Conflict between resource use and adaptation to a mutualist

Suppose two mutualistic species help each other best if their (scaled) trait values are the same. The same traits are, however, also involved in adaptation to resource use, and the resources of the two species are best utilised with different trait values. There is thus a conflict between resource use (which is best if the two species have two different, externally determined trait values) and mutualism (which is maximal when the two species' traits match).

We model adaptation to the optimal use of different resources by assuming that the carrying capacity of the species, $K_1(x_1)$ and $K_2(x_2)$, reach their maxima at different trait values; without loss of generality, we may assume that the maxima are at $x_1 = -x_0$ and $x_2 = x_0$, respectively, where x_0 is a constant. For numerical work, assume a Gaussian function with some constant "background" resource added,

$$K_1(x_1) = c + \exp\left(-\frac{(x_1 + x_0)^2}{2\sigma_K^2}\right)$$

$$K_2(x_2) = c + \exp\left(-\frac{(x_2 - x_0)^2}{2\sigma_K^2}\right)$$

(1)

(note that by scaling the trait values, $\sigma_K = 1$ may be assumed without loss of generality).

For mutualism, we define the total "amount" of help given by one individual of species 2 to all individuals of species 1 as the total number of offspring produced by species 1 which could not be produced without the helping individual of species 2. Since the number of offspring must be proportional to the density of species 1 (N_1), the total amount of help equals aN_1. If there are different strategies within species 1, however, then those with trait values nearer to the species 2 individual receive more help. Assume that there are two strategies within species 1, $x_1^{(1)}$ and $x_1^{(2)}$, with frequencies p_1 and p_2, respectively. The amount of help given to all individuals $x_1^{(1)}$ by one individual of species 2 is then

$$\frac{p_1 \alpha(x_1^{(1)} - x_2)}{p_1 \alpha(x_1^{(1)} - x_2) + p_2 \alpha(x_1^{(2)} - x_2)} aN_1$$

(2)

where $\alpha(x_1 - x_2)$ is maximal when the traits match; we assume the Gaussian function

$$\alpha(x_1 - x_2) = \exp\left(-\frac{(x_1 - x_2)^2}{2\sigma_\alpha^2}\right) \tag{3}$$

We embed the above assumptions into a simple Lotka-Volterra model where the population dynamics of the two species are given by

$$\frac{dN_1}{dt} = rN_1\left(1 - \frac{N_1}{K_1(x_1)} + aN_2\right)$$

$$\frac{dN_2}{dt} = rN_2\left(1 - \frac{N_2}{K_2(x_2)} + aN_1\right) \tag{4}$$

where N_1 and N_2 denote the population densities of the two species, x_1 and x_2 are the corresponding trait values, and a measures the strength of mutualism. As follows from formula (2), as long as each species has only one strategy, function $\alpha(x_1 - x_2)$ does not play a role. When a mutant y_1 (y_2) enters species 1 (species 2), however, its dynamics are

$$\frac{dM_1}{dt} = rM_1\left(1 - \frac{\hat{N}_1}{K_1(y_1)} + a\frac{\alpha(y_1 - x_2)}{\alpha(x_1 - x_2)}\hat{N}_2\right)$$

$$\frac{dM_2}{dt} = rM_2\left(1 - \frac{\hat{N}_2}{K_2(y_2)} + a\frac{\alpha(y_2 - x_1)}{\alpha(x_2 - x_1)}\hat{N}_1\right) \tag{5}$$

where M_1 and M_2 denote the (small) density of the mutant of species 1 and of species 2, respectively. At any one time, there is only one mutant (either M_1 or M_2). The resident densities $\hat{N}_1$ and $\hat{N}_2$ are determined from the equilibrium of equations (4).

(a) In the full model, two traits (one for each species) are evolving even in a monomorphic resident population. Therefore, we need to construct an isocline plot to find the monomorphic evolutionary singularity. Convergence stability is also more difficult than for a single trait: If necessary, use the canonical equation assuming equal and constant mutation rates and mutational variances to see whether the singularity is convergence stable. Establish whether the singularity is a fitness maximum or fitness minimum for each species.

(b) As one extreme case, assume that one of the two species evolves much slower than the other. Fix the second species at an arbitrary trait value OR at its singular trait value as determined in (a), and assume that only the first species evolves. (By symmetry, fixing the first species and letting the second species evolve yields analogous results.) Construct PIPs for species 1. Can you find evolutionary branching? Explore evolution of species 1 after branching while keeping species 2 fixed.

(c) If time permits, consider the case when both species mutate at similar speeds. Due to symmetry, one can expect if one species branches then both branches simultaneously. Further, symmetry suggests that the trait values of the two dimorphic populations will be close to the symmetric arrangement $x_1^{(1)} = -x_2^{(2)}$, $x_1^{(2)} = -x_2^{(1)}$ (deviations from this symmetric arrangement are due to small variations in the emerging mutations). In this case, one has to track only two evolving variables; for example, $x_2^{(1)}$ and $x_2^{(2)}$ fully characterise the four strategies present. Explore the coevolution of two strategies in each of the two species assuming this symmetry constraint.