Adaptive Dynamics Course
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Evolution of Dormancy

Dormancy is advantageous in temporally stochastic environments. As a simple example, consider an annual plant living in an environment where in some years, the crop fails entirely. Without seed dormancy, the plant is extinct in the first such year. A variety with seed dormancy however survives, and thus clearly does better in the long term even if dormancy entails a survival cost.

In this project, we study the evolution of dormancy - or, equivalently, of seed germination - and in particular, the diversification of germination strategies in annual plants. Let x denote the fraction of seeds that germinate in any one year and let $N(t)$ be the number of seeds in year t prior to germination. If a seed germinates, it produces $\frac{k}{xN(t)+a}$ new seeds in favourable years; in unfavourable years, no plant survives to yield crop. The yield depends on the number of germinated seeds in year t, i.e., on the number of competing plants. k is a constant which contains the probability of survival from germination to reproduction and maximum fecundity, whereas a controls how fast the entire crop produced by the population, $xN(t)Y(t)$, saturates with the number of competing plants (this is the so-called saturating yield model of density dependent crop).

Favourable and unfavourable years occur with probability p and 1-p, respectively, and are temporally uncorrelated. The per capita yield is therefore given by

$$Y(t) = \begin{cases} \dfrac{k}{xN(t)+a} & \text{with probability } p \\ 0 & \text{with probability } 1-p \end{cases} \tag{1}$$

$N(t)$ fluctuates in time due to the random alternation of favourable and unfavourable years according to

$$N(t+1) = \left[(1-x)z + xY(t)\right]N(t) \tag{2}$$

where z is the constant probability of survival in the seed bank.

Consider now a rare mutant strategy with germination fraction y. The dynamics of the mutant population are

$$M(t+1) = \left[(1-y)z + yY(t)\right]M(t) \tag{3}$$

where $Y(t)$ is the same as for the resident and is therefore determined by the resident density $N(t)$. Unfortunately, there is no way one could calculate the distribution of $N(t)$ explicitly in fluctuating environments. Hence the resident population dynamics must be simulated using equations (1)-(2), and $N(t)$ must be extracted from the simulation. From $N(t)$, one gets the yield $Y(t)$ according to eq. (2), and can calculate the annual growth rate of the mutant in year t, $\left[(1-y)z + yY(t)\right]$. The long-term growth rate is the geometric mean of the annual growth rates, or, equivalently, the arithmetic mean of the log annual growth rates, over a large number of years (see lecture).

Next, we extend the model to two habitats that differ in the probability of survival in the seed bank: in the "safe" habitat the probability of survival is z_1 and in the "dangerous" habitat it is $z_2 < z_1$. A fraction d of newly produced seeds disperse to the alternative habitat. The resident population thus follows the dynamics

$$\begin{aligned} N_1(t+1) &= (1-x)z_1N_1(t) + x(1-d)Y_1(t)N_1(t) + xdY_2(t)N_2(t) \\ N_2(t+1) &= (1-x)z_2N_2(t) + x(1-d)Y_2(t)N_2(t) + xdY_1(t)N_1(t) \end{aligned} \tag{4}$$

where N_1 and N_2 are respectively the number of seeds in the first and in the second habitat. We assume that the two habitats experience synchronous above-ground environmental conditions (e.g. synchronous changes in weather). The yields in the two habitats thus differ only because they depend on the local population density, i.e., in a favourable year the yield in the first habitat is $\frac{k}{xN_1(t)+a}$ whereas the yield in the second habitat is $\frac{k}{xN_2(t)+a}$. Analogously to eq. (3), a mutant population with germination fraction y grows according to

$$\begin{aligned} M_1(t+1) &= (1-y)z_1M_1(t) + y(1-d)Y_1(t)M_1(t) + ydY_2(t)M_2(t) \\ M_2(t+1) &= (1-y)z_2M_2(t) + y(1-d)Y_2(t)M_2(t) + ydY_1(t)M_1(t) \end{aligned} \tag{5}$$

One has to simulate the resident dynamics in eqs. (4) and calculate the habitat-specific yields in order to simulate the growth of the mutant population. Notice that in the extended model, not only the habitat-specific annual growth rates fluctuate but also the population structure (the ratio of M_1 and M_2) changes between years, which also influences overall growth. In the simulation, measure the annual growth of the entire mutant population $\left[\left(M_1(t+1)+M_2(t+1)\right)/\left(M_1(t)+M_2(t)\right)\right]$ and calculate the long-term geometric mean of these annual growth rates to obtain invasion fitness. To avoid the exponential explosion of mutant numbers, divide both M_1 and M_2 with the annual growth rate in each year but be careful to preserve the population structure as given by the simulation.

Start with the analysis of the first model (single habitat). Show that in a constant environment (p=1), dormancy is selected against such that x=1 is the optimal strategy. Construct PIPs to show that with environmental fluctuations, x<1 may be ESS, i.e., some dormancy is selected for. Show that in a single habitat, two germination strategies may coexist but there is always a globally stable ESS (no evolutionary branching). Study how the ESS germination fraction depends on the probability of seed survival, z.

Next, investigate the model with two habitats. Construct an example for evolutionary branching (hint: choose small dispersal fractions) and investigate the coevolution of two strategies using isocline plots. Study how the evolutionary singularities change with changing dispersal.