Question 1 (20%) Here we investigate the demography of a mustard plant, *Boechera stricta*, following Cotto *et al.* (2019).

B. stricta has two key stages: immature (non-reproductive) and mature (reproductive). A fraction s_I of immature individuals survive each year, of which a proportion m mature. Each mature individual produces f seeds that survive to become immature individuals in the following year, and a proportion s_M of mature individuals survive and remain mature.

(a) (4%) Write down recursion equations for the number of immature, I, and matrure, M, individuals. Write out the corresponding transition matrix, $\mathbf{M}$.

Solution

The recursion equations for I and M are

$$\begin{aligned} I(t+1) &= s_I(1-m)I(t) + fM(t) \\ M(t+1) &= s_I m I(t) + s_M M(t) \end{aligned}$$

This gives transition matrix

$$\mathbf{M} = \begin{pmatrix} s_I(1-m) & f \\ s_I m & s_M \end{pmatrix}$$

(b) (4%) Write down the characteristic polynomial for $\mathbf{M}$.

Solution

The characteristic polynomial is

$$\begin{aligned} |\mathbf{M} - \lambda \mathbf{I}| &= \begin{vmatrix} s_I(1-m) - \lambda & f \\ s_I m & s_M - \lambda \end{vmatrix} \\ &= (s_I(1-m) - \lambda)(s_M - \lambda) - f s_I m \\ &= \lambda^2 - (s_I(1-m) + s_M)\lambda + s_I(1-m)s_M - f s_I m \\ &= \lambda^2 - \mathrm{Tr}(\mathbf{M})\lambda + \mathrm{Det}(\mathbf{M}) \end{aligned}$$

Cotto *et al.* (2019) used published data to estimate parameters values for *B. stricta* and found that the two eigenvalues are approximately $\lambda = 3$ and $\lambda = 1/2$. With their estimated parameter values the right eigenvector associated with $\lambda = 3$ is approximately $\begin{pmatrix} 1/10 \\ 9/10 \end{pmatrix}$ and the right eigenvector associated with $\lambda = 1/2$ is approximately $\begin{pmatrix} 11/10 \\ -1/10 \end{pmatrix}$. The left eigenvector associated with $\lambda = 3$ is approximately $\begin{pmatrix} 1 & 15 \end{pmatrix}$ and the left eigenvector associated with $\lambda = 1/2$ is approximately $\begin{pmatrix} 1 & -1/10 \end{pmatrix}$. Use these estimates in your answers below.

(c) (4%) What is the leading eigenvalue? Is the population expected to grow or decline?

Solution

The leading eigenvalue in discrete-time is the one with the largest absolute value, here $\lambda = 3$. Because this is larger than 1 we expect the population to grow.

(d) (2%) What fraction of the population do we expect to be reproductively mature in the long-run?

Solution

The fraction of each type in the long-term is given by the right eigenvector associated with the leading eigenvalue, $\begin{pmatrix} 1/10 \\ 9/10 \end{pmatrix}$. Since this already sums to one we can simply read off that 1/10 of the population will be immature and 9/10 of the population with be mature in the long-run.

(e) (2%) What is the reproductive value of a mature individual relative to an immature individual?

Solution

The reproductive value of each type is given by the left eigenvector associated with the leading eigenvalue, $\begin{pmatrix} 1 & 15 \end{pmatrix}$. Since this is already normalized relative to the reproductive value of an immature individual we can simply read off that the relative reproductive value of a mature individual is 15.

(f) (4%) The general solution for this system can be written $\vec{n}(t) = \mathbf{A}\mathbf{D}^t\mathbf{A}^{-1}\vec{n}(0)$. Write out the entries of $\mathbf{D}$ and $\mathbf{A}$.

Solution

The matrix $\mathbf{D}$ is a diagonal matrix with the eigenvalues on the diagonal

$$\mathbf{D} = \begin{pmatrix} 3 & 0 \\ 0 & 1/2 \end{pmatrix}$$

The matrix $\mathbf{A}$ contains the right eigenvectors as columns (in the same order as the eigenvalues in $\mathbf{D}$)

$$\mathbf{A} = \begin{pmatrix} 1/10 & 11/10 \\ 9/10 & -1/10 \end{pmatrix}$$

Question 2 (30%) Here we analyze a model to understand how species compete for essential nutrients (e.g., plants need certain inorganic nutrients to grow). Our approach follows Loreau (2011).

Let R represent the available stock of an essential nutrient, which flows into the system at rate I and is lost from the system at rate qR. Let N_1 be the biomass of a plant species that requires this nutrient. We assume the plants uptake the nutrient at a rate of $a_1 R N_1$, of which e_1 is converted into new plant biomass. Plant biomass is lost at a rate of $m_1 N_1$. The rate of change in the nutrient stock and plant biomass is then

$$\begin{aligned}\frac{\mathrm{d}R}{\mathrm{d}t} &= I - qR - a_1 R N_1 \\ \frac{\mathrm{d}N_1}{\mathrm{d}t} &= e_1 a_1 R N_1 - m_1 N_1.\end{aligned}$$

(a) (10%) Find all equilibria of this model.

Solution

We start with the N_1 equation, which implies that at equilibrium

$$\begin{aligned}0 &= \frac{\mathrm{d}N_1}{\mathrm{d}t} \\ 0 &= e_1 a_1 R N_1 - m_1 N_1 \\ 0 &= N_1(e_1 a_1 R - m_1)\end{aligned}$$

so that either $N_1 = 0$ or $R = m_1/(e_1 a_1)$.

Taking $N_1 = 0$ first, the R equation then says

$$\begin{aligned}0 &= \frac{\mathrm{d}R}{\mathrm{d}t} \\ 0 &= I - qR - a_1 R N_1 \\ 0 &= I - qR \\ R &= I/q\end{aligned}$$

This is one equilibrium, $\hat{R} = I/q$ and $\hat{N}_1 = 0$.

Next taking $R = m_1/(e_1 a_1)$, the R equation then says

$$\begin{aligned}0 &= \frac{\mathrm{d}R}{\mathrm{d}t} \\ 0 &= I - qR - a_1 R N_1 \\ 0 &= I - q m_1/(e_1 a_1) - m_1 N_1/e_1 \\ N_1 &= \frac{I - q m_1/(e_1 a_1)}{m_1/e_1} \\ N_1 &= I e_1/m_1 - q/a_1\end{aligned}$$

This is the other equilibrium, $\hat{R} = m_1/(e_1 a_1)$ and $\hat{N}_1 = Ie_1/m_1 - q/a_1$.

(b) (10%) Use the Jacobian to determine when the equilibrium with the plant present, $\hat{N}_1 > 0$, is stable (assuming all parameters are positive). [Hint: look at the sign of the trace and determinant.] We'll call the value of R at this equilibrium the "R star" of species 1, R_1^*.

Solution

The Jacobian is

$$\begin{aligned}\mathbf{J} &= \begin{pmatrix} \frac{\mathrm{d}}{\mathrm{d}R}\frac{\mathrm{d}R}{\mathrm{d}t} & \frac{\mathrm{d}}{\mathrm{d}N_1}\frac{\mathrm{d}R}{\mathrm{d}t} \\ \frac{\mathrm{d}}{\mathrm{d}R}\frac{\mathrm{d}N_1}{\mathrm{d}t} & \frac{\mathrm{d}}{\mathrm{d}N_1}\frac{\mathrm{d}N_1}{\mathrm{d}t} \end{pmatrix} \\ &= \begin{pmatrix} -q - a_1 N_1 & a_1 R \\ e_1 a_1 N_1 & e_1 a_1 R - m_1 \end{pmatrix}\end{aligned}$$

Evaluating at $R = \hat{R} = m_1/(e_1 a_1)$ and $N_1 = \hat{N}_1 = Ie_1/m_1 - q/a_1$ gives

$$\mathbf{J}_1 = \begin{pmatrix} -a_1 e_1 I/m_1 & -m_1/e_1 \\ e_1(Ie_1 a_1/m_1 - q) & 0 \end{pmatrix}$$

We'll determine stability with the Routh-Hurwitz conditions for a 2x2 matrix, which requires a negative trace and positive determinant.

The trace of this matrix is $-a_1 e_1 I/m_1$, which is always negative.

The determinant of this matrix is

$$\begin{aligned}\mathrm{Det}(\mathbf{J}_1) &= (-a_1 e_1 I/m_1)0 - (-m_1/e_1)e_1(Ie_1 a_1/m_1 - q) \\ &= Ie_1 a_1 - m_1 q\end{aligned}$$

So the equilibrium is stable when

$$\begin{aligned}&0 < \mathrm{Det}(\mathbf{J}_1) \\ &0 < Ie_1 a_1 - m_1 q \\ &0 < Ie_1/m_1 - q/a_1 \\ &0 < \hat{N}_1\end{aligned}$$

i.e., it is stable when the equilibrium abundance of the plant is positive.

(c) (2%) Now consider a second plant species whose dynamics follow

$$\frac{\mathrm{d}N_2}{\mathrm{d}t} = e_2 a_2 R N_2 - m_2 N_2.$$

If it were the only plant species present, with $N_2 > 0$, use this equation to get the equilibrium value of the resource. We call this the "R star" of the second species, R_2^*.

Solution

Since N_2 has the same dynamics as N_1, we can just switch the subscripts from above, so that the equilibrium with just N_2 present is $\hat{R} = m_2/(e_2 a_2)$ and $\hat{N}_2 = Ie_2/m_2 - q/a_2$.

(d) (4%) Now to understand how competition for essential nutrients works, replace R with R_1^* in the equation for $\frac{\mathrm{d}N_2}{\mathrm{d}t}$. Dividing by N_2 gives the growth rate of species 2 when it attempts to establish in a habitat where only species 1 was present beforehand. Show that species 2 can only establish when $R_2^* < R_1^*$.

Solution

From above we have $R_1^* = m_1/(e_1 a_1)$. Setting $R = R_1^*$ in the equation for N_2 gives

$$\begin{aligned}\frac{\mathrm{d}N_2}{\mathrm{d}t} &= e_2 a_2 R N_2 - m_2 N_2 \\ &= e_2 a_2 \frac{m_1}{e_1 a_1} N_2 - m_2 N_2\end{aligned}$$

Dividing by N_2 gives the growth rate of species 2 when rare

$$\frac{1}{N_2}\frac{\mathrm{d}N_2}{\mathrm{d}t} = e_2 a_2 \frac{m_1}{e_1 a_1} - m_2$$

Species 2 will only establish if it's growth rate when rare is positive

$$\begin{aligned}0 &< \frac{1}{N_2}\frac{\mathrm{d}N_2}{\mathrm{d}t} \\ 0 &< e_2 a_2 \frac{m_1}{e_1 a_1} - m_2 \\ \frac{m_2}{e_2 a_2} &< \frac{m_1}{e_1 a_1} \\ R_2^* &< R_1^*\end{aligned}$$

(e) (4%) What does it mean, biologically, that a species can only replace another when it has a lower R^*?

Solution

It means that a species can only replace another if it can grow using less resources. In this way, continual replacement will lead to the "most efficient" (smallest R^*) species excluding all others, and minimizing the amount of nutrient in the system.

Question 3 (40%) Here we analyze a "Levene-type" model to understand how environmental heterogeneity can produce genetic polymorphism. This treatment follows Doebeli (2011).

Imagine a species occupying two environments, which we'll call patch 1 and patch 2. Each generation, an individual with trait value x survives to reproductive age with probability $w_1(x) = e^{-(x+d)^2/(2\sigma^2)}$ if it is in patch 1 or with probability $w_2(x) = e^{-(x-d)^2/(2\sigma^2)}$ if it is in patch 2. That is, trait value $x = -d$ maximizes survival in patch 1 and trait value $x = d$ maximizes survival in patch 2. The parameter d determines how different the two patches are while σ (assumed to be positive) describes how quickly survival drops off as trait values deviate from those maximizing survival (larger σ cause slower drop offs). Survivors produce offspring, asexually, of which cN from patch 1 and $(1-c)N$ from patch 2 are chosen to start the next generation (e.g., c, which is between 0 and 1, could be the quality of patch 1 relative to patch 2). We assume the total population size across the two patches, N, is constant. The offspring then randomly disperse into the two habitat patches to start the next generation.

Now imagine a population where individuals have either trait x or trait y. The frequency of y in the next generation is then determined by the sum of the classic haploid selection recursion in each patch, weighted by the contribution of each patch to the next generation,

$$q(t+1) = c\frac{q(t)w_1(y)}{(1-q(t))w_1(x) + q(t)w_1(y)} + (1-c)\frac{q(t)w_2(y)}{(1-q(t))w_2(x) + q(t)w_2(y)}.$$

Here we'll do an evolutionary invasion analysis, assuming x is the resident trait value and y is the trait value of a rare mutant. To find the invasion fitness of a rare mutant we take the derivative of $q(t+1)$ with respect to $q(t)$ and evaluate at $q(t) = 0$, giving

$$\lambda(y,x) = c\frac{w_1(y)}{w_1(x)} + (1-c)\frac{w_2(y)}{w_2(x)}.$$

(a) (10%) Calculate the selection gradient, $D(x) = \frac{\partial\lambda(y,x)}{\partial y}\Big|_{y=x}$, which describes the direction of evolution from x. [Hint: using the chain rule, the derivative of $f(x) = e^{-(x-a)^2/(2\sigma^2)}$ is $(-(x-a)/\sigma^2)f(x)$.]

Solution

$$
\begin{aligned}
D(x) &= \frac{\partial \lambda(y,x)}{\partial y}\Big|_{y=x} \\
&= \frac{\partial}{\partial y}\left(c\frac{w_1(y)}{w_1(x)} + (1-c)\frac{w_2(y)}{w_2(x)} \right)_{y=x} \\
&= \frac{c}{w_1(x)}\frac{\partial}{\partial y}\left(w_1(y)\right)_{y=x} + \frac{1-c}{w_2(x)}\frac{\partial}{\partial y}\left(w_2(y)\right)_{y=x} \\
&= \frac{c}{w_1(x)}\left((-(y+d)/\sigma^2)w_1(y)\right)_{y=x} + \frac{1-c}{w_2(x)}\left((-(y-d)/\sigma^2)w_2(y)\right)_{y=x} \\
&= \frac{c}{w_1(x)}(-(x+d)/\sigma^2)w_1(x) + \frac{1-c}{w_2(x)}(-(x-d)/\sigma^2)w_2(x) \\
&= -c(x+d)/\sigma^2 - (1-c)(x-d)/\sigma^2 \\
&= -\frac{c(x+d)+(1-c)(x-d)}{\sigma^2} \\
&= -\frac{x-d(1-2c)}{\sigma^2}
\end{aligned}
$$

(b) (4%) At a singular strategy, $\hat{x}$, there is no directional selection. Show that $\hat{x} = d(1-2c)$ is a singular strategy.

Solution

There is no directional selection when

$$
\begin{aligned}
0 &= \frac{\partial \lambda(y,x)}{\partial y}\Big|_{y=x} \\
0 &= -\frac{x-d(1-2c)}{\sigma^2} \\
0 &= x-d(1-2c) \\
x &= d(1-2c)
\end{aligned}
$$

meaning that $\hat{x} = d(1-2c)$ is a singular strategy.

(c) (4%) Calculate $\frac{\mathrm{d}D(x)}{\mathrm{d}x}\big|_{x=\hat{x}}$, describing how the selection gradient changes with the resident strategy near the singular point.

Solution

$$\left.\frac{\mathrm{d}D(x)}{\mathrm{d}x}\right|_{x=\hat{x}} = \frac{\mathrm{d}}{\mathrm{d}x}\left(-\frac{x-d(1-2c)}{\sigma^2}\right)_{x=\hat{x}}$$
$$= \left(-\frac{1}{\sigma^2}\right)_{x=\hat{x}}$$
$$= -\frac{1}{\sigma^2}$$

(d) (2%) When is $\hat{x}$ convergence stable? (Hint: use your answer in (c).)

Solution

The singular strategy $\hat{x}$ is convergence stable when the selection gradient has a negative slope at that point, which we see from above is always true.

(e) (10%) Calculate $\left.\frac{\partial^2\lambda(y,x)}{\partial y^2}\right|_{y=\hat{x},x=\hat{x}}$, describing the curvature of the fitness function when the resident trait value is at the singular strategy.

Solution

$$\left.\frac{\partial^2\lambda(y,x)}{\partial y^2}\right|_{y=\hat{x},x=\hat{x}} = \frac{\partial}{\partial y}\left(\frac{\partial\lambda(y,x)}{\partial y}\right)_{y=\hat{x},x=\hat{x}}$$
$$= \frac{\partial}{\partial y}\left(\frac{c}{w_1(x)}(-(y+d)/\sigma^2)w_1(y) + \frac{1-c}{w_2(x)}(-(y-d)/\sigma^2)w_2(y)\right)_{y=\hat{x},x=\hat{x}}$$
$$= \left(\frac{c}{w_1(x)}\left(\frac{-w_1(y)}{\sigma^2} + \left(\frac{y+d}{\sigma^2}\right)^2 w_1(y)\right) + \frac{1-c}{w_2(x)}\left(\frac{-w_2(y)}{\sigma^2} + \left(\frac{y-d}{\sigma^2}\right)^2 w_2(y)\right)\right)_{y=\hat{x},x=\hat{x}}$$
$$= c\left(\frac{-1}{\sigma^2} + \left(\frac{\hat{x}+d}{\sigma^2}\right)^2\right) + (1-c)\left(\frac{-1}{\sigma^2} + \left(\frac{\hat{x}-d}{\sigma^2}\right)^2\right)$$
$$= \frac{-1}{\sigma^2} + c\left(\frac{\hat{x}+d}{\sigma^2}\right)^2 + (1-c)\left(\frac{\hat{x}-d}{\sigma^2}\right)^2$$
$$= \frac{-1}{\sigma^2} + c\left(\frac{d(1-2c)+d}{\sigma^2}\right)^2 + (1-c)\left(\frac{d(1-2c)-d}{\sigma^2}\right)^2$$
$$= \frac{-1}{\sigma^2} + c\left(\frac{2d(1-c)}{\sigma^2}\right)^2 + (1-c)\left(\frac{2dc}{\sigma^2}\right)^2$$
$$= \frac{-1}{\sigma^2} + c(1-c)\left(\frac{2d}{\sigma^2}\right)^2$$

(f) (4%) Assuming the two patches contribute equally, $c = 0.5$, show that $\hat{x}$ is evolutionarily *un*stable when $\sigma < d$. (Hint: use your answer in (e).)

Solution

$\hat{x}$ is evolutionarily *un*stable when

$$0 < \frac{\partial^2 \lambda(y,x)}{\partial y^2}\Big|_{y=\hat{x},x=\hat{x}}$$
$$0 < \frac{-1}{\sigma^2} + c(1-c)\left(\frac{2d}{\sigma^2}\right)^2$$

Plugging in $c = 1/2$

$$0 < \frac{-1}{\sigma^2} + (1/2)^2\left(\frac{2d}{\sigma^2}\right)^2$$
$$0 < \frac{-1}{\sigma^2} + \left(\frac{d}{\sigma^2}\right)^2$$
$$\frac{1}{\sigma^2} < \left(\frac{d}{\sigma^2}\right)^2$$
$$\sigma^2 < d^2$$
$$\sigma < d$$

(g) (4%) Give a biological interpretation for why we see evolutionary instability at $\hat{x}$ when d is large relative to σ (assuming $c = 0.5$). Note that $\hat{x} = d(1-2c)$ represents a strategy that is a comprimise between the two patches.

Solution

Since $\hat{x} = d(1-2c)$ is a comprimise between the two patches, as the difference in the optima between these two patches, d, grows, eventually the comprimise means that $\hat{x}$ does poorly in both patches, and it is therefore better to specialize in one. This is all relative to σ because σ determines how quickly fitness declines as the trait value moves away from either optima.

(h) (2%) Given the parameter values are such that $\hat{x}$ is convergent stable but not evolutionarily stable, how does environmental heterogeneity affect genetic polymorphism?

Solution

When $\hat{x}$ is convergent stable but not evolutionarily stable it means that $\hat{x}$ is an evolutionary branching point. I.e., when the two patches have very different optima, $d > \sigma$, this environmental heterogeneity promotes genetic polymorphism (specialists in each patch).

Question 4 (10%) Here we use probability theory derive a classic result in the coalescent model, a model which describes how alleles sampled from present-day individuals have lineages that "coalesce" into common ancestors as we look into the past.

(a) (2.5%) In a diploid population of constant size N, the probability the lineages of two sampled alleles coalesce in the previous generation is the probability they have the same parent allele. When we choose parent alleles at random this is $1/(2N)$. If the two sample lineages do not coalesce in that generation the probability of them coalescing in the generation before that is again $1/(2N)$, and so on. What is the name (or equation) of the probability distribution that most accurately describes the number of generations until the two lineages coalesce, $\Pr(T = t)$?

Solution

Each generation there is a Bernoulli trial with probability $p = 1/(2N)$ that determines if the two lineages coalesce. We want to know how many generations until the first coalescence, T. This describes a geometric distribution, $\Pr(T = t) = (1 - p)^{t-1}p$.

(b) (2.5%) Given it takes $T = t$ generations until the two lineages coalesce, there will be a branch of length t leading from each sampled allele to their most recent common ancestor. That means the two sampled alleles are separated by $2t$ generations. Given mutations – all of which are unique – occur *continuously* at a rate of μ per generation, what is the name (or equation) of the probability distribution that most accurately describes the number of mutations that occur in $2t$ generations, $P(M = m|2t)$?

Solution

A Poisson distribution describes the number of events that occur in a given amount of time when those events occur at a constant rate. The Poisson has just one parameter, the mean, which in this case is $2t\mu$, the expected number of mutations differentiating the two sampled alleles when they are seperated by $2t$ generations.

(c) (2.5%) Use the law of total expectation to write the expected number of mutations, $\mathbb{E}(M)$, as a sum of conditional expectations, where the conditioning is the time until coalescence, $\mathbb{E}(M|T = t)$.

Solution

We sum over all the potential coalescence times, weighting by the probability of each

$$\mathbb{E}[M] = \sum_{t=0}^{t=\infty} \mathbb{E}(M|T = t) \Pr(T = t)$$

(d) (2.5%) We find that the answer to (c) can be written $\mathbb{E}(M) = 2\mu\mathbb{E}(T)$. Based on your answer in (a), what is $\mathbb{E}(T)$? You now have the expected number of mutational differences between two randomly sampled alleles!

Solution

From (a) we know that T is geometrically distributed with parameter $p = 1/(2N)$. Since the expectation of a geometric distribution is $1/p$ we have $\mathbb{E}(T) = 2N$. This then gives

$\mathbb{E}(M) = 4N\mu.$