

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

S.A.H. GERITZ,<sup>1,2\*</sup> É. KISDI,<sup>1,3</sup> G. MESZÉNA<sup>4</sup> and J.A.J. METZ<sup>2,5</sup>

<sup>1</sup> *Collegium Budapest, Institute for Advanced Study, Szentháromság u. 2, H-1014 Budapest, Hungary*

<sup>2</sup> *Institute of Evolutionary and Ecological Sciences, Kaiserstraat 63, NL-2311 GP Leiden, The Netherlands*

<sup>3</sup> *Department of Genetics, Eötvös University, Múzeum krt. 4/A, H-1088 Budapest, Hungary*

<sup>4</sup> *Department of Atomic Physics, Eötvös University, Puskin u. 5–7, H-1088 Budapest, Hungary*

<sup>5</sup> *International Institute for Applied System Analyses, A-2361 Laxenburg, Austria*

## Summary

We present a general framework for modelling 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 neighbourhood. Of particular interest is a type of singular strategy that is an evolutionary attractor from a great distance, but once in its neighbourhood a population becomes dimorphic and undergoes disruptive selection leading to evolutionary branching. Modelling the adaptive growth and branching of the evolutionary tree can thus be considered as a major application of the framework. A haploid version of Levene's 'soft selection' model is developed as a specific example to demonstrate evolutionary dynamics and branching in monomorphic and polymorphic populations.

**Keywords:** adaptive dynamics; evolutionarily singular strategy; evolutionary branching; evolutionary modelling

## 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 remains to be seen whether during the course of evolution the ESS will actually become established at all. It

\* Address all correspondence to Stefan A.H. Geritz, Department of Zoology, University of Maryland, College Park, MD 20742, USA.

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 it is also convergence-stable.

In this paper, we integrate various concepts and techniques from modern ESS-theory into a single mathematical framework for modelling the dynamics of long-term phenotypic evolution. We introduce the concept of an ‘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 neighbourhood. These four properties are to a large extent 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 it 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 modelling 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 multidimensional (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 always to be a protected polymorphism in the sense that each strategy present is protected against extinction by a positive growth rate when rare. 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. 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

$$r(x, E_x) = 0 \quad (1)$$

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 of the mutant is therefore equal to

$$s_x(y) = r(y, E_x) \quad (2)$$

What  $s_x(y)$  exactly looks like depends on the particular biological problem at hand. A specific example is given later. 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

$$s_x(y) = s_x(x) + D(x)(y - x) \quad (3)$$

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

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

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  $D(x) > 0$ , then 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 neighbourhood 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 analysed 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  $y$  (Fig. 1; for other examples of pairwise invasibility plots, see Van Tienderen and De Jong, 1986; Metz *et al.*, 1992; Kisdi and Meszena, 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 another line on which  $s_x(y)$  is zero corresponds to an evolutionarily singular strategy. If mutations

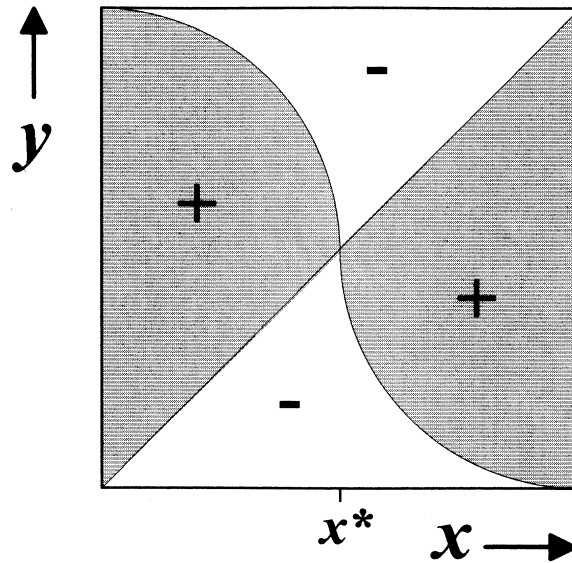


Figure 1. Example of a pairwise invasibility plot. The resident's and mutant's strategy are denoted by  $x$  and  $y$ , respectively. The shaded area indicates combinations of  $x$  and  $y$  for which the mutant's fitness,  $s_x(y)$ , is positive. The singular strategy is denoted by  $x^*$ .

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 (Fig. 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 neighbourhood. 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 neighbourhood of  $x^*$ . In the pairwise invasibility plot, the vertical line through  $x^*$  lies completely inside a region marked '-' (Figs 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

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

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

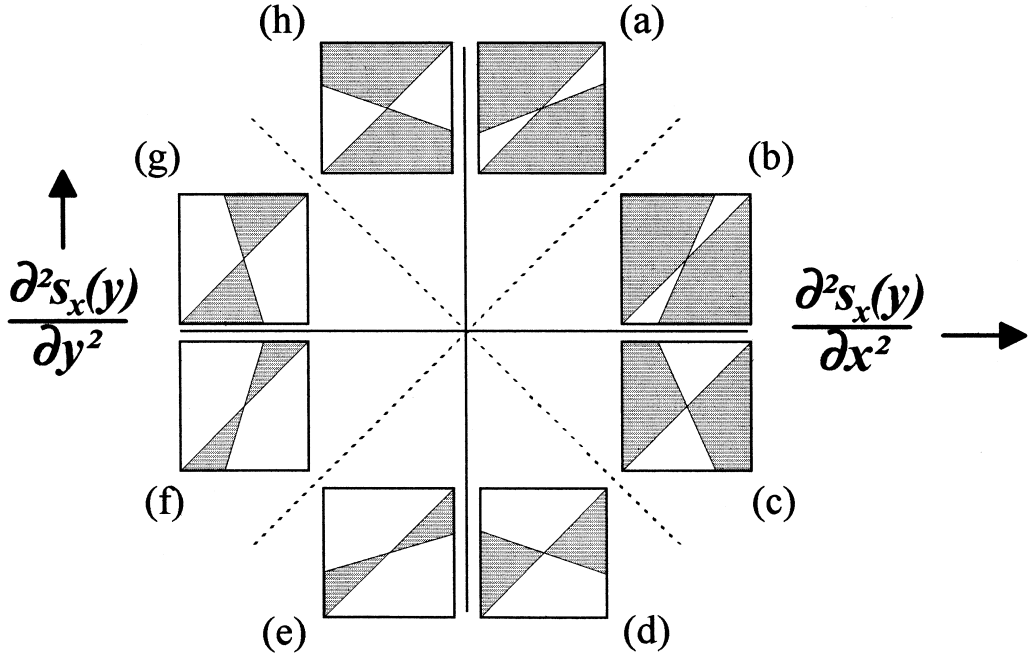


Figure 2. The eight possible generic local configurations of the pairwise invasibility plot and their relation to the second-order derivatives of  $s_x(y)$ . In the shaded regions within the separate plots,  $s_x(y)$  is positive.

$x < y < x^*$  and  $x^* < y < x$ . In the pairwise invasibility plot, there is a ‘+’ above the diagonal on the left, and below the diagonal on the right of  $x^*$  (Figs 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

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

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

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

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

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

(Figs 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 neighbourhood of  $x^*$ . In the pairwise invasibility plot, the horizontal line through  $x^*$  on the  $y$ -axis lies entirely inside a region marked ‘+’ (Figs 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

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

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 invisable 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 (Fig. 3). This set is non-empty if, and only if, the secondary diagonal lies inside a '+' region (Figs 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  $-45^\circ$  must be positive, that is,

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

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

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

(Figs 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 Fig. 2. For example, a singular strategy can be ESS-stable but not convergence-stable (Fig. 2f), or convergence-stable but not ESS-stable (Fig. 2b) (for examples, see Eshel and Motro, 1981; Eshel, 1983; Christiansen, 1991; Brown and Pavlovic, 1992; Abrams *et al.*, 1993b; Kisdi and Meszena, 1993, 1995; Meszena *et al.*, in press). A singular strategy that is both an ESS and convergence-stable (Figs 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 (Fig. 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 Meszena, 1993, 1995). If mutual invasibility is possible near a singular strategy that lacks convergence stability, the popu-

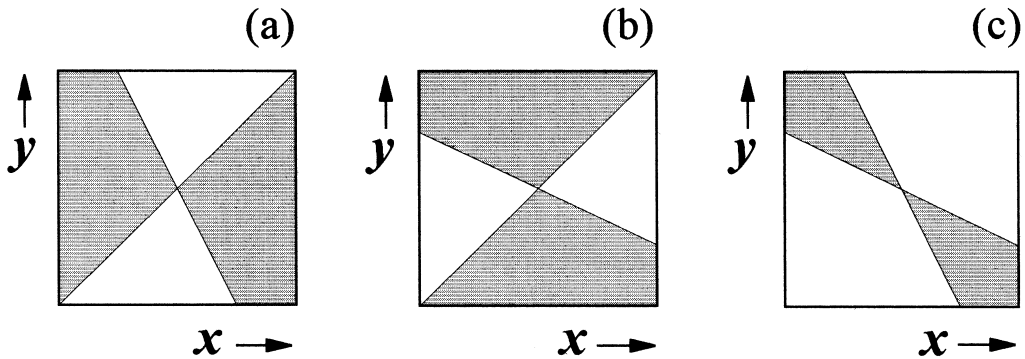


Figure 3. Graphic representation of the set of mutually invisable strategies. (a) Sign of  $s_x(y)$ ; (b) sign of  $s_y(x)$ ; and (c) superposition of (a) and (b).

Table 1. Properties of the singular strategies

Property	Characterization
ESS-stable	$b < 0$
Convergence-stable	$a - b > 0$
Singularity can spread	$a > 0$
Nearby dimorphisms	$a + b > 0$

$$a = \partial^2 s_x(y) / \partial x^2; b = \partial^2 s_x(y) / \partial y^2.$$

lation may evolve away before it has a chance of becoming dimorphic (Figs 2a,h). However, if the singular strategy is convergence-stable, then an initially monomorphic population inevitably sooner or later becomes dimorphic (Figs 2b,c). As until now we have 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 invisable strategies are necessarily on opposite sides of  $x^*$  (Fig. 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 1). 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 (Fig. 4a). The case of a dimorphic resident population with strategies  $x_1$  and  $x_2$  close to  $x^*$  can be considered 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 (Fig. 4b). Mutants in between the two resident types, therefore, can invade, whereas

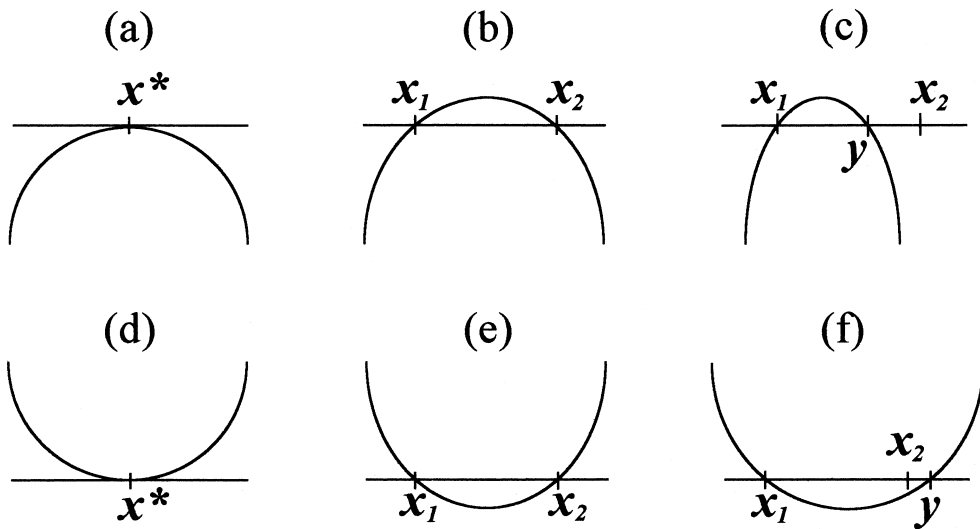


Figure 4. A mutant's fitness in a dimorphic population with strategies  $x_1$  and  $x_2$  as a perturbation from the fitness in a monomorphic population with a single strategy  $x^*$  that is an ESS (a–c) or not an ESS (d–f).

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 (Fig. 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 (Fig. 2b), then a mutant can invade if, and only if,  $y < x_1$  or  $x_2 < y$  (see Appendix 1). To see this intuitively, note that in a monomorphic resident population at a singular strategy that is not an ESS, all nearby mutants can invade (Fig. 2b), and hence have a positive fitness (Fig. 4d). A slight perturbation leads to the case of a dimorphic resident population with strategies  $x_1$  and  $x_2$  close to  $x^*$  (Fig. 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 (Fig. 4f). With each successive invasion, therefore, the two remaining strategies become more and more distinct. In the long term, the population effectively splits up into two diverging subpopulations. This process of phenotypic divergence in an initially monomorphic population we call ‘evolutionary branching’. The corresponding singular strategy we will refer to as the ‘evolutionary branching point’. An example of evolutionary branching is given later (for other examples of branching, see Metz *et al.*, 1992, 1996; Meszéna *et al.*, in press).

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  $E_{x_1, \dots, x_n}$  denote the environment in a population with strategies  $x_1, \dots, x_n$  at its demographic attractor, and let  $r(x_i, E_{x_1, \dots, x_n})$  denote the long-term growth rate of the  $x_i$ -phenotype. Since the long-term exponential growth rate of each resident type is zero,  $E_{x_1, \dots, x_n}$  must satisfy

$$r(x_i, E_{x_1, \dots, x_n}) = 0 \quad (12)$$

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 co-exist (MacArthur and Levins, 1964; Tilman, 1982). The actual number of co-existing 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. Fig. 3).



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

$$s_{x_1, \dots, x_n}(y) = r(y, E_{x_1, \dots, x_n}) \quad (13)$$

(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:

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

(cf. Equation 4). Combinations of strategies for which  $D_i(x_1, \dots, x_n)$  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 co-evolutionary 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  $x_1^*, \dots, x_n^*$ , such that  $D_i(x_1^*, \dots, x_n^*)$  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

$$\left[ \frac{\partial^2 s_{x_1, \dots, x_n}(y)}{\partial y^2} \right]_{y=x_i^*} < 0 \quad (15)$$

$x_j = x_j^* \quad \forall j$

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; see also the example in the next section). Mutual invasibility of a mutant and the resident from which it was derived is possible near a singular coalition if, and only if,

$$\left[ \frac{\partial^2 s_{x_1, \dots, x_n}(y)}{\partial x_i^2} \right]_{y=x_i^*} < - \left[ \frac{\partial^2 s_{x_1, \dots, x_n}(y)}{\partial y^2} \right]_{y=x_i^*} \quad (16)$$

$x_j = x_j^* \quad \forall j$

(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 Condition (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 but Equation 15 is not) will lead to further branching of the evolutionary tree (see Appendix 1).

### A specific example

We develop here 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  $x_1, \dots, x_n$  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  $K_1, \dots, K_m$  respectively. The total number of established individuals with strategy  $x_i$  ( $i = 1, \dots, n$ ) 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,

$$\sum_{i=1}^n N_i = \sum_{j=1}^m K_j \quad (17)$$

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  $j^{\text{th}}$  patch, the fraction of the available space in the  $j^{\text{th}}$  patch allocated to individuals with strategy  $x_i$  is

$$f_j(x_i)N_i / \sum_{h=1}^n f_j(x_h)N_h \quad (18)$$

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

$$N'_i = \sum_{j=1}^m \left( K_j f_j(x_i)N_i / \sum_{h=1}^n f_j(x_h)N_h \right) \quad (19)$$

At equilibrium,  $N'_i = N_i$  for all  $i$ . For the population to maintain  $n$  strategies at equilibrium, the number of patches must be greater than or equal to the number of co-existing 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  $x_1, \dots, x_n$ . The resident population at its equilibrium determines the level of competition in the various patches as experienced by the mutant. As long as the mutant is still rare, the environment as set by the residents remains unaffected by the mutant's presence itself. Let  $\hat{N}_i$  denote the number of resident individuals with strategy  $x_i$  at equilibrium. For the number of mutants,  $N_{\text{mut}}$ , in successive years, we thus have as a first-order approximation

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

(cf. Equation 19). Consequently, the mutant's exponential growth rate is

$$S_{x_1, \dots, x_n}(y) = \log \frac{N'_{\text{mut}}}{N_{\text{mut}}} = \log \sum_{j=1}^m \left( K_j f_j(y) / \sum_{h=1}^n f_j(x_h) \tilde{N}_h \right) \quad (21)$$

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,

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

each with the same height ( $\alpha$ ) and width ( $\sigma$ ), 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 2, we show that based on the above assumptions there is a unique evolutionarily singular strategy  $x^* = 0$  that is convergence-stable, that can invade other populations, and in the neighbourhood 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 (Fig. 5a). The long-term evolutionary outcome then consists of a single generalist 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 (Fig. 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 (Fig. 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 Fig. 5b and its mirror image along the main diagonal (cf. Fig. 3). The resulting set is necessarily symmetric in the main diagonal. The isoclines, given by

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

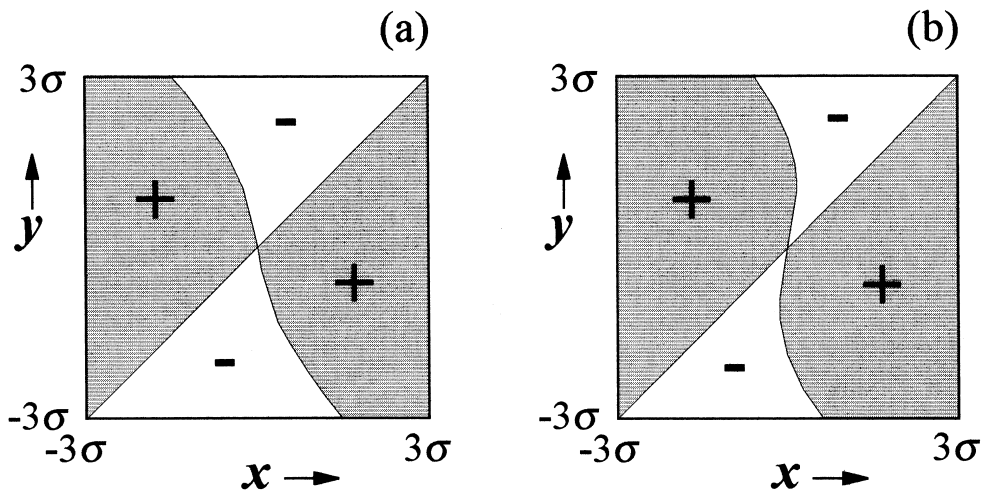


Figure 5. Pairwise invasibility plots for Levene's (1953) haploid selection model with three patches for (a)  $d/\sigma = 1$  and (b)  $d/\sigma = 1.5$ .

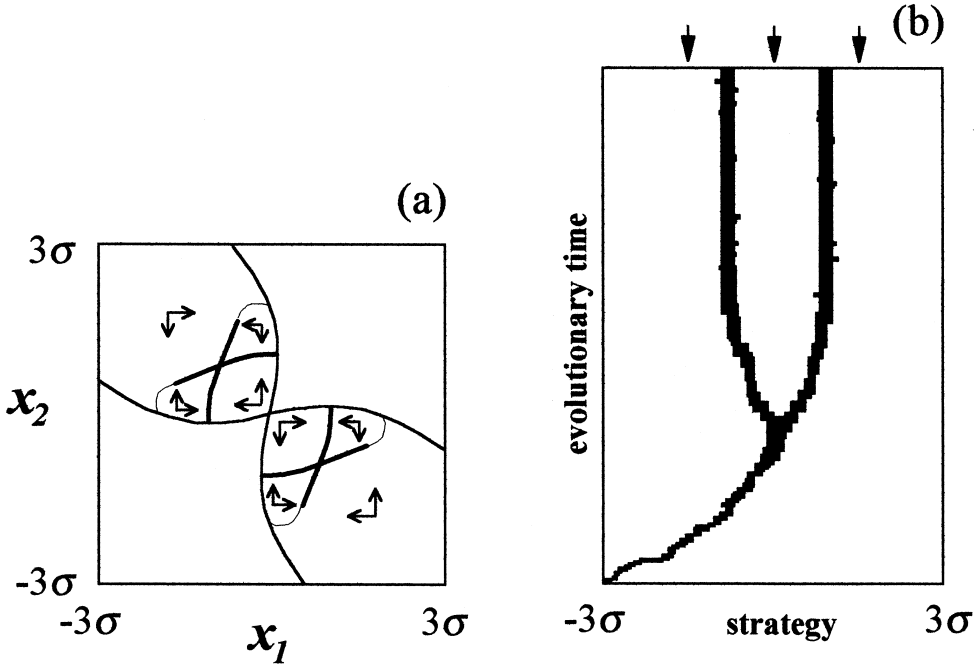


Figure 6. (a) Set of potential protected dimorphisms with invasion cones and isoclines for  $d/\sigma = 1.5$ . Thick isoclines are ESS-stable, thin isoclines lack ESS-stability. (b) Simulated evolutionary tree. The arrows at the top indicate the within-patch optimal strategies.

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 (Fig. 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 Fig. 6a) if

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

(cf. Equation 15), and a local minimum (thin lines in Fig. 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 (Fig. 6a). Therefore, after branching at  $x^* = 0$ , the population evolves towards a stable dimorphism in which the middle patch is exploited by both strategies, while the remaining two patches are both monopolized by only one strategy each (Fig. 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 coalitions (Fig. 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

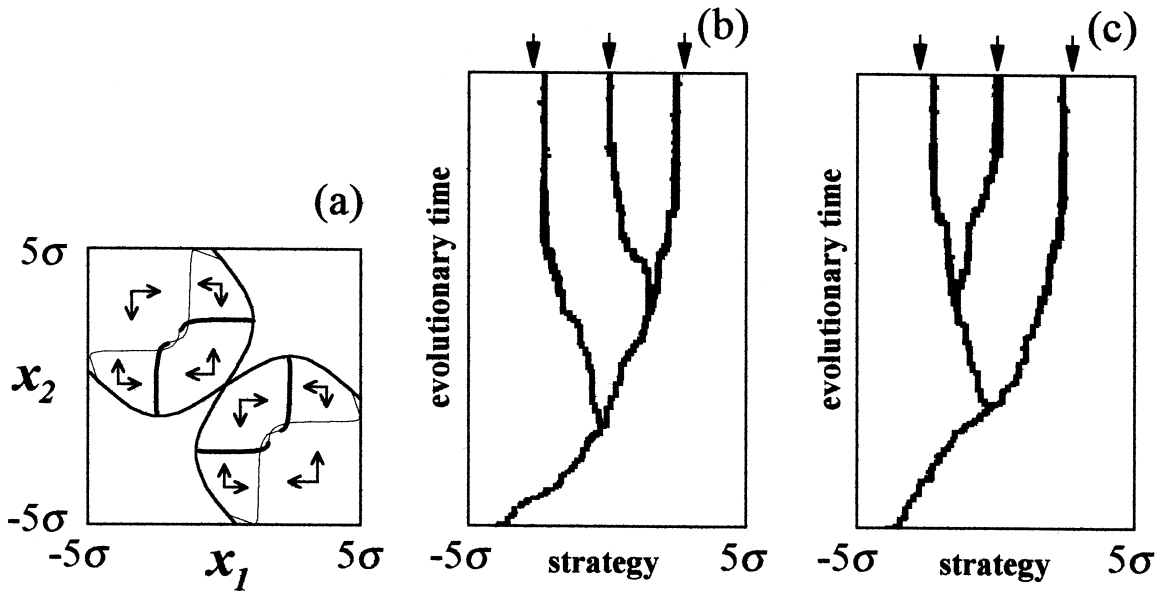


Figure 7. (a) Set of possible protected dimorphisms with invasion cones and isoclines for  $d/\sigma = 2.5$ . Thick isoclines are ESS-stable, thin isoclines lack ESS-stability. (b,c) Simulated evolutionary trees with alternative branching patterns. The arrows at the top indicate the within-patch optimal strategies.

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 the population will evolve first, the population eventually ends up as a stable trimorphism with each strategy adapted to its own specific patch (Figs 7b,c).

The dynamics of evolution as predicted by the model are confirmed by numerical simulations (Figs 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  $d/\sigma$  becomes larger than 1.22 (Fig. 8a). The dimorphic singularity first appears when the monomorphic singularity becomes a branching point (Fig. 8b). As patch difference increases, the strategies of the dimorphic coalition also grow further apart. At  $d/\sigma = 2.10$ , the dimorphic sin-

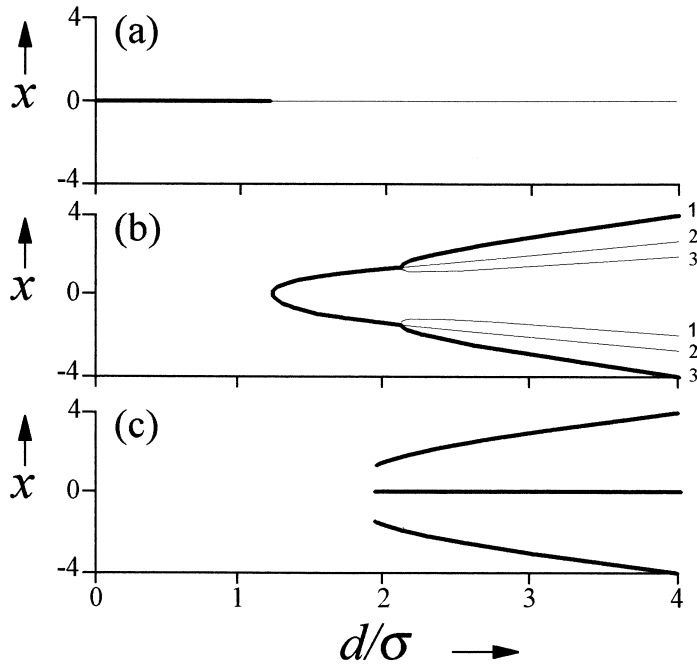


Figure 8. Bifurcation plot with  $d/\sigma$  as the bifurcation parameter for (a) the monomorphic singular strategy, (b) the dimorphic singular coalition (different strategy pairs are labelled 1–3), and (c) the trimorphic singular coalition. Thick lines indicate ESS-stability, thin lines indicate lack of ESS-stability of the corresponding strategy.

gularity 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 Fig. 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 dimorphism 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  $d/\sigma = 2.10$  (Fig. 8c). As patch difference decreases, the frequency of the middle strategy of the trimorphism becomes zero when  $d/\sigma$  approaches 1.93. At the same time, the other two strategies of the trimorphism converge to the dimorphic coalition (Fig. 8c). As patch difference increases, the strategies of the trimorphism converge to the within-patch optimal strategies  $\mu_1$ ,  $\mu_2$  and  $\mu_3$ .

Meszéna *et al.* (in press) demonstrated evolutionary branching in a monomorphic population in a similar model with two patches and limited migration between the patches (for recent related models, see 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 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 (Fig. 2), we can distinguish three main groups: singular strategies that lack convergence stability and therefore act as evolutionary repellers (Figs

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; Figs 2c–e), and hence represent final outcomes of an evolutionary process; and, finally, the singular strategy that is convergence-stable but not ESS-stable, that is, the evolutionary branching point (Fig. 2b). This latter type stands out in particular, because from a great 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 neighbourhood 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 neighbourhood 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; Mesz ena *et al.*, in press). However, in contrast with our basic assumptions, in the simulations new mutants often come along 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. Below we consider the significance of some of the other assumptions of the framework.

The present modelling is confined to one-dimensional strategies only (or to one-dimensional parameterizations of multidimensional 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 a fixed point, a limit cycle or an ergodic stochastic attractor (but see Rand *et al.*, 1994 and Ferriere and Gatto, 1995 for complications in the case of chaotic attractors). If there were more than one attractor, then the resident

population could no longer 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). Note, however, that neither evolutionary branching nor extinction of branches is 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 modelled 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 discrete step approach, but the dynamical properties are different. In particular, with infinitesimally small mutation steps, evolutionary branching does not occur. To see this, note that mutual invasibility is possible only within the neighbourhood 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 neighbourhood 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, mutual invasibility, and hence evolutionary branching, are no longer possible.

The dimensionality of the environment sets an upper limit to the number of different strategies that can co-exist 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 individuals 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 Meszena, 1993, 1995; Mylius and Dieckmann, 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 (Fig. 9a), both of which are degenerate cases in our general classification of the singular strategies (Fig. 2).



Another general prerequisite for evolutionary branching is that the mutant's fitness is a non-linear function of the mutant's strategy. This excludes branching in all cases where  $s_x(y)$  is given as the (weighted) arithmetic average over two alternative pure strategies (like in the case of matrix games) with  $x$  and  $y$  denoting the mixing frequencies for the resident and the mutant respectively. 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 (Fig. 9b), both of which are non-generic cases in the general classification of Fig. 2. Once the singular has been established, all mutations are neutral (Fig. 9b; cf. the 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 (Fig. 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 depends on the extent 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 sexual populations is the following. Assume that there is a continuum of potential allele types on a single, diploid locus, and that there exists a function  $\phi$  such that  $\phi(x_1, x_2)$  is the phenotype of an individual with alleles  $x_1$  and  $x_2$ . Moreover, we assume that the phenotype of a heterozygote is always intermediate between that of the two homozygotes. Note that this does not necessarily imply that the heterozygote also has an intermediate fitness. Consider an initially rare mutant allele  $y$  in a randomly mating monomorphic resident population with allele  $x$ . As long as the mutant allele is still 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

$$s_x(y) = r \langle \phi(x, y) E_{\phi(x, x)} \rangle \quad (25)$$

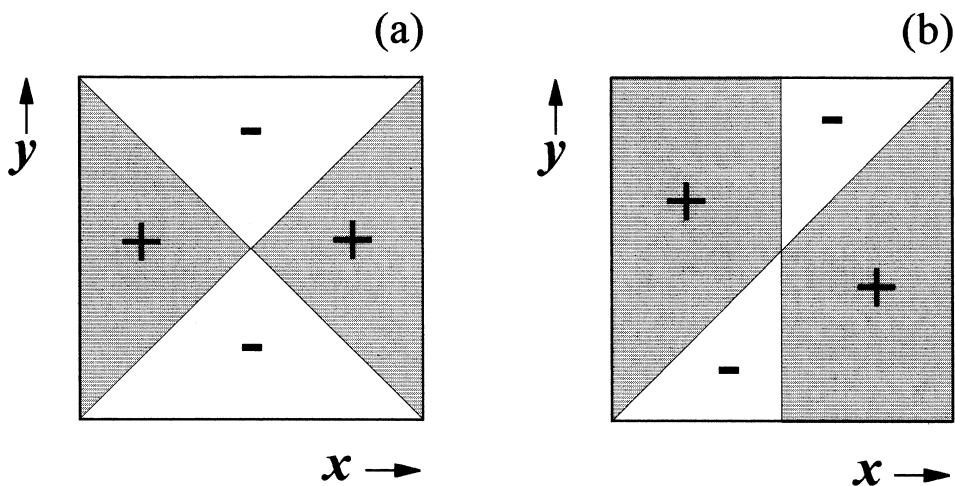


Figure 9. (a) Local configuration of the pairwise invasibility plot near a local fitness maximum (i.e. optimal strategy) if the environment is one-dimensional; the signs are opposite near a local fitness minimum (i.e. pessimal strategy). (b) Pairwise invasibility plot in the case of an ESS if the mutant's fitness is a linear function of the mutant's strategy (for a non-ESS the signs are opposite).

(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.

Depending on the particular problem at hand, all eight local configurations (Fig. 2) of the pairwise invasibility plot for allele types are theoretically possible, including the branching point. Branching in allele space leads to genetic polymorphisms where random mating also gives rise to heterozygotes with intermediate phenotypes. A necessary prerequisite for the evolution of reproductive isolation between two branches is that these heterozygote offspring have a lower fitness than homozygotes within the branches, while at the same time the genetic polymorphism in the population as a whole is preserved. During the process of evolutionary branching, both conditions are fulfilled. The heterozygotes have intermediate phenotypes that are selected against (Fig. 4e), and still the dimorphism is protected due to frequency-dependent selection. Evolutionary branching of alleles thus yields a stable dimorphism with partial post-zygotic isolation of the branches (that is, heterozygote inferiority). Under appropriate conditions, pre-zygotic reproductive isolation may indeed evolve, resulting in the formation of two distinct species (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).

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## Appendix 1

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

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

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

$$s_{x_1, x_2}(y) = s_{x_2, x_1}(y) \quad (\text{A2})$$

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

$$\beta_1 = \beta_2, \quad \gamma_{11} = \gamma_{22}, \quad \gamma_{13} = \gamma_{23} \quad (\text{A3})$$

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

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

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

$$\begin{aligned} \alpha &= 0 \\ \beta_1 &= \beta_2 = \beta_3 = 0 \\ \gamma_{11} &= \gamma_{22} = 0 \\ \gamma_{13} + \frac{1}{2}\gamma_{33} &= \gamma_{23} + \frac{1}{2}\gamma_{33} = 0 \\ \gamma_{12} + \gamma_{23} &= \gamma_{12} + \gamma_{13} = 0 \end{aligned} \quad (\text{A5})$$

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

$$s_{x^*, x^*}(y) = s_{x^*}(y) \quad (\text{A7})$$

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

$$s_{x^*}(y) = s_{x^*}(x^*) + \left[ \frac{\partial s_x(y)}{\partial y} \right]_{\substack{x=x^* \\ y=x^*}} (y - x^*) + \frac{1}{2} \left[ \frac{\partial^2 s_x(y)}{\partial y^2} \right]_{\substack{x=x^* \\ y=x^*}} (y - x^*)^2 \quad (\text{A8})$$

in which the first term is zero because of the selective neutrality of residents among themselves. The second term is also zero, because the local fitness gradient vanishes at the singular strategy. Equating (A1) with (A8) for  $x_1 = x_2 = x^*$  thus gives

$$\gamma_{33} = \left[ \frac{\partial^2 s_x(y)}{\partial y^2} \right]_{\substack{x=x^* \\ y=x^*}} \quad (\text{A9})$$

If we combine the information given in (A3), (A5) and (A9), and use this to simplify Equation (A1), we get

$$s_{x_1, x_2}(y) = \left[ \frac{\partial^2 s_x(y)}{\partial y^2} \right]_{\substack{x=x^* \\ y=x^*}} (y - x_1)(y - x_2) \quad (\text{A10})$$

It follows that the graph of  $s_{x_1, x_2}(y)$  as a function of  $y$  is a parabola with zeros at  $y = x_1$  and  $y = x_2$ . If  $x^*$  is ESS-stable, the coefficient in (A10) is negative (see Equation 5), so that the parabola has a maximum and is positive for  $y$  in between  $x_1$  and  $x_2$  (Fig. 4b). If  $x^*$  lacks ESS-stability, the coefficient in (A10) is positive (see Equation 5), and the parabola has a minimum and is positive for  $y$  outside  $x_1$  and  $x_2$  (Fig. 4e).

Equation (A10) readily generalizes to cases of mutual invasibility of nearby types in the vicinity of a singular coalition. Consider a protected polymorphism  $x_1, \dots, x_n$  close to a singular coalition  $x_1^*, \dots, x_n^*$ . 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 a 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

$$s_{x_1, \dots, x_i, x_i', \dots, x_n}(y) = \left[ \frac{\partial^2 s_{x_1, \dots, x_i, \dots, x_n}(y)}{\partial y^2} \right]_{\substack{y=x_i^* \\ x_j=x_i^* \forall j}} (y - x_i)(y - x_i') \quad (\text{A11})$$

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 2

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  $j^{\text{th}}$  patch, and let the pre-competitive survival probability,  $f_j(x)$ , for an individual with strategy  $x$  in the  $j^{\text{th}}$  patch be given by Equation (22). Then, the fitness of an initially rare mutant with strategy  $y$  in an equilibrium resident population with strategy  $x$  is

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

(cf. Equation 21), where the total population size  $\Sigma N_i$  is equal to  $\Sigma K_i$  (cf. Equation 17). At a singular strategy,  $x^*$ , the local fitness gradient by definition is zero, that is,

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

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

$$x^* = \sum_{j=1}^m c_j \mu_j \quad (\text{B3})$$

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

$$\frac{\partial^2 s_x(y)}{\partial x^2} = \sum_{j=1}^m c_j \left(\frac{x^* - \mu_j}{\sigma^2}\right)^2 + \frac{1}{\sigma^2} \quad (\text{B4})$$

and

$$\frac{\partial^2 s_x(y)}{\partial y^2} = \sum_{j=1}^m c_j \left(\frac{x^* - \mu_j}{\sigma^2}\right)^2 - \frac{1}{\sigma^2} \quad (\text{B5})$$

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

$$\frac{\partial^2 s_x(y)}{\partial x^2} + \frac{\partial^2 s_x(y)}{\partial y^2} = 2 \sum_{j=1}^m c_j \left(\frac{x^* - \mu_j}{\sigma^2}\right)^2 \quad (\text{B6})$$

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

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

but lacks ESS-stability if

$$\sum_{j=1}^m c_j \frac{(x^* - \mu_j)^2}{\sigma^2} > 1 \quad (\text{B8})$$

(cf. Equation 5). In other words,  $x^*$  is an ESS as long as  $\sigma$  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

$$\frac{\partial^2 s_x(y)}{\partial x^2} - \frac{\partial^2 s_x(y)}{\partial y^2} = \frac{2}{\sigma^2} \quad (\text{B9})$$

which is positive (cf. Equation 8). Consequently, if  $x^*$  is not an ESS, it is 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 Inequalities (B7) and (B8) respectively become  $d/\sigma < \sqrt{1.5}$  ( $\approx 1.22$ ) and  $d/\sigma > \sqrt{1.5}$ .