Adaptive Dynamics Course
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Evolution in heterogeneous environments

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 doing poorly in alternative habitats). To investigate the evolution of habitat specialization, we set up a model for an annual organism in discrete time. We assume that fecundity in habitat *i* is a Gaussian-type function of phenotype *x* with a habitat-specific optimum,

$$\lambda_i(x) = a \exp\left[-\frac{(x-\mu_i)^2}{2\sigma^2} \right] + c \tag{1}$$

Offspring undergo density-dependent mortality according to the Beverton-Holt model of population dynamics (see e.g. P. Yodzis: Introduction to theoretical ecology, Harper & Row, 1989), such that the probability of survival in patch *i*, if it initially contains N_i offspring, is given by

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

Here b_i characterizes the size of patch *i* (large values of *b* correspond to small patches that can carry only few individuals). With only a single patch, the year-to-year dynamics is given by

$$N(t+1) = \lambda(x)\, f(N(t)) N(t) \tag{3}$$

where *N* denotes population size after reproduction and just before the stage of density dependent survival.

When the population inhabits several patches, then the patches are connected via dispersal. We assume that dispersal occurs after density dependence and before reproduction, i.e., the life cycle is reproduction - density-dependent survival - dispersal - reproduction - ... At dispersal, a fraction m_{ij} of the individuals present in patch *j* migrate into patch *i*. Dispersal entails no cost (e.g., there is no risk of mortality due to dispersal). The joint dynamics of *n* patches is then given by the system of difference equations

$$N_i(t+1) = \lambda_i(x) \sum_{j=1}^{n} m_{ij} f_j(N_j(t)) N_j(t) \qquad (4)$$

for $i = 1,...,n$, where we define $m_{ii} = 1 - \sum_{j \neq i} m_{ji}$ the fraction of individuals which stay in patch *i*.

Different strategies differ in only their phenotype *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 patch, irrespectively of which strategies they are. Denoting the number of individuals with phenotype x_k in patch *i* by $N_i^{(k)}(t)$, the dynamics for *K* different strategies follows

$$N_i^{(k)}(t+1) = \lambda_i(x_k) \sum_{j=1}^{n} m_{ij} f_j\left(\sum_{l=1}^{K} N_j^{(l)}(t)\right) N_j^{(k)}(t) \qquad (5)$$

Consider first only two patches of equal size ($b_1 = b_2$) and with symmetric dispersal ($m_{12} = m_{21} = m$). Let *d* denote the difference between the habitat-specific optimal phenotypes and scale *x* such that $\sigma = 1$ and $\mu_1 = -d/2$, $\mu_2 = d/2$. By scaling *N*, one can also set $b_1 = 1$ without loss of generality. Explore the adaptive dynamics for different values of *d* and *m* (for the other parameters, $a/c = 1.5$ and $\beta c = 1$ are good starting values). Obtain bifurcation diagrams for the monomorphic evolutionary singularity, and construct at least one example for the evolution of coexisting strategies after branching. Next, vary the relative size of the two patches (b_2/b_1), and study its effect on monomorphic and dimorphic evolution. Argue that as long as the population attains a stable fixed point, no more than two strategies will coexist.

If time permits, it is interesting to extend the model to three patches. Assume that the patches are of equal size and dispersal distributes all offspring equally over all patches ($m_{ij} = 1/n$ where *n* is the number of patches). 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 a single generalist is not evolutionarily stable.