

## Dynamics of Adaptation and Evolutionary Branching

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We present a formal framework for modeling evolutionary dynamics with special emphasis on the generation of diversity through branching of the evolutionary tree. Fitness is defined as the long term growth rate which is influenced by the biotic environment leading to an ever-changing adaptive landscape. Evolution can be described as a dynamics in a space with variable number of dimensions corresponding to the number of different types present. The dynamics within a subspace is governed by the local fitness gradient. Entering a higher dimensional subspace is possible only at a particular type of attractors where the population undergoes evolutionary branching. [S0031-9007(97)02628-8]

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Evolution by natural selection is the grand unifying theory of biology. In the simplest selection models each phenotype has a fixed fitness value, and the fittest type eventually outcompetes all others. This constant fitness picture, however, is unable to explain the enormous diversity of life on Earth: how could any type but the fittest survive? For instance, in the spin-glass models [1,2] as well as in the prebiotic model of Eigen [3] either a single, localized (quasi)species is present or the high mutation rate destroys any organization in the genotype space. Speciation has been explained by stochastic models ignoring selection processes altogether [4,5]. In these models, however, the concept of adaptation has no meaning. We suggest that speciation can be understood on the basis of natural selection if one takes into account the fact that the fitness function itself is modified by the evolutionary process. We suppose a clear separation of the (slow) evolutionary and the (fast) population dynamical time scales, that is, mutations, occurs only infrequently and has only a small phenotypic effect. (This is a very realistic assumption for almost all evolutionary situations.)

We confine ourselves to asexual populations, and assume that different types can be characterized by a single, one-dimensional quantity, referred to as strategy. Fitness is a smooth function of the strategy parameter. This description, which has some similarity to the “fitness space” approach [6], is much easier to handle than the “genotype space” models.

Fitness can be generally defined as the long term population growth rate of a given type [7]. The growth rate can NOT be fixed, because exponential population growth cannot be sustained indefinitely. Consider a population with a single strategy  $x$ . The growth of the population can be described by

$$\frac{d}{dt} N = M(x, E) \cdot N, \quad (1)$$

where  $N$  is the state vector of the population (i.e., the number of individuals in different age groups, state, location, etc.). The projection matrix  $M(x, E)$  contains the demographic parameters for birth, death, and migration, and depends on strategy  $x$  as well as on the environment  $E$ . For any given, fixed condition of the environment the population would increase exponentially with growth rate  $\varrho(x, E)$ , which is the (real) leading eigenvalue of the matrix  $M(x, E)$ . We suppose that  $\varrho$  is a smooth function of the strategy as well as the environmental parameters. As the population increases, the environment deteriorates. Consequently, the growth rate decreases and eventually becomes zero when the population reaches an equilibrium. The condition of the environment at the equilibrium is denoted by  $E_x$ , which is a solution of  $\varrho(x, E) = 0$ , and which we assume to be unique.

Next, consider a new mutant with strategy  $y$  emerging in an equilibrium population of  $x$  strategists. As long as the mutant is rare, its effect on the environment as set by the  $x$  strategy is negligible, so that the mutant’s growth rate is given by

$$s_x(y) = \varrho(y, E_x). \quad (2)$$

If  $s_x(y) < 0$  the mutant dies out, but if  $s_x(y) > 0$  it will spread. If mutations are small, then the sign of the local fitness gradient

$$D(x) = \left[ \frac{\partial s_x(y)}{\partial y} \right]_{y=x} \quad (3)$$

determines what mutants can invade. If  $D(x) > 0$ , mutants with  $y > x$  can invade  $x$ , whereas if  $D(x) < 0$ , this is only possible for mutants with  $y < x$ . If  $y$  is near enough to  $x$   $s_x(y) > 0$  implies  $s_y(x) < 0$ , because the local fitness gradient does not change sign during the transition  $x \rightarrow y$ . That is, the  $x$  strategy cannot recover once the mutant has become common and the  $x$  strategy itself

has become rare. We shall assume that the mutant eventually takes over the whole population in this case.

The population thus evolves in the direction of the local fitness gradient until it reaches the neighborhood of a “singular strategy,”  $x^*$ , where the local fitness gradient is zero. Close to a singular strategy it may happen that  $s_x(y) > 0$  and  $s_y(x) > 0$ , so that both  $x$  and  $y$  are protected against extinction, and the population necessarily becomes dimorphic.

As a convenient graphical means to see what mutants can spread in a given population we use a “pairwise invasibility plot” (PIP) to indicate the sign of  $s_x(y)$  for all possible values of  $x$  and  $y$  (Fig. 1). On the main diagonal  $s_x(y)$  is always zero, because by definition  $s_x(x) = \varrho(x, \mathbf{E}_x) = 0$ . A “+” just above the diagonal and a “-” just below indicate a positive fitness gradient, whereas the opposite indicates a negative fitness gradient. The intersection of the diagonal with another curve on which  $s_x(y)$  is zero corresponds to a singular strategy.

Close to a singular strategy  $x^*$  there are only eight possible (generic) local configurations of the PIP (Fig. 2). For their algebraic characterization we will use that at the singular strategy

$$\frac{\partial^2 s_x(y)}{\partial x^2} + 2 \frac{\partial^2 s_x(y)}{\partial x \partial y} + \frac{\partial^2 s_x(y)}{\partial y^2} = 0, \quad (4)$$

which follows from  $s_x(x) = 0$  for all  $x$ . Each configuration represents a different evolutionary scenario that can be interpreted in terms of the four properties of the singular strategy discussed below.

(1) A singular strategy  $x^*$  is evolutionarily stable (ESS) if no initially rare mutant can invade, in other words, if  $s_{x^*}(y) < 0$  for all  $y \neq x^*$ . In the PIP the vertical line through  $x^*$  lies entirely within a region marked “-” [Figs. 2(c)–2(f)]. Since  $s_{x^*}(y)$  as a function of  $y$  has a maximum for  $y = x^*$ , at the singular strategy we have

$$\frac{\partial^2 s_x(y)}{\partial y^2} < 0. \quad (5)$$

An ESS is an evolutionary trap in the sense that once established in a population, no further evolutionary change is possible [8].

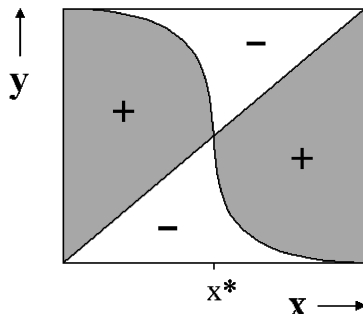


FIG. 1. Example of pairwise invasibility plot.

(2) A singular strategy is convergence stable [9] if a population of nearby phenotypes can be invaded by mutants that are even closer to  $x^*$ , that is, if  $s_x(y) > 0$  for  $x < y < x^*$  and  $x^* < y < x$ . In the PIP there is a “+” above the diagonal on the left, and below the diagonal on the right of  $x^*$  [Figs. 2(b)–2(e)]. Since at  $x^*$  the local fitness gradient is a decreasing function of  $x$ , it follows that at the singular strategy we have

$$\frac{dD(x)}{dx} = \frac{\partial^2 s_x(y)}{\partial x \partial y} + \frac{\partial^2 s_x(y)}{\partial y^2} < 0, \quad (6)$$

or, using Eq. (4),

$$\frac{\partial^2 s_x(y)}{\partial x^2} > \frac{\partial^2 s_x(y)}{\partial y^2}. \quad (7)$$

A convergence stable singular strategy is an evolutionary attractor in the sense that a monomorphic population will remain within its neighborhood. A singular strategy that is not convergence stable is a repeller from which populations tend to evolve away. A singular strategy can be ESS but not convergence stable [Fig. 2(f)], or convergence stable but not ESS [Fig. 2(b)] [10].

(3) A singular strategy can spread in other populations when itself is initially rare if  $s_x(x^*) > 0$  for all  $x \neq x^*$ , in other words, if in the PIP the horizontal line through  $x^*$  on the  $y$  axis lies entirely in a region marked “+” [Figs. 2(a)–2(d)]. Since  $s_x(x^*)$  as a function of  $x$  has a minimum for  $x = x^*$ , it follows that at the singular strategy we have

$$\frac{\partial^2 s_x(y)}{\partial x^2} > 0. \quad (8)$$

A singular strategy that is ESS and convergence stable may nevertheless be incapable of invading other populations if initially rare itself [Fig. 2(e)]. Such a singular strategy can be reached only asymptotically through a series of ever-decreasing evolutionary steps [Fig. 2(e)] [11,12].

(4) Two strategies  $x$  and  $y$  can mutually invade, and hence give rise to a dimorphic population, if  $s_x(y) > 0$  and

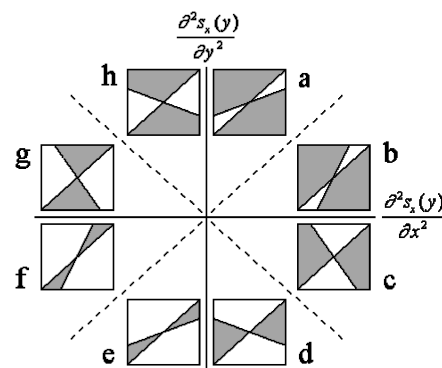


FIG. 2. Classification of the singular strategies according to the second partials of  $s_x(y)$ . The small plots are the local PIPs near to the singular point characterized by these partials.

$s_y(x) > 0$ . The set of pairs of mutually invincible strategies near  $x^*$  is given by the overlapping parts of the “+” regions in the PIP and its mirror image taken along the main diagonal. The set is nonempty if and only if the secondary diagonal lies entirely in a “+” region [Figs. 2(a)–2(c), 2(h)]. Since along the secondary diagonal  $s_x(y)$  has a local minimum for  $y = x = x^*$ , at the singular strategy we have

$$\frac{\partial^2 s_x(y)}{\partial x^2} - 2 \frac{\partial^2 s_x(y)}{\partial x \partial y} + \frac{\partial^2 s_x(y)}{\partial y^2} > 0, \quad (9)$$

or, equivalently,

$$\frac{\partial^2 s_x(y)}{\partial x^2} > -\frac{\partial^2 s_x(y)}{\partial y^2}. \quad (10)$$

The evolutionary significance of mutual invincibility depends on the combination with the other properties of the singular strategy. If  $x^*$  is convergence stable and ESS, then mutually invincible strategies are necessarily on opposite sides of  $x^*$  [Fig. 2(c)]. A mutant with strategy  $y$  can invade a population with  $x_1$  and  $x_2$  (with  $x_1 < x_2$ ) only if  $x_1 < y < x_2$  [Fig. 3(a)]. The mutant may replace both  $x_1$  and  $x_2$ , or only the one that is on the same side of  $x^*$  but farther away. In the long run the dimorphism effectively disappears as the population gradually evolves towards  $x^*$  through a series of monomorphic and (converging) dimorphic population states.

However, if  $x^*$  is convergence stable but not ESS [Fig. 2(b)], then a strategy  $y$  can invade only if  $y < x_1$  or  $y > x_2$  [Fig. 3(b)]. Since it is always the middle strategy that is ousted, the two remaining strategies become progressively more distinct with each successive invasion. This process of divergence of strategies we call “evolutionary branching,” and the singular strategy in the associated PIP we call a “branching point.”

Figure 4 shows numerical simulation of evolutionary branching in a population inhabiting two patches with different optimal strategies and migration between them [13]. (A similar model was analyzed by [14] using the genotype space approach.)

After branching the two coexisting strategies soon evolve too far apart for the local approximation of the mutant’s fitness used in Fig. 3 above to be valid. To

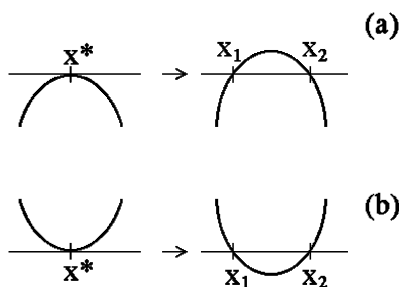


FIG. 3. Mutant’s fitness in a population with  $x_1$  and  $x_2$  as a perturbation from the fitness in a population with a strategy  $x^*$  that is (a) ESS or (b) not ESS. (Horizontal axis: strategy, vertical axis: fitness.)

generalize the formalism to populations with an arbitrary number of strategies, let  $\mathbf{E}_{x_1, \dots, x_n}$  denote the condition of the environment in an equilibrium population with strategies  $x_1, \dots, x_n$ , i.e.,

$$\varrho(x_i, \mathbf{E}_{x_1, \dots, x_n}) = 0 \quad (11)$$

for all  $i$ . Generically,  $\mathbf{E}_{x_1, \dots, x_n}$  can satisfy Eq. (11) only if the environment can be represented as a vector with at least  $n$  independently adjustable components [15]. The dimensionality of the environment thus sets an upper limit to the number of different types that can coexist, and hence to the maximum diversity that can be reached by branching of the evolutionary tree.

The growth rate of an initially rare mutant with strategy  $y$  in an equilibrium population with strategies  $x_1, \dots, x_n$  is given by

$$s_{x_1, \dots, x_n}(y) = \varrho(y, \mathbf{E}_{x_1, \dots, x_n}) \quad (12)$$

[cf. Eq. (2)]. The direction of a possible evolutionary change in the  $x_i$  strategy is indicated by the local fitness gradient

$$D_i(x_1, \dots, x_n) = \left[ \frac{\partial s_{x_1, \dots, x_n}(y)}{\partial y} \right]_{y=x_i} \quad (13)$$

[cf. Eq. (3)]. We call  $x_1^*, \dots, x_n^*$  an “evolutionarily singular coalition” if for each strategy the fitness gradient is zero. The classification above can be used for each member population of this coalition. A singular coalition that is an evolutionary attractor but some of its members are not in an ESS point will lead to further branching of the evolutionary tree.

The picture of evolution that arises is that of a random walk in a state space of a dimension that is given by the number of the different strategies present. The direction of the steps is given by the local fitness gradient. (This random walk can be approximated by a deterministic dynamics of the strategy parameters in the appropriate limit [16].) At each branching event the dimension of the state space increases. In some cases there is no attractor in the  $n$ -dimensional space, and the population leaves the volume containing the strategy combinations that can coexist

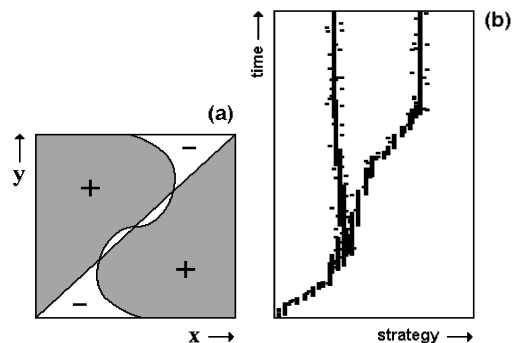


FIG. 4. Evolutionary branching in a specific model [13]. (a) PIP with two branching points and a repeller, and (b) simulated evolutionary tree.

as an  $n$  morphism. In this case one or several strategies may go extinct, so that the population falls back to a lower dimensional state space again. (See [17,18] for further discussion and generalizations.) According to the numerical experiments, like the one presented on Fig. 4, this behavior is not very sensitive for the time-scale separation. If the random component of the directional evolution is not negligible, but still small enough, the picture of an evolving and, sometimes, branching quasispecies emerges.

Although evolutionary branching is reminiscent of speciation, in the present context of asexual populations the species concept is not well defined. Applied to sexual populations, the framework could describe evolution in allele space rather than in strategy space. Branching in allele space can be interpreted as speciation only if the separate branches do not interbreed. Matings between different branches produce intermediate offspring (heterozygotes). As during the process of branching intermediate types are selected against [cf. Fig. 3(b)], types that mate more within branches than between branches are at a selective advantage, so that reproductive isolation might evolve indeed [19].

Many models of adaptive evolution assume a one-dimensional environment, usually represented by the equilibrium population density [20]. In these models coexistence of different types, and hence evolutionary branching, is not possible, and convergence stability always implies ESS stability as well. Fixed, though multi-peaked, fitness landscapes like in spin-glass models do not allow for coexistence and branching either. As the separate fitness peaks generically are of unequal height, the type at the highest peak will in the long run out-compete all others. In the present framework, however, fitnesses of the coexisting populations are self-organized to be zero [cf. Eq. (11)], that is, to be exactly equal to each other.

This self-organization has a clear biological message: if two (or more) species have been living together for millions of years, it is meaningless to ask which of them is the fittest or the least fit. This is in contradiction with the assumptions of Bak and Sneppen [21]. Their model is similar to ours in one respect: the fitness landscape of each species is affected by the other species. However, the number of species is fixed, and within species diversification is prohibited in the Bak and Sneppen model. Their model is an interesting candidate for an effective model explaining the long-term statistics of the evolutionary process. Our approach is intended to be a precursor of an underlying theory unifying diversification and adaptation into a single framework.

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