

Chapter 6

Adaptive dynamics

An organism is regarded as adapted to a particular situation, or to the totality of situations which constitutes its environment, only insofar as we can imagine an assemblage of slightly different organic forms, which would be less well adapted to that environment. Ronald Fisher

6.1 Evolutionary invasion analysis

Until now, we have considered evolutionary dynamics on a short time scale, where only two alleles segregate in a population, and which results in either the maintenance of polymorphism or the fixation of an allele. However, once an allele has been fixed by selection under such **short-term evolution**, a new allele may arise through mutation that may again be favored by selection.

By the repeated invasion of mutant alleles, a quantitative phenotypic trait (for example body size, enzymatic flux, temporal discount rate, date of first flowering, or maximum flight speed) may then evolve by a gradual (i.e., step-by-step) transformation and eventually converge to a stable **evolutionary equilibrium**. This is a point where a change in the trait can no longer occur by natural selection. This process of successive allelic invasion and replacement, which results in continuous change of a phenotype, is called **adaptive dynamics**. We also refer to this process as **long-term evolution** because, due to the fact that the mutation rate is usually small (recall chapter 4), a longer time scale is required for mutations to appear. Hence, gradual phenotypic change occurs on a slower time scale as allele frequency change, which is often referred to as **short-term evolution**.

In order to model long-term evolution we consider that each individual in the population is characterized by a quantitative phenotype; that is to say a real valued variable. We will use the insights gained from studying models with two alleles in order to characterize long-

term evolutionary equilibria, while in reality every individual in a population may have a different phenotype. We thus assume that only two alleles can segregate in the population. Allele A, whose carriers express phenotype x , and allele B, whose carriers express phenotype y , where both are assumed to code for quantitative phenotypes, respectively, x and $y \in \mathbb{R}$.

6.1.1 The fate of a single mutant copy

We denote by $w(x, y)$ the fitness of a *single* A individual (expressing phenotype x) introduced into a population otherwise monomorphic for the B allele, where individuals thus express phenotype y . We denote by $w(y, y)$ the fitness of a single B individual in a monomorphic B population, which is assumed to be at its demographic equilibrium (say for number n^* of individuals). Since at a demographic equilibrium an individual just replaces itself, fitness must be equal to one (recall eq. 2.10 and/or eq. 3.20), whereby

$$w(y, y) = 1. \quad (6.1)$$

If we assume that the B-monomorphic population size is large (say $n^* \geq 1000$), then the fitness of a B individual is virtually not affected by the introduction of a single A individual into that population, and is still given by $w(y, y) = 1$. This can be understood by considering that a randomly sampled B individual is unlikely to interact with the very single A individual, since the probability of such an interaction is $1/n^* < 0.001$ as there is one A individual and $n^* - 1$ individuals with allele B. Hence, the selection coefficient on allele A when introduced as a single copy into the B population is¹

$$s = w(x, y) - w(y, y) = w(x, y) - 1. \quad (6.2)$$

Since the sign of the selection coefficient (eq. 3.9) determines the direction of selection on allele A, it is not favored by selection if $s \leq 0$, in other words when

$$w(x, y) \leq 1. \quad (6.3)$$

This says that if an individual carrying A is introduced as a single copy in a monomorphic B population and produces less or exactly one successful offspring over a single demographic time period, then B cannot be invaded by A. By contrast, when $w(x, y) > 1$, a carrier of A produces more than one successful offspring and will then invade the B population (when neglecting the effect of genetic drift). Note that the term “invasion” refers to the spread of the allele when rare but does not imply fixation in the population, as a stable polymorphism may occur between A and B.

Because this account focuses only on the initial fate—(invasion or not)—of the A allele arising as a single copy by mutation in the backdrop of a B population, the A allele is often called the “mutant” allele, while B is referred to as the “resident” or “wild-type” allele. We will endorse this language here.

¹In terms of the notations used in chapter 3, e.g., eq. 3.10, we have $w_A = w(x, y)$, $w_B = w(y, y)$, and the selection coefficient is $s = w_A - w_B$.

6.1.2 Uninvadability

We say that a phenotype y is an **uninvadable strategy** if

$$w(x, y) \leq 1 \quad \forall x \in \mathcal{X}, \quad (6.4)$$

where \mathcal{X} is the phenotype space, that is, the set of feasible alternative phenotypes (or “strategies”) that an individual can implement. This is taken in this course as either the entire set of real numbers, \mathbb{R} , or some subset of it, for instance if x is a probability.

An uninvadable strategy cannot be invaded by any alternative strategy in the phenotypic space and thus characterizes an evolutionary equilibrium. Indeed, eq. (6.4) says that for an uninvadable strategy, eq. (6.3) holds for any possible mutant attempting an invasion of the resident population. Eq. (6.4) also says that an uninvadable strategy maximizes fitness for a resident population at the uninvadable state. Hence, if y is uninvadable, then it solves the maximization problem

$$\max_{x \in \mathcal{X}} w(x, y), \quad (6.5)$$

which means that y is the best strategy against itself. As such, an uninvadable strategy can also be interpreted as a Nash equilibrium of a symmetric game between two players with payoff function given by the fitness function.

6.1.3 Necessary conditions for uninvadability

A useful quantity to characterize uninvadable strategies is the so-called *selection gradient*

$$S(y) = \left. \frac{\partial w(x, y)}{\partial x} \right|_{x=y} \quad (6.6)$$

on the evolving trait at point y . The selection gradient is the marginal change in the fitness of an individual when it varies its strategy in a population expressing strategy y . This can be thought of as the “gains from switching” trait value to x for an individual in a population where everybody else plays y . There are no gains of switching when the selection gradient is equal to zero. A strategy y^* will be called a **singular strategy** when it solves

$$S(y^*) = 0 \quad (6.7)$$

This is the first-order necessary condition for a function to have a maximum, and thus a necessary condition for a strategy to be uninvadable is that it is a singular strategy.

A singular strategy may be a **fitness maximum or minimum** (recall that first-order derivatives locate both maxima and minima of a function), and for a singular strategy to be uninvadable, we thus require that it also satisfies the second-order condition

$$\left. \frac{\partial^2 w(x, y)}{\partial x^2} \right|_{x=y=y^*} \leq 0, \quad (6.8)$$

which, along with eq. (6.7), is sufficient to characterize a local maximum of fitness.

6.2 Long-term evolution under constant selection

6.2.1 Stabilizing selection

Biological assumptions

In order to illustrate and understand the concept of uninvasability, we assume a population with haploid individuals undergoing the following life cycle. (1) Adult individuals gather resources (possibly involving density-dependent competition). (2) Individuals produce offspring according to the amount of resources they obtain (fecundity). (3) All adults die and offspring survive to adulthood (possibly involving density-dependent competition) to form the next generation of adults. All events in this life cycle—resource gathering, offspring production (fecundity), and survival—may depend on the strategies (phenotypes) of the individuals in the population.

Suppose we focus on a quantitative phenotype, such as size, weight, or maximum running speed of an individual. These are phenotypes that are subject to a so-called **stabilizing selection**. That is, there are physiological constraints (trade-offs) acting on the organism such that an ‘optimal value’ of the phenotype, say y_{op} , maximizes resource uptake and reproduction of an individual under given environmental conditions. As a concrete example, let us assume that the fitness of an individual with phenotype x introduced into a large resident population with individuals having phenotype y as follows a Gaussian function

$$w(x, y) = k(y) \exp \left(-\frac{(x - y_{\text{op}})^2}{2\sigma_w^2} \right). \quad (6.9)$$

Here, $k(y)$ is a constant of proportionality determining the maximal possible fitness of the individual when it expresses the optimal phenotype, $x = y_{\text{op}}$ (because then $\exp \left(-\frac{(x - y_{\text{op}})^2}{2\sigma_w^2} \right) = \exp(0) = 1$ and thus $w(y_{\text{op}}) = k$), and σ_w is the characteristic width of the fitness function (see Derivation 1). The larger the value of σ_w the more slowly fecundity declines as the distance between x and y_{op} increases (see the lecture slides). In other words, fecundity declines when the phenotype expressed by an individual departs from this optimal phenotype and the larger σ_w the slower the decline, because σ_w appear in the denominator of eq. (6.9) and increasing its value flattens the fecundity function.

Owing to our life-cycle, we can let fitness be determined by a Beverton-Holt model of density-dependent competition (eq. 2.7) so that the constant of proportionality in eq. (6.9) is given by

$$k(y) = \frac{f_b}{1 + \gamma n^*(y)}, \quad (6.10)$$

is the factor decreasing fecundity as a result of density-dependent competition, with f_{max} being the maximal possible fecundity, and $n^*(y)$ the demographic equilibrium of the resident (monomorphic) population and thus depending on the traits of individuals in the resident population. The regulating factor $k(y)$ takes values between one (in the absence of density-

dependent competition) and a small number when the resident population is large. In such a population, the equilibrium population size is

$$n^*(y) = \frac{f_{\max} \exp\left(-\frac{(y-y_{\text{op}})^2}{2\sigma_w^2}\right) - 1}{\gamma}, \quad (6.11)$$

which is eq. (2.11) where fecundity $f = f_{\max} \exp\left(-\frac{(y-y_{\text{op}})^2}{2\sigma_w^2}\right)$ depends only on the trait y of the resident population (since we assume the resident population is monomorphic).

Two things should be noted about eq. (6.9).

- The strategy of an individual with phenotype x does not affect the regulating factor $k(y)$. This stems from the fact that we assumed that individual phenotype does not affect any feature interacting with population size. In other words, we assumed *density-independent selection*.

- For density-independent selection, the fitness of an individual can generally be put under the form of eq. (6.9), where the effect of density-dependent competition population size comes as a proportionality factor, which implies that the direction of selection will not depend on population size.

Writing fitness as in eq. (6.9) where density-dependent effects are absorbed in a constant of proportionality $k(y)$ often simplifies many calculations as we don't need to track explicitly population size. This is without real loss of generality and we endorse the assumption of density-independent selection for the rest of the course and for simplicity of notation write the regulated factor $k(y)$ simply as k (but keeping in mind that any population is subject to density-dependent competition regulating population size when resources are limiting).

Uninvadability analysis

Let us now identify the uninvadable strategy under stabilizing selection. Using fitness (eq. 6.9) and the chain rule to compute derivatives, the selection gradient (eq. 6.6) on the evolving phenotype is

$$\begin{aligned} S(y) &= \frac{\partial w(x, y)}{\partial x} \\ &= k \frac{d}{dx} \left[\exp\left(-\frac{(x-y_{\text{op}})^2}{2\sigma_w^2}\right) \right] \Big|_{x=y} \\ &= k \exp\left(-\frac{(y-y_{\text{op}})^2}{2\sigma_w^2}\right) \frac{d\left(-\frac{(x-y_{\text{op}})^2}{2\sigma_w^2}\right)}{dx} \Big|_{x=y}. \end{aligned} \quad (6.12)$$

Here, (and throughout) all derivatives are evaluated at $x = y$ and the third line follows from the property of derivatives of exponential functions [i.e., $d \exp(g(x)) / dx = (dg(x)/dx) \times \exp(g(x))$].

Carrying out the derivative of the last line of eq. (6.12) yields that the selection is

$$S(y) \propto - \left(\frac{y - y_{\text{op}}}{\sigma_w^2} \right). \quad (6.13)$$

Hence, when $y < y_{\text{op}}$, increasing the trait value increases fitness, while if $y > y_{\text{op}}$, increasing the trait value decreases fitness. From the selection gradient, the single singular strategy (satisfying $S(y^*) = 0$, eq. 6.7) is

$$y^* = y_{\text{op}}, \quad (6.14)$$

which is precisely the optimal phenotype. This is also a local fitness maximum (recall eq. 6.8) owing to the fact that at $y = y_{\text{op}}$, we have

$$\left. \frac{\partial^2 w(x, y)}{\partial x^2} \right|_{x=y=y_{\text{op}}} = - \frac{k}{\sigma_w^2} < 0. \quad (6.15)$$

Since there is only a single singular point, this implies that the strategy $y = y_{\text{op}}$ is uninvadable.

Considering that reproduction follows a Beverton-Holt model, the equilibrium population size at the uninvadable strategy satisfies eq. (6.11) and is given at $y = y_{\text{op}}$ by

$$n^* = \frac{f_{\text{max}} - 1}{\gamma}. \quad (6.16)$$

(since $\exp\left(-\frac{(y - y_{\text{op}})^2}{2\sigma_w^2}\right) = 1$ when $y = y_{\text{op}}$). Hence, the model predicts both the uninvadable strategy $y = y_{\text{op}}$ and its associated equilibrium population size, which is maximized by natural selection.

6.2.2 Trade-off between quality and quantity

Biological assumptions

Stabilizing selection is the outcome of trade-offs on the values that phenotypes can take. We go into more details of one of these trade-offs; namely, the trade-off between the quality and quantity of offspring produced, which is typical in many organisms, from plants to humans. This trade-off affects, for instance, the size of the offspring that are produced by an individual. Indeed, offspring of larger size are expected to have higher survival (i.e., be of higher “quality”), but producing offspring of larger size also entails producing fewer number of offspring (“quantity”), as there is a constraint on the total number of resources available for an individual to produce offspring.

To analyze this quality-quantity trade-off, let us denote by x the size at conception/birth of an offspring produced by a focal individual and consider that this individual has gathered r_e units of resources to produce offspring. Our key assumption will be that the number of offspring of size x produced by the focal individual is

$$n_J(x) = \frac{r_e}{x}. \quad (6.17)$$

This says that the number of offspring produced is proportional to the per-capita amount of resources allocated to reproduction. The smaller the offspring, the more offspring can be produced, since each then uses up less resources. Hence, $n_J(x)$ is a monotonic decreasing function of size x . We assume that the probability that any offspring survives to adulthood is a monotonically increasing and saturating function of its size (i.e., diminishing returns in size) and is given by the function

$$s_J(x) = \frac{x^2}{1+x^2}, \quad (6.18)$$

which is concave (bent upwards). Hence, the larger the offspring, the larger its survival probability.

Because $n_J(x)$ is decreasing, while $s(x)$ is increasing with offspring size x , there is a trade-off between number of offspring produced (“quantity”) and their survival to adulthood (“quality”). For this situation and assuming density-independent selection, we can let the fitness of a focal individual with strategy x in a resident population with strategy y be given by

$$w(x, y) = kn_J(x)s_J(x), \quad (6.19)$$

where $n_J(x)s_J(x)$ is the maximal number of offspring reaching adulthood (offspring production times their survival) in the absence of density-dependent competition and k is the regulating factor taking density-dependent competition into account (treated as a constant as in eq. 6.9).

Uninvadability analysis

We now have all the elements to evaluate the uninvadable strategy and from the fitness function (eq. 6.19), the selection gradient (eq. 6.6) on offspring size is

$$S(y) = k \left[n_J(y) \frac{ds_J(x)}{dx} \Big|_{x=y} + s_J(y) \frac{dn_J(x)}{dx} \Big|_{x=y} \right]. \quad (6.20)$$

The first term is the marginal benefit from increasing allocation to survival (increasing x will increase survival), while the second term is the marginal cost (increasing x will decrease number of offspring produced).

Substituting the explicit survival and offspring number functions (eq. 6.17 and eq. 6.18), into eq. (6.20), the selection gradient on resource allocation becomes

$$S(y) = k \left[\frac{2r}{(y^2 + 1)^2} - \frac{r(y^2 + 1)}{(y^2 + 1)^2} \right] = \frac{kr}{(y^2 + 1)^2} [2 - (y^2 + 1)]. \quad (6.21)$$

The singular points satisfying $S(y^*) = 0$ are $y = 1$ and $y = -1$ (satisfying $2 - (y^2 + 1) = 0$). Only positive size makes biological sense. Hence the unique relevant singular strategy for this model is

$$y^* = 1. \quad (6.22)$$

Substituting eq. (6.17)–(6.19) into (6.8) shows that this strategy is uninvadable; specifically, we have

$$\left. \frac{\partial^2 w(x, y)}{\partial x^2} \right|_{x=y=1} = -\frac{kr_e}{2} < 0. \quad (6.23)$$

6.3 Invasion implies substitution

We characterized uninvadability in terms of the maximization of the fitness of an individual carrying a mutant phenotype. We saw in the lecture slides that under individual based simulations, a population far from an uninvadable strategy will actually converge to it by successive allelic replacement (see slides’ figures at the end of the course “Adaptive dynamics, session 1”). Hence, the model exhibits the **invasion implies substitution** feature that we encountered under short term evolution when selection was constant (e.g., eq. 3.12). We will now see that the “invasion implies substitution” rule stands true regardless of the complexity of interactions between individuals, as long as mutations have small effects on phenotypes. This underlies the view, going back to Darwin, that evolution is a gradual, step-by-step transformation of the individual phenotypes in a population and it will pave the way to a general analysis of evolutionary dynamics and

Allele frequency change

To understand the conditions under which “invasion implies substitution”, we consider our usual two alleles segregating in the population; that is, allele A (whose bearers have phenotype x) and allele B (whose bearers have phenotype y). We write the phenotype of a A carrier as

$$x = y + \delta. \quad (6.24)$$

Hence, we regard the mutant phenotype of x as a deviation of magnitude δ from the resident phenotype y . The mutation thus alters the phenotype with an effect size of δ , which, in experimental settings, is usually found to be small.

Recall that the fitness of a single A individual in an otherwise monomorphic B population is denoted $w(x, y)$ (see eq. 6.2). Assuming that δ is small, we can, by way of a so-called Taylor expansion around the point $\delta = 0$, write this fitness as

$$w(x, y) = \underbrace{w(y, y)}_1 + \delta S(y) + O(\delta^2), \quad (6.25)$$

where

$$S(y) = \left. \frac{\partial w(x, y)}{\partial x} \right|_{x=y} \quad (6.26)$$

is the selection gradient at point y (eq. 6.6). The term $O(\delta^2)$ is a remainder term of order δ^2 (see Derivation 2 in the Appendix). This means that $O(\delta^2)$ is of magnitude δ^2 , e.g., if $\delta = 0.01$, then the magnitude of $O(\delta^2)$ is 0.0001, a small number.

Hence, when δ is small, $O(\delta^2)$ can be neglected and eq. (6.25) says that whether A has a larger or smaller fitness than B is predicted by the selection gradient alone. Indeed, we can show that $S(y)$ is the linear approximation of the fitness differential difference between alleles when δ is small. This can be done by substituting eq. (6.25) into eq. (6.2) to express the selection coefficient on allele A as

$$s = \delta S(y) + O(\delta^2). \quad (6.27)$$

Hence, for small phenotypic differences between mutant and residents, $O(\delta^2)$ is neglected, and the selection gradient $S(y)$ allows to predict the direction of evolution. When $S(y) > 0$ then a mutant with $\delta > 0$ (the mutation increases the phenotype relative to the resident) is favored by selection while a mutant with $\delta < 0$ (the mutation decreases the phenotype relative to the resident) is counter-selected.

Suppose A invades and reaches an appreciable frequency $p \gg 0$, how does that affect the values of s ? Remarkably eq. (6.27) holds at all allele frequencies, since the fitness difference between a resident and mutant is always given by $\delta S(y)$. Indeed, this is the only thing that distinguishes mutant and resident, whoa are otherwise are assumed to be subject to the same environmental conditions. Thus, irrespective of the frequency p of A in the population, the change Δp in mutant frequency over one generation is given by

$$\Delta p = \frac{p(1-p)}{\bar{w}} (\delta S(y) + O(\delta^2)). \quad (6.28)$$

Since $S(y)$ is frequency independent, allele A is favored by selection if $S(y) > 0$ at all frequencies (when δ is small) and will go to fixation [eq. 6.28 is equivalent to eq. 3.9 with $s = \delta S(y) + O(\delta^2)$]. Remarkably, this holds regardless of how population size changes as a result of selection, since $S(y)$ is not affected by that change. We call this the “invasion implies substitution” result².

Convergence stability

The invasion implies substitution result (eq. 6.28) applies to any mutant-resident allele pair (not only allele A and B). Suppose then that $S(y) > 0$ for some resident trait value $y < y^*$ where y^* is a singular strategy, which must satisfy $S(y^*) = 0$. Then, by eq. (6.28) any mutant increasing the trait value ($\delta > 0$) will invade and substitute, thereby moving the population closer to the singular point. Conversely, suppose $S(y) < 0$ for $y > y^*$. Then, eq. (6.28) again tells us that a mutant allele decreasing the trait value ($\delta < 0$) will invade and substitute the resident, thereby moving the population closer to the singular strategy.

This shows that such a singular strategy y^* with the above features is an attractor of the evolutionary dynamics: it will be gradually approached by the evolution dynamics. And this

²A detailed proof of this result is beyond the scope of this course but can be found, for instance in the book “Analysis of Evolutionary Processes: The Adaptive Dynamics Approach and Its Applications” by Dercole and Rinaldi (2008), Princeton University Press.

occurs if the selection gradient $S(y)$ is a monotonic decreasing function in y (since $S(y) > 0$ is positive for $y < y^*$ and $S(y) < 0$ for $y^* > y$). This implies that a singular strategy y^* is an evolutionary attractor if the derivative of the selection gradient is negative when the population is monomorphic for this strategy; namely, if

$$\left. \frac{dS(y)}{dy} \right|_{y=y^*} < 0. \quad (6.29)$$

A strategy satisfying this condition is called a **convergence stable strategy**.

It can be checked that for the two examples we worked out above (“stabilizing selection” and “quantity-quality trade-off”), the uninvadable strategies are indeed convergence stable and thus attractors of the evolutionary dynamics³. Since these convergence stable strategies are uninvadable they are final stops of evolution. However, as we will later see, nothing guarantees that a convergence stable strategy is actually uninvadable.

6.4 Summarizing the main long term evolution concepts

One of the central question one can ask under long-term evolution is whether one can find a phenotype (strategy) such that no mutation can invade the population when rare and if one finds such a strategy, will the population converge to it by gradual evolution? The key notions to answer this questions are the follow characterization of strategies.

- A **singular strategy** y^* satisfies $S(y^*)=0$ where $S(y) = \left. \frac{\partial w(x,y)}{\partial x} \right|_{x=y=y^*}$ is the phenotypic selection gradient on a mutant trait value evaluated in a resident population at the singular strategy. A singular strategy is a candidate end-point of the evolutionary dynamic and is either a (local) minimum or maximum of fitness.

- A singular strategy is a local attractor of the evolutionary dynamic and thus a **convergence stable strategy** when $dS(y)/dy|_{y=y^*} < 0$. Hence, when a population is in the neighborhood of a convergence stable strategy, it will converge to it by gradual evolution.

- A convergence stable strategy is a locally **uninvadable strategy** if $\partial^2 w(x,y)/\partial x^2|_{x=y=y^*} \leq 0$. Such a strategy cannot be displaced by mutation with small effect size.

³Under the model of stabilizing selection (eq. 6.13), the convergence stability condition is at the uninvadable strategy y is $dS(y)/dy = -(kf_{\max})/\sigma_w^2 < 0$, while for the model of survival-fecundity trade-offs (eq. 6.21), one can check that $dS(y)/dy = -\frac{k r_e}{2} < 0$.

6.5 Examples of long-term evolution under frequency-dependent selection

We now apply the results from adaptive dynamics to the evolution of traits affecting competition for resources where we consider two different types of competition.

6.5.1 Exploitation competition

Biological assumptions

Individuals in a population usually compete for the use/exploitation of a range of resources, and each individual is constrained to the range of resources it can physically exploit (e.g., hominins cannot digest cellulose and are thus limited by the type of resources we can use as food). The range of resources an individual uses is called its **resource utilization niche**, and the full range of conditions (biotic such as predation and abiotic, such as temperature or humidity) under which an individual can survive and reproduce is called its **fundamental niche**.

We will here address the evolution of the resource utilization niche. To that end, we assume that there is a distribution of resources in the population that can be indexed along an one-dimensional axis and denote by $a(q)$ the abundance of resources of type or quality $q \in \mathbb{R}$. This resource quality axis could, for instance, be the size of a prey. Resource abundance is assumed to follow a Gaussian function

$$a(q) = a_{\max} \exp\left(-\frac{(q - q_{\max})^2}{2\sigma_a^2}\right), \quad (6.30)$$

where q_{\max} is the value (say size) of the prey that has maximum abundance a_{\max} . The parameter σ_a is the width of the resource type or quality. A larger resource width means a more uniform distribution of the resource types (see lecture slides).

Individuals cannot exploit all resources with the same efficiency (there are trade-offs) and we assume that an evolving phenotypic trait x maps directly on the resource axis. For instance, this could be size of the beak allowing a bird to catch different sizes of preys. Hence, the phenotype x describes the match between the feeding apparatus of the individual and the structure of the resource. An individual with phenotype $x = q$ is best at exploiting preys of type q . We assume a Gaussian resource utilization function for a focal individual with phenotype x exploiting resource of type q , such that

$$u(x, q) = \exp\left(-\frac{(x - q)^2}{2\sigma_u^2}\right) \quad (6.31)$$

for some parameter $\sigma_u > 0$ that describes the resources utilization width. This can be thought of as the amount of resources of quality q that an individual with phenotype x

can exploit. In short, this gives the resource utilization niche. When σ_u is increased, an individual with a given value of x can use a larger spectrum of resources; that is, when q is varied around x the individual can still extract resources not matching precisely x . Hence, σ_u measures the extent to which an individual is a **generalist**. When σ_u goes to zero an individual with phenotype x can only exploit a resource of type $q = x$ and is thus a **specialist**.

In order to address the evolution of the resource utilization function via the trait x , we assume that individuals compete for resources in the population, and that the share of resources of type q obtained by a single individual with phenotype x in a resident y population is increasing with its relative efficiency at extracting resources, $r_e(q, x, y)$, as follows:

$$r_e(x, y, q) = \frac{u(x, q)}{u(x, y)} = \frac{\exp\left(-\frac{(x-q)^2}{2\sigma_u^2}\right)}{\exp\left(-\frac{(y-q)^2}{2\sigma_u^2}\right)}. \quad (6.32)$$

The numerator is the ability of exploiting resource of type q by the focal individual and the denominator is the ability of an individual of the resident population to exploit the very same resource.

If we assume density-independent selection and that the expected number of offspring produced by an individual is proportional to its share of resources, the fitness of a single individual with phenotype x in an otherwise monomorphic resident population y can be assumed to be given by

$$w(x, y) = k \int_{-\infty}^{\infty} a(q) r_e(x, y, q) dq, \quad (6.33)$$

where the constant k encapsulates density dependent-competition that we do not model explicitly (recall the explanations behind eq. 6.9). The integral averages the relative efficiency of extracting resources over all resource types that an individual can encounter in its habitat, with the distribution of resource types being given by eq. (6.30). Carrying out the integration one eventually gets

$$w(x, y) = K \exp\left(-\frac{(x-y)^2}{2\sigma_u^2}\right) \left(x \left(1 - \frac{\sigma_a^2}{\sigma_u^2}\right) + y \left(1 + \frac{\sigma_a^2}{\sigma_u^2}\right) - 2q_{\max}\right), \quad (6.34)$$

where $K = ka_{\max}\sqrt{2\pi}\sigma_a > 0$ is a constant of proportionality. With this fitness function we can now carry out the uninvasibility analysis.

Uninvasibility and convergence stability analysis

Substituting eq. 6.34 into the selection gradient $S(y) = \partial w(x, y)/\partial x$ (eq. 6.6), and carrying out the derivative and evaluating it (as usual) at $x = y$, the selection gradient on the resource exploitation is

$$S(y) = -K \left(\frac{y - q_{\max}}{\sigma_u^2} \right). \quad (6.35)$$

This selection gradient is qualitatively of the same form as the model of stabilizing selection (eq. 6.13), and is indeed a form of stabilizing selection: when the trait value in the resident population is below that of q_{\max} an individual expressing a higher trait value is favored by selection, while when the trait value in the resident population is above that of q_{\max} an individual expressing a lower trait value is favored by selection. Hence, the only singular point satisfying $S(y) = 0$ is

$$y = q_{\max}. \quad (6.36)$$

This is also a convergence stable strategy since the derivative of the selection gradient is negative at that point:

$$\left. \frac{dS(y)}{dy} \right|_{y=q_{\max}} = -\frac{K}{\sigma_u^2} < 0. \quad (6.37)$$

Hence, $y = q_{\max}$ is an evolutionary attractor and a population starting away from it will actually converge to it. The left panel of Fig. 6.1 shows that, using individual-based simulations, a population starting away from the convergence point will converge to it by long-term evolution.

Is the singular strategy $y = q_{\max}$ locally uninvadable? From eq. (6.8) we need $\partial^2 w(x, y)/\partial x^2 < 0$ for the trait to be uninvadable, and one can show that

$$\left. \frac{\partial^2 w(x, y)}{\partial x^2} \right|_{x=y=q_{\max}} = \frac{K}{\sigma_u^2} \left(\frac{\sigma_a^2}{\sigma_u^2} - 1 \right). \quad (6.38)$$

Now, if

$$\sigma_a^2 > \sigma_u^2 \implies \sigma_a > \sigma_u \implies \left. \frac{\partial^2 w(x, y)}{\partial x^2} \right|_{x=y=q_{\max}} > 0, \quad (6.39)$$

the second-order condition for uninvadability is not satisfied and the point $y = q_{\max}$ is invadable. This means that mutants with phenotypic values $x \neq q_{\max}$ can invade the population, for a population at the convergence stable state!

What the condition $\sigma_a > \sigma_u$ in eq. (6.39) means is that if the prey distribution is more broad than the resource utilization function, then individuals are specialists (relative to the resource distribution) and actually benefit from exploiting a type of resources that is different from the most common one for which competition is strongest. Hence, if in a population all individuals are using the most common resource, a mutant inducing its carrier to exploit a less abundant resource will face reduced competition by exploiting an alternative resource and has increased fitness.

The consequence of a singular point to be invadable is displayed in Fig. 6.1. This shows by way of individual-based simulations that at the convergence stable strategy the population becomes split into a bimodal distribution of phenotypes resulting in the coexistence of two “types” of phenotypes exploiting different ranges of the resource. For this reason, a singular convergence stable point where the second derivative of fitness with respect to an individual’s phenotype is positive is called an **evolutionary branching** point.

Evolutionary branching results in polymorphism being maintained in the population because individuals with different trait values coexist at an evolutionary equilibrium. In the above example it means that individuals with different values of the evolving trait y will exploit a different range of the resource. Eq. (6.39) shows that if individuals are constrained to be specialists (small σ_u) and the distribution of resources is broad (large σ_a), then polymorphism will generally occur with individuals evolving to specialize on the uptake of different types of resources or preys. This is an example of the concept of **limiting similarity**, which says that coexistence between different types is possible only if the niches of the different types do not overlap too much. Otherwise if individuals use the same niches we have competitive exclusion, and one type will eventually dominate the population.

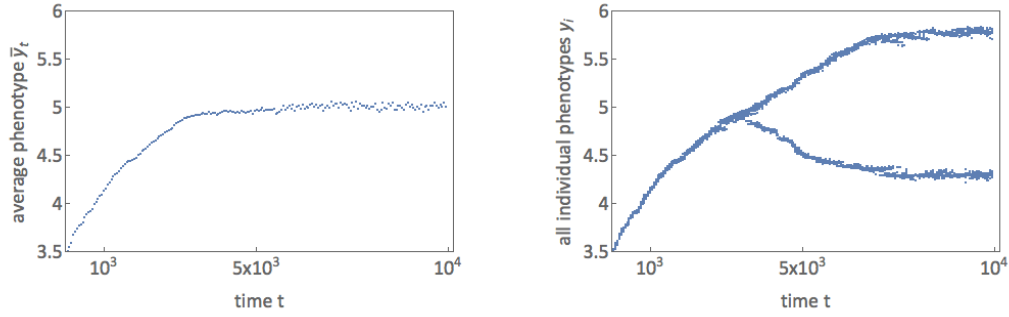


Figure 6.1: Left panel: average trait value \bar{y}_t in the population under individual-based simulations as a function of time t (measured in number of generations) for the resource exploitation competition model. Parameter values $q_{\max} = 5$, $\sigma_a = 2$, $\sigma_u = 1$ with a Beverton-Holt demographic model. The mutation rate in the simulation is $\mu = 0.01$ per individual with phenotypic step size sampled from a Normal distribution with mean zero and standard deviation 0.01. Starting with an initial value where all individuals have a trait value of 3.5, the adaptive dynamics first converges to the convergence stable strategy $y = 5$, which is the value predicted by the model (eq. 6.36). However, since this point is invadable, evolutionary branching should occur. The right panel depicts the phenotypic values of each individual in the population and shows that once the convergence stable point has been reached, the population divides in two clusters: evolutionary branching indeed occurs and this results in a bimodal phenotypic distribution.

6.5.2 Interference competition and evolutionary suicide

We saw that competition for exploiting resources along a gradient of resources can lead to the coexistence between different phenotypes in the population. Competition for resources

can thus lead to diversification. We now investigate another facet of competition and see that sometimes natural selection can drive a population to extinction.

Biological assumptions

We assume that individuals compete for resources but that this competition partly destroys the amount of material resources individuals have access to. For instance bacteria produce toxins, which can partly destroy nutrients used by other individuals in the population. This is an example of **interference competition**, where individuals can prevent the foraging by other individuals or directly prevent their establishment in the habitat.

In order to model the evolution of interference competition, we assume that a focal individual expresses a trait x , which describes its level of competitive ability (competitiveness for short). The more competitive, the more resources an individual obtains. But the level of competitiveness is assumed to destroy resources in the population or limit the access of individuals to them. To capture this trade-off between individual advantage and deleterious effect on the population, we assume (as usual) density-independent selection and that the fitness of a single individual with level of competitiveness x in an otherwise monomorphic resident population with level of competitiveness y is given by

$$w(x, y) = \frac{x}{y} a (1 - y) k. \quad (6.40)$$

Here, a is the amount (or abundance) of resources individuals have potentially access to, which is decreased by the level of competitiveness in the population. That is, $(1 - y)$ measures the extent to which competition between individuals destroys population resources. The term x/y is the relative individual efficiency at extracting resource. Hence, if the focal individual is more competitive than individuals in the population, he will extract more resources. The constant $k > 0$ is the regulating factor capturing the effects of density-dependent competition on fitness (recall eq. ??).

Uninvadability analysis and convergence stability analysis

Substituting fitness (eq. 6.40) into the selection gradient (eq. 6.6), we find that the direction of selection on level of competitiveness is

$$S(y) = a \frac{(1 - y)}{y} k. \quad (6.41)$$

This selection gradient is positive for all levels of competitiveness, which takes values between zero and one ($0 \leq y \leq 1$) to be biologically realistic. This means that the level of competitiveness is selected to increase at all trait values. By gradual evolution, competitiveness will eventually reach a value where the population will go extinct since fitness is selected to go down with increasing y (the term $(1 - y)$ in eq. 6.40 decreases fitness as y increases).

To make this conclusion more explicit, suppose population dynamics follows a Beverton-Holt model so that the regulating factor can be taken to be given by eq. 6.40, namely

$$k = \frac{1}{1 + \gamma n^*}. \quad (6.42)$$

This implies that for a resident population equilibrium population size is

$$n^* = \frac{a(1 - y) - 1}{\gamma} \quad (6.43)$$

(obtained by using eq. 6.40 with eq. 6.42, setting $w(y, y) = 1$ and solving for n). The equilibrium population size n^* is decreasing with y , and eventually takes a value of zero when $y = (a - 1)/a$. Hence for large a , n tends to zero as y tends to one.

Since competitiveness y is selected to increase at all trait values, we have that the population must go extinct in the long run ($n^* \rightarrow 0$). The model thus predicts *selection driven population extinction*; that is,

$$S(y) > 0 \text{ for all } y \implies y \text{ increases} \implies n^* \rightarrow 0. \quad (6.44)$$

This is an example of *evolutionary suicide*. Fig. 6.2 displays the results of an individual-based simulation of this situation and shows that the evolutionary process indeed results in an increase in the level of competition, which causes the population to go extinct.

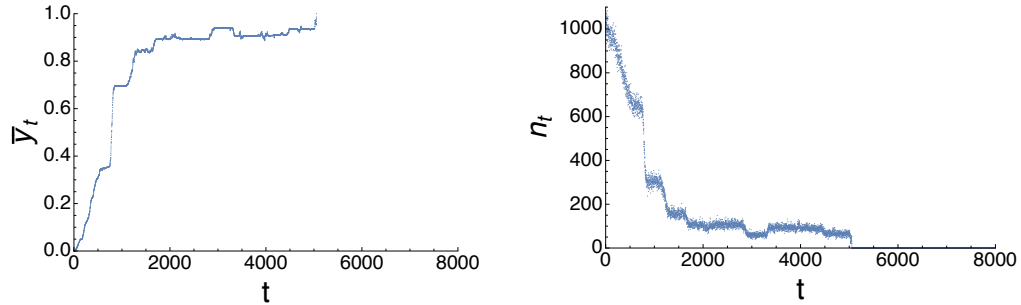


Figure 6.2: Average trait value \bar{y}_t and population size n_t in the population under individual-based simulations as a function of time t (measured in number of generations) for the competitiveness model with Beverton-Holt demography. Parameter values are $\gamma = 1$, $a = 1000$, $\bar{y}_0 = 0$, $n_0 \approx 1000$. The assumptions about the mutation process: mutation rate of $\mu = 10^{-3}$ per individual with phenotypic step size sampled from a Normal distribution with zero mean and standard deviation 0.05. The asymptotic values converge to the strategies predicted by the analytical results, which are $y \rightarrow 1$ and $n^* \rightarrow 0$.

6.6 Appendix

Derivation 1. A Gaussian function $f(x)$ in x refers to a function of the form

$$f(x) = \alpha \exp\left(-\frac{(x - \mu)^2}{2\sigma^2}\right), \quad (6.45)$$

for some parameters α , μ , and σ . The parameter α is the height of the bell shaped curve's peak, μ is the position of the center of the peak, and σ tunes the width of the curve. A normalized Gaussian function (satisfying $\int_{-\infty}^{\infty} f(x) dx = 1$) provides a probability distribution, in which case $\alpha = 1/\sqrt{2\pi\sigma^2}$, μ gives the mean, and σ the standard deviation (σ^2 is the variance). The standard deviation is approximately 1.25 times the mean absolute deviation from the mean.

Derivation 2. Recall that a first-order Taylor series (or expansion) of $f(x)$ about point x_0 is

$$f(x) = f(x_0) + \frac{df(x)}{dx}(x - x_0) + O((x - x_0)^2). \quad (6.46)$$

where $O((x - x_0)^2)$ is the remainder term. Using this result for $w(x, y)$ by Taylor expanding about point $x_0 = y$ and using $\delta = x - y$ gives eq. (6.25).
