Evolutionary Singular Strategies and the Adaptive Growth and Branching of the Evolutionary Tree

Geritz, S.A.H., Kisdi, E., Meszena, G. & Metz, J.A.J.

Working Paper

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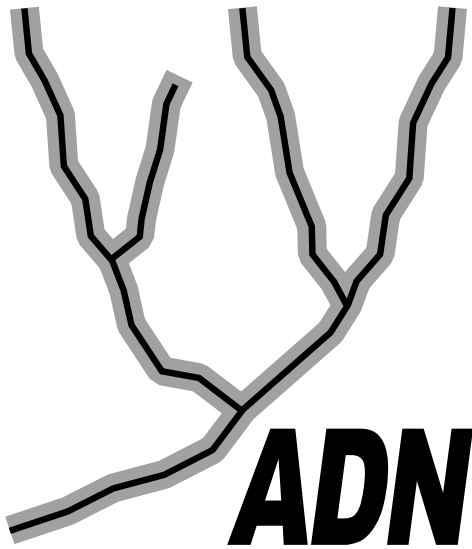**IIASA** International Institute for Applied Systems Analysis □ A-2361 Laxenburg □ Austria

Telephone: +43 2236 807 □ Fax: +43 2236 71313 □ E-Mail: info@iiasa.ac.at

IIASA STUDIES IN ADAPTIVE DYNAMICS   NO. 12

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Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree

S.A.H. GERITZ [1,2], É. KISDI [1,3], G. MESZÉNA [4], J.A.J. METZ [2,5]

[1] *Collegium Budapest, Institute for Advanced Study, Szentháromság u. 2, H-1014 Budapest, Hungary*
[2] *Institute of Evolutionary and Ecological Sciences, Kaiserstraat 63, NL-2311 GP Leiden, The Netherlands*
[3] *Department of Genetics, Eötvös University, Múzeum krt. 4/A, H-1088 Budapest, Hungary*
[4] *Department of Atomic Physics, Eötvös University, Puskin u. 5-7, H-1088 Budapest, Hungary*
[5] *Adaptive Dynamics Network, International Institute for Applied System Analyses, A-2361 Laxenburg, Austria*

Summary

We present a general framework for modeling adaptive trait dynamics in which we integrate various concepts and techniques from modern ESS-theory. The concept of evolutionarily singular strategies is introduced as a generalization of the ESS-concept. We give a full classification of the singular strategies in terms of ESS-stability, convergence stability, the ability of the singular strategy to invade other populations if initially rare itself, and the possibility of protected dimorphisms occurring within the singular strategy's neighborhood. Of particular interest is a type of singular strategy that is an evolutionary attractor from a large distance, but once in its neighborhood a population becomes dimorphic and undergoes disruptive selection leading to evolutionary branching. Modeling the adaptive growth and branching of the evolutionary tree thus can be considered as a major application of the framework. A haploid version of Levene's 'soft selection' model is developed as a specific example in order to demonstrate evolutionary dynamics and branching in monomorphic and polymorphic populations.

Keywords: adaptive dynamics; evolutionarily singular strategy; evolutionary branching; evolutionary modeling.

Introduction

The evolutionarily stable strategy (or ESS; Maynard Smith and Price, 1973), effectively defined as an evolutionary trap, has become the main tool for predicting the outcomes of long term phenotypic evolution when fitness depends on the frequencies of the various phenotypes present in a population. A major advantage of the ESS is that it can be resolved from phenotypic considerations alone without having to account explicitly for the (often unknown) underlying genetic detail. Moreover, by circumventing the intricacies of diploid Mendelian inheritance, more complex ecological interactions and adaptations can be explored than is usually possible with a fully genetic approach. In those cases where a comparison with more complete approaches is possible, ESS-theory has been shown to be largely compatible with both quantitative genetics (Charlesworth, 1990; Taper and Case, 1992; Abrams *et al.*, 1993a) and population genetics (Eshel and Feldman, 1982, 1984; Eshel, 1991, 1996; Hammerstein and Selten, 1993; Hammerstein, 1996; Matessi and Di Pasquale, 1996; Weissing, 1996).

　　　Notwithstanding its strength and elegance, the ESS has a serious drawback: It always still remains to be seen whether during the course of evolution the ESS will actually become established at all. It now has been generally acknowledged that ESS-stability (which renders a population

immune against invasion by any new mutant) and convergence stability (which ensures the gradual approach through a series of small evolutionary steps) are two totally independent stability concepts that can occur in any combination (Eshel and Motro, 1981; Eshel, 1983; Taylor, 1989; Christiansen, 1991; Abrams *et al.*, 1993b). A phenotype that is convergence stable is an evolutionary attractor in the sense that a population that starts off with a different phenotype can always be invaded by phenotypes nearer by. If a phenotype is not convergence stable, then any such initial perturbation tends to increase. The significance of the ESS as a long term evolutionary predictor thus depends on whether or not is also convergence stable.

In this paper we integrate various concepts and techniques from modern ESS-theory into a single mathematical framework for modeling the dynamics of long-term phenotypic evolution. We introduce the concept of 'evolutionarily singular strategy' as a generalization of the ESS-concept. Our main result is a classification of the singular strategies in terms of ESS-stability, convergence stability, the ability of the singular strategy to invade other populations if initially rare itself, and the possibility of protected dimorphisms occurring within the singular strategy's neighborhood. These four properties are to a large extend independent of one another and can occur in many combinations. Each combination represents a qualitatively different evolutionary scenario. A type of singular strategy that stands out in particular is convergence stable but lacks ESS-stability. We show that from larger distances it acts as an evolutionary attractor, but once nearby the population undergoes disruptive selection and splits up into two subsequently phenotypically diverging subpopulations. We therefore consider modeling the adaptive growth and branching of the evolutionary tree as a major application of the classification.

We first develop the framework for monomorphic resident populations, and generalize some of our results to polymorphic populations later. We formulate a haploid version of Levene's (1953) 'soft selection' model as a specific example to demonstrate evolutionary branching in both monomorphic and polymorphic populations. A more formal approach of the framework including generalizations for multi-dimensional (that is, vector-valued) strategies was presented by Metz *et al.* (1996).

The framework

Assumptions

We assume that individuals reproduce asexually, and that the offspring are phenotypically identical to the parent. Phenotypes are denoted by their strategy, which can vary continuously. We consider one-dimensional (that is, scalar-valued) strategies only.

The strategies in a given resident population can be considered as a set of model parameters that implicitly specify a unique attractor for the resident population dynamics. Mutations occur sufficiently infrequently so that the population has reached its attractor before a new mutant comes along. On the longer time-scale of mutations, therefore, a population can be represented by merely listing all strategies that are present.

A polymorphic resident population is assumed to be always a protected polymorphism in the sense that each strategy present is protected against extinction by a positive growth rate when rare, at least untill the next mutant comes along. Consequently, what strategies remain once the

population has settled down again in a new demographic attractor after the successful invasion of a new mutant, can be described purely in terms of the growth rates of each strategy if rare.

Finally, we assume that phenotypic mutations are small but random. We explicitly do not assume infinitesimally small evolutionary changes giving rise to a continuous adaptive dynamic, because that would rule out a number of our results (see Discussion). Evolution thus proceeds by small but discrete steps.

Monomorphic populations

Fitness is the long-term exponential growth rate of a phenotype in a given environment (Metz *et al.*, 1992). The environment contains abiotic as well as biotic factors, including the number and frequencies of the various phenotypes themselves. Once a population has reached its demographic attractor there are no long-lasting trends towards population decline or growth. The fitness of all phenotypes present, therefore, has become zero. Let E_x denote the environment in a population of a single phenotype with strategy x, and let $r(x,E_x)$ denote the population's long-term exponential growth rate. At the demographic attractor we thus have

$$r(x, E_x) = 0. \tag{1}$$

Next, consider a new mutant with strategy y emerging in a population of residents with strategy x. As long as the mutant is still rare, its effect on the environment E_x as set by the residents is negligible. The fitness, $s_x(y)$, of the mutant is therefore equal to

$$s_x(y) = r(y, E_x). \tag{2}$$

What $s_x(y)$ exactly looks like depends on the particular biological problem at hand. A specific example is given in a later section. We here merely assume that $s_x(y)$ is a known function of x and y, and develop a theory of adaptive dynamics in terms of properties of $s_x(y)$ only.

If $s_x(y) > 0$ the mutant can spread (but will not necessarily always do so as a result of random extinction due to the small initial size of the mutant population). If $s_x(y) < 0$ it will die out. If $s_x(y) > 0$ and $s_y(x) < 0$, then the mutant can spread but the resident cannot recover when rare itself. A protected dimorphism of x and y is therefore not possible, and eventually the mutant will replace the resident and take over the whole population. If mutations are small, so that x and y are very similar to one another, we have as a linear approximation of the mutant's fitness

$$s_x(y) = s_x(x) + D(x)(y - x). \tag{3}$$

where $D(x)$ is the local fitness gradient defined as

$$D(x) = \left[\frac{\partial s_x(y)}{\partial y} \right]_{y=x}. \tag{4}$$

Since by definition $s_x(x) = r(x,E_x) = 0$ for all x (see Equations 1 and 2), the sign of $D(x)$ determines what mutants can invade. If $D(x) > 0$, only mutants with $y > x$ can invade and take over the population, whereas if $D(x) < 0$, then this is only possible for mutants with $y < x$. The population thus evolves in the direction of the local fitness gradient until it reaches the neighborhood of a strategy for which $D(x)$ is zero. A strategy for which the local fitness gradient is zero we call an 'evolutionarily singular strategy'. Near a singular strategy there is no longer directional selection, and it may happen that both $s_x(y) > 0$ and $s_y(x) > 0$. In this case neither strategy can eliminate the other, and the population necessarily becomes dimorphic.

The evolution of a monomorphic population can be analyzed graphically by means of a 'pairwise invasibility plot', that is, a graph of the sign of $s_x(y)$ as a function of x and y (Figure 1; for other examples of pairwise invasibility plots, see Van Tienderen and De Jong, 1986; Metz *et al.*, 1992; Kisdi and Meszéna, 1993, 1995). To see what mutants can spread in a given resident population we look along a vertical line through a point on the x-axis representing the resident's strategy. The parts of this line inside a region marked '+' correspond to strategies on the y-axis for which $s_x(y) > 0$, and hence denote potentially invading mutants. The parts of the line inside a region marked '-' correspond to mutants for which $s_x(y) < 0$, and which therefore cannot invade. On the principal diagonal $s_x(y)$ is by definition zero (cf. Equations 1 and 2). The intersection of the diagonal with an other line on which $s_x(y)$ is zero corresponds to an evolutionarily singular strategy. If mutations are small we need to consider only strategies within a narrow band along the diagonal. A '+' just above and a '-' just below the diagonal indicates a positive fitness gradient, whereas a '-' above and a '+' below indicates a negative fitness gradient.

Close to a singular strategy there are only eight possible generic local configurations of the pairwise invasibility plot that can be algebraically characterized in terms of the second-order derivatives of $s_x(y)$ evaluated at the singular strategy (Figure 2). Each configuration represents a different evolutionary scenario that can be interpreted in terms of ESS-stability, convergence stability, the ability of the singular strategy to invade other populations if initially rare itself, and the possibility of protected dimorphisms occurring within the singular strategy's neighborhood. We first consider each of these four properties of the singular strategy separately before we investigate their possible combinations and the corresponding evolutionary scenarios.

Properties of the singular strategy

A singular strategy x^* is (locally) ESS-stable (Maynard Smith, 1982) if no nearby mutant can invade, in other words, if $s_{x^*}(y) < 0$ for all $y \neq x^*$ in a neighborhood of x^*. In the pairwise invasibility plot the vertical line through x^* lies completely inside a region marked '-' (Figure 2c-f). Since along this vertical line $s_x(y)$ as a function of y has a maximum for $y = x^*$, it follows that at the singular strategy

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

A singular strategy that is ESS-stable is an evolutionary trap in the sense that once it has become established in a population, no further evolutionary change is possible by small mutations.

A singular strategy is (locally) convergence stable (Christiansen, 1991) if a population of a nearby phenotype 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 pairwise invasibility plot there is a '+' above the diagonal on the left of x^*, and below the diagonal on the right of x^* (Figure 2b-e). In other words, the local fitness gradient points towards the singular strategy. Since at x^* the sign of the local fitness gradient changes from positive to negative, $D(x)$ is a (locally) decreasing function of x, and hence at the singular strategy we have

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

(Eshel, 1983). Notice that as on the diagonal of the pairwise invasibility plot $s_x(y)$ is always zero, also the second-order directional derivative of $s_x(y)$ under a slope of plus 45° must also be zero on the diagonal, that is,

$$\frac{\partial^2 s_x(y)}{\partial x^2} + 2\frac{\partial^2 s_x(y)}{\partial x \partial y} + \frac{\partial^2 s_x(y)}{\partial y^2} = 0. \tag{7}$$

If we use this to eliminate the cross-derivative in Equation (6), we get

$$\frac{\partial^2 s_x(y)}{\partial x^2} > \frac{\partial^2 s_x(y)}{\partial y^2} \tag{8}$$

(Figure 2b-e). For a monomorphic population a singular strategy that is convergence stable is an evolutionary attractor. A singular strategy that is not convergence stable is an evolutionary repeller from which an initially monomorphic population evolves away.

A singular strategy can spread in populations of a slightly different phenotype when initially rare itself if $s_x(x^*) > 0$ for all $x \neq x^*$ in a neighborhood of x^*. In the pairwise invasibility plot the horizontal line through x^* on the y-axis lies entirely inside a region marked '+' (Figure 2a-d). Since along this horizontal line $s_x(y)$ as a function of x has a minimum for $x = x^*$, it follows that at the singular strategy

$$\frac{\partial^2 s_x(y)}{\partial x^2} > 0. \tag{9}$$

Two strategies x and y can mutually invade, and hence give rise to a dimorphic population, if both $s_x(y) > 0$ and $s_y(x) > 0$. The set of all pairs of mutually invasible strategies near a singular strategy is given by the overlapping parts of the '+' regions in the pairwise invasibility plot and its mirror image taken along the main diagonal (Figure 3). This set is non-empty if, and only if the secondary diagonal lies inside a '+' region (Figure 2a-c,h). Since along the secondary diagonal $s_x(y)$

has a local minimum for $x = y = x^*$, the second-order directional derivative of $s_x(y)$ at the singular strategy under a slope of minus 45° must be positive, that is,

$$\frac{\partial^2 s_x(y)}{\partial x^2} - 2\frac{\partial^2 s_x(y)}{\partial x \partial y} + \frac{\partial^2 s_x(y)}{\partial y^2} > 0 \, . \tag{10}$$

If we use Equation (7) to eliminate the cross-derivative, we find

$$\frac{\partial^2 s_x(y)}{\partial x^2} > -\frac{\partial^2 s_x(y)}{\partial y^2} \tag{11}$$

(Figure 2a-c,h). With small evolutionary steps an initially monomorphic population can become dimorphic only within the vicinity of a singular strategy that satisfies the above condition.

The four properties of the singular strategy and their algebraic relationship are summarized in Table 1. Although not fully independent of one another, the four properties can be combined in various ways, yielding the eight basic configurations presented in Figure 2. (Complete independence would give sixteen different combinations). For example, a singular strategy can be ESS-stable but not convergence stable (Figure 2f), or convergence stable but not ESS-stable (Figure 2b; for examples, see, e.g., Eshel and Motro, 1981; Eshel, 1983; Christiansen, 1991; Brown and Pavlovic, 1992; Abrams *et al.*, 1993b; Kisdi and Meszéna, 1993, 1995; Meszéna *et al.*, 1996). A singular strategy that is both an ESS and convergence stable (Figure 2c-e) is called a 'continuously stable strategy' or CSS (Eshel and Motro, 1981; Eshel, 1983). A continuously stable strategy may still be incapable of invading other populations if initially rare itself (Figure 2e), in which case it can be approached only monotonically (that is, either from the left or from the right) by an infinite series of ever decreasing evolutionary steps (Kisdi and Meszéna, 1993, 1995). If mutual invasibility is possible near a singular strategy that lacks convergence stability, the population may evolve away before it has a chance of becoming dimorphic (Figure 2a,h). However, if the singular strategy is convergence stable, then an initially monomorphic population inevitably sooner or later becomes dimorphic (Figure 2b,c). As till now we assumed monomorphic resident populations, the occurrence of mutual invasibility giving rise to protected dimorphisms poses a potential problem that is dealt with below.

Dimorphisms near a singular strategy and evolutionary branching

The evolutionary significance of mutual invasibility near a convergence stable singular strategy x^* depends on whether or not it is also ESS-stable. If x^* is convergence stable and an ESS, then mutually invasible strategies are necessarily on opposite sides of x^* (Figure 2c). A mutant with strategy y can invade a resident population with strategies x_1 and x_2 (with $x_1 < x_2$) if, and only if $x_1 < y < x_2$ (see Appendix A). The reason for this can be seen intuitively as follows. In a monomorphic resident population at the ESS no mutant can invade. The mutant's fitness, $s_{x^*}(y)$, as a function of the mutant's strategy, y, has a maximum at $y = x^*$ where it is zero, but elsewhere the fitness is negative (Figure 4a). The case of a dimorphic resident population with strategies x_1 and x_2 close to x^* can be

considered as a small perturbation of this situation. As the mutant's fitness is zero for $y = x_1$ and $y = x_2$, the maximum of the mutant's fitness now lies between x_1 and x_2 where it is positive (Figure 4b). Mutants in between the two resident types, therefore, can invade, whereas mutants outside cannot. A mutant that is sufficiently close to the ESS replaces both residents, and renders the population monomorphic again. Otherwise only the type that is on the same side of x^* as the mutant, but further away, is ousted, and the population remains dimorphic (Figure 4c). In the long run, however, any dimorphism eventually disappears as the population gradually evolves towards the ESS through a series of monomorphic and (converging) dimorphic population states.

If x^* is convergence stable but not an ESS (Figure 2b), then a mutant can invade if, and only if $y < x_1$ or $x_2 < y$ (see Appendix A). To see this intuitively, notice that in a monomorphic resident population at a singular strategy that is not ESS all nearby mutants can invade (Figure 2b), and hence have a positive fitness (Figure 4d). A slight perturbation leads to the case of a dimorphic resident population with strategies x_1 and x_2 close to x^* (Figure 4e). Only mutants outside the two resident types have a positive fitness and can invade, whereas mutants in between cannot. After invasion it is always the strategy in the middle that is ousted (Figure 4f). With each successive invasion, therefore, the two remaining strategies become more and more distinct. On the long run the population effectively splits up into two diverging sub-populations. This process of phenotypic divergence in an initially monomorphic population we call 'evolutionary branching'. The corresponding singular strategy we will refer to as 'evolutionary branching point'. An example of evolutionary branching is given in a later section (for other examples of branching, see Metz *et al.*, 1992, 1996; Meszéna *et al.*, 1997).

We thus conclude that, irrespective of whether or not mutual invasibility near a singular strategy is possible, singular strategies that are convergence stable as well as ESS-stable (that is, the continuously stable strategies sensu Eshel and Motro, 1981; Eshel, 1983) give rise to stabilizing selection in both monomorphic and nearby dimorphic populations. These singular strategies therefore represent the final, monomorphic outcomes of an evolutionary process. In contrast, singular strategies that are convergence stable but not ESS-stable (that is, the branching points) are attractors for monomorphic populations but repellers for nearby dimorphic populations. Once an initially monomorphic population has come sufficiently close to the singular strategy it will become dimorphic and subsequently undergo disruptive selection, leading to two phenotypically distinct and diverging subpopulations.

Polymorphic populations

After branching the two resident strategies soon grow too far apart for the local approximation of the mutant's fitness in a dimorphic resident population near the branching point as used above to be valid anymore. To see how evolution proceeds after branching, we generalize the formalism to populations with an arbitrary number of different phenotypes. Let $E_{x1,..,xn}$ denote the environment in a population with strategies $x_1,..,x_n$ at its demographic attractor, and let $r(x_i, E_{x1,..,xn})$ denote the long-term growth rate of the x_i-phenotype. Since the long-term exponential growth rate of each resident type is zero, $E_{x1,..,xn}$ must satisfy

$$r(x_i, E_{x_1,..,x_n}) = 0 \qquad\qquad (12)$$

for all *i* (cf. Equation 1). In general this is possible only if the environment can be represented by a vector of at least n independent components. For example, this is the case if individuals affect one another through the availability of n different kinds of resources, the abundance of which in turn depends on the frequencies of the various types of individuals present. The dimensionality of the environment thus sets a theoretical upper limit to the number of phenotypes that could possibly coexist on the same trophic level (MacArthur and Levins, 1964; Tilman, 1982). The actual number of coexisting types, however, may at any time be smaller. For *n* = 2 the set of possible protected dimorphisms is given by the overlapping '+' regions of the pairwise invasibility plot and its mirror image taken along the principal diagonal (cf. Figure 3).

The growth rate of an initially rare mutant with strategy *y* in a resident population with strategies $x_1,..,x_n$ at its demographic attractor is equal to

$$s_{x_1,...,x_n}(y) = r(y, E_{x_1,...,x_n}) \tag{13}$$

(cf. Equation 2). With small mutations the direction of evolution in the x_i-strategy is indicated by the sign of the local fitness gradient

$$D_i(x_1,..,x_n) = \left[\frac{\partial s_{x_1,...,x_n}(y)}{\partial y} \right]_{y=x_i} \tag{14}$$

(cf. Equation 4). Combinations of strategies for which $D_i(x_1,..,x_n)$ is zero lie on a *n*-1 dimensional manifold that we shall refer to as the x_i-isocline. For *n* = 2, the x_1- and x_2-isoclines are lines that divide the set of protected dimorphisms into a number of separate regions with different coevolutionary directions (Figs 6a and 7a). On the x_i-isocline there is no longer directional selection in the x_i-strategy. If the *n*-1 other strategies were fixed and did not evolve, then each point on the x_i-isocline would correspond to a singular strategy in an environment set by the other strategies. However, the *n*-1 other strategies are not fixed and continue to evolve (and possibly move the population away from the x_i-isocline again) unless the local fitness gradient is zero for all strategies at the same time, that is, at the point of intersection of all isoclines. We call a polymorphism consisting of the strategies $x_1^*,..,x_n^*$ such that $D_i(x_1^*,..,x_n^*)$ is zero for all resident strategies simultaneously, an 'evolutionarily singular coalition'.

The individual strategies of a singular coalition can each be classified in a similar way as singular strategies. A singular coalition is evolutionarily stable so that no new mutants can invade the population if, and only if all its constituent strategies are ESS, that is, if

$$\left[\frac{\partial^2 s_{x_1,...,x_n}(y)}{\partial y^2} \right]_{\substack{y=x_i^* \\ x_j=x_j^* \forall j}} < 0 \tag{15}$$

8

for all *i* (cf. Equation 5; Brown and Vincent, 1987, 1992; Vincent and Brown, 1989; Brown and Pavlovic, 1992). Generalization of convergence stability is less straightforward and depends on the relative size and frequency of mutations in the various resident strategies. It is neither sufficient nor necessary that the condition for convergence stability in a monomorphic population (Equation 8) applies to each individual strategy of the singular coalition separately (Matessi and Di Pasquale, 1996). However, unambiguous examples of convergence stability for *n* = 2 have been recognized (Motro, 1994; Matessi and Di Pasquale, 1996; also, see example in the next section).

Mutual invasibility of a mutant and its resident progenitor is possible near a singular coalition if, and only if

$$\left[\frac{\partial^2 s_{x_1,..,x_n}(y)}{\partial x^2}\right]_{\substack{y=x_i^* \\ x_j=x_j^* \forall j}} < -\left[\frac{\partial^2 s_{x_1,..,x_n}(y)}{\partial y^2}\right]_{\substack{y=x_i^* \\ x_j=x_j^* \forall j}} \tag{16}$$

(cf. Equation 11). Mutual invasibility has no long-term consequences if the strategy is at the same time evolutionarily stable, that is, if it also satisfies Equation (15). A singular coalition that is both ESS and convergence stable represents a final, polymorphic outcome of the evolutionary process. A singular coalition that is convergence stable but for which at least one strategy lacks ESS stability and allows for mutual invasibility nearby (that is, for which Equation 16 is satisfied while Equation 15 is not) will lead to further branching of the evolutionary tree (see Appendix A).

A Specific Example

We here develop a haploid version of Levene's (1953) 'soft selection' model with continuous strategies as a specific example to demonstrate evolutionary dynamics and branching in monomorphic and polymorphic populations. Consider a resident population with strategies $x_1,..,x_n$ of an organism with discrete, non-overlapping generations in a spatially heterogeneous environment consisting of *m* different patches. Each patch can support only a limited number of established individuals denoted by $K_1,..,K_m$ respectively. The total number of established individuals with strategy x_i (*i*=1,..,*n*) summed over all patches is denoted by N_i. We assume that all patches are occupied to maximum capacity, so that the total population size in each generation is always constant, that is,

$$\sum_{i=1}^{n} N_i = \sum_{j=1}^{m} K_j . \tag{17}$$

During dispersal, the offspring are distributed randomly into the different patches such that the number of juveniles with a given strategy landing in a given patch is proportional to the frequency of that particular strategy among the dispersing offspring. Assuming that all established individuals have the same fecundity irrespective of their strategy or patch, the number of juveniles with strategy x_i landing in a given patch is thus proportional to N_i.

Within a patch, juveniles first undergo a period of frequency-independent selection followed by a period of non-selective 'contest' competition during which the available living-space is allocated at random among the survivors. With $f_j(x_i)$ denoting the pre-competitive survival probability for an individual with strategy x_i in the jth patch, the fraction of the available space in the jth patch allocated to individuals with strategy x_i is

$$f_j(x_j)N_i \bigg/ \sum_{h=1}^{n} f_j(x_h)N_h \,. \tag{18}$$

For the total number of established individuals with strategy x_i in the next generation summed over all patches we consequently have

$$N_i' = \sum_{j=1}^{m} \left(K_j f_j(x_j)N_i \bigg/ \sum_{h=1}^{n} f_j(x_h)N_h \right). \tag{19}$$

At equilibrium $N_i' = N_i$ for all i. In order for the population to maintain n strategies at equilibrium, the number of patches must be greater than or equal to the number of coexisting strategies, that is, $m \geq n$. Whenever an equilibrium with n strategies is possible, it is unique and stable (Gliddon and Strobeck, 1975; Strobeck, 1979).

Consider an initially rare mutant with strategy y in a resident population with strategies $x_1,..,x_n$. The resident population at its equilibrium determines the level of competition in the various patches as experienced by the mutant. The resident equilibrium densities, denoted by $\hat{N}_1,..,\hat{N}_n$, depend on the resident strategies. As long as the mutant is rare, the environment as set by the residents remains unaffected by the mutant's presence itself. For the number of mutants, N_{mut}, in successive years we thus have as first-order approximation

$$N_{mut}' = \sum_{j=1}^{m} \left(K_j f_j(y)N_{mut} \bigg/ \sum_{h=1}^{n} f_j(x_h)\hat{N}_h \right) \tag{20}$$

(cf. Equation 19). The mutant's exponential growth rate consequently is

$$s_{x_1,..,x_n}(y) = \log\left(\frac{N_{mut}'}{N_{mut}} \right) = \sum_{j=1}^{m} \left(K_j f_j(y) \bigg/ \sum_{h=1}^{n} f_j(x_h)\hat{N}_h \right). \tag{21}$$

Below we confine ourselves to the case of three patches, each with the same carrying capacity, that is, $K_1 = K_2 = K_3$. Moreover, we assume that the pre-competitive survival probabilities in the different patches are bell-shaped functions of strategy, that is,

$$f_j(x) = \alpha \exp\left(-\frac{(x-\mu_j)^2}{2\sigma^2}\right), \tag{22}$$

each with the same height (α) and width (σ), but with different though evenly spaced optima $\mu_1 = -d$, $\mu_2 = 0$, and $\mu_3 = +d$ for some fixed value d representing patch difference.

In Appendix B, we show that with above assumptions there is a unique evolutionarily singular strategy $x^* = 0$ that is convergence stable, that can invade other populations, and in the neighborhood of which there are always pairs of strategies that can mutually invade. If the patches are sufficiently similar to one another, that is, if $d/\sigma < 1.22$, then the singular strategy is also evolutionarily stable (Figure 5a). The long term evolutionary outcome then consists of a single generalists strategy that, although optimally adapted to the middle patch, also exploits the other two patches. If the patches are further apart ($d/\sigma > 1.22$), however, then the singular strategy is a branching point (Figure 5b). After having reached the singular strategy, the population now undergoes evolutionary branching during which the generalist gives way to a dimorphic coalition of more specialized strategies (Figure 6b).

Figure 6a gives the set of potential protected dimorphisms for $d/\sigma = 1.5$, and was obtained by taking the overlapping parts of the '+' regions of the pairwise invasibility plot in Figure 5b and its mirror image along the main diagonal (cf. Figure 3). The resulting set is necessarily symmetric in the main diagonal. The isoclines, given by

$$D_i(x_1, x_2) = \left[\frac{\partial s_{x_1,x_2}(y)}{\partial y}\right]_{y=x_i} = 0, \tag{23}$$

for $i = 1, 2$ (cf. Equation 14), were computed numerically using Equation (21), and divide the set of potential dimorphisms into eight regions (four symmetrically on each side of the diagonal). Within each region the set of permissible directions of evolutionary change, that is, the 'invasion cone' (Matessi and Di Pasquale 1996), follows from the local fitness gradients (Equation 14 with Equation 21) and is indicated by arrows (Figure 6a). The intersection of the isoclines corresponds to an evolutionarily singular coalition. The invasion cones determine whether or not the singular coalition is convergence stable. The mutant's fitness as a function of its own strategy has a local maximum on the x_i-isocline (thick lines in Figure 6a) if

$$\left[\frac{\partial^2 s_{x_1,x_2}(y)}{\partial y^2}\right]_{y=x_i} < 0 \tag{24}$$

(cf. Equation 15), and a local minimum (thin lines in Figure 6a) if the inverse inequality is true. A singular coalition is evolutionarily stable only if at the point of intersection both isoclines correspond to fitness maxima, that is, if both isoclines are thick. If the patches are not too far apart ($1.22 < d/\sigma < 2.10$), then there is a unique singular coalition that is both convergence stable and ESS-stable (Figure 6a). Therefore, after branching at $x^* = 0$, the population evolves towards a stable

11

dimorphism in which the middle patch is exploited by both strategies, while the remaining two patches are both monopolized by only one strategy each (Figure 6b).

If the difference between the patches is larger ($d/\sigma > 2.10$), then the isoclines intersect at three points corresponding to three different evolutionarily singular coalition (Figure 7a). On inspection of the invasion cones it can be seen that two of these are convergence stable, separated by a convergence unstable singular coalition. To which of the two convergence stable coalitions the population will actually evolve is a matter of chance. Neither coalition is evolutionarily stable (one of the intersecting isoclines is always a thin line), so that once the population has come sufficiently nearby it will undergo further branching. Both convergence stable dimorphic coalitions consist of a specialist adapted to either the first or third patch, and a relative generalist exploiting the two remaining patches. It is always this generalist that undergoes further branching, giving way to more specialized strategies. Independent of the dimorphic coalition to which of the population will evolve first, the population eventually ends up as a stable trimorphism with each strategy adapted to its own specific patch (Fig 7b,c).

The dynamics of evolution as predicted by the model is confirmed by numerical simulations (Figure 6b and 7b,c). In these simulations we use Equation (19) to calculate the number of individuals with different strategies in successive generations. Starting with a monomorphic population, new types are generated with a low probability per generation by small but random mutations from strategies already present. The new mutants are added to the population with a low initial frequency. By iteration of Equation (19) some mutants will increase in number, whereas others remain rare or gradually vanish. When the frequency of a given strategy drops below a certain pre-set threshold, the strategy is considered to have gone extinct and is removed from the population. Details of the simulation (like the precise mutation rate, mutation radius, inoculation and extinction thresholds) do not qualitatively affect the outcome of the simulations.

Figure 8 shows how the number, the stability properties, and the positions of the singular strategy and the singular coalitions change due to changes in patch difference. The monomorphic singularity does not change its position, but it loses ESS-stability and becomes a branching point when d/σ becomes larger than 1.22 (Figure 8a). The dimorphic singularity first appears when the monomorphic singularity becomes a branching point (Figure 8b). As patch difference increases, the strategies of the dimorphic coalition grow also further apart. At $d/\sigma = 2.10$ the dimorphic singularity undergoes a 'pitchfork' bifurcation yielding three dimorphic singularities, two of which are convergence stable but not ESS-stable (pairs of strategies numbered 1 and 3 in Figure 8b) separated by a convergence unstable dimorphic singularity (pair numbered 2). The trimorphic singular coalition already emerges at $d/\sigma = 1.93$, that is, before the dimorphisms has lost its ESS-stability. Although ESS-stable, the trimorphism remains unreachable for an initially monomorphic or dimorphic population until the dimorphic coalition loses ESS-stability at $d/\sigma = 2.10$ (Figure 8c). As patch difference decreases, the frequency of the middle strategy of the trimorphism becomes zero when d/σ approaches 1.93. At the same time the other two strategies of the trimorphism converge to the dimorphic coalition (Figure 8c). As patch difference increases, the strategies of the trimorphism converge to the within-patch optimal strategies μ_1, μ_2 and μ_3.

Meszéna *et al.* (1997) demonstrated evolutionary branching in monomorphic populations in a similar model with two patches and limited migration between the patches (for recent related models, see, e.g., Brown and Pavlovic, 1992; Brown, 1996).

Discussion

Starting from four basic assumptions, we model evolution as a sequence of monomorphic or polymorphic population states, where each time the transition from one state to the next occurs when an advantageous mutant comes around and spreads. The evolutionarily singular strategies play a key-role in the evolutionary dynamics of an initially monomorphic population. Among the eight possible different types of singular strategies (Figure 2) we can distinguish three main groups: Singular strategies that lack convergence stability and therefore act as evolutionary repellers (Figure 2a,f-h). Singular strategies that are both evolutionarily and convergence stable (that is, the 'continuously stable strategies' sensu Eshel and Motro, 1981; Eshel, 1983; Figure 2c-e), and hence represent final outcomes of an evolutionary process. And finally, the singular strategy that is convergence stable but not ESS, that is, the evolutionary branching point (Figure 2b). This latter type stands out in particular, because from a large distance it acts as an evolutionary attractor, but once nearby, the population undergoes disruptive selection leading to evolutionary branching. With small evolutionary steps, an initially monomorphic population can become distinctively dimorphic only if it passes first through the neighborhood of a singular strategy of this type. The branching point, therefore, plays a central role in the adaptive growth and branching of the evolutionary tree. Disruptive selection at singular strategies that are convergence stable but not evolutionarily stable has also been indicated in specific models by Christiansen and Loeschcke (1980), Brown and Pavlovic (1992), Metz *et al.* (1992) and Abrams *et al.* (1993b).

The generalization of the singular strategy for polymorphic populations is the evolutionarily singular coalition. Each individual strategy of a singular coalition can be classified in the same way as a monomorphic singular strategy. A singular coalition each strategy of which is an ESS given the other strategies represents a final evolutionary stop for a polymorphic population. Evolution towards a singular coalition consisting of one or more branching points will lead to further branching of the evolutionary tree. Depending on the number of branching points contained in the singular coalition one or more new branches may develop (nearly) simultaneously (for an example of simultaneous branching in a dimorphic population, see Metz *et al.*, 1996). Like in the case of monomorphic populations, with small mutations a polymorphic population can reach a higher level of (protected) polymorphism only if it first passes through the neighborhood of a singular coalition with at least one branching point. Extinction of branches may occur when a population evolves towards the boundary of the set of possible protected polymorphisms, in which case the population falls back again to a lower level of polymorphism (see, e.g., Metz *et al.*, 1996). In polymorphic populations evolutionary cycles are also possible (Marrow *et al.*, 1992; Dieckmann *et al.*, 1995; Abrams and Matsuda, 1996).

The predictions from our framework are confirmed by numerical simulations (see the example in the previous section; for other examples, see Metz *et al.*, 1992, 1996; Meszéna *et al.*, 1997). Notwithstanding our basic assumptions, in the simulations new mutants often come along

13

before the population has reached its demographic attractor and before disadvantageous mutants have disappeared. The simulations, therefore, show that relaxation of the assumption that the resident population has reached its demographic attractor before a new mutant comes along, and that a polymorphic population is always a protected polymorphism, does not qualitatively affect the results. In the simulations the predictions also prove to be fairly robust with respect to larger mutations as well. Below we consider the significance of some of the other assumptions of the framework.

The present modeling is confined to one-dimensional strategies only (or to one-dimensional parametrizations of multi-dimensional strategies). Extension of the framework to multiple traits under simultaneous selection is not straightforward. In particular the meaning of convergence stability becomes ambiguous and more complex (but see Motro, 1994; Matessi and Di Pasquale, 1996). Some generalizations to multiple traits have been discussed by Metz *et al.* (1996). For a specific example of multiple traits in a population genetics context see Christiansen and Loeschcke (1987).

In this article we assume that for each possible coalition of strategies there is a unique demographic attractor that determines the long-term exponential growth rate of an emerging mutant strategy (Equations 2 and 13). The demographic attractor may be either a fixed point, a limit cycle or an ergodic stochastic attractor (but see Rand *et al.*, 1994; Ferriere and Gatto, 1995 for complications in the case of chaotic attractors). If there were more than one attractor, then the resident population no longer could be represented by its strategies alone. Two populations with the same strategies but in different demographic states may follow different evolutionary courses, because the biotic environment in the two populations is not the same (cf. Rand *et al.*, 1994). However, if mutations are small, and moreover, a small change in strategies is accompanied by a small change in population dynamics, then during the course of evolution a population may track gradual changes in the initial demographic attractor instead of jumping back and forth between different parallel attractors. Consequently, for a monomorphic resident population there will be different pairwise invasibility plots depending on the initial demographic state of the population. Obviously, this picture no longer holds if, as a consequence of the evolutionary change in the resident strategies, the population dynamics undergo a bifurcation such that the demographic attractor undergoes an abrupt change, loses its population dynamical stability or ceases to exist altogether (e.g. Matsuda and Abrams, 1994). Notice, however, that neither evolutionary branching nor extinction of branches are necessarily accompanied by a discontinuous change in the population dynamics. Repeated alternations between parallel demographic states due to environmental disturbances on an ecological time-scale could best be modeled as a single, multi-peaked stochastic attractor rather than as different deterministic population states. This is not possible, however, if the alternations occur on a longer time-scale.

In this article we assume that mutations are small but finite. This leads to an evolutionary dynamics with small but discrete steps in the phenotype space. A similar approach with discrete evolutionary steps in a population genetics context was followed by Matessi and Di Pasquale (1996). Many other authors, however, assume infinitesimally small steps leading to a continuous adaptive dynamics (in time as well as in phenotype space) in which the change per unit time is proportional to the fitness gradient (e.g. Hofbauer and Sigmund, 1990; Marrow *et al.*, 1992, 1996; Abrams *et al.*, 1993b; Dieckmann *et al.*, 1995, Dieckmann and Law, 1996). The fixed-points (or

equilibria) of the continuous adaptive dynamics coincide with the singular strategies or singular coalitions of our descrete step approach, but the dynamical properties are different. In particular, with infinitesimally small mutation steps evolutionary branching does not occur. To see this, notice that mutual invasibility is possible only within the neighborhood of a singular strategy of a size proportional to the mutation step size itself. As the mutation step size decreases, an initially monomorphic population necessarily has to come closer to the singular strategy before the population can become dimorphic. In the limit of continuous dynamics the step size has become zero, so that the neighborhood in which mutual invasibility can occur has collapsed to a single point, that is, the fixed-point itself. Since with continuous adaptive dynamics fixed-points can be approached but are never actually reached, mutually invasibility, and hence evolutionary branching are not possible.

The dimensionality of the environment sets a theoretical upper limit to the number of different strategies that can coexist as a protected polymorphism, and hence to the maximum diversity that can be reached through branching of the evolutionary tree. One general prerequisite for branching, therefore, is that individals affect one another via at least two environmental variables that in turn depend on the frequencies of the various strategies present. If individuals affect one another via only a single environmental variable (such as population equilibrium density, or the abundance of a single resource), then only one strategy can persist at a time, and mutual invasibility, and hence evolutionary branching are not possible. In such a one-dimensional environment, a (local) ESS is always a (locally) optimal strategy that maintains the highest equilibrium density or lowest resource abundance (Tilman, 1982; Kisdi and Meszéna, 1993, 1995; Mylius and Diekmann, 1995). The pairwise invasibility plot is necessarily anti-symmetric along the main diagonal, and there are only two possible local configurations of the pairwise invasibility plot (Figure 9a), both of which are degenerate cases in our general classification of the singular strategies (Figure 2).

Another general prerequisite for evolutionary branching is that the mutant's fitness is a nonlinear function of the mutant's strategy. This excludes branching in all cases where $s_x(y)$ is given as the (weighed) arithmetic average over two alternative pure strategies (like in the case of matrix games) with x and y denoting the mixing frequencies for respectively the resident and the mutant. If the mutant's fitness is a linear function of the mutant's strategy, then the second-order derivative of $s_x(y)$ with respect to y is zero (cf. Equation 5), and there are only two local configurations of the pairwise invasibility plot possible (Figure 9b), both of which are non-generic cases in the general classification of Figure 2. Once the singular has been established, all mutations are neutral (Figure 9b; cf. Bishop-Cannings theorem, 1978). In matrix games the singular strategy is then ESS-stable if it can invade other populations if initially rare itself (Maynard Smith, 1982, p.14). If this is the case, then the ESS is also automatically convergence stable (Figure 9b; Taylor, 1989; Eshel, 1996). Mutual invasibility near the ESS is possible, but branching does not occur.

Although evolutionary branching is reminiscent of speciation, in the present context of asexually reproducing organisms the species concept has no clear meaning. The possible connection between branching and speciation in a more general context depends on the extend to which our results generalize to diploid and sexual organisms, and in particular whether reproductive isolation evolves between the emerging branches. One possible way of applying our approach to diploid and sexually reproducing organisms is the following. Assume that there is a continuum of

potential allele types on a single, diploid locus (or, equivalently, that there are many loci with very tight linkage). Moreover, assume that there exists a function ϕ such that $\phi(x_1,x_2)$ is the phenotype of an individual with alleles x_1 and x_2. Finally, assume that the phenotype of a heterozygote is always intermediate between that of the two homozygotes. Notice that this not necessarily implies that the heterozygote also has an intermediate fitness. Next, consider an initially rare mutant allele y in a randomly mating monomorphic resident population with allele x. As long as the mutant allele is rare, its exponential growth rate is equal to the exponential growth rate of the number of heterozygotes. For the mutant's fitness we thus find

$$s_x(y) = r\left(\phi(x, y), E_{\phi(x,x)}\right) \tag{24}$$

(cf. Equation 2), where $\phi(x,y)$ is the phenotype of the heterozygote, and $\phi(x,x)$ is the phenotype of the resident homozygote. Using this definition of $s_x(y)$, the framework can be applied to sexual populations with Mendelian inheritance describing evolution in allele space rather than in phenotype space. Thus, depending on the particular problem at hand, all eight local configurations (Figure 2) of the pairwise invasibility plot for allele types are theoretically possible, including the branching point.

Branching in allele space leads to a genetic dimorphism (or to genetic polymorphisms after repeated branching events). Mating between individuals from different genetic branches, however, produces heterozygotes, so that on a phenotypic level we also see intermediate types. During branching, these intermediate types necessarily have a lower fitness than the homozygotes and are selected against (cf. Figure 4e). Types that mate more frequently within branches than between branches are therefore at a selective advantage. Consequently, branching in allele space may favor the evolution of assortative mating and of reproductive isolation. Two prerequisites for the evolution of assortative mating are that a genetic polymorphism is maintained within the population while at the same time heterozygotes are selected against. Various possible scenarios for the evolution of assortative mating have been modeled elsewhere (see, e.g., Maynard Smith, 1966; Balkau and Feldman, 1973; Dickinson and Antonovics, 1973; Felsenstein, 1981; Seger, 1985; Diehl and Bush, 1989; de Meeûs *et al.*, 1993). In most population genetic models, which lack frequency-dependent selection, the maintenance of a genetic polymorphism and heterozygote inferiority are mutually exclusive. However, within our evolutionary framework, during evolutionary branching, both conditions arise in a very natural way.

Appendix A

Dimorphisms near a singular strategy

Consider a dimorphic resident population with strategies x_1 and x_2 near a singular strategy x^*, and let $s_{x1,x2}(y)$ denote the fitness of an initially rare mutant with strategy y. Second-order Taylor expansion of $s_{x1,x2}(y)$ for x_1, x_2, and y close to x^* yields

$$
\begin{aligned}
s_{x_1,x_2}(y) = {} & \alpha + \beta_1(x_1 - x^*) + \beta_2(x_2 - x^*) + \beta_3(y - x^*) \\
& + \tfrac{1}{2}\gamma_{11}(x_1 - x^*)^2 + \tfrac{1}{2}\gamma_{22}(x_2 - x^*)^2 + \tfrac{1}{2}\gamma_{33}(y - x^*)^2 \\
& + \gamma_{12}(x_1 - x^*)(x_2 - x^*) + \gamma_{13}(x_1 - x^*)(y - x^*) + \gamma_{23}(x_2 - x^*)(y - x^*),
\end{aligned} \tag{A1}
$$

where the coefficients β_i, γ_{ij} (i, j = 1, 2, 3) denote the first- and second-order derivatives of $s_{x1,x2}(y)$ evaluated at $x_1 = x_2 = y = x^*$. Since the order of the numbering of the resident strategies is arbitrary, we have

$$
s_{x_1,x_2}(y) = s_{x_2,x_1}(y). \tag{A2}
$$

If we apply this to Equation (A1), we find that

$$
\beta_1 = \beta_2, \quad \gamma_{11} = \gamma_{22}, \quad \gamma_{13} = \gamma_{23}. \tag{A3}
$$

Further, as residents are selectively neutral among themselves, we necessarily have

$$
s_{x_1,x_2}(x_1) = s_{x_1,x_2}(x_2) = 0 \tag{A4}
$$

which, if applied to Equation (A1), yields the additional conditions

$$
\begin{aligned}
& \alpha = 0 \\
& \beta_1 = \beta_2 = \beta_3 = 0 \\
& \gamma_{11} = \gamma_{22} = 0 \\
& \gamma_{13} + \tfrac{1}{2}\gamma_{33} = \gamma_{23} + \tfrac{1}{2}\gamma_{33} = 0 \\
& \gamma_{12} + \gamma_{23} = \gamma_{12} + \gamma_{13} = 0.
\end{aligned} \tag{A5}
$$

Finally, as the set of potential protected dimorphisms connects to the diagonal of the pairwise invasibility plot exactly at the singular strategy (Figure 3), we have

$$
s_{x^*,x^*}(y) = s_{x^*}(y). \tag{A6}
$$

Second-order Taylor expansion of $s_{x^*}(y)$ for y close to x^* gives

$$s_{x*}(y) = s_{x*}(x*) + \left[\frac{\partial s_{x*}(y)}{\partial y}\right]_{y=x*} (y-x*) + \frac{1}{2}\left[\frac{\partial^2 s_{x*}(y)}{\partial y^2}\right]_{y=x*} (y-x*)^2. \tag{A7}$$

The first term is zero because of the selective neutrality of residents among themselves. The second term is equal to the local fitness gradient at the singular strategy, and therefore is also zero. Substitution of Equations (A1) and (A7) into Equation (A6) with $x_1 = x_2 = x*$ gives

$$\gamma_{33} = \left[\frac{\partial^2 s_{x*}(y)}{\partial y^2}\right]_{y=x*}. \tag{A8}$$

If we combine the information given in Equations (A3), (A5) and (A8), and use this to simplify Equation (A1), we get

$$s_{x_1,x_2}(y) = \left[\frac{\partial^2 s_{x*}(y)}{\partial y^2}\right]_{y=x*} (y-x_1)(y-x_2). \tag{A9}$$

It follows that for given resident strategies x_1 and x_2, the graph of $s_{x1,x2}(y)$ as a function of y is a parabola with zeros at $y = x_1$ and $y = x_2$. Moreover, if $x*$ is ESS-stable, the coefficient in Equation (A9) is negative (see Equation 5), so that the parabola has a maximum and is positive for y in between x_1 and x_2 (Figure 4b). If, however, $x*$ lacks ESS-stability, the coefficient in Equation (A9) is positive (see Equation 5), and the parabola has a minimum and is positive for y outside x_1 and x_2 (Figure 4e).

Equation (A9) readily generalizes to cases of mutual invasibility of nearby types in the vicinity of a singular coalition. Consider a protected polymorphism $x_1,..,x_n$ close to a singular coalition $x_1*,..,x_n*$. For given i, let x_i' denote a mutant derived from x_i that can coexist with all the other strategies including x_i itself. Proceeding in a similar manner as before, we get as second-order Taylor approximation of the fitness of a new mutant with strategy y close to x_i and x_i' in the now $(n+1)$-morphic population gives

$$s_{x_1,..,x_i,x_i',..,x_n}(y) = \left[\frac{\partial^2 s_{x_1*,..,x_n*}(y)}{\partial y^2}\right]_{y=x_i*} (y-x_i)(y-x_i'). \tag{A10}$$

For a mutant close to x_i* the fitness as a function of its own strategy is a parabola with zeros at $y = x_i$ and $y = x_i*$. If x_i* is ESS stable (cf. Equation 15), then only mutants in between x_i and x_i' can invade, whereas otherwise only mutants outside can invade.

Appendix B

We here derive algebraically the singular strategies and their stability properties in Levene's (1953) 'soft selection' model for haploids with m different patches. Let $c_j = K_j/\Sigma K_j$ denote the relative size of the jth patch, and let the pre-competitive survival probability, $f_j(x)$, for an individual with strategy x in the jth patch be given as in Equation (22). The fitness of an initially rare mutant with strategy y in an equilibrium resident population with strategy x then is

$$s_x(y) = \log \sum_{j=1}^{m} c_j \frac{f_j(y)}{f_j(x)} = \log \sum_{j=1}^{m} c_j \exp\left(-\frac{(y-\mu_j)^2 - (x-\mu_j)^2}{2\sigma^2}\right) \tag{B1}$$

(cf. Equation 21), where we used that the total population size ΣN_i is equal to ΣK_i (cf. Equation 17). At a singular strategy, x^*, the local fitness gradient by definition is zero, that is,

$$\left[\frac{\partial s_{x^*}(y)}{\partial y}\right]_{y=x^*} = -\sum_{j=1}^{m} c_j \left(\frac{x^*-\mu_j}{\sigma^2}\right) = 0. \tag{B2}$$

Solving Equation (B2) for x^*, we find

$$x^* = \sum_{j=1}^{m} c_j \mu_j, \tag{B3}$$

that is, the weighted average of the within-patch optimal strategies. For the stability properties of the singular strategy we need

$$\left[\frac{\partial^2 s_x(y)}{\partial x^2}\right]_{\substack{y=x^* \\ x=x^*}} = \sum_{j=1}^{m} c_j \left(\frac{x^*-\mu_j}{\sigma^2}\right)^2 + \frac{1}{\sigma^2} \tag{B4}$$

and

$$\left[\frac{\partial^2 s_x(y)}{\partial y^2}\right]_{\substack{y=x^* \\ x=x^*}} = \sum_{j=1}^{m} c_j \left(\frac{x^*-\mu_j}{\sigma^2}\right)^2 - \frac{1}{\sigma^2}. \tag{B5}$$

Since Equation (B4) is always positive, it follows that x^* can always spread in populations with a different strategy (cf. Equation 9). Moreover, summation of Equations (B4) and (B5) gives

$$\left[\frac{\partial^2 s_x(y)}{\partial x^2}\right]_{\substack{y=x^* \\ x=x^*}} + \left[\frac{\partial^2 s_x(y)}{\partial y^2}\right]_{\substack{y=x^* \\ x=x^*}} = 2\sum_{j=1}^{m} c_j \left(\frac{x^*-\mu_j}{\sigma^2}\right)^2, \tag{B6}$$

19

which is also positive, so that mutual invasibility within the singular strategy's neighborhood is also always possible (cf. Equation 11). From Equation (B5) it can be seen that x^* is ESS-stable if

$$\sum_{j=1}^{m} c_j \frac{(x^* - \mu_j)^2}{\sigma^2} < 1,$$ (B7)

but lacks ESS-stability if the inverse inequality is true (cf. Equation 5). In other words, x^* is an ESS as long as σ is sufficiently large, that is, as long as the overlap of the fitness functions in the different patches is sufficiently large. The singular strategy is always convergence stable, however, independently of whether or not it is an ESS, because

$$\left[\frac{\partial^2 s_x(y)}{\partial x^2} \right]_{\substack{y=x^* \\ x=x^*}} - \left[\frac{\partial^2 s_x(y)}{\partial y^2} \right]_{\substack{y=x^* \\ x=x^*}} = \frac{2}{\sigma^2},$$ (B8)

which is always positive (cf. Equation 8). Consequently, if x^* is not an ESS, it must be a branching point. With three patches of equal size ($c_1 = c_2 = c_3 = 1/3$), and with equally spaced within-patch optima with difference d ($\mu_1 = -d$, $\mu_2 = 0$, $\mu_3 = +d$), the Equation (B7) becomes $d/\sigma < \sqrt{1.5}$ (≈ 1.22).

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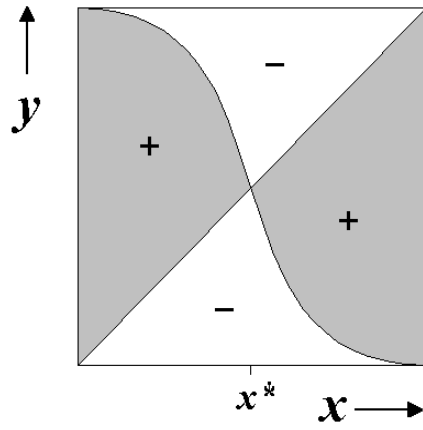
Figure 1. Example of a pairwise invasibility plot. The resident's and mutant's strategy are denoted by x and y, respectively. The shaded area indicates combinations of x and y for which the mutant's fitness, $s_x(y)$, is positive. The singular strategy is denoted by x^*.
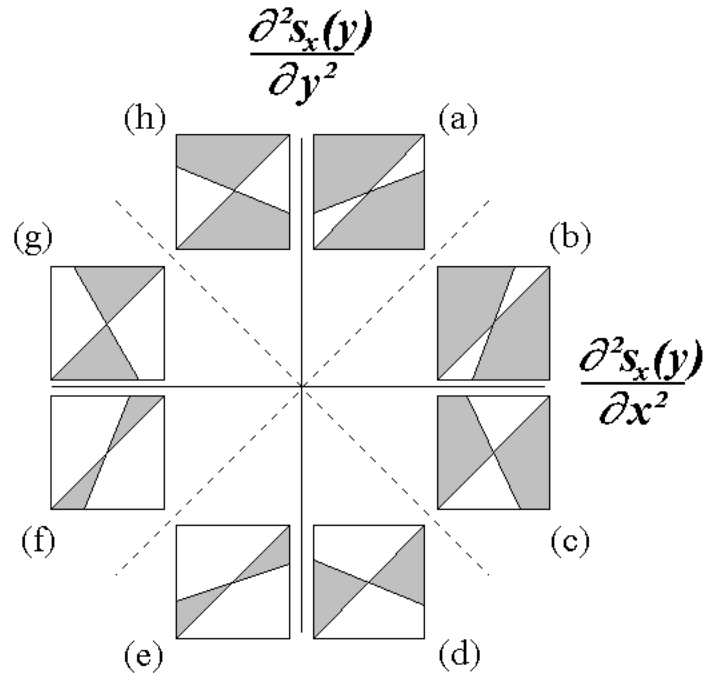
Figure 2. The eight possible generic local configurations of the pairwise invasibility plot and their relation to the second-order derivatives of $s_x(y)$. Inside the shaded regions within each separate plot, $s_x(y)$ is positive.
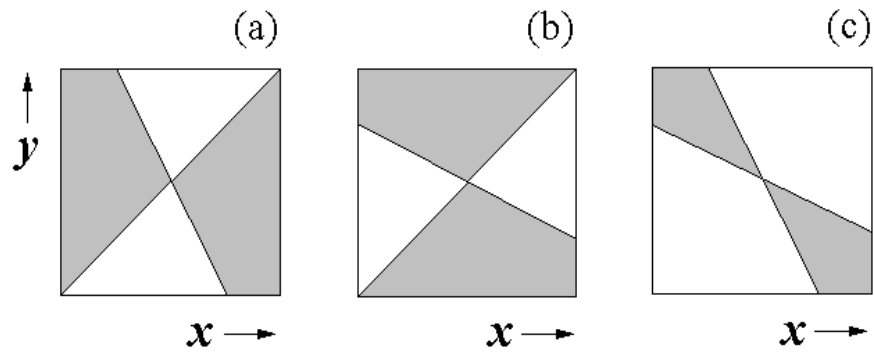
Figure 3. Graphic representation of the set of mutually invasible strategies. (a) Sign of $s_x(y)$; (b) sign of $s_y(x)$; and (c) superposition of (a) and (b).
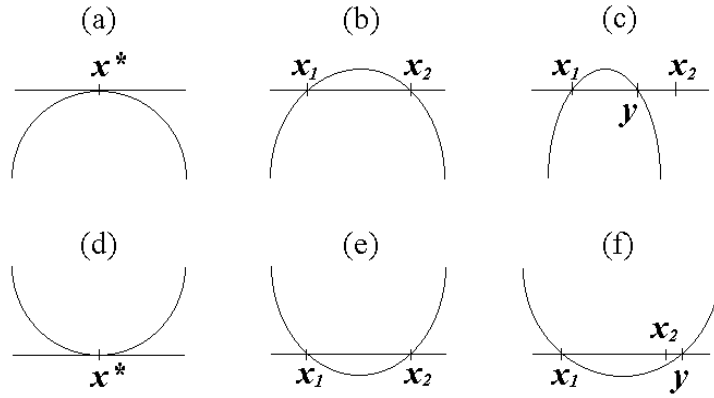
Figure 4. A mutant's fitness as a function of its own strategy y in a dimorphic population with strategies x_1 and x_2 as a perturbation from the fitness in a monomorphic population with a single strategy x^* that is an ESS (a-c) or not an ESS (d-f).
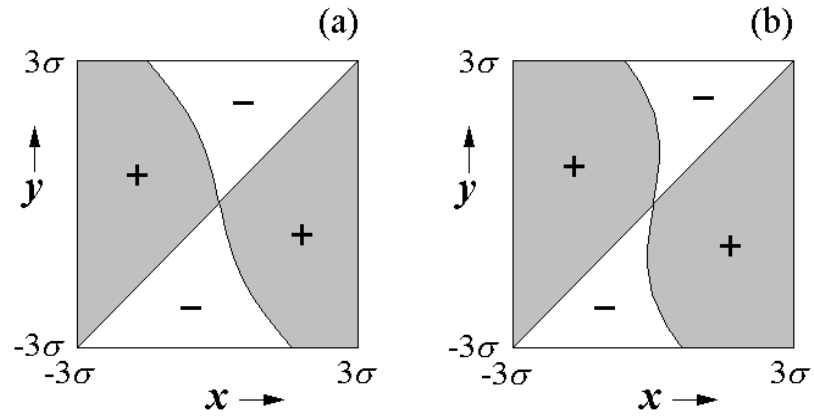
Figure 5. Pairwise invasibility plot for Levene's (1953) haploid selection model with three patches for (a) $d/\sigma = 1$, and (b) $d/\sigma = 1.5$.
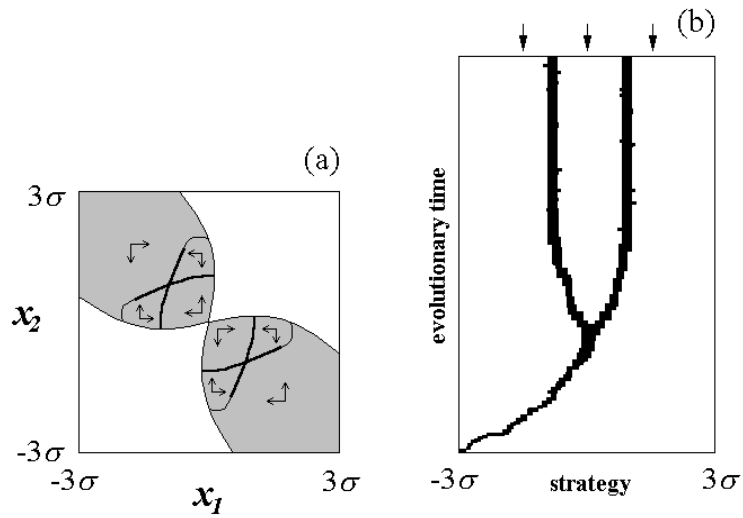
Figure 6. (a) Set of potential protected dimorphisms (shaded regions) with invasion cones and isoclines for $d/\sigma = 1.5$. Thick isoclines are ESS-stable, thin isoclines lack ESS-stability. (b) Simulated evolutionary tree. The arrows at the top of indicate the within-patch optimal strategies.
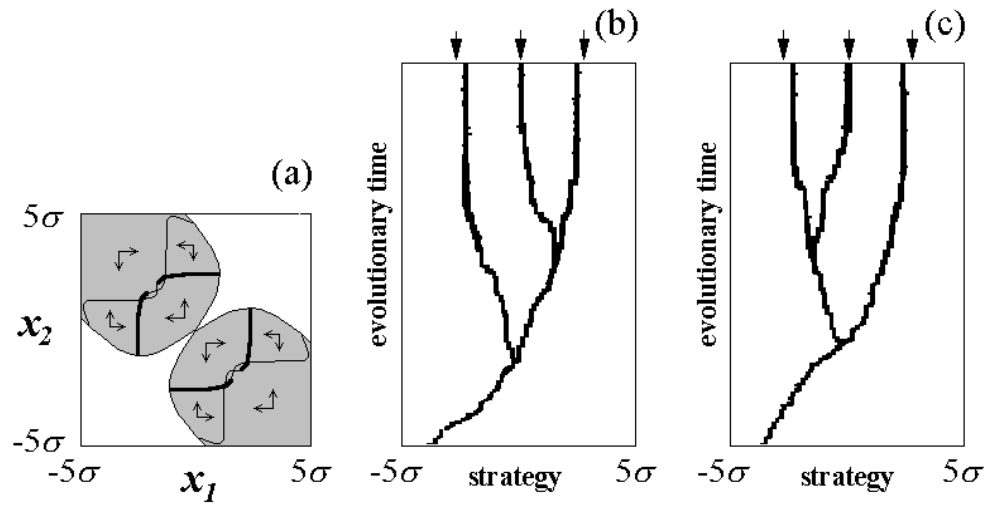
Figure 7. (a) Set of potential protected dimorphisms (shaded regions) with invasion cones and isoclines for $d/\sigma = 2.5$. Thick isoclines are ESS-stable, thin isoclines lack ESS-stability. (b,c) Simulated evolutionary tree. The arrows at the top of indicate the within-patch optimal strategies.
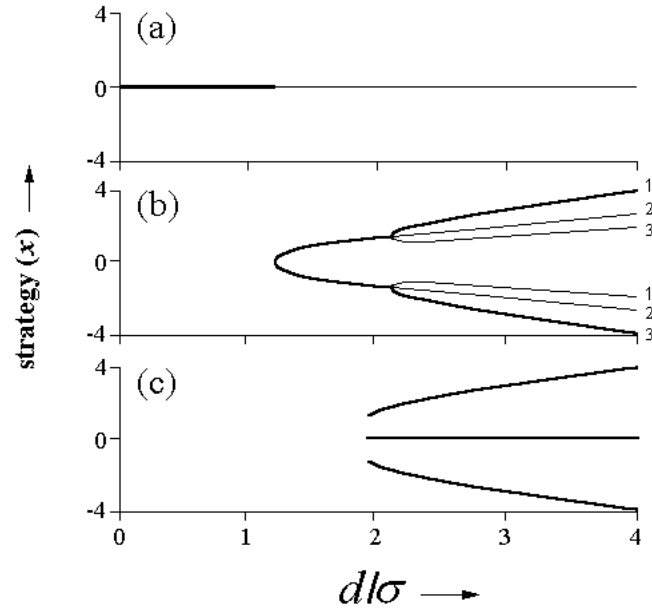
Figure 8. Bifurcation plot with d/σ as bifurcation parameter for (a) the monomorphic singular strategy, (b) the dimorphic singular coalition (the different strategy pairs are labeled 1-3), and (c) the trimorphic singular coalition. Thick lines indicate ESS-stability, thin lines indicate lack of ESS-stability of the corresponding strategy.
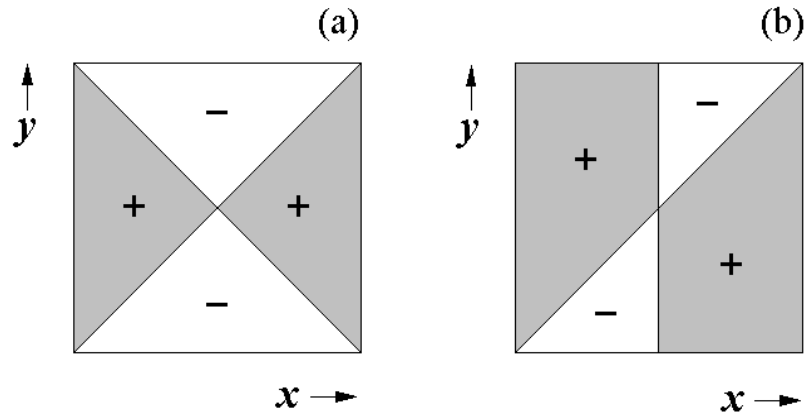
Figure 9. (a) Local configuration of the pairwise invasibility plot near a local fitness maximum (i.e., optimal strategy) if the environment is one-dimensional; the signs are opposite near a local fitness minimum (i.e., 'pessimal' strategy). (b) Pairwise invasibility plot in the case of an ESS if the mutant's fitness is a linear function of the mutant's strategy (for a non-ESS the signs are opposite).