

Evolutionary branching with adaptive resource choice

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We are interested in the branching behavior of an asexual model where resource choice approaches optimal, or adaptive, choice. We study the properties of the model in an adaptive dynamics framework, i.e. here we derive expected outcomes of selection alone. Additional processes involved in speciation in sexual organisms, such as recombination, drift or eco-evolutionary feedbacks, are not investigated here. Instead, we assume a large monomorphic population of organisms with clonal reproduction, where mutations occur at a slow pace compared to ecological dynamics. Given a monomorphic resident population, we study the fitness of a mutant arising in that population. If the fitness of a mutant is greater than that of the resident, the mutant invades and becomes the resident. We use fitness gradients to predict the singularities of the evolutionary dynamics, and study their stability to know under what conditions branching points are expected.

1 Non-adaptive resource choice

Suppose a population of n individuals feeding on two resources, R_1 and R_2 . Here, R_1 and R_2 also refer to the concentrations of those two resources. Individuals feed on R_1 with feeding efficiency $e_1(x)$ and on R_2 with feeding efficiency $e_2(x)$, where e_1 and e_2 both depend on an underlying ecological trait, x . Specifically, the feeding efficiencies are $e_1(x) = \exp(-s(x+1)^2)$ and $e_2(x) = \exp(-s(x-1)^2)$, where s is the ecological selection coefficient, which controls the strength of the trade-off between both feeding efficiency functions (depicted in Figure 1). The ecological trait x is continuous and can be seen, for example, as beak size for a species of bird, and feeding efficiency on R_1 is maximized when $x = -1$ and feeding efficiency on R_2 is maximized when $x = 1$.

In this model, individuals feed on both resources depending on resource availability and their own feeding efficiency. The invasion fitness, i.e. that of a mutant with ecological trait value y in a monomorphic resident population x , is

$$w(y, x) = e_1(y)R_1 + e_2(y)R_2 \tag{1}$$

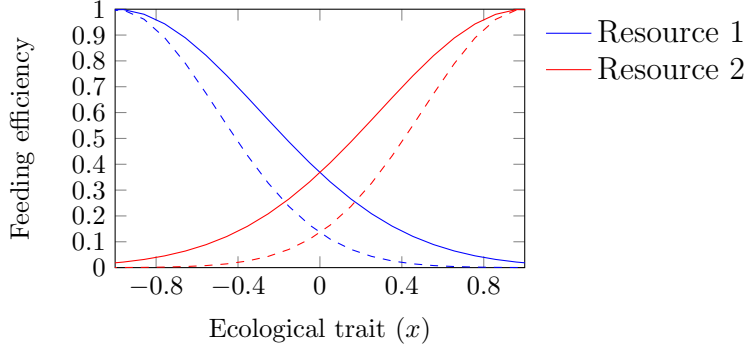


Figure 1: Feeding efficiency on both resources as a function of the ecological trait. The ecological selection coefficient s determines the strength of the trade-off: solid lines, $s = 1$, dashed lines, $s = 2$.

R_1 and R_2 are calculated from the resource dynamics. Our system behaves like a chemostat, where

$$\frac{dR_i}{dt} = I_i - R_i/c_i - R_i n e_i(x) \quad (2)$$

Here, I_i is the inflow of resource R_i per unit time, c_i is the renewal time of resource R_i and $n e_i(x)$ is the proportion of R_i that is consumed by the population. This yields the equilibrium concentration

$$R_i = \frac{I_i c_i}{1 + c_i n e_i(x)} \quad (3)$$

We find the singularities of the evolutionary dynamics by finding the roots of the fitness gradient. The fitness gradient $g(x)$ is the slope of the invasion fitness with respect to the mutant's phenotype, evaluated at the resident's phenotype x , so

$$g(x) = \left. \frac{\partial w}{\partial y} \right|_{y=x} \quad (4)$$

In the current scenario, the fitness gradient becomes

$$g(x) = -2s(x * w(x) + \Delta(x)) \quad (5)$$

where $\Delta(x) = e_1(x)R_1 - e_2(x)R_2$ is the payoff differential between the two resources.

We numerically found the roots of the fitness gradient for a range of selection coefficient values, and systematically evaluated the convergence and evolutionary stability of the singularities. Convergence stability defines whether a

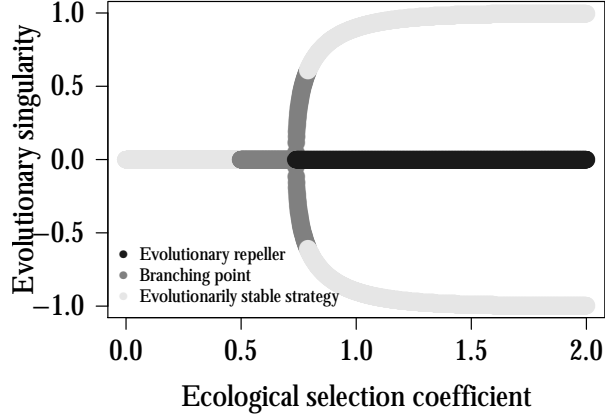


Figure 2: Adaptive dynamics of a population with non-adaptive resource usage in sympatry. Branching is expected only for narrow range of selection intensities, or niche widths. If selection is too weak, a generalist is favored. If selection is too strong, a specialist is favored. Parameters: $n = 1,000$, $I_1 = I_2 = 2$, $c_1 = c_2 = 0.001$.

singularity is evolutionarily attainable from a nearby point in phenotype space. A singularity x^* is convergent stable if the derivative of the fitness gradient with respect to the resident's trait is negative at x^* , or in other words, if the fitness gradient is positive below x^* and negative above. Evolutionary stability defines whether, once reached, the singularity is a fitness maximum subject to stabilizing selection, or a fitness minimum subject to disruptive selection. A singularity x^* is evolutionarily stable if the second derivative of the invasion fitness evaluated at x^* is negative, i.e. the singularity is a fitness peak. A branching point is a singularity that is convergent stable but evolutionarily unstable, i.e. attainable but a fitness minimum once reached, which leads to divergence. The results are shown in Fig. 2. Under this scenario, we see that branching is expected in a rather narrow band of selection coefficient values. In the next section, we will study the effect of adaptive resource choice on evolutionary branching, by letting individuals to a variable extent choose what food is best for them.

2 Adaptive resource choice

Let us assume now that individuals can choose to some extent the resource they feed on. We define β as the resource choice parameter. When $\beta = 0$, individuals behave as in the previous scenario. However, as β increases, individuals gain the ability to increase their uptake of the resource, of the two resources, that is most

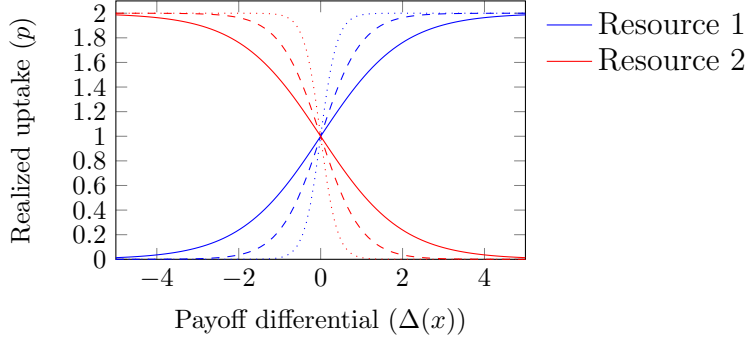


Figure 3: Realized uptake, as a proportion of the feeding efficiency, is a function of the payoff differential i.e. how advantageous is each resource. The higher the resource choice parameter β , the steeper these curves become close to zero, and they approach a step function as $\beta \rightarrow \infty$, which corresponds to full resource choice. Solid lines, $\beta = 1$; dashed lines, $\beta = 2$; dotted lines, $\beta = 5$.

advantageous to them. This is equivalent to saying that each individual reduces its consumption of the least advantageous resource, say R_i , by a factor p_i , which represents the realized uptake of resource R_i such that the actual amount of R_i consumed by an individual is $p_i e_i(x)$. p_i depends on β such that when $\beta > 0$, $p_i < 1$ for the least advantageous resource (i.e. resource uptake is reduced), but is equal to 1 for the most advantageous resource. At the extreme, i.e. when $\beta \rightarrow \infty$, individuals consume only the most advantageous resource. How advantageous R_1 is compared to R_2 is given by the payoff differential $\Delta(x) = e_1(x)R_1 - e_2(x)R_2$ introduced in the previous section. A suitable expression for p_1 and p_2 is a logistic function represented in Fig. 3, of the form

$$p = \frac{2}{1 + \exp(-\beta\Delta(x))} \quad (6)$$

Both resource uptake functions approach a step function as β becomes very large, which corresponds to a full resource choice where individuals feed only on the most advantageous resource, no matter how much more advantageous it is.

Under this new scenario, the resource equilibrium is now

$$R_i = \frac{I_i c_i}{1 + c_i n p_i e_i(x)} \quad (7)$$

From there, we can rewrite the payoff differential as

$$\Delta(x) = e_1(x)R_1 - e_2(x)R_2 = \frac{e_1(x) I_1 c_1}{1 + c_1 n p_1 e_1(x)} - \frac{e_2(x) I_2 c_2}{1 + c_2 n p_2 e_2(x)} \quad (8)$$

We can then substitute Equation 8 into Eq. 6 and Eq. ?? and numerically solve for p_1 and p_2 .