



## Evolutionary Branching under Asymmetric Competition

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I investigate the evolution of a continuous trait, such as body size or arms level, which affects the outcome of competitive contests such that the contestant with the larger trait value has a higher probability of winning. I show that a polymorphism of distinctly different strategies can evolve in an initially monomorphic population even if mutations have only small phenotypic effect. In a simple Lotka–Volterra-type model of asymmetric competition, I derive the conditions under which two strategies can gradually evolve from a single ancestral strategy; the evolution of higher level polymorphisms is studied by numerical analysis and computer simulations of specific examples. High levels of polymorphism may build up during evolution. The coevolution of strategies in polymorphic populations, however, may also lead to extinction, which decreases the level of polymorphism. I discuss whether the evolution of several haploid strategies from a single initial strategy may correspond to the evolution of several sympatric species in a diploid outbreeding population.

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### Introduction

The outcome of competitive interactions often depend on traits which influence or indicate competitive ability, such as body size, weight, armament, or costly signals of strength (e.g. Clutton-Brock *et al.*, 1979; Clutton-Brock & Albon, 1979; Weiner, 1986, 1990; Weiner & Thomas, 1986; Carroll & Salamon, 1995; Luiselli, 1996; Mitani *et al.*, 1996; Roberts, 1996; Simmons & Scheepers, 1996). The contestant with the larger trait value has a higher probability of winning the contest; large values of the trait, however, are costly in terms of reduced survival probability or reduced fecun-

dity. Competitive asymmetry between members of a population has been recognized as an important factor for example in shaping within-population variability (Begon, 1984; Begon *et al.*, 1996) and in stabilizing population dynamics (Lomnicki, 1989). Asymmetry is also prevalent in between-species competition (Lawton & Hassell, 1981; Connell, 1983; Schoener, 1983; Englund *et al.*, 1992), where the larger species is usually superior in interference competition (Persson, 1985; Alatalo & Moreno, 1987; Dickman, 1988; Thompson & Fox, 1993).

A wide range of evolutionary dynamics may occur for traits that determine competitive success. It is intuitively appealing that the competitive advantage of individuals larger than the rest of the population may lead to runaway evolution or an “arms race” (Dawkins & Krebs,

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1979; Maynard Smith & Brown, 1986). The evolutionary increase of the trait value, however, may come to a halt either because the cost of large trait values increases and eventually outweighs the advantage, or because population size decreases such that competition is relaxed (Parker, 1983; Abrams & Matsuda, 1994). The population may reach a unique stable strategy, but multiple attractors are also possible (Abrams & Matsuda, 1994). Evolution may lead to extinction either because the trait value increases without limit and the associated population density asymptotically decreases to zero, or because the evolutionarily stable population has such a low density that it is endangered by demographic or environmental stochasticity (Matsuda & Abrams, 1994).

A population of large individuals may be invaded by considerably smaller mutants, which cannot win competitive contests against the residents, but which are free from the costs of large size. Invasion of small mutants may give rise to a stable dimorphism (Abrams & Matsuda, 1994), or to evolutionary cycles in which runaway evolution towards large trait values is reset when small mutants take over the population (Maynard Smith & Brown, 1986). Asymmetric competition can also maintain a continuous evolutionarily stable distribution of trait values (Maynard Smith & Brown, 1986; Geritz, 1995).

A series of coevolutionary models assumed that size differences not only influence competitive superiority but also imply niche differentiation (Roughgarden, 1979; Rummel & Roughgarden, 1985; Brown & Vincent, 1987; Taper & Case, 1992). These models yield either a stable coalition of several species, or taxon cycles started by the invasion of a new species, followed by directional coevolution, extinction, and reconstitution of the initial species assemblage. Coevolution of two species with different within- and between-species competition was modelled by Law *et al.* (1997), who found multiple evolutionary attractors, parallel evolution or character convergence, evolutionary cycles, and extinction of one species.

In this paper, I investigate the evolution of polymorphism under asymmetric competition. Previous models with evolutionarily stable polymorphic populations or multispecies co-

alitions either did not consider the dynamics of evolution leading to polymorphism, or assumed that invaders had the best strategy given the present composition of the resident population. Though the latter procedure is apt to identify evolutionarily stable coalitions, it may be unrealistic for the actual dynamics of evolution [Taper & Case (1992) discuss this assumption in more detail]. Here I assume that mutants are phenotypically similar to the resident strategies already present, and investigate how polymorphisms of distinctly different strategies can evolve by small mutational steps.

In most cases when a slightly different mutant appears in a resident population, it either invades and replaces the former resident strategy, or dies out; repeated invasions result in directional evolution of the trait (Eshel, 1983; Taylor, 1989). The resident and the mutant can coexist only when directional evolution ceases, i.e. near a so-called evolutionarily singular point. The evolutionary singularity where directional evolution arrives at may be an ESS; it also may, however, lack evolutionary stability. Near a singularity of the latter type, the invading mutant can coexist with the former resident; moreover, the two strategies undergo divergent coevolution, which gives rise to two phenotypically distinct strategies (Metz *et al.*, 1992, 1996; Eshel *et al.*, 1997; Geritz *et al.*, 1997, 1998). The emergence of a dimorphism in an initially monomorphic population (or of an  $n + 1$ -morphism in an  $n$ -morphic population) followed by the gradual differentiation of the two initially similar strategies is called evolutionary branching, and the singular point at which the process initiates a branching point (Metz *et al.*, 1996; Geritz *et al.*, 1997, 1998).

Assuming small mutations, the level of polymorphism can increase only by evolutionary branching. Hence I explore the evolution of polymorphism under asymmetric competition primarily by searching for evolutionary branching points. However, as I will also demonstrate, the coevolution of strategies which have arisen by evolutionary branching can lead to the extinction of a strategy later, thus the population can fall back to a lower level of polymorphism again.

The specific model I assume is a Lotka–Volterra competition model, where the com-

petitive coefficients are determined by the differences between the trait values of the contestants. First I investigate under which conditions a monomorphic population can undergo evolutionary branching and thus become dimorphic. This part of the model analysis can be done without restricting generality by assuming specific functional forms in the model. Second, I explore the evolutionary dynamics of polymorphic populations. Since this is possible only by numerical analysis, I give three examples with different functions assumed. The examples illustrate repeated evolutionary branching leading to high levels of polymorphism, evolutionarily stable polymorphisms, and extinction. Qualitatively similar results have been obtained by Geritz *et al.* (1999), under significantly different model assumptions.

### The Model

I investigate the evolution of a single continuous trait such as body size or arms level. The trait has two effects on fitness. First, individuals of the population engage in competitive interactions, where a trait value larger than that of the contestant confers an advantage. Asymmetric competition thus exerts frequency-dependent selection for larger trait values. Second, large values of the trait imply a cost in terms of low survival and/or fecundity, irrespectively of other individuals. Frequency-independent selection may be either stabilizing (both small and large trait values are disadvantageous, intermediate trait values are favoured) or directional (large trait values are costly, small trait values are favoured). For example, stabilizing selection is likely to operate on body size. Armaments used solely to gain competitive advantage monotonously decrease fitness in a competition-free environment.

Let  $n$  denote the number of strategies present in the population, with trait values  $x_1, \dots, x_n$  and population densities  $N_1, \dots, N_n$ . Population dynamics are described by the Lotka–Volterra equations,

$$\frac{dN_i}{dt} = N_i \left[ \rho(x_i) - \sum_{j=1}^n \alpha(x_i - x_j) N_j \right] \quad (1)$$

where  $\rho(x_i)$  is the intrinsic growth rate of strategy  $x_i$  in a competition-free environment, and  $\alpha(x_i - x_j)$  is the competition coefficient which describes the effect of strategy  $x_j$  on strategy  $x_i$ .  $\rho(x)$  is a decreasing function at least for large values of  $x$ . The competitive coefficient,  $\alpha(x_i - x_j)$ , is a decreasing function of the difference between the trait value of the individual and that of its contestant: individuals with large trait value experience little competition by small individuals, while small individuals suffer from high competition by large individuals. The concave–convex function

$$\alpha(x_i - x_j) = c \left( 1 - \frac{1}{1 + v \exp(-k(x_i - x_j))} \right) \quad (2)$$

shown in Fig. 1 is a flexible way of modeling this situation.

This model is similar to the one investigated recently by Law *et al.* (1997), with the following differences: (i) they considered two species with a single resident strategy for each; (ii) the intrinsic growth rate function ( $\rho(x)$ ) was assumed to be linear, and the competition coefficients were given by eqn (2) with  $v = 1$ ; and (iii) different intensities of interspecific and intraspecific asymmetric competition [i.e. different values of  $k$  and  $c$  in eqn (2) for within- and between-species competition] were allowed for.

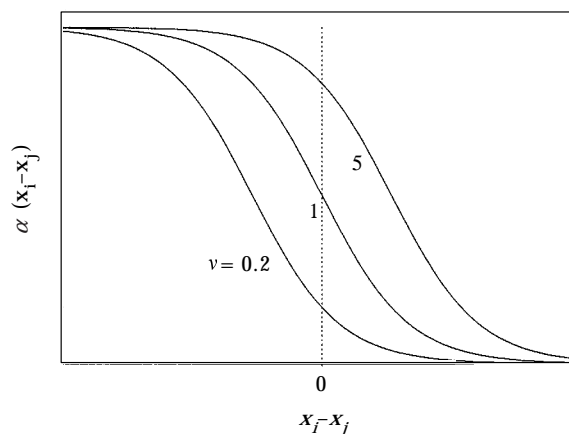


FIG. 1. Concave–convex shape of  $\alpha$  as given by eqn (2) ( $v = 0.2$ ; 1; 5;  $c = 2$ ;  $k = 4$ ).

Here I consider an arbitrary number of coexisting strategies in a population, and assume that competition is determined solely by the trait values of the contestants. Except in the examples, I do not assume any particular function for  $\rho(x)$  or  $\alpha(x_i - x_j)$ .

In order to analyse the dynamics of evolution, I assume that mutations are of small phenotypic effect. Evolution is mutation-limited, i.e. mutations occur infrequently such that a mutant strategy either has spread or has been excluded, and the population has reached its equilibrium, by the time the next mutant comes along.

### Adaptive Dynamics under Asymmetric Competition

In this section I start with a population of a single resident strategy, and investigate under which conditions this strategy can undergo evolutionary branching giving rise to two resident strategies. At the end of this section I briefly describe the generalized analysis for polymorphic resident populations.

Consider a rare mutant strategy  $y$  in the resident population of strategy  $x$ . The mutant increases in number if its growth rate,

$$r_x(y) = \rho(y) - \alpha(y - x)N(x) \quad (3)$$

is positive [cf. eqn (1)]; a mutant with negative growth rate dies out. The resident population has zero growth rate ( $r_x(x) = 0$ ) at the equilibrium population density  $N(x) = \rho(x)/\alpha(0)$ . It follows that a mutant strategy  $y$  slightly larger than  $x$  can invade and replace the resident if the fitness gradient

$$\left. \frac{\partial r_x(y)}{\partial y} \right|_{y=x} = \rho'(x) - \alpha'(0)\rho(x)/\alpha(0) \quad (4)$$

is positive; smaller mutants can invade if the fitness gradient is negative. Notice that since the resident and its slightly different mutant take part in competition, the shape of function  $\alpha(y - x)$  is relevant only near  $y - x = 0$ .

Repeated invasions and substitutions result in directional evolution until the population reaches an evolutionary singularity, where the fitness gradient is zero. At the singular strategy  $x^*$ , the proportionate cost of increasing the trait,

$|\rho'(x^*)/\rho(x^*)|$ , must balance the constant advantage given by  $|\alpha'(0)/\alpha(0)|$  [cf. eqn (4)]. If the cost is too high for all trait values, then frequency-independent selection drives evolution towards decreasing trait values despite the competitive advantage of being larger. Runaway evolution leads to increasing trait values if the proportionate cost is smaller than the advantage for all trait values. Notice, however, that if  $\rho(x)$  becomes zero at some  $x_{max}$ , then the proportionate cost must exceed the advantage as  $x$  increases, and therefore evolution must reach a singularity before  $x_{max}$ .

Whether or not the population can undergo evolutionary branching at a singularity depends on two stability criteria (Metz *et al.*, 1996; Geritz *et al.*, 1997, 1998; Eshel *et al.*, 1997). First, the singular strategy must be convergence stable such that directional evolution of a monomorphic population can approach it. This condition is fulfilled if

$$\frac{d}{dx} \left[ \left. \frac{\partial r_x(y)}{\partial y} \right|_{y=x} \right]_{x=x^*} = \left[ \frac{\partial^2 r}{\partial x \partial y} + \frac{\partial^2 r}{\partial y^2} \right]_{y=x=x^*} < 0 \quad (5)$$

(Eshel, 1983; Taylor, 1989; Christiansen, 1991). Second, the singularity must lack evolutionary stability, i.e.

$$\left[ \left. \frac{\partial^2 r_x(y)}{\partial y^2} \right|_{y=x=x^*} \right] > 0 \quad (6)$$

(Maynard Smith, 1982). Substituting  $r_x(y)$  from eqn (3) into inequalities (5) and (6), a singular strategy is a branching point if

$$\rho''(x^*) - \frac{\alpha'(0)}{\alpha(0)} \rho'(x^*) < 0 \quad (7)$$

and

$$\rho''(x^*) - \alpha''(0) \frac{\rho(x^*)}{\alpha(0)} > 0 \quad (8)$$

The singularities that are both convergence stable and evolutionarily stable [i.e. satisfy inequality (7) and the opposite of inequality (8)] are final stops of evolution; these were called continuously stable strategies or CSSs by Eshel (1983). Convergence unstable singularities [that

TABLE 1  
Possible evolutionary singularities with different functional forms  $\rho$  and  $\alpha$

	$\alpha$ near zero		
	Concave ( $\alpha''(0) < 0$ )	Linear or inflection ( $\alpha''(0) = 0$ )	Convex ( $\alpha''(0) > 0$ )
Concave $\rho$ ( $\rho''(x^*) < 0$ )	CSS or branching point	CSS	CSS
Linear $\rho$ ( $\rho''(x^*) = 0$ )	Branching point	Degenerate	CSS
Convex $\rho$ ( $\rho''(x^*) > 0$ )	Branching point or repellor	Branching point or repellor	CSS, branching point or repellor

do not satisfy inequality (7)] are evolutionary repellers.

The first derivatives in inequality (7) are both negative:  $\alpha'(0)$  is negative by definition, and  $\rho'(x^*)$  must be negative otherwise the fitness gradient [eqn (4)] cannot be zero at  $x^*$ . It follows from inequality (7) that the singularity is always convergence stable if  $\rho(x)$  is concave or linear, and may be convergence stable if  $\rho(x)$  is convex. (Throughout the paper, I use the terms “concave” and “convex” as seen from below, i.e. a concave function has a negative second derivative.) Inequality (8) shows that a locally concave shape of  $\alpha(y-x)$  near  $y-x=0$  promotes evolutionary branching; so does the convexity of  $\rho(x)$  as long as the singularity remains convergence stable. Table 1 summarizes the possible outcomes of evolution for different shapes of  $\rho$  and  $\alpha$ .

If  $\alpha''(0) = 0$  and  $\rho(x)$  is linear, then the monomorphic singular strategy is degenerate in the sense that  $\partial^2 r_x(y)/\partial y^2|_{y=x=x^*} = 0$ , i.e. the singularity just undergoes a bifurcation between an ESS and a branching point. Since both the first and the second derivatives of the fitness function vanish at the singularity, it is the third derivative  $\partial^3 r_x(y)/\partial y^3|_{y=x=x^*}$  that determines which mutants can invade. If the third derivative is positive, then mutants smaller than  $x^*$  cannot invade the singular strategy, whereas a larger mutant can invade and coexist with  $x^*$ . A negative third derivative leads to the opposite result. The details of evolutionary dynamics in dimorphic populations near such a singularity are quite complicated, and will be presented

elsewhere (Kisdi, *in prep.*). Ultimately, however, the population undergoes evolutionary branching at the degenerate singularity.

Evolutionary branching gives rise to a polymorphism of two substantially different strategies in an initially monomorphic population. The subsequent coevolution of the coexisting strategies can be modelled similarly to the monomorphic populations (Geritz *et al.*, 1998). The fitness of a rare mutant  $y$  in the population of resident strategies  $x_1, \dots, x_n$  is

$$r_{x_1, \dots, x_n}(y) = \rho(y) - \sum_{j=1}^n \alpha(y-x_j)N_j \quad (9)$$

[cf. eqn (1)]. The fitness gradient

$$\left. \frac{\partial r_{x_1, \dots, x_n}(y)}{\partial y} \right|_{y=x_i} = \rho'(x_i) - \sum_{j=1}^n \alpha'(x_i-x_j)N_j \quad (10)$$

determines the direction of evolution of the resident strategy  $x_i$ . Notice that in polymorphic populations the shape of function  $\alpha$  is significant not only near zero, because mutants of one resident must compete also with other, substantially different residents.

Polymorphic evolutionary singularities are coalitions of resident strategies where the fitness gradient of each strategy is zero. Unfortunately, a general condition for convergence stability is not straightforward in polymorphic populations (Matessi & Di Pascuale, 1996). If the population arrives near the singular coalition, a particular

resident strategy  $x_i$  can undergo evolutionary branching if it is evolutionarily unstable, i.e. if

$$\left. \frac{\partial^2 r_{x_1, \dots, x_n}(y)}{\partial y^2} \right|_{y=x_i} = \rho''(x_i) - \sum_{j=1}^n \alpha''(x_i - x_j) N_j \quad (11)$$

is positive. This condition is necessary; however, it is sufficient only if all the other strategies of the singular coalition are evolutionarily stable, and hence remain at the singularity. If other strategies also lack evolutionary stability, and they evolve with different speed, then the fastest of them can undergo branching while the others may lag behind. As branching in one strategy generally changes the frequency-dependent fitness function [eqn (9)], the slower evolving strategies may no longer be near a branching point, i.e. they may have missed the opportunity for branching. Faster evolution of a strategy is possible if it is present in greater number (since the speed of evolution is limited by the appearance of new mutants, and the number of mutants is proportional to the number of individuals), or if the rate or size of mutations depends on the trait value.

Polymorphic populations with asymmetric competition may have very rich adaptive dynamics, a full exploration of which is beyond the scope of this paper. The following examples illustrate the possibility of evolution to a stable polymorphism, repeated evolutionary branching, “missed” branching, and extinction following evolutionary branching.

### Examples

The following three examples assume different functional forms for the intrinsic growth rate  $\rho(x)$ . The competitive coefficient function  $\alpha(y - x)$  remains unspecified; in the numerical analyses of polymorphic populations, however, I use eqn (2) for  $\alpha(y - x)$  with different values of  $v$ . If  $v < 1$  then  $\alpha$  is convex, if  $v > 1$  then  $\alpha$  is concave, and if  $v = 1$  then  $\alpha$  has an inflection point at  $y - x = 0$ .

#### EXAMPLE 1: LINEAR $\rho(x)$

If the intrinsic growth rate is a linearly decreasing function of the trait value,

$$\rho(x) = \beta - bx \quad (12)$$

then  $\partial r_x(y)/\partial y|_{y=x=x^*} = 0$  can be solved explicitly for the monomorphic singular strategy

$$x^* = \frac{\beta}{b} + \frac{\alpha(0)}{\alpha'(0)} \quad (13)$$

The singularity is always convergence stable; evolutionary branching occurs if  $\alpha$  is concave near zero (Table 1).

Coevolution following evolutionary branching can be analysed numerically using eqns (10) and (11). The results are shown in Fig. 2(a) for a dimorphic population where  $\alpha$  is given by eqn (2). For each pair of coexisting strategies, the direction of evolution of  $x_1$  and  $x_2$  can be

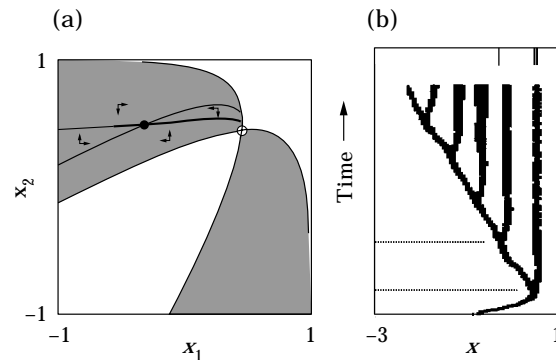


FIG. 2. (a) Isocline plot with linear  $\rho(x)$ . Strategy pairs inside the shaded area can form a protected dimorphism. The direction of evolution of  $x_1$  ( $x_2$ ) is shown by horizontal (vertical) arrows as determined from eqn (10). Thick isoclines are evolutionarily stable [eqn (11) is negative]; thin isoclines are evolutionarily unstable [eqn (11) is positive]. (○) indicates the branching point ( $x_1 = x_2 = x^* = 0.45$ ), (●) corresponds to the dimorphic singular coalition, ( $x_1^* = -0.32, x_2^* = 0.49$ ). At the singular coalition,  $x_1$  (i.e. the smaller strategy) is evolutionarily unstable,  $x_2$  (the larger strategy) is evolutionarily stable; (b) simulated evolutionary tree. Starting with a monomorphic population, evolution first converges to  $x^* = 0.45$  where it undergoes evolutionary branching; the two branches evolve to ( $x_1^* = -0.32, x_2^* = 0.49$ ), where the smaller strategy undergoes branching again. Subsequent evolution leads to increasing levels of polymorphism by repeated branching. The position of the branching point and the dimorphic singular coalition, as read from the isocline plot, are shown by the vertical bars above the tree; horizontal dotted lines indicate when the population is at the monomorphic and dimorphic singularities. Parameter values:  $\beta = 1, b = 1, c = 2, v = 1.2, k = 4$ .

determined from eqn (10): in Fig. 2(a), these are indicated by horizontal and vertical arrows, respectively, within the set of protected dimorphisms. Directional evolution of one or the other resident strategy ceases at the so-called isoclines. The intersection of the isoclines thus corresponds to the dimorphic evolutionary singularity.

The expected course of evolution of the dimorphic population can be read from the isocline plot in Fig. 2(a) as follows. For convenience, I assume that the smaller strategy of the coalition is denoted by  $x_1$  and the larger one is  $x_2$  (that is, I consider the upper half of the plot above the  $x_2 = x_1$  diagonal). At the beginning of evolutionary branching, the population contains two strategies both near  $x^*$ , which undergo disruptive coevolution, i.e.  $x_1$  decreases and  $x_2$  increases. Evolution soon arrives at the  $x_2$ -isocline, and proceeds along this isocline towards the singular coalition  $(x_1^*, x_2^*)$ . Since the  $x_2$ -isocline is nearly horizontal, the larger strategy will stay approximately constant while the smaller strategy evolves towards even smaller trait values. In the singular coalition, the large strategy is evolutionarily stable, but the small strategy is evolutionarily unstable [as determined from eqn (11) and indicated by the thickness of the isoclines]. The small strategy thus undergoes secondary branching, giving rise to a trimorphic population. Subsequent evolution can be analysed similarly to the dimorphic case; however, I do not pursue the numerical analysis further because the results cannot be visualized.

With linear  $\rho(x)$ , a strategy  $x_i$  in the  $n$ -morphic singular coalition lacks evolutionary stability if  $-\Sigma\alpha''(x_i - x_j)N_j$  is positive [cf. eqn (11)]. Notice that this condition is always satisfied for the smallest strategy of the coalition, provided that  $\alpha$  is concave-convex and  $\alpha''(0) < 0$ . The first branching is thus followed by a series of further evolutionary branching events; the series of repeated branching is interrupted only if the smallest possible trait value is reached. Depending on the model parameters, some of the larger strategies can undergo further branching as well.

I also performed direct simulations of the evolutionary process in order to confirm the

model predictions, and to illustrate the evolutionary dynamics of three and more coexisting strategies [Fig. 2(b)]. In the simulations, I iterated the population dynamics according to eqn (1), starting with a monomorphic population. Mutant strategies were generated by small deviations from strategies already present, and were introduced at a low initial frequency. By the iteration of the population dynamics some strategies grew in number, others declined. If the frequency of a strategy dropped below a low threshold, the strategy was considered extinct and was removed from the iteration. The evolutionary tree shows the strategies present at various times during the simulation. The simulations were not mutation-limited, i.e. mutants appeared before the previous mutants reached their equilibrium density or went extinct. As a consequence, there was always some variation within a branch of the evolutionary tree. This variation, however, did not confound the model predictions: the first branching in the simulation took place near the monomorphic branching point ( $x^*$ ) as determined above, the lower branch evolved downwards while the upper branch remained approximately constant, and the second branching happened near the singular coalition  $(x_1^*, x_2^*)$ .

#### EXAMPLE 2: GAUSSIAN $\rho(x)$

Stabilizing selection on the trait can be modelled by assuming that the intrinsic growth rate is a Gaussian function of the trait value,

$$\rho(x) = a \exp\left(-\frac{(x - m)^2}{2\sigma^2}\right) \quad (14)$$

In this case, there is a single monomorphic singularity at

$$x^* = m - \frac{\alpha'(0)}{\alpha(0)} \sigma^2 \quad (15)$$

that is larger than the optimal trait value in a competitive-free environment ( $m$ ) because  $\alpha'(0)$  is negative. The singular strategy is always convergence stable [inequality (5) reduces to

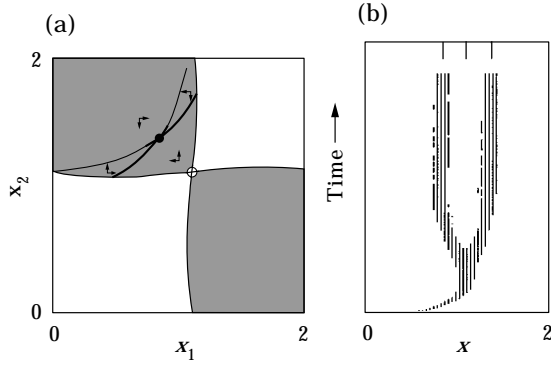


FIG. 3. (a) Isocline plot with Gaussian  $\rho(x)$ ; (b) simulated evolutionary tree. The monomorphic population has a branching point at  $x_1 = x_2 = x^* = 1.1$ ; there is an evolutionarily stable dimorphic coalition at  $(x_1^* = 0.84, x_2^* = 1.37)$ . Notations as in Fig. 2. Parameter values:  $a = 1, m = 0, \sigma = 1, c = 2, v = 1, k = 2.2$ .

$-\rho(x^*)/\sigma^2 < 0$ ]. The monomorphic population undergoes evolutionary branching if

$$\left. \frac{\partial^2 r_x(y)}{\partial y^2} \right|_{y=x=x^*} = \rho(x^*) \left[ \left( \frac{\alpha'(0)}{\alpha(0)} \right)^2 - \frac{1}{\sigma^2} - \frac{\alpha''(0)}{\alpha(0)} \right] > 0 \quad (16)$$

Evolutionary branching is hence promoted if (i)  $|\alpha'(0)/\alpha(0)|$  is large, i.e. there is strong asymmetry in competition, (ii)  $\sigma^2$  is large, i.e. stabilizing selection is weak, and (iii)  $\alpha$  is concave at zero.

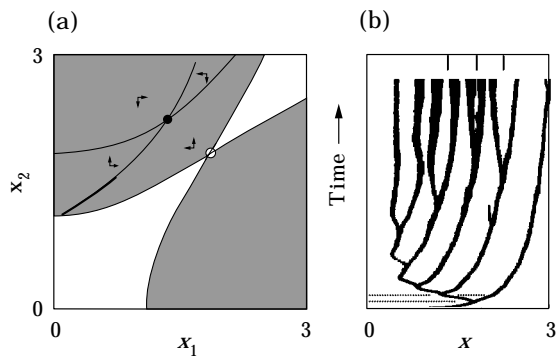


FIG. 4. (a) Isocline plot with Gaussian  $\rho(x)$ . (b) Simulated evolutionary tree. The monomorphic population has a branching point at  $x_1 = x_2 = x^* = 1.81$ . In the dimorphic singular coalition  $(x_1^* = 1.33, x_2^* = 2.24)$ , both strategies lack evolutionary stability; in the simulation, however, the larger strategy at the two-strategy stage misses evolutionary branching. Notations as in Fig. 2. Parameter values:  $a = 1, m = 0, \sigma = 1, c = 2, v = 1.2, k = 4$ .

Strong asymmetry and weak stabilizing selection result in a large  $x^*$  [cf. eqn (15)], such that the Gaussian function  $\rho(x)$  is convex at  $x^*$ , which favors branching (Table 1).

Following evolutionary branching, the population may reach an evolutionarily stable coalition of two strategies provided that the competitive asymmetry is sufficiently weak, i.e.  $k$  is sufficiently small in eqn (2) (Fig. 3). With stronger asymmetry, however, further evolutionary branching occurs. The isocline plot in Fig. 4(a) shows an example where both strategies of the dimorphic singular coalition lack evolutionary stability. The population density of the smaller strategy is higher, hence it produces more mutants and evolves faster. Once the smaller strategy has undergone branching, the fitness function [eqn (9)] slightly changes such that the singularity shifts away from the present trait value of the larger strategy. Whether or not the larger strategy will still undergo branching depends on the size of mutations relative to the magnitude of this shift: if mutations are not very small, then the larger strategy can still branch, but if mutations are of sufficiently small phenotypic effect, then the opportunity for evolutionary branching in the larger strategy is missed. Figure 4(b) illustrates a simulation with missed branching; an analogous simulation with somewhat larger mutations led to branching in both strategies of the dimorphic coalition.

Repeated evolutionary branching can lead to high levels of polymorphism [Fig. 4(b)]. Unlike in the case of linear  $\rho(x)$ , the coexisting strategies are confined in range such that all strategies are larger than  $m$ , the optimal trait value in a competition-free environment: strategies below  $m$  are disadvantageous with respect to both stabilizing selection and asymmetric competition, and therefore would experience strong selection towards larger trait values.

#### EXAMPLE 3: CONVEX $\rho(x)$

If the intrinsic growth rate is a convex function of the trait value, then a monomorphic population may have multiple evolutionary singularities. Here I assume the monotonically decreasing, convex function

$$\rho(x) = -a - b(x - \sqrt{x^2 + d}) \quad (17)$$



with non-negative  $a$  and positive  $b$  and  $d$ . For large negative values of  $x$ , this function is approximately linear with slope  $-2b$ . As  $x$  increases, the function becomes less steep; for large positive values of  $x$ , it asymptotically converges to  $-a$ .

If  $a = 0$ , i.e. if even very large strategies have positive growth rates in a competition-free environment, then there are two monomorphic evolutionary singularities at

$$x_{1,2}^* = \pm \sqrt{\left(\frac{\alpha(0)}{\alpha'(0)}\right)^2 - d} \quad (18)$$

The larger singular strategy is always convergence unstable, hence an initial population above this singularity undergoes runaway evolution towards large trait values. The smaller singularity is a branching point unless  $\alpha$  is too convex (Table 1). If competitive asymmetry is strong such that  $(\alpha(0)/\alpha'(0))^2 < d$ , then there is no evolutionarily singular strategy: runaway evolution leads to ever increasing trait values unless the strategy set is constrained. As the trait value increases, the equilibrium population density,  $N(x) = \rho(x)/\alpha(0)$ , decreases: the population evolves towards extinction (Matsuda & Abrams, 1994).

If  $a > 0$ , then  $\rho(x)$  is negative for large trait values, and therefore runaway evolution is not possible. The monomorphic evolutionary singularities are the roots of a third-degree polynomial; the largest one is always convergence stable. Figure 5 shows the singular trait values as a function of competitive asymmetry. If  $\alpha$  is convex near zero [Fig. 5(a)], then there may be one or two convergence stable ESSs; if  $\alpha$  is concave [Fig. 5(b)], then all convergence stable singularities are branching points (cf. Table 1).

Evolutionary branching gives rise to protected polymorphism. It does not guarantee, however, that the polymorphism is persistent on an evolutionary time-scale: coevolution of the coexisting strategies can lead to extinction, and thus the population can fall back to a lower level of polymorphism. Such an evolutionary scenario is illustrated in Fig. 6. There are two convergence stable monomorphic evolutionary singularities, an ESS and a branching point, with a repellor in between. A monomorphic population above the

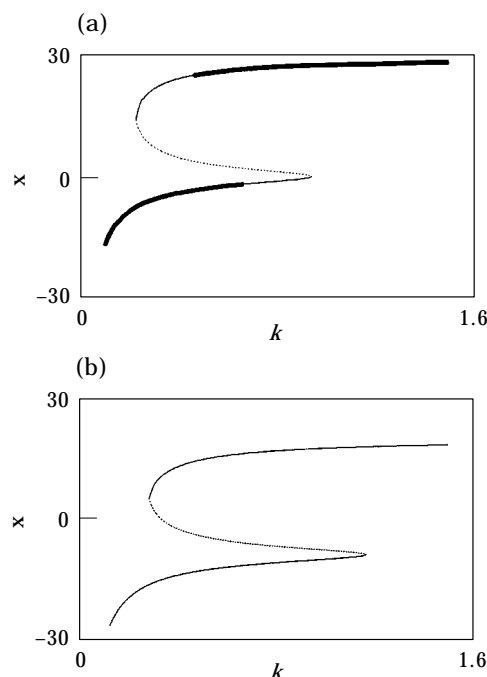


FIG. 5. The monomorphic evolutionary singularities for convex  $\rho(x)$  as given by eqn (17).  $\alpha$  is specified by eqn (2); increasing  $k$  corresponds to increasingly asymmetric competition. (—) denotes evolutionarily stable strategies, (---) branching points, and (· · ·) evolutionary repellers. (a)  $\alpha$  is convex near zero ( $v = 0.7$ ); (b)  $\alpha$  is concave near zero ( $v = 1.1$ ). Parameter values:  $a = 0.6$ ,  $b = 10$ ,  $d = 3.5$ ,  $c = 2$ .

repellor evolves to the branching point and becomes dimorphic. However, there is no dimorphic singularity in the domain of protected dimorphisms in which the population is evolving. Therefore the population eventually leaves the set of protected dimorphisms, and the larger strategy of the dimorphism goes extinct. The remaining monomorphic population is below the repellor and hence evolves to the monomorphic ESS.

### Discussion

In a simple asymmetric competition model based on the Lotka–Volterra equations, I have demonstrated the possibility for evolutionary branching, i.e. the evolution of polymorphism by small mutational steps in an initially monomorphic population. Repeated evolutionary branching readily leads to high levels of polymorphism [e.g. Figs 2(b) and 4(b)].

Evolutionary branching is possible only if a large and a small strategy can coexist in a

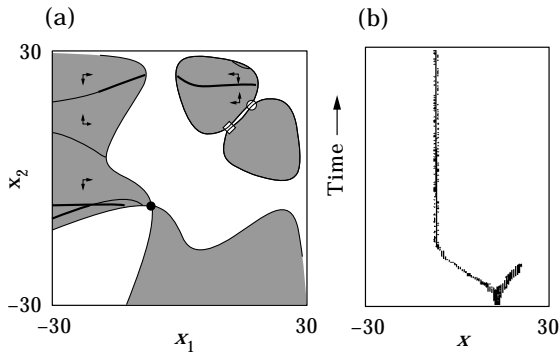


FIG. 6. (a) Isocline plot with convex  $\rho(x)$  as given by eqn (17). The monomorphic population has three singularities, an ESS at  $x_1 = x_2 = x^* = -6.86$  ( $\bullet$ ), a repeller at  $x_1 = x_2 = x^* = 11.37$  ( $\diamond$ ), and a branching point at  $x_1 = x_2 = x^* = 17.22$  ( $\circ$ ); other notations as in Fig. 2; (b) simulated evolutionary tree. Starting with a monomorphic population above the repeller, the population evolves to the branching point and undergoes evolutionary branching; the dimorphic population, however, leaves the area of protected dimorphism, i.e. the larger strategy goes extinct. The remaining monomorphic population is below the repeller and therefore evolves to the ESS. Parameter values:  $a = 0.6$ ,  $b = 10$ ,  $d = 3.5$ ,  $c = 2$ ,  $v = 0.7$ ,  $k = 0.24$ .

protected dimorphism. A large strategy can invade the population of small individuals by its competitive superiority. A small strategy can, however, also invade the population of large individuals. Though small individuals cannot win a contest against large ones, they have a good chance to avoid any such contest altogether, because the large strategy can maintain only a low population density due to the cost of large trait values. The few contests encountered and lost by small individuals is overcompensated by their greater intrinsic growth rate, i.e. by not bearing the cost of large size.

When runaway evolution proceeds up to large trait values, then even a slightly smaller mutant can invade and coexist with the former resident. This sets the initial stage of evolutionary branching. If the two coexisting strategies experience disruptive selection (which is mathematically equivalent to there being no evolutionarily stable strategy sufficiently similar to them), then divergent coevolution gives rise to two phenotypically distinct branches.

For simplicity, I always started with a monomorphic population and investigated whether it can undergo evolutionary branching. Evolutionary branching, however, may occur

more easily in an initially polymorphic population. Such an example is shown in Fig. 7. Here the monomorphic population has an ESS, therefore no polymorphism evolves [Fig. 7(a)]. If, however, the initial population is dimorphic, then the smaller strategy undergoes repeated evolutionary branching whereby a high level of polymorphism can evolve [(Fig. 7b)]. This implies that there may be a threshold level of polymorphism above which higher level polymorphisms can be evolutionarily restored. If some environmental catastrophe were to kill all but two strategies of the rich coalition built up in Fig. 7(b), then highly polymorphic coalitions can evolve again provided that the two remaining strategies are able to coexist and evolve to the dimorphic branching point. If only one strategy is left, then it will evolve to the ESS, thus the polymorphism cannot be regained.

#### EVOLUTIONARY BRANCHING IN OTHER MODELS OF ASYMMETRIC COMPETITION

The Lotka–Volterra type model used in this paper is perhaps the simplest model of asymmetric competition. It is not, however, a mechanistic model, i.e. it is not derived from underlying elementary processes of individual life histories. When trading off ecological realism for simplicity, it is crucial to ask how robust the predictions are with respect to structural modifications of the model.

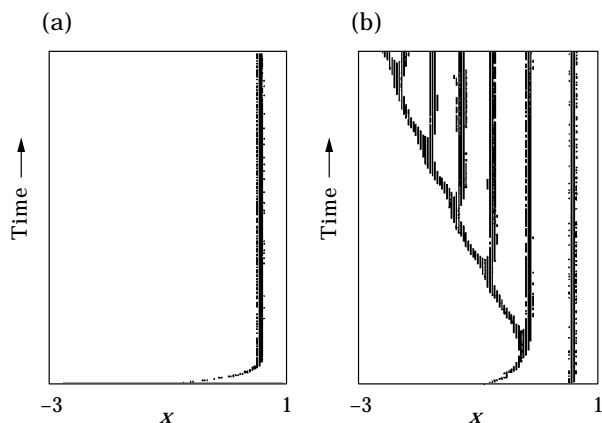


FIG. 7. Simulated evolutionary trees. (a) Starting with a monomorphic population, evolution converges to an ESS; (b) starting with a dimorphic population, the smaller strategy undergoes repeated evolutionary branching.  $\rho(x)$  is linear [eqn (12)],  $\alpha$  is given by eqn 2; parameter values are  $\beta = 1$ ,  $b = 1$ ,  $c = 2$ ,  $v = 0.8$ ,  $k = 4$ .

A short preliminary analysis of the asymmetric competition model proposed by Roughgarden in order to explain taxon cycles (Roughgarden, 1979; Rummel & Roughgarden, 1985; Brown & Vincent, 1987; Taper & Case, 1992) also indicated evolutionary branching. In this model, however, different strategies exploit partially different niches in addition to the differences in their competitive ability. Niche segregation is known to promote evolutionary branching without competitive asymmetry (Metz *et al.*, 1996).

In a model constructed specifically for the evolution of seed size in plants, the results obtained by Geritz *et al.* (1999) were strikingly similar to the present study, including evolutionary branching, repeated branching, and extinction. This is surprising because their model was rather different from the simple Lotka–Volterra model used here. Seeds were assumed to disperse randomly into safe-sites, such that the number of seeds per site was variable. Competition was restricted to seeds within the same site. Individuals competed according to a weighted lottery, where an increase in seed size conferred a disproportionate advantage as larger seedlings oppress smaller ones by shading. Larger seeds also had higher precompetitive survival probability; large seeds, however, could be produced in less number given the limited resources provided by a safe site. The fitness function incorporating these ecological details is analytically untractable and much more complicated than eqn (3). Nevertheless the predicted evolutionary scenarios are similar, which may reflect a fundamental similarity of the evolutionary mechanism operating in the two models: the evolutionary increase of the trait value promoted by competitive asymmetry leads to low population density, where competition is relaxed and smaller mutants can invade.

It would be premature, however, to conclude that competitive asymmetry facilitates evolutionary branching in general. Reanalysing four asymmetric competition models used by Abrams & Matsuda (1994), I found that evolutionary branching is possible in only two of them: Branching may occur in the constant density “free for all” competition model and in the variable density “pairwise” competition model,

but branching is not possible in the variable density “free for all” model and in the constant density “pairwise” model of Abrams & Matsuda (1994). Further research is required in order to identify the critical ecological factors which determine whether asymmetric competition can lead to evolutionary branching.

#### EVOLUTIONARY BRANCHING AND DIPLOID MULTILOCUS GENETICS

As in most previous models with evolutionary branching (Metz *et al.*, 1996; Doebeli & Ruxton, 1997; Meszéna *et al.*, 1997; Geritz *et al.*, 1998, 1999; Geritz & Kisdi, in press; Mathias & Kisdi, in press; Meszéna & Metz, in press), I modelled evolution on a phenotypic level and assumed that strategies breed true (i.e. there is haploid or clonal inheritance). In diploid outbreeding species, recombination may severely affect the outcome of evolution. As long as the population is monomorphic and undergoes directional evolution, the phenotypic adaptive dynamics (termed often as the “ESS-approach”) are largely compatible with the quantitative genetic models (Charlesworth, 1990; Iwasa *et al.*, 1991; Taper & Case, 1992; Abrams *et al.*, 1993a,b; Taylor, 1996). At an evolutionary branching point, however, random mating and recombination recreates the intermediate phenotypes that are selected against during evolutionary branching, and thereby prevent the emergence of two phenotypically separate branches. If mating is random and recombination is free, the evolution of polygenic traits will get stuck at the branching point, in spite of that the population is at a fitness minimum and thus experiences disruptive selection (Abrams *et al.*, 1993a).

Evolutionary branching may occur under diploid multilocus inheritance only if recombination is prevented by reproductive isolation between the emerging branches. Although the evolution of reproductive isolation in sympatry is still controversial, there is some empirical evidence which seems to support the possibility (e.g. Coyne & Orr, 1989, 1997; Rice & Hostert, 1993; Johannesson *et al.*, 1995; Noor, 1995; Saetre *et al.*, 1997; Rundle & Schluter, 1998).

If the trait under selection (henceforth referred to as the primary trait) determines mate choice,

then evolutionary branching immediately results in prezygotic isolation (Templeton, 1981; Rice, 1984; Smith, 1988; Rice & Salt, 1990; Rice & Hostert, 1993; Galis & Metz, 1998). In an explicit multilocus genetic model, Doebeli (1996) and Doebeli and Dieckmann (in press) demonstrated that disruptive selection leads to bimodal phenotypic distribution (the multilocus equivalent of branching) under assortative mating. A realistic example for this scenario may involve body size as the primary trait: body size has a strong influence on mate choice, and disruptive selection on body size is thought to lead to sympatric speciation in several species (Schluter & Nagel, 1995; Nagel & Schluter, 1998). Body size is often a main factor in competitive asymmetry. It is thus reasonable to expect that asymmetric competition, by generating disruptive selection on body size at an evolutionary branching point, may cause sympatric speciation when mating is size-assortative.

If there is no assortative mating in the initial population, it may still evolve when the population is at the evolutionary branching point. Under disruptive selection on the primary trait, an allele influencing mate choice such that carriers prefer mates with primary trait similar to their own is spread by selection (Maynard Smith, 1966; Seger, 1985; Doebeli, 1996; Doebeli & Dieckmann, in press). Assortative mating based on the primary trait evolves easily because no linkage disequilibrium is needed between the primary trait and the mate choice loci (Felsenstein, 1981; Rice & Hostert, 1993).

Reproductive isolation may also evolve independently of the primary trait, for example by sexual selection (Turner & Burrows, 1995). Two reproductively isolated groups, or species, cannot coexist permanently without niche differentiation. However, if the isolated groups appear in a population that has been stuck at a branching point, then any initial difference in the primary trait will be amplified by disruptive selection: the population will undergo evolutionary branching such that the two isolated groups evolve into the two branches, and thereby gain the differentiation necessary for stable coexistence as separate species (Galis & Metz, 1998).

Multilocus inheritance is also likely to violate the assumption of mutation-limited evolution: the more loci affect the trait, the more mutations occur, and therefore the less likely it is that a new mutant appears only after the population has reached its equilibrium. The assumption of mutation-limited evolution greatly simplifies the analysis of the model. However, as the direct simulations demonstrate, the model predictions are robust with respect to the frequency of mutations.

Multilocus genetic models often assume that each locus has only two alternative alleles. This is, however, not necessarily true *a priori*. If there is a continuum of different potential alleles at a locus, and mutations give rise to phenotypically similar alleles, then the adaptive dynamics framework can be applied to the evolution of alleles within a locus. In a one-locus diploid model, Kisdi and Geritz (in press, 1999) showed that alleles undergo evolutionary branching much like haploid strategies in the phenotypic model, giving rise to a protected genetic polymorphism of two distinctly different alleles. It is not yet known to what extent this result generalizes to several loci.

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