Adaptive Dynamics Course
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Evolution in heterogeneous environments - I

Many species live in habitat patches with different environments (such as dryer or wetter) or exploit different kinds of hosts (e.g. different plant species for a phytophagous insect). Different habitats often need different adaptations. A species inhabiting different patches may evolve into a generalist (a jack-of-all-trades, which is not particularly well adapted to either environment but can exploit all) or a habitat specialist (which is adapted to one but doing poorly in alternative habitats).

To investigate the evolution of habitat specialization, in this project we set up a model for an annual organism in discrete time. We start with two habitats and assume that fecundity is a Gaussian-type function of trait *x* with a habitat-specific optimum,

$$\begin{aligned} \lambda_1(x) &= a\exp\left[-\frac{(x-\mu_1)^2}{2\sigma^2}\right]+c \\ \lambda_2(x) &= a\exp\left[-\frac{(x-\mu_2)^2}{2\sigma^2}\right]+c \end{aligned} \tag{1}$$

where μ_1 and μ_2 are the optimal trait values in habitat 1 and 2, respectively. Without loss of generality, one can scale trait *x* such that $\sigma = 1$ and $\mu_1 = -d/2$, $\mu_2 = d/2$, where *d* is the difference between the habitat-specific optima μ_1 and μ_2.

Offspring undergo density-dependent mortality such that the probability of survival to adulthood in habitats *i* (*i*=1 or 2), if the habitat contains *N* offspring, is given by

$$f_i(N) = \frac{\beta}{1+b_i N} \tag{2}$$

Here b_i characterizes the size of habitat *i*: large values of *b* correspond to small habitats where adding a single individual has a relatively large effect on survival. Note that by scaling *N*, one can set $b_1 = 1$ without loss of generality (or in other words, the adaptive dynamics of trait *x* depends only on the ratio b_2/b_1).

The habitats are connected via dispersal. We assume that dispersal occurs after density dependent survival and before reproduction, i.e., the life cycle is survival - dispersal - reproduction - survival... During dispersal, a fraction *m* of the individuals born in one habitat migrate to the other. Dispersal entails no cost (e.g., there is no risk of mortality due to dispersal).

The above assumptions lead to the population dynamical equations

$$\begin{aligned} N_1(t+1) &= \left[(1-m)\,f_1(N_1(t))N_1(t) + mf_2(N_2(t))N_2(t)\right]\lambda_1(x) \\ N_2(t+1) &= \left[(1-m)\,f_2(N_2(t))N_2(t) + mf_1(N_1(t))N_1(t)\right]\lambda_2(x) \end{aligned} \tag{3}$$

where N_i denotes the number of juveniles in habitat *i* just prior to density-dependent survival (i.e., immediately after reproduction).

Different strategies differ in only their strategy *x* and in their habitat-specific fecundity $\lambda_i(x)$, but share all other properties. In particular, density-dependent survival is determined by the total number of individuals within a habitat, irrespectively of their strategies. The population dynamics of a rare mutant *y* in the equilibrium population of resident *x* are thus given by

$$\begin{aligned} M_1(t+1) &= \left[(1-m)\,f_1(\hat{N}_1)M_1(t) + mf_2(\hat{N}_2)M_2(t)\right]\lambda_1(y) \\ M_2(t+1) &= \left[(1-m)\,f_2(\hat{N}_2)M_2(t) + mf_1(\hat{N}_1)M_1(t)\right]\lambda_2(y) \end{aligned} \tag{4}$$

where M_i is the number of mutants in habitat *i* and $\hat{N}_i$ denotes the equilibrium number of residents obtained from equations (3). Notice that the population is structured by the habitat. To calculate the invasion fitness of the mutant, rewrite equations (4) into the matrix form

$$\begin{pmatrix} M_1 \\ M_2 \end{pmatrix}_{t+1} = \begin{bmatrix} (1-m)\,f_1(\hat{N}_1)\lambda_1(y) & mf_2(\hat{N}_2)\lambda_1(y) \\ mf_1(\hat{N}_1)\lambda_2(y) & (1-m)\,f_2(\hat{N}_2)\lambda_2(y) \end{bmatrix} \begin{pmatrix} M_1 \\ M_2 \end{pmatrix}_t \tag{5}$$

Elements of the matrix in the brackets are constant. The mutant population thus grows exponentially, and the annual growth rate is given by the dominant eigenvalue of the matrix.

Assume first that the two habitats are of equal size ($b_1 = b_2$) and find examples for different types of singular strategies. Investigate how the number and stability of singularities change as a function of *d* for at least two different values of *m* (bifurcation analysis). Construct an isocline plot and investigate the coevolution of two strategies in an example with evolutionary branching. Next, vary the relative size of the two habitats (b_2 / b_1), and study its effect on monomorphic and dimorphic evolution.

If time permits, extend the model to three habitats. Assume that the habitats are of equal size and all offspring are equally distributed over all habitats (1/3 stays where it was born, 1/3 goes to one alternative habitat and 1/3 goes to the other alternative habitat). By symmetry, one expects either a single generalist strategy to evolve or three habitat specialists. Evolutionary branching can however split the population only into two, not three, branches. Explore how the population evolves when the generalist is not evolutionarily stable.