(\delta)\, \{n_i(x-\delta,t) - n_i(x,t)\}\, \mathrm{d}\delta\end{aligned} \tag{S15.4.1}$$

The first term represents that rate at which individuals from other locations move into location *x*, and the second term represents the rate at which individuals move away from *x* to other locations. We further assume that the changes in number are sufficiently small that the difference equation for $\Delta n_i(x,t)$ can be well approximated by a differential equation $\frac{\partial n_i(x,t)}{\partial t}$ (see Box 2.6). Equation (S15.4.1) is more general than a diffusion equation, as it allows individuals to move any amount, δ.

Next, let's define the frequency of type *A* at location *x* as $p(x,t) = n_A(x,t)/(n_A(x,t) + n_a(x,t))$. Thus, a differential equation for *p* is:

$$\frac{\partial p}{\partial t} = \frac{1}{N}\frac{\partial n_A}{\partial t} - \frac{p}{N}\frac{\partial N}{\partial t}, \tag{S15.4.2}$$

where $N = n_A + n_a$. Substituting equation (S15.4.1) into (S15.4.2) and performing a series of rearrangements gives:

$$\begin{aligned}\frac{\partial p}{\partial t} &= \frac{1}{N(x,t)}\int \kappa(\delta)\,\{n_A(x-\delta,t) - n_A(x,t)\}\,\mathrm{d}\delta - \frac{p(x,t)}{N(x,t)}\int \kappa(\delta)\,\{N(x-\delta,t) - N(x,t)\}\,\mathrm{d}\delta \\ &= \int \kappa(\delta)\left\{\frac{n_A(x-\delta,t)}{N(x-\delta,t)}\frac{N(x-\delta,t)}{N(x,t)} - p(x,t)\right\}\mathrm{d}\delta - \int \kappa(\delta)p(x,t)\left\{\frac{N(x-\delta,t)}{N(x,t)} - 1\right\}\mathrm{d}\delta \\ &= \int \kappa(\delta)\left\{p(x-\delta,t)\frac{N(x-\delta,t)}{N(x,t)} - p(x,t)\frac{N(x-\delta,t)}{N(x,t)}\right\}\mathrm{d}\delta \\ &= \int \kappa(\delta)\frac{N(x-\delta,t)}{N(x,t)}\{p(x-\delta,t) - p(x,t)\}\,\mathrm{d}\delta\end{aligned}. \tag{S15.4.3}$$

(For further details and a different application of this model, see Day 2000.)

Equation (S15.4.3) describes how the frequency, *p*, changes for arbitrary dispersal kernels, $\kappa(\delta)$. If individuals move only small distances in a small amount of time, then δ will be small, and we can expand the last integrand in equation (S15.4.3) using a Taylor series:

$$\begin{aligned}\frac{\partial p}{\partial t} &= \int \kappa(\delta)\left\{-\frac{\partial p}{\partial x}\delta + 2\frac{\partial N}{\partial x}\frac{1}{N}\frac{\partial p}{\partial x}\frac{\delta^2}{2} + \frac{\partial^2 p}{\partial x^2}\frac{\delta^2}{2} + \ldots\right\}\mathrm{d}\delta \\ &= -\mu\frac{\partial p}{\partial x} + \sigma^2\frac{\partial N}{\partial x}\frac{1}{N}\frac{\partial p}{\partial x} + \frac{\sigma^2}{2}\frac{\partial^2 p}{\partial x^2},\end{aligned} \tag{S15.4.4}$$

where μ and σ^2 are the drift and diffusion coefficients describing the movement of individuals according to a diffusion process (Day 2000; Pease *et al.* 1989).

Equation (S15.4.4) provides a general description of how diffusive movement affects the distribution of allele frequencies over space. In the hybrid zone model described by equation (S15.3.1), we assumed diffusion without drift ($\mu = 0$), corresponding to symmetric dispersal.

We also assumed that the population density is constant across space, so that $\partial N/\partial x = 0$. These assumptions allow us to simplify equation (S15.4.4) considerably:

$$\frac{\partial p}{\partial t} = \frac{\sigma^2}{2}\frac{\partial^2 p}{\partial x^2}. \tag{S15.4.5}$$

To complete the model we assume that natural selection acts next at each spatial location. As a result, we add a 'reaction' term to equation (S15.4.5) to account for the way in which selection alters the frequency of A, just as we did in equation (S15.3.1). According to equation (3.13), the change in allele frequency due to selection in discrete time is

$$\Delta p = \frac{p(t)^2 W_{AA} + p(t)\, q(t) W_{Aa}}{p(t)^2 W_{AA} + 2p(t)\, q(t) W_{Aa} + q(t)^2 W_{aa}} - p(t), \tag{S15.4.6}$$

If selection is weak, we can approximate (S15.4.6) with a continuous-time model (see Problem 3.20):

$$\frac{\mathrm{d}p}{\mathrm{d}t} = p\,(1-p)\left(p\,(W_{AA} - W_{Aa}) + (1-p)\,(W_{Aa} - W_{aa})\right) \tag{S15.4.7}$$

Combining both forces – dispersal over space described by equation (S15.4.5) and selection at each point in space described by equation (S15.4.7) – we get:

$$\frac{\partial p}{dt} = \frac{\sigma^2}{2}\frac{\partial^2 p}{dx^2} + p\,(1-p)\left(p\,(W_{AA} - W_{Aa}) + (1-p)\,(W_{Aa} - W_{aa})\right). \tag{S15.4.8}$$

Assuming that heterozygotes have a relative fitness of 1 – s and that homozygotes are equally fit, $p\,(W_{AA} - W_{Aa}) + (1-p)\,(W_{Aa} - W_{aa}) = s(2p-1)$, and equation (S15.4.7) becomes equation (S15.3.1).

Supplementary Problems

Problem S15.1: Using integration by parts, demonstrate that equation (S15.1.3) can be obtained from (S15.1.2) using the forward Kolmogorov equation (15.8). Remember that the integrals are evaluated over the range of possible values of x, from $-\infty$ and $+\infty$. You will need to assume that the probability distribution $\phi(x,t|x_0,t_0)$ decays to zero for very large and very small values of x; use your results to specify exactly what must be assumed about $\phi(x,t|x_0,t_0)$ as x goes to $+\infty$ and $-\infty$.

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