Exercise 3: the evolution of local adaptation

Environmental conditions often vary across space, favouring different trait values in different locations. However, individuals may disperse across habitats, potentially constraining local adaptation.

When does natural selection favour specialisation versus generalism?

Consider a population subdivided into two large patches of equal size, with the following life cycle:

1. Adults produce a large number of offspring and then die.
2. Offspring compete randomly within patches to survive density dependent regulation, which is such that each patch carries the same number of offspring (i.e. selection is "soft").
3. Offspring either disperse to the other patch with probability m or remain in their natal one with probability $1 - m$ (so random dispersal occurs when $m = 1/2$).

Exercise 3 (continued)

The evolving trait z is a morphological or physiological trait affecting adaptation to local conditions. In patch $i \in \{1, 2\}$, the fecundity of an individual with trait z is:

$$f_i(z) = f_{\max} \exp\left(-\frac{(z-\theta_i)^2}{\sigma^2}\right),$$

where θ_i is the local optimum and $\sigma > 0$ controls the strength of stabilising selection. Assume $\theta_1 = -1$ and $\theta_2 = 1$.

a. Define the mean matrix $\boldsymbol{W}(y,x)$, where the (i,j)-th entry $w_{ij}(y,x)$ gives the expected number of mutants in patch i produced by a mutant in patch j.

Exercise 3 (continued)

b. Compute the left and right eigenvectors of the mean matrix under neutrality $\boldsymbol{W}(x, x)$:

- The reproductive values $\boldsymbol{v}^\circ = (v_1^\circ, v_2^\circ)$
- The class distribution of a neutral lineage $\boldsymbol{q}^\circ = (q_1^\circ, q_2^\circ)$

Use these results to:

- Describe the balance between selection in patch 1 and patch 2.
- Derive the selection gradient $S(x)$ and identify the singular strategy x^*
- Determine whether x^* is convergence stable

Exercise 3 (continued)

c. In this model, the sensitivity of the class distribution of the mutant lineage to its trait is given by:

$$\left.\frac{\partial q_1(y,x^*)}{\partial y}\right|_{y=x^*} = \frac{1}{\sigma^2}\frac{2m-1}{2m}, \qquad \left.\frac{\partial q_2(y,x^*)}{\partial y}\right|_{y=x^*} = \frac{1}{\sigma^2}\frac{1-2m}{2m}.$$

- Interpret these expressions: how does an increase in trait value in a mutant lineage affects the probability that a mutant is in a patch of type 1 vs 2? Why?
- Use these expressions to compute the coefficient of disruptive selection $H(x^*)$.
- Determine the condition under which evolutionary branching occurs. Explain why and when spatial heterogeneity can favour the coexistence of specialist types using the decomposition $H(x^*) = H_{\mathrm{w}}(x^*) + 2H_{\mathrm{q}}(x^*)$.

Exercise 4: the emergence of life-history polymorphism

Organisms exhibit striking diversity in their life histories. Some species are short-lived and reproduce once before dying (e.g. annual plants), while others reproduce across many generations with little or no senescence.

Most of this variation occurs among species — but can such life-history differences emerge and persist within species?

Consider a well-mixed population with two discrete age classes (1 and 2). Individuals:

- Reproduce at age 1 and age 2,
- Compete within age classes for reproductive resources or opportunities,
- Die after age 2.

Exercise 4 (continued)

The evolving trait $z \in [0, 1]$ is the fraction of resources allocated to reproduction at age 1. This:

- increases fecundity at age 1 linearly,
- reduces survival to age 2: $s_1(z) = 1 - z$,
- reduces fecundity at age 2 linearly.

Density regulation occurs among newborns before entry into age 1.

Exercise 4 (continued)

Given these assumptions, the effective fecundities of a mutant y in a resident population x at ages 1 and 2 are:

$$b_1(y,x) = k(x) f_1 \cdot \frac{y}{x},$$
$$b_2(y,x) = k(x) f_2 \cdot \frac{1-y}{1-x},$$

respectively, where $f_1 > 0$ and $f_2 > 0$ are parameters setting the maximum fecundity at ages 1 and 2, and where $k(x) = 1/[f_1 + f_2(1-x)]$ is the probability that a newborn survives density dependent regulation to age 1.

Survival to age 2 is:

$$s_1(y) = 1 - y.$$

Exercise 4 (continued)

a. Write the Leslie matrix $\boldsymbol{W}(y, x)$ and characterise the selection gradient $S(x)$. Use it to find the singular strategy x^*. Is it convergence stable?

b. Calculate the coefficient of disruptive selection via its two components $H(x^*) = H_{\mathrm{w}}(x^*) + 2H_{\mathrm{q}}(x^*)$. Use it to determine when evolutionary branching occurs. What maintains alternative life-history strategies here?