

Evolutionary Dynamics of Seed Size and Seedling Competitive Ability

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We present a model for the evolutionary dynamics of seed size when there is a trade-off between seed size and seed number, and seedlings from large seeds are better competitors and have a higher precompetitive survival than seedlings from small seeds. We find that strong competitive asymmetry, high resource levels, and intermediate harshness of the precompetitive environment favor coexistence of plants with different seed sizes. If the evolution of seed size is mutation-limited and single mutations have only a small phenotypic effect, then an initially monomorphic population reaches the final evolutionarily stable polymorphic state through one or more discrete evolutionary branching events. At each such branching event, a given lineage already present in the population divides into two phenotypically diverging daughter lines, each with its own seed size. If the precompetitive survival of seeds and seedlings is high for small and large seeds alike, however, evolutionary branching may be followed by the extinction of one or more lineages. Various results presented here are model-independent and point the way to a more general evolutionary bifurcation theory describing how the number and stability properties of evolutionary equilibria may change as a consequence of changes in model parameters. © 1999 Academic Press

Key Words: seed size evolution; seedling competition; frequency-dependent selection; adaptive dynamics; evolutionary branching; extinction; evolutionary bifurcation theory.

1. INTRODUCTION

An important element in the reproductive strategy of a plant is the partitioning of its seed output into many small seeds or a few large ones. Large seeds tend to produce seedlings that have a higher probability of survival and a higher reproductive output when established but cannot be produced in as large numbers as small seeds (Fenner, 1985). Smith and Fretwell (1974) formulated a model for the optimal balance between the size and the number of seeds. In their model, the fitness,

W , of a plant with seed size m and a total amount of R resources is given by

$$W = \frac{R}{m} f(m), \quad (1)$$

where $f(m)$ is the expected reproductive yield per seed as a function of seed size. The optimal seed size, m_{opt} , that maximizes fitness corresponds to the point of contact where the graph of $f(m)$ is tangent to a straight line through the origin (Fig. 1a). Independently of the exact shape of $f(m)$, there is always a single best seed size that

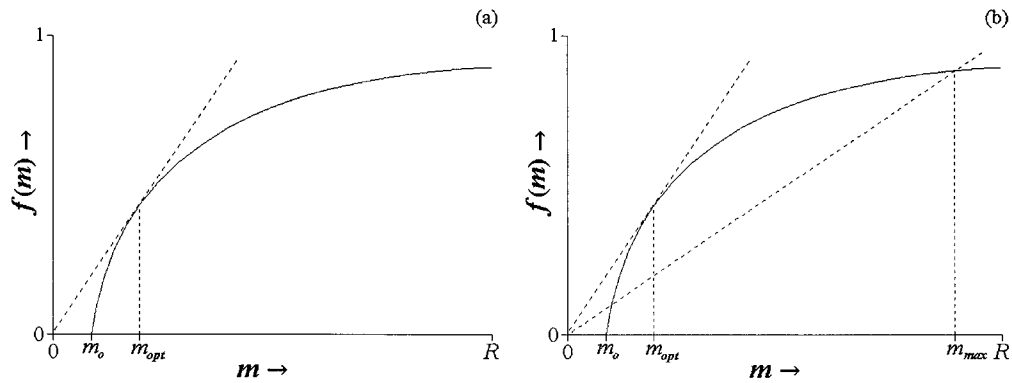


FIG. 1. (a) Optimization of offspring size in the Smith–Fretwell (1974) model. The optimal offspring size, m_{opt} , coincides with the point of contact where the graph of $f(m)$ is touched by a straight line through the origin. (b) Evolutionarily stable seed size distribution in the model of Geritz (1995). The ESS includes all seed sizes between the Smith–Fretwell optimum, m_{opt} , and m_{max} , which is given the intersection of the graph of $f(x)$ with the main diagonal.

is moreover independent of the amount of resources available per plant. Thus, according to the model of Smith and Fretwell (1974) all plants in a given population should produce seeds of one size only.

Still, variation in seed size is common both among and within individual plants in the same population (Michaels *et al.*, 1988; Westoby *et al.*, 1992). To explain this variation as an adaptation (rather than as a constraint on a plant's ability to produce seeds of uniform size) various alternative models have been proposed, each of which emphasizes different aspects of a plant's life history or its environment (see, e.g., Kaplan and Cooper, 1984; Venable, 1985; Begon and Parker, 1986; Parker and Begon, 1986; Temme, 1986; Lloyd, 1987; McGinley and Charnov, 1988; McGinley *et al.*, 1987; García-Dorado, 1990; Lalonde, 1991; Venable, 1992; Geritz, 1995; Sakai, 1995; Sakai and Sakai, 1995; Rees and Westoby, 1997; Geritz, 1998).

In this paper we investigate how competition among seedlings can affect the evolution of seed size when

seedlings from large seeds are better competitors and have a higher precompetitive survival than seedlings from small seeds. We use an extension of the Smith–Fretwell (1974) model based on a competition model for annual plants without a seed bank as described by Geritz *et al.* (1988) and Geritz (1995). In the model, seeds are dispersed randomly into a large number of discrete germination sites such that the number of seeds landing in any one site is Poisson-distributed. During dispersal, germination, and early seedling growth, the offspring first undergo a period of frequency-independent selection due to predation, burial, desiccation, and so forth. The survival probability for seeds of size m during this period of frequency-independent selection is denoted by $f(m)$ and is given by

$$f(m) = \max\{0, 1 - 2 \cdot \exp(-\beta m)\} \quad (2)$$

(Fig. 2a). Different values of β correspond to different habitat types: High values of β are typical for open, moist

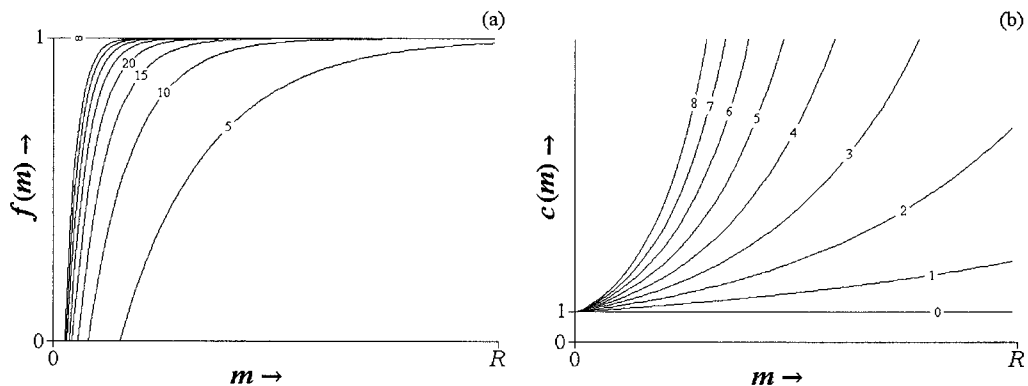


FIG. 2. (a) Precompetitive seed and seedling survival, $f(m)$, for different values of βR representing different types of environments. (b) Seedling competitive ability, $c(m)$, for different values of αR representing different levels of competitive asymmetry.

conditions that favor seedling establishment for both small and large seeds (Gross and Werner, 1982; Gross, 1984; Stanton, 1984; Wulff, 1986a). Low values of β , on the other hand, represent harsher conditions under perennial vegetation or litter where seedling establishment is low and where large seeds have a significant precompetitive advantage relative to smaller seeds (Grime and Jeffrey, 1965; Haskins and Gorz, 1975; Gross and Werner, 1982; Gross, 1984; Winn, 1985). In the limit for β approaching infinity, all seeds survive and produce established plants irrespectively of their size. Additional, non-selective (i.e., seed size-independent) precompetitive mortality due to seed landings outside of suitable germination sites, trampling or flooding, and so forth, will be implicitly accounted for by reducing the amount of available resources.

Seedlings that survive the initial phase of frequency-independent selection compete for the locally available resources within a germination site. Individual seedlings may have different expected future fecundities depending on the amount of resources obtained. The total amount of resources per germination site is denoted by R . We assume that in a site with a total number of k competitors with, respectively, seeds of sizes m_1, \dots, m_k , the fraction of R gained by an individual seedling with seed size m_i ($i = 1, \dots, k$) is equal to

$$\frac{c(m_i)}{c(m_1) + \dots + c(m_k)}, \quad (3)$$

where $c(m)$ is a measure of the competitive ability of a seedling with seed size m . Alternatively, Eq. (3) can be interpreted as the probability of establishment when there is room for only one established plant per germination site so that competition affects survival rather than fecundity (see, e.g., Chesson and Warner, 1981; Fagerström and Ågren, 1979; Ågren and Fagerström, 1984; Geritz *et al.*, 1988; Geritz, 1995). The two interpretations are mathematically equivalent, however, and give the same demographic and evolutionary outcomes.

In various species, seed size has been shown experimentally to affect the competitive ability of seedlings in favor of larger seeds (Black, 1958; Stanton, 1985; Wulff, 1986b). We assume that the competitive ability of a seedling is given by

$$c(m) = \exp(\alpha m) \quad (4)$$

(Fig. 2b). Different values of α correspond to different levels of competitive asymmetry: if α is zero, seed size has no effect on the competitive ability of seedlings, and all seedlings in a given germination site get the same amount of resources irrespectively of their seed size (i.e., symmetric

competition). Differences in fitness between plants with different seed sizes are then due only to differences in precompetitive seed and seedling survival, $f(m)$, so that we effectively recover the Smith–Fretwell (1974) model. With symmetric competition, therefore, we find a single optimal seed size excluding all other seed sizes (Fig. 1a). For larger values of α , however, a large seed size gives a competitive advantage relative to smaller seeds. In the limit for α approaching infinity, only the single seedling from the largest seed present in a given germination site obtains resources while all other seedlings in the same site get none at all and thus fail to reproduce (i.e., extremely asymmetric competition). With extremely asymmetric competition there is no longer a single, optimal seed size, because a population with a single seed size can always be invaded by plants with slightly larger seeds or by plants with sufficiently smaller but (due to the size–number trade-off) more numerous seeds (Geritz *et al.*, 1988). Instead, there is an evolutionarily stable seed polymorphism with a continuum of seed sizes (Fig. 1b). Plants with small seeds survive because they are better colonizers (because of their larger seed number) which enables them to exploit sites that by chance remain unoccupied by the larger (but less numerous) seeds of their competitors (Geritz, 1995).

In this paper we investigate the evolutionary consequences of intermediate levels of competitive asymmetry (α), different types of precompetitive environment (β), and different amounts of resources per germination size (R). We explore how the two extreme outcomes of the model (i.e., a single optimal seed size with symmetric competition on the one hand, and a continuum of coexisting seed sizes with extremely asymmetric competition on the other) are connected to one another via intermediate levels of competitive asymmetry. At intermediate levels of competitive asymmetry the model is very hard to analyze algebraically, and we therefore resort to numerical analyses instead. To this end we assume that each individual plant produces seeds of one size only, and that the offspring always have the same seed size as the mother. In the Discussion we shall argue how the results can be interpreted in the context of sexual reproduction. We further assume that phenotypic mutations in seed size occur only very infrequently, and only one at a time, so that the resident population has reached its demographic equilibrium before the next mutant comes along. Finally, we assume that the effect of a single mutation on seed size is small but finite so that evolution proceeds by small but discrete individual steps. We analyze the model within the context of a theoretical framework for modeling evolutionary dynamics developed by Metz *et al.* (1996) and Geritz *et al.* (1997, 1998).

2. EVOLUTIONARILY SINGULAR STRATEGIES

Resident Population Dynamics

Consider a resident population with n different plant types, each with its own seed size denoted by m_i ($i = 1, \dots, n$), and let $N_{i,t}$ denote the density in year t of plants with seed size m_i expressed as the average number of established plants per germination site. The fraction of resources obtained per seedling with seed size m_i in a germination site together with k_1, \dots, k_n seedlings with, respectively, seeds of sizes m_1, \dots, m_n is given by

$$\frac{c(m_i)}{c(m_i) + k_1 c(m_1) + \dots + k_n c(m_n)} \quad (5)$$

(cf. Eq. (3)). Modeling a trade-off between seed size and seed number in the same way as in the model of Smith and Fretwell (1974), and taking into account that only a fraction $f(m_i)$ of all seeds of size m_i survive the precompetitive phase and eventually become established plants, the number of established offspring produced by a plant with seed size m_i in a germination site together with k_1, \dots, k_n other plants with seeds of sizes m_1, \dots, m_n is

$$f(m_i) \frac{R}{m_i} \left(\frac{c(m_i)}{c(m_i) + k_1 c(m_1) + \dots + k_n c(m_n)} \right). \quad (6)$$

Assuming Poisson-distributed seed numbers per germination site, the numbers of competing seedlings per germination site, k_1, \dots, k_n , are also Poisson-distributed with expectations $N_{1,t}, \dots, N_{n,t}$, so that the expected number of established offspring per plant with seed size m_i is given by

$$f(m_i) \frac{R}{m_i} \cdot \left(\sum_{k_1=0}^{\infty} \dots \sum_{k_n=0}^{\infty} \frac{c(m_i)}{c(m_i) + k_1 c(m_1) + \dots + k_n c(m_n)} \times \frac{(N_{1,t}^{k_1} \dots (N_{n,t})^{k_n})}{k_1! \dots k_n!} e^{-N_{1,t} - \dots - N_{n,t}} \right). \quad (7)$$

By re-scaling seed size as the fraction of the available resources per germination site (i.e., using m_i/R instead of m_i as a relative measure of seed size) it follows from Eqs. (2), (4), and (7) that the outcome of the model will depend only on the two products αR and βR instead of each parameter individually.

At demographic equilibrium the expected per capita number of established offspring (Eq. (7)) is equal to one for all plant types present in the population. In a monomorphic resident population with only seeds of size m ,

there is a single, positive, and asymptotically stable equilibrium density whenever $f(m) R/m > 1$ (Geritz *et al.*, 1988). The equilibrium depends on the resident's seed size and hence will be denoted by $N(m)$. If $f(m) R/m \leq 1$, the per capita number of established offspring is too low to maintain a positive population density.

Mutant's Fitness

Next, consider a mutant plant with seed size m' in a monomorphic resident population with seed size m at demographic equilibrium. During the early phase of invasion when the mutant is still rare, the probability of two or more mutant seeds landing in the same germination site is assumed to be negligible. Mutant seedlings, therefore, initially compete only with resident seedlings and not among themselves. For the mutant's per capita number of established offspring, that is, its fitness, denoted by $W_m(m')$, we thus find

$$W_m(m') = f(m') \frac{R}{m'} \cdot \left(\sum_{k=0}^{\infty} \frac{c(m')}{c(m') + k \cdot c(m)} \times \frac{(N(m))^k}{k!} e^{-N(m)} \right). \quad (8)$$

Notice that $W_m(m')$ is equal to the mutant's fitness, $f(m') R/m'$, as in the Smith–Fretwell (1974) model (cf. Eq. (1)), times a correction factor that takes into account the effects of competition. Other authors have used the logarithmic growth rate, that is, $\ln(W_m(m'))$, as a measure of the mutant's fitness (see, e.g., Metz *et al.*, 1996; Geritz *et al.*, 1997, 1998; Mészéna *et al.*, 1997).

If $W_m(m') < 1$, the mutant dies out. If $W_m(m') > 1$, the mutant may spread (but need not always do so, because of the possibility of random extinction due to drift when there are still only very few copies of the mutant around). If the mutant spreads and in addition we have $W_{m'}(m) < 1$ (so that the resident cannot recover once rare itself), then the mutant will eventually replace the resident and take over the population. We shall refer to this as a substitution. If, however, the mutant spreads but in addition $W_{m'}(m) > 1$ (so that the resident is protected against extinction and cannot be replaced), then the population necessarily becomes dimorphic with both the resident and the mutant living together.

Evolutionarily Stable Singular Strategies

Figure 3a shows for which combinations of resident and mutant seed sizes $W_m(m')$ is larger or smaller than

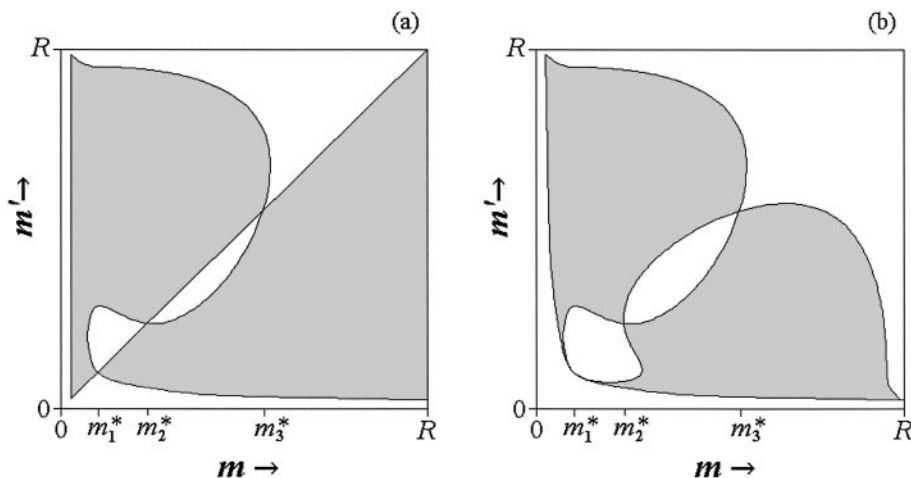


FIG. 3. (a) Pairwise invasibility plot for $\alpha R = 6$ and $\beta R = 25$. Shaded regions indicate where $W_m(m') > 1$. (b) Area of coexistence for the same parameter values. The shaded regions indicate combinations of m and m' that can mutually invade, and hence can coexist as a protected dimorphism.

one when $\alpha R = 6$ and $\beta R = 25$. To see what mutants can spread in a given resident population we look along a vertical line through the point on the m -axis representing the resident's seed size. The parts of this line inside a region for which $W_m(m') > 1$ (shaded regions) correspond to potentially invading mutants, and the parts of the line inside a region for which $W_m(m') < 1$ (unshaded regions) correspond to mutants that cannot invade. Of particular interest are the so-called evolutionarily singular strategies m_1^* , m_2^* , and m_3^* , characterized by

$$\left[\frac{\partial W_m(m')}{\partial m'} \right]_{m'=m} = 0 \quad (9)$$

(Metz *et al.*, 1996; Geritz *et al.*, 1997, 1998). Looking along a vertical line through m_1^* , it can be seen that no nearby mutants can invade a resident population in which all plants have seed size m_1^* . In other words, m_1^* is a (locally) evolutionarily stable strategy or ESS (Maynard Smith, 1982). For the mutant, an ESS corresponds to a local fitness maximum, and is therefore characterized by

$$\left[\frac{\partial^2 W_m(m')}{\partial m'^2} \right]_{m'=m} < 0 \quad (10)$$

(Maynard Smith, 1982). Notice that m_1^* is not a global ESS, because mutants further away (i.e., between $m' = 0.29 \cdot R$ and $m' = 0.95 \cdot R$) could invade if only they happened to appear. Assuming sufficiently small evolutionary steps, however, these seed sizes cannot be generated by a single mutation of m_1^* , and can therefore be ignored. Neither m_2^* nor m_3^* is (locally) evolutionarily stable.

Convergence Stable Singular Strategies

Figure 3b shows what combinations of resident and mutant seed sizes can coexist as a protected dimorphism (shaded regions). The figure was obtained by first taking the mirror image of Fig. 3a along its main diagonal (which gives all combinations of seed sizes for which $W_{m'}(m) > 1$), and putting it on top of the original. The overlapping parts of the shaded regions in the mirror image and in its original correspond to seed sizes for which both $W_m(m') > 1$ and $W_{m'}(m) > 1$ and which therefore can coexist as a protected dimorphism. We shall refer to the set of possible protected dimorphisms (Fig. 3b) as the area of coexistence. The area of coexistence reaches the diagonal only at the singular strategies m_1^* , m_2^* , and m_3^* (Fig. 3b). Coexistence of two very similar seed sizes is therefore only possible near a singular strategy and nowhere else. Consequently, with small evolutionary steps, any mutant that can spread in a given resident population will also replace the resident, that is, as long as the population stays away from the singular strategies.

Starting with a resident population with a seed size smaller than m_1^* , it can be seen from Fig. 3a that mutants with slightly larger seeds can invade (and subsequently replace the resident), whereas mutants with smaller seeds cannot. Similarly, a resident population on the other side of m_1^* can be invaded (and replaced) only by mutants with smaller seeds. Thus, with small evolutionary steps, m_1^* is an evolutionary attractor in the sense that an initially monomorphic population will gradually evolve toward m_1^* . Evolutionary attractors in the above sense are also called convergence stable (Christiansen, 1991), and are algebraically characterized by

$$\frac{d}{dm} \left\{ \left[\frac{\partial W_m(m')}{\partial m'} \right]_{m'=m} \right\} = \left[\frac{\partial^2 W_m(m')}{\partial m \partial m'} \right]_{m'=m} + \left[\frac{\partial^2 W_m(m')}{\partial m'^2} \right]_{m'=m} < 0 \quad (11)$$

(Eshel, 1983). Metz *et al.* (1996) and Geritz *et al.* (1997, 1998) have used different but equivalent conditions. From Fig. 3a it can also be seen that m_2^* lacks convergence stability (and thus is an evolutionary repeller from which an initially monomorphic resident population tends to evolve away), whereas m_3^* , again, is convergence stable.

Evolutionary Branching

Evolutionary stability and convergence stability are two fully independent properties that can occur in any combination (Eshel and Motro, 1981; Eshel, 1983; Eshel *et al.*, 1997; Taylor, 1989; Christianson, 1991; Abrams *et al.*, 1993; Eshel *et al.*, 1997). The evolutionary significance of protected dimorphisms nearby a singular strategy depends on the particular combination of the two types of stability. If a singular strategy is both convergence stable and evolutionarily stable (like in the case of m_1^* , Fig. 3a), only mutants with a seed size in between the two resident seed sizes can invade. In the long run the population converges to the singular strategy through a series of monomorphic or dimorphic population states (Metz *et al.*, 1996; Geritz *et al.*, 1997, 1998). Such a singular strategy (also called a continuously stable strategy, or CSS; Eshel and Motro, 1981; Eshel, 1983) represents a final, monomorphic stop of the evolutionary process.

In the case of m_2^* , which is an evolutionary repeller, the population most probably will evolve away before it has a chance of becoming dimorphic. Its main significance is that it separates the domains of attraction of m_1^* and of m_3^* .

The case of m_3^* (which is convergence stable but not evolutionarily stable) stands out in particular. For a monomorphic population it acts as an evolutionary attractor, but in a population in which all plants have seeds of size m_3^* , any nearby mutant can invade (Fig. 3a). Once the population has become dimorphic near the singular strategy, only mutants with a seed size outside the two resident seed sizes can invade, so that with each successive invasion the two resident types grow further and further apart (Metz *et al.*, 1996; Geritz *et al.*, 1997, 1998). We call this process of phenotypic divergence in an initially monomorphic resident population evolutionary branching. A singular strategy that is convergence

stable but not evolutionarily stable we call an evolutionary branching point.

Figure 4 shows the results of numerical simulations of the evolutionary process using Eq. (7) to calculate the change in plant density from one generation to the next in a population with an arbitrary number of different plant types. Starting with a monomorphic population at the beginning of the simulation (i.e., $n = 1$), new mutants are generated with a low probability per offspring by a small but random mutation from types already present. With each new mutation an extra equation for the mutant's population density is added to the system (i.e., n is increased by one). New mutants are introduced initially at a very low frequency, but may increase or decrease during subsequent generations. When the frequency of a given type falls below a certain predefined threshold, it is considered to have gone extinct and is removed from the population (i.e., n is decreased by one).

The simulations confirm the predictions of the theory: depending on the initial seed size, the population either evolves toward m_1^* (Fig. 4a) or evolves toward m_3^* where it undergoes evolutionary branching (Fig. 4b). Neither the precise density at which mutants are introduced or eliminated, nor the mutation rate or size, qualitatively affects the outcomes of the simulations. Moreover, in the simulations new mutants often come along before the resident population has reached its equilibrium and before inferior mutants have been eliminated, which demonstrates that the assumption of separate timescales

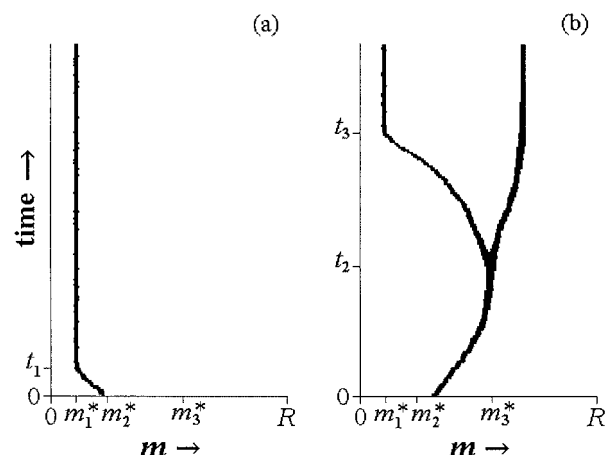


FIG. 4. Simulated evolutionary trees with different initial seed sizes for $\alpha R = 6$ and $\beta R = 25$. (a) The population starting left of the repeller m_2^* reaches the evolutionarily stable seed size m_1^* at time t_1 . (b) The population that starts on the right side of m_2^* evolves to the branching point m_3^* and undergoes disruptive selection at time t_2 . The population reaches a dimorphic evolutionarily stable state at time t_3 .

for selection and mutation is not very critical. The thickness of the trunk and branches in Fig. 4 gives the width of the phenotype distribution. Increasing the mutation rate or size increases the width of the trunk and branches, and also affects the timescale of the evolutionary dynamics. The occurrence of branching, however, remains unaffected. As the population approaches the branching point, directional selection becomes weaker and evolution slows down while the width of the phenotype distribution increases. The acceleration of evolution toward smaller seed sizes in the left branch in Fig. 4b is a consequence of smaller seeds being produced in larger numbers, leading to a larger total number of mutant offspring per plant.

Changes in Number and Stability Properties of Evolutionary Singular Strategies

The number and the stability properties of the singular strategies depend on the values of αR and βR . Figure 5 shows the invasion plots for various combinations of different parameter values (cf. Fig. 3a). we first consider the row with $\beta R = 25$. At low values of αR , there is only a single, convergence stable, and globally evolutionarily stable singular strategy (Fig. 5; $\alpha R = 4.5$, $\beta R = 25$). At higher values of αR , the singular strategy loses its global evolutionary stability and becomes a local ESS ($\alpha R = 5.0$, $\beta R = 25$). As αR increases further, two new singular strategies (i.e., a repeller and a branching point) appear when the curved line defined by $W_m(m') = 1$ first touches and then intersects the main diagonal at two additional points ($\alpha R = 5.5, 6.0$, and 6.5 , $\beta R = 25$). In a similar but reversed process at still higher values of αR , the lower two intersection points with the main diagonal move closer together and finally merge and annihilate one another, so that in the end only the branching point remains ($\alpha R = 7.0$, $\beta R = 25$). Just before the two singularities meet and disappear, however, the ESS first loses its evolutionary stability and becomes a branching point (Fig. 6).

At higher values of βR , increasing αR may lead to the simultaneous appearance of the repeller and the branching point before the ESS loses its global stability (e.g., Fig. 5; $\alpha R = 5.5$, $\beta R = 45$). The ESS then is globally evolutionarily stable but only locally convergence stable, which is possible because of the independence of evolutionary stability and convergence stability. At lower values of βR , the ESS may lose its global and local evolutionary stability without the appearance of additional singular strategies (e.g., Fig. 5; $\alpha R = 5.0$, $\beta R = 15$ and $\alpha R = 5.5$, $\beta R = 15$).

Figure 7a shows how the number and stability properties of the singular strategies change as αR and βR vary continuously. The figure was produced using Eqs. (9), (10), and (11) to numerically identify and characterize singular strategies in terms of their stability properties. For parameter values inside the hatched region the precompetitive seed and seedling survival is too low for maintaining a positive population density; that is, $f(m) R/m$ is always smaller than one. The seed size that maximizes fitness in the Smith–Fretwell (1974) model is then optimal in the sense that it minimizes the rate of population decline. For parameter values above the hatched region, but left of the dotted line, there is a single, convergence stable and globally evolutionarily stable singular strategy. On the other side of the dotted line the ESS has lost its global character and has become only a local ESS. The thin solid line indicates where the ESS loses its evolutionary stability altogether and turns into a branching point. Only at point P, where the dotted line and the thin solid line touch one another does the ESS lose both its global and its local evolutionary stability at the same time and turn directly into a branching point.

Inside the wedge-shaped domain formed by the thick solid lines there are three singular strategies. The left edge of the wedge indicates where the repeller and the branching point first appear when in the pairwise invasibility plot the curve on which $W_m(m')$ is equal to one touches and then intersects the main diagonal at two additional points. The right edge indicates where the repeller and the former ESS merge and disappear together. In classical bifurcation theory, the mutual annihilation of two singularities or the simultaneous appearance of two singularities as a consequence of changing model parameters is called a fold bifurcation. The tip of the wedge-shaped domain where the two fold bifurcations meet and cancel one another is a so-called cusp-bifurcation point (see, e.g., Kuznetsov, 1995). The significance of point Q is discussed later.

Figure 7b gives a horizontal cross section through the wedge-shaped domain in Fig. 7a at $\beta R = 35$ to show how the actual values of the singular strategies depend on αR . The thick solid line indicates ESSs, the thin solid line branching points, and the thin dashed line evolutionary repellers. Point S indicates where the global ESS becomes a local ESS. The change from a local ESS into a branching point occurs just before the curve bends upward and connects to the repeller, but the resolution of the figure is too low to show this clearly. Figure 7c is a cross section at $\beta R = 5$, illustrating that for values of βR below the cusp point in Fig. 7a the fold has disappeared and stretched out into a monotonously increasing line.

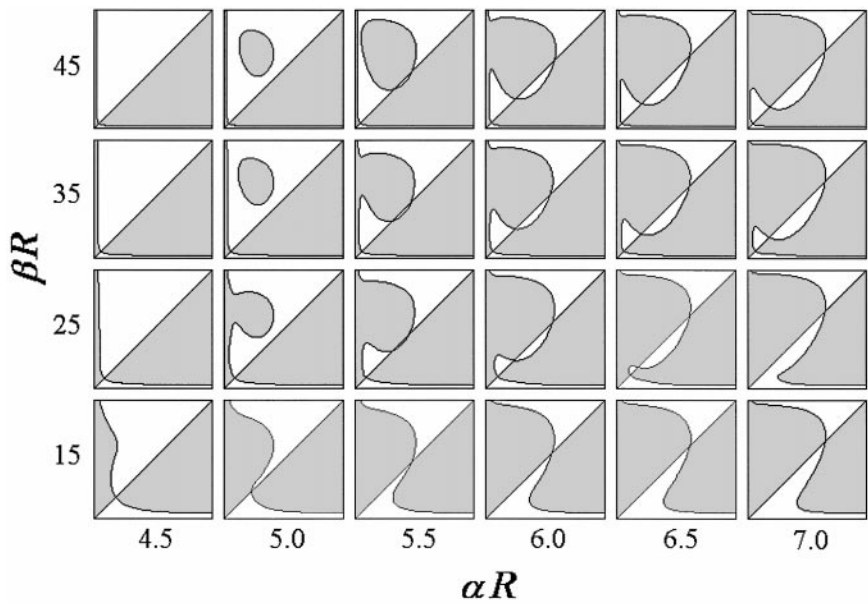


FIG. 5. Pairwise invasibility plots for different values of αR and βR . In each plot the scale of the axis runs from zero to R .

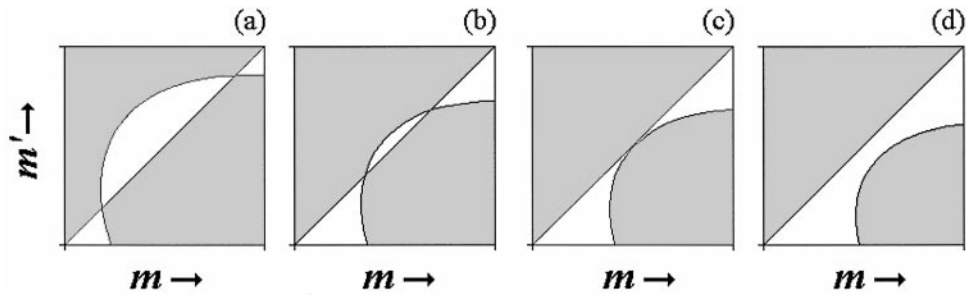


FIG. 6. Detail of pairwise invasibility plots for (a) $\alpha R = 6.754$, (b) $\alpha R = 6.763$, (c) $\alpha R = 6.766$, and (d) $\alpha R = 6.769$ and fixed $\beta R = 25$. The ESS in (a) must first lose its evolutionary stability in (b) before it collides with the repeller in (c), resulting in their mutual annihilation in (d). Axis scales are between $0.13R$ and $0.15R$.

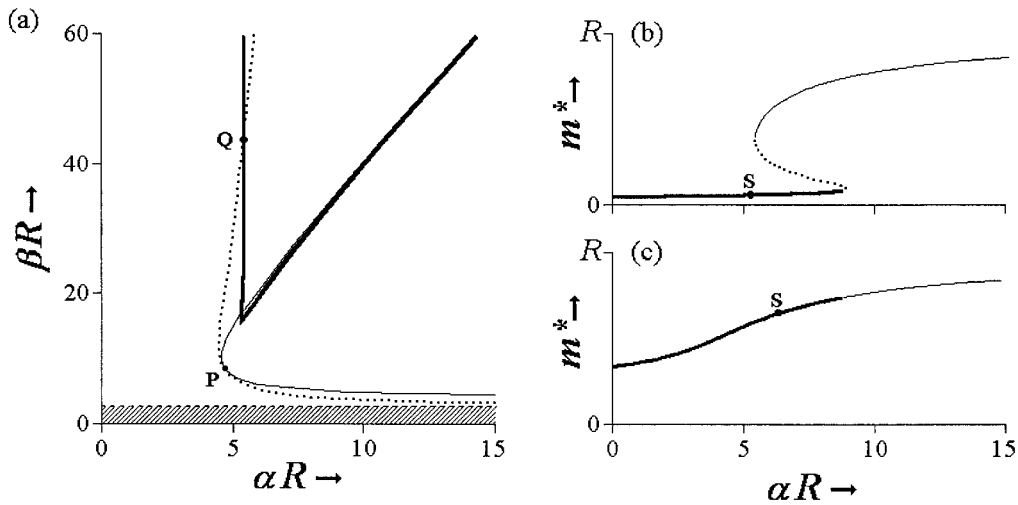


FIG. 7. (a) Number and stability properties of the singular strategies as a function of αR and βR . (b) The actual values of the singular strategies for fixed $\beta R = 35$, and (c) $\beta R = 5$. See text for further explanation.

3. EVOLUTIONARILY SINGULAR COALITIONS

Resident Population Dynamics and Mutant's Fitness

To see what happens after evolutionary branching when the population has become distinctively dimorphic, we consider a resident population with two plant types with seed sizes m_1 and m_2 . The full dynamics of the population follow from Eq. (7) with $n = 2$. Coexistence of two plant types is possible only if m_1 and m_2 are inside the area of coexistence (cf. Fig. 3b). Geritz *et al.* (1988) showed that if coexistence is possible, then there is a single, asymptotically stable population dynamical equilibrium with both types present at positive densities. The average number of established plants per germination site at the equilibrium depends on m_1 and m_2 , and will be denoted by, respectively, $N_1(m_1, m_2)$ and $N_2(m_1, m_2)$. At the boundary of the area of coexistence where $W_{m_1}(m_2) = 1$ or $W_{m_2}(m_1) = 1$, the equilibrium densities of, respectively, m_2 and m_1 become zero.

The fitness, $W_{m_1, m_2}(m')$, of an initially rare mutant with seed size m' in a resident population with seed sizes m_1 and m_2 at its equilibrium is derived in a similar way as in the case of a monomorphic population, and is found to be

$$\begin{aligned} W_{m_1, m_2}(m') &= f(m') \frac{R}{m'} \cdot \left(\sum_{k_1, k_2=0}^{\infty} \frac{c(m')}{c(m') + k_1 c(m_1) + k_2 c(m_2)} \right. \\ &\quad \times \frac{N_1(m_1, m_2)^{k_1} N_2(m_1, m_2)^{k_2}}{k_1! k_2!} e^{-N_1(m_1, m_2) - N_2(m_1, m_2)} \Big) \end{aligned} \quad (12)$$

(cf. Eq. (8)). The mutant can invade if $W_{m_1, m_2}(m') > 1$, and dies out if $W_{m_1, m_2}(m') < 1$. After the mutant has invaded, the population dynamics can in essence follow four possible patterns. For convenience, assume that it was m_1 that mutated. The most common pattern (i) is that the mutant just ousts the resident to which it is most similar, that is, its progenitor m_1 . Apart from such simple substitutions there are three other patterns that are relatively more rare, but that do occur regularly in the course of the evolutionary trajectories, and are moreover essential in determining the shape of those trajectories. In pattern (ii) all three types coexist until the occurrence of the next successful mutant, which for m' close to m_1 is only possible near the so-called evolutionary isocline for

m_1 to be discussed in the next paragraph. Pattern (iii) occurs only when the population is near the boundary of the area of coexistence where the frequency of m_2 becomes zero and the combination of m' and m_2 falls just outside the area of coexistence. In this case the mutant replaces both former resident types, so that the population becomes monomorphic again. We shall refer to this as an extinction event. Finally, in pattern (iv) m_2 dies out while m' and m_1 remain, which is possible only at the confluence of the conditions that we gave for patterns (ii) and (iii). Although trajectories containing pattern (iv) have but a negligibly small probability of occurring and have moreover never been observed for the present model, the possibility cannot *a priori* be excluded.

Isoclines and Evolutionarily Singular Coalitions

Since by assumption mutations occur only one at a time, a single evolutionary step inside the area of coexistence is always either horizontal or vertical depending on which particular resident produces the next successfully invading mutant first. With small evolutionary steps, the direction of a possible change in m_i ($i = 1, 2$) is given by the sign of the local fitness gradient,

$$\left[\frac{\partial W_{m_1, m_2}(m')}{\partial m'} \right]_{m' = m_i}. \quad (13)$$

The fitness gradients of m_1 and m_2 together define the so-called invasion cone, that is, the set of admissible evolutionary change given the present state of the resident population (Matessi and Di Pasquale, 1996). Figure 8 shows the area of coexistence for $\alpha R = 6$ and $\beta R = 25$ with the invasion cones indicated by arrows. We refer to the lines inside the area of coexistence on which the local fitness gradient for m_i is zero as the evolutionary isocline for m_i , or simply the m_i -isocline. For a mutant in a resident population on the m_i -isocline, the isocline corresponds to a local fitness maximum if

$$\left[\frac{\partial^2 W_{m_1, m_2}(m')}{\partial m'^2} \right]_{m' = m_i} < 0, \quad (14)$$

or a fitness minimum if the reverse is true. Parts of isoclines corresponding to local fitness maxima are indicated by thick solid lines, whereas parts corresponding to fitness minima are indicated by thin lines (Fig. 8).

As long as the population stays well inside the area of coexistence and away from isoclines, we always have pattern (i); that is, a successfully invading mutant will just oust the resident to which it is most similar after which the population remains dimorphic. Close to an

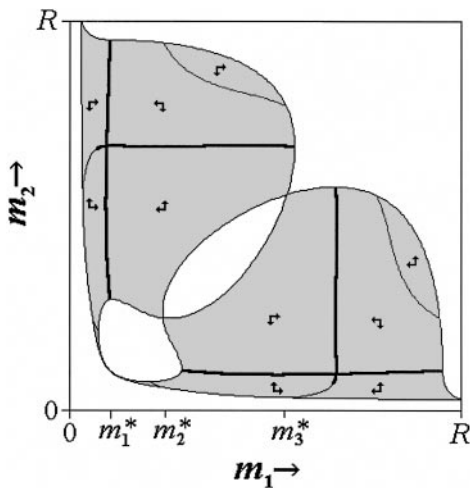


FIG. 8. Area of coexistence with isoclines and invasion cones for $\alpha R = 6$ and $\beta R = 25$. Thick lines correspond to local fitness maxima for the mutant, whereas thin lines correspond to local fitness minima. The monomorphic singular strategies are denoted by m_1^* , m_2^* , and m_3^* .

isocline, however, we may also have pattern (ii); that is, the mutant and both former resident types may coexist so that the population becomes trimorphic, at least until the next successful mutant comes along. To understand this we can do a thought experiment in which m_2 is fixed and does not evolve. The corresponding point on the m_1 -isocline then can be considered as a singular strategy for m_1 in a population in which m_2 is merely an environmental parameter. This means that we can study the fate of m_1 -mutants near the isocline in the same manner as we studied the fate of mutants near singular strategies in monomorphic resident populations. We thus find that mutual invasibility of a mutant and its resident progenitor in a dimorphic resident population is possible only in the neighborhood of isoclines. Evolutionary branching may occur if the isocline corresponds to a local fitness minimum, but is unlikely to persevere if evolution in the other resident type moves the population away from the vicinity of the isocline. Near the intersection of two isoclines where directional selection has ceased for both resident types at the same time, however, mutual invasibility leads to evolutionary branching if at the point of intersection either or both isoclines correspond to local fitness minima.

The points of intersection of isoclines are so-called evolutionarily singular coalitions (Metz *et al.*, 1996; Geritz *et al.*, 1997, 1998). Due to the diagonal symmetry of the area of coexistence, singular coalitions always occur in reciprocal pairs, one on each side of the diagonal (Fig. 8). Both represent the same population, that is, with

the same seed sizes, but with a different order of numbering the resident strategies. A singular coalition is evolutionarily stable (i.e., no mutant can invade) if at the point of intersection both isoclines correspond to local fitness maxima (Vincent and Brown, 1988). Generalization of convergence stability is less straightforward because of the higher degree of freedom of evolutionary change in populations with two or more resident strategies. Unlike convergence in monomorphic populations, convergence at higher levels of polymorphism may depend on the relative mutation rates and step sizes of the different resident strategies (Abrams *et al.*, 1993). Unambiguous examples of convergence in dimorphic populations can sometimes be constructed graphically using the invasion cones (Matessi and Di Pasquale, 1996). Like in the monomorphic case, evolutionary stability and convergence stability of dimorphic singular coalitions are fully independent properties that can occur in any combination. A singular coalition that is convergence stable but not evolutionarily stable for at least one of the resident types gives rise to disruptive selection and further branching of the evolutionary tree.

For $\alpha R = 6$ and $\beta R = 25$ there is a single evolutionarily singular coalition (Fig. 8; we consider the singularities on either side of the diagonal as identical). It can be seen from the invasion cones that the singular coalition will be reached from most places inside the area of coexistence, and therefore is convergence stable. In particular, an initially monomorphic population that enters the area of coexistence near the point (m_3^*, m_3^*) on the diagonal inevitably will end up near the singular coalition. The singular coalition is evolutionarily stable, because at the point of intersection both isoclines correspond to local fitness maxima. The singular coalition thus represents a final stop of the evolutionary process. The corresponding simulated evolutionary tree is given in Fig. 4b.

Figure 9a gives the area of coexistence with isoclines and invasion cones for $\alpha R = 9.5$ and $\beta R = 35$. Now there are three different evolutionarily singular coalitions. None of these is evolutionarily stable, because at each intersection point one or both isoclines correspond to fitness minima. From the invasion cones it can be seen that the middle of the three singular coalitions is an evolutionary repeller, whereas the other two are convergence stable. For an initially monomorphic population that enters the area of coexistence near the point (m^*, m^*) , the probability of reaching the attractor furthest away from the diagonal is negligibly small, as it would require mutations to occur systematically much more frequently in one resident strategy than in the other. Instead, the population evolves toward the singular coalition that is closest to the diagonal. Lacking

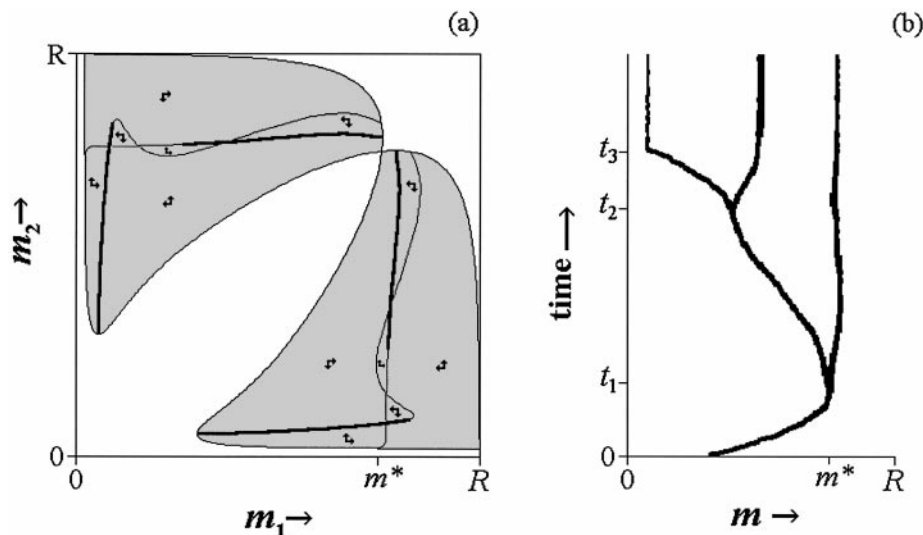


FIG. 9. (a) Area of coexistence with isoclines and invasion cones for $\alpha R = 9.5$ and $\beta R = 35$, and (b) simulated evolutionary tree. At time t_1 the population reaches the branching point, m^* , and undergoes evolutionary branching. At time t_2 the dimorphic population reaches the dimorphic singularity where it for a second time undergoes disruptive selection. At t_3 the population reaches an evolutionarily stable trimorphism.

evolutionary stability, the population then undergoes for a second time disruptive selection and evolutionary branching. The corresponding simulated evolutionary tree is given in Fig. 9b.

Change in Number and Stability Properties of Evolutionary Singular Coalitions

Figure 10a shows how the number and stability properties of the singular coalitions in a dimorphic resident population depend on αR and βR . Dimorphic singularities do not exist for parameter values inside the hatched

region. The border of this region exactly coincides with the boundary between local and global stability of the monomorphic ESS (dotted line in Fig. 7a). In the Appendix we show that this is not a coincidence and explain why this should be so. For a population settled at the monomorphic ESS, loss of global evolutionary stability has no consequences if evolution proceeds by small steps only, and the potentially invading mutants are too dissimilar from the resident type to be generated by a single mutation. The dimorphism, therefore, may remain unreachable until (at some higher value of αR) the monomorphic ESS loses its local evolutionary

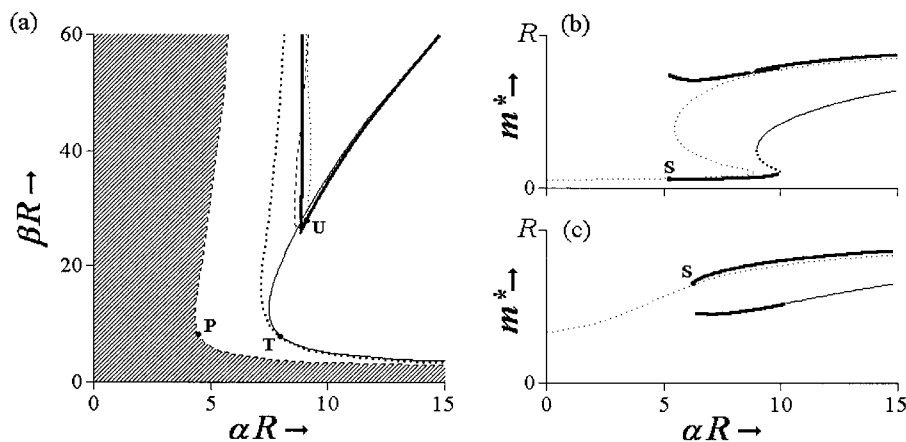


FIG. 10. (a) Number and stability properties of the dimorphic singular coalitions as a function of αR and βR . (b) The actual values of the dimorphic singularities as functions of αR for fixed $\beta R = 35$, and (c) $\beta R = 5$. The thin dotted curves in (b) and (c) indicate the monomorphic singularities. See text for further explanation.

stability and becomes a branching point. Only at point P (where the monomorphic ESS loses its global and local evolutionary stability and turns into a branching point all at the same time; also see Fig. 7a) does the dimorphic singularity appear just when the ESS becomes a branching point.

For parameter values between the hatched region and the heavy dotted line, there is a single convergence stable and globally evolutionarily stable dimorphic singular coalition. On the other side of the dotted line, the dimorphism has lost its global evolutionary stability but retains its local evolutionary stability. (The dotted line also corresponds to the first occurrence of an evolutionarily stable trimorphism; see the Appendix.) The thin solid line indicates where the smaller seed size of the dimorphism loses its evolutionary stability and becomes a local fitness minimum that may give rise to evolutionary branching. At point T, where the dotted line and the thin solid line touch one another, the population loses both its global and local evolutionary stability simultaneously. When we cross the hatched line (which partly lies inside the wedge-shaped domain formed by the thick solid lines, and which smoothly connects to the right edge of the wedge at point U), the larger seed size of the coalition (instead of the smaller seed size) loses its evolutionary stability. Disruptive selection and the ensuing evolutionary branching thus may occur in either the left or the right branch of the evolutionary tree, depending on the exact values of αR and βR .

The left edge of the wedge-shaped domain corresponds to a fold bifurcation that gives rise to two new singularities when the isoclines first touch and then intersect one another at two additional points. The two new singularities thus formed are respectively a convergence stable but evolutionarily unstable singular coalition and an evolutionary repeller. Inside the parameter range shown, the lack of evolutionary stability of the new attractor is due to the smaller seed size representing a local fitness minimum. The larger seed size of the attractor may also turn into a fitness minimum, but only so at much higher values of βR outside the range shown in the figure. The light dotted line inside the wedge shows where the larger seed size of the repeller becomes a fitness minimum. The smaller seed size of the repeller always corresponds to a fitness minimum. The right edge of the wedge indicates a fold bifurcation where the repeller and the former evolutionarily stable singular coalition merge and disappear.

Figure 10b is a horizontal cross section through the wedge-shaped domain at $\beta R = 35$ showing the actual values of the dimorphic singular coalitions as functions of αR . For the sake of comparison, the monomorphic singular strategies have been indicated by the thin dotted

line (cf. Fig. 7b). The more heavy curves denote the dimorphic singular coalitions. The lower curve indicates the smaller seed size of the coalition, and the upper curve the larger seed size. The thick solid lines correspond to local fitness maxima, the thin solid lines correspond to local fitness minima, and the dashed lines indicate evolutionary repellers. A singular coalition is evolutionarily stable only where both curves are thick and solid. The double fold lies exactly in between the edges of the wedge-shaped domain in Fig. 10a. The flatness of the fold in the upper curve is directly related to the fact that the isocline for the larger seed size in most a straight line parallel to one of the axes (cf. Fig. 9a). Approaching point S from the right, the frequency of the larger seed size of the dimorphism gradually becomes zero whereas the smaller seed size converges to the monomorphic ESS indicated by the thin dotted line (Fig. 10b). In cross sections through Fig. 10a below point P, however, it is always the smaller seed size that goes extinct while the larger seed size connects to the monomorphic ESS (Fig. 10c). In cross sections exactly through point P where the monomorphic singularity loses both its global and its local evolutionary stability and becomes a branching point all at the same time, both seed sizes of the dimorphism connect to the monomorphism.

Generalization to Higher Levels of Polymorphism

Graphical analyses using pairwise invasibility plots and isoclines are no longer possible for resident populations with three or more coexisting phenotypes. Generalization of the algebraic approach to higher levels of polymorphisms (including the problems with convergence stability) is straightforward (Metz *et al.*, 1996; Geritz *et al.*, 1997, 1998). The fitness, $W_{m_1, \dots, m_n}(m')$, of an initially rare mutant with seed size m' in a resident population with seed sizes m_1, \dots, m_n at its demographic equilibrium directly follows from Eq. (13) but with n resident types instead of 2. Demographic stability and uniqueness of the resident population equilibrium was verified by simulation of the resident population dynamics using Eq. (6). With small evolutionary steps, the direction of evolutionary change in each resident seed size is given by the sign of the corresponding local fitness gradient (cf. Eq. (13)). The isoclines, where the local fitness gradient is zero, are no longer lines but $(n - 1)$ -dimensional manifolds. An evolutionarily singular coalition is a protected polymorphism such that the local fitness gradient is zero for all resident types at the same time (i.e., where all isoclines intersect), and can be found using standard numerical

methods for solving systems of nonlinear equations. A singular coalition is evolutionarily stable if at the singular coalition the mutant's fitness as a function of its own strategy has a local maximum at each of the resident strategies (cf. Eq. (14)).

Figure 11 shows that changes in the number and stability properties of the singular coalitions due to changes in αR and βR exhibit similar patterns at all levels of polymorphism. Loss of global evolutionary stability always coincides with the emergence of an evolutionarily stable singularity at a higher level of polymorphism (dotted lines in Fig. 11). For parameter values inside the regions numbered I through VI (separated from one another by the dotted lines) there exist globally evolutionarily stable singular strategies or singular coalitions with, respectively, one up to six different coexisting seed sizes. (Higher levels of polymorphism occur at larger values of αR .) Crossing the border between two such regions from the left to the right, the globally evolutionarily stable singular strategy or coalition on the left side loses its global stability and becomes only locally evolutionarily stable. At the same time a new globally evolutionarily stable singular coalition appears, consisting of one more resident type (see the Appendix). Local evolutionary stability, however, can be lost in various ways, depending on which of the resident seed sizes of the coalition turns into a local fitness minimum first (not shown in Fig. 11, but see Fig. 10a for loss of local evolutionary stability of dimorphic singularities). At each level of polymorphism there is a wedge-shaped parameter region, the edges of which correspond to a fold bifurcation where two singularities simultaneously appear or

disappear (thick solid lines in Fig. 11). The left edge of each wedge has a vertical asymptote, while the right edge converges to a straight line with a positive slope that is the same for all levels of polymorphism. Below the horizontal dotted line near the bottom of Fig. 11, there are no evolutionary singularities.

Extinction of Evolutionary Branches

For parameter combinations inside the dotted region in Fig. 11 (formed by the intersection at point Q of the left most wedge-shaped domain and region I), there are three monomorphic singularities: an ESS, a repeller, and a branching point. There are no singularities with two or more coexisting seed types, however. Figure 12a shows the area of coexistence with isoclines and invasion cones for $\alpha R = 6$ and $\beta R = 100$, which is well inside this parameter region. Since the isoclines inside the area of coexistence do not intersect, there are no dimorphic singularities. An initially monomorphic population starting inside the domain of attraction of the branching point, m_3^* , will undergo evolutionary branching and will enter the area of coexistence near the point (m_3^*, m_3^*) . There being no dimorphic singularity, however, the population evolves along the thick isocline until it reaches the edge of the area of coexistence. Near the edge, the next successful mutant will move the population outside the area of coexistence, so that the population falls back again to a monomorphic condition close to, and inside, the domain of attraction of the ESS m_1^* . This corresponds to the extinction of one of the branches of the evolutionary tree and was described as invasion pattern (iii) at the beginning of this section. The corresponding simulated evolutionary tree is given in Fig. 12b. (N.B., extinctions are also possible for parameter combinations inside a narrow strip along the outside of the right edge of the dotted region in Fig. 11, but which is too narrow to be seen. For parameter values inside this strip there actually does exist a dimorphic evolutionarily stable singular coalition, but it lies inside a part of the area of coexistence that is unconnected to the part entered by the population during branching, and therefore cannot be reached.)

Extinction is also possible at a higher level of polymorphism. For example, consider parameter combinations inside the crosshatched region in Fig. 11 formed by the intersection at point W of the second wedge-shaped domain and region II. Inside this region there are in addition to the three monomorphic singular strategies also three dimorphic singularities: a dimorphic evolutionarily stable singular coalition, a dimorphic attractor lacking evolutionary stability (i.e., a dimorphic branching point), and a dimorphic repeller separating the two. There are

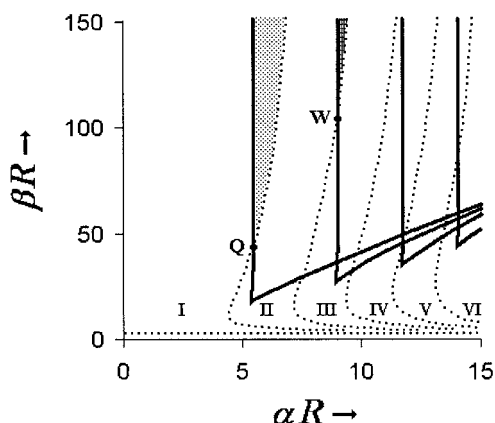


FIG. 11. Different levels of evolutionarily stable polymorphisms inside the regions I through VI separated by the dotted lines. Thick lines indicate fold bifurcations for singularities with one through four seed types present. Notice the different vertical scale compared to Figs. 7a and 10a. See text for further explanation.

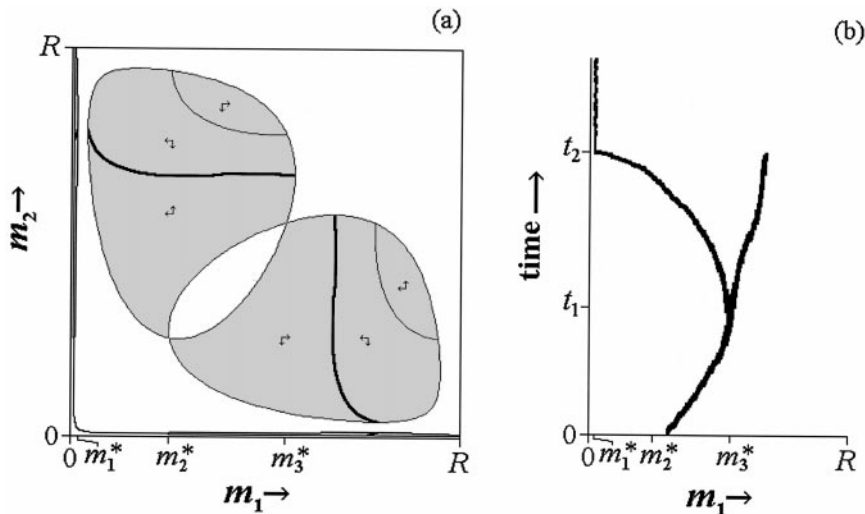


FIG. 12. (a) Area of coexistence with isoclines and invasion cones for $\alpha R = 6$ and $\beta R = 100$, and (b) corresponding simulated evolutionary tree. The initially monomorphic population starting inside the domain of attraction of m_3^* undergoes evolutionary branching and enters the area of coexistence at time t_1 . The population reaches the edge of the area of coexistence and falls back to a monomorphic state somewhere inside the domain of attraction of m_1^* at time t_2 .

no singularities with three or more coexisting resident types, however. An initially monomorphic population starting inside the domain of attraction of the branching point will undergo evolutionary branching twice, that is, at the monomorphic branching point, and next inside the area of coexistence near the dimorphic branching point. The dimorphic evolutionarily stable singular coalition is virtually unreachable because of the repeller in between (cf. Fig. 9a). As there are no trimorphic singularities, the population inevitably will fall back again to a dimorphic condition as it reaches the edge of the volume of protected trimorphisms. The new dimorphic coalition, however, is on the other side of the repeller and inside the domain of attraction of the evolutionarily stable dimorphism. A corresponding example of a simulated evolutionary tree for $\alpha R = 9.2$ and $\beta R = 150$ is given in Fig. 13a.

As βR increases, more and more different kinds of extinction patterns become possible, including cascades of extinctions where a population may drop several levels of polymorphism in succession within a very short time (i.e., “mass extinctions”). For example, at $\alpha R = 9$ and $\beta R = 925$ (which is outside the parameter range shown in Fig. 11, however), the right edge of region I enters the second wedge-shaped domain (not shown), forming a parameter region inside the crosshatched region in which the dimorphic evolutionarily stable singular coalition is missing. Thus, after two rounds of evolutionary branching and a single extinction event, the population will leave the volume of protected trimorphisms and find itself inside the area of coexistence again, but on the other

side of the repeller. However, unlike the previous example, there now is no evolutionarily stable dimorphic coalition, nor can the population return to the former attractor because of the repeller in between. Instead, the population will evolve to the edge of the area of coexistence where it will fall back to a monomorphic condition inside the domain of attraction of the monomorphic ESS. The population thus experiences two branching and two extinction events. The corresponding simulated evolutionary tree for $\alpha R = 9.04$ and $\beta R = 1100$ is given in Fig. 13b.

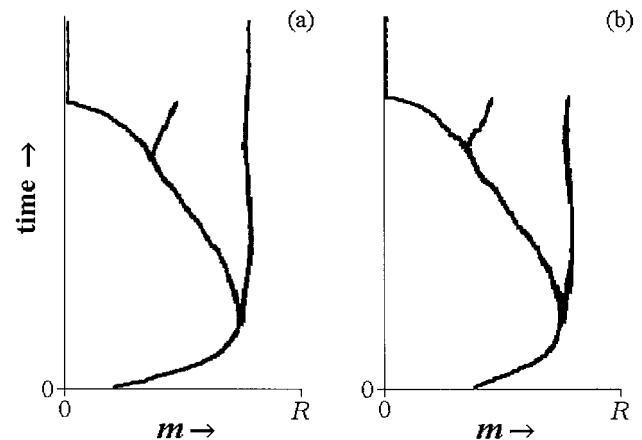


FIG. 13. Simulated trees with different extinction patterns for (a) $\alpha R = 9.2$ and $\beta R = 150$ giving rise to one branch that goes extinct, and (b) $\alpha R = 9.04$ and $\beta R = 1100$ with two extinct branches.

4. DISCUSSION

In this paper we investigated how competitive asymmetry due to differences in seed size affects the evolution of seed size in a number of different circumstances. We found that the results depend only on the parameter combinations αR and βR such that high values of αR and intermediate values of βR favor coexistence of plants with different seed sizes (Fig. 11).

Varying the strength of competitive asymmetry (α) while keeping the amount of resources per germination site (R) and the precompetitive environment (β) constant amounts to moving along a horizontal line through the parameter space in Fig. 11. For small α , the competitive advantage of having a larger seed size is small, so that differences in fitness are mainly due to differences in survival during the precompetitive phase of frequency-independent selection rather than to competition. Consequently, like in the model of Smith and Fretwell (1974), we find only a single optimal seed size. As α increases, the monomorphic ESS eventually loses its evolutionary stability and evolutionarily stable polymorphisms with progressively larger numbers of different seed sizes become possible. High values of α favor coexistence of plants, with different seed sizes, because the competitive advantage of having large seeds then is sufficient to compensate for the lower per capita seed number. At the same time, plants with small seeds have sufficiently many seeds to exploit sites that by chance remain unoccupied by the larger seeds of their superior competitors.

Varying the total amount of resources per germination site (R) while the competitive asymmetry (α) and the precompetitive environment (β) remain constant amounts to moving along a straight line through the origin in Fig. 11. The slope of this line is given by β/α . High values of β/α correspond to large seeds having only a small advantage relative to small seeds, either during the precompetitive phase (large β) or during competition (small α), or both. Varying R has very much the same effect as changing α . For small R , plant densities are too low for competition to be a significant evolutionary factor, so that we effectively recover the Smith–Fretwell (1974) model with only a single optimal seed size. As R increases, evolutionarily stable polymorphisms with a progressively larger number of different seed sizes become possible. However, if β/α is greater than the asymptotic slope of the right edge of the wedge-shaped domain in Fig. 7a, the monomorphic ESS retains its evolutionary stability also at higher values of R .

Changing the precompetitive environment (β) while the competitive asymmetry (α) and the amount of resources

per germination site (R) remain constant amounts to moving along a vertical line in Fig. 11. For small values of β , precompetitive survival is generally low but depends on seed size. Hence, the outcome of evolution is then determined mainly by frequency-independent selection during the precompetitive phase, leading a single optimal seed size. If, on the other hand, β is large, then seedling establishment is high for small and large seeds alike, so that small seeds no longer are selected against during the precompetitive phase. Since small seeds can be moreover produced in larger numbers, large seeds are selected against. The highest possible levels of evolutionarily stable seed polymorphism are therefore reached at intermediate values of β .

Various patterns of change in the number and stability properties of evolutionarily singular strategies or coalitions due to changes in model parameters are generic and model-independent. For example, loss of global evolutionary stability, in general, coincides with the appearance of a new evolutionary singularity at a higher level of polymorphism. The new evolutionary singularity emerges first on the boundary and then moves into the interior of the set of protected polymorphisms. Moreover, the new singularity will be both evolutionarily stable and convergence stable. This is a direct consequence of how isoclines connect to the boundary of the set of protected polymorphisms (see the Appendix). Thus, if the former singularity retains some local evolutionary stability after having lost its global stability, there will be two simultaneous evolutionarily stable outcomes with different numbers of coexisting strategies.

A different but also generic way of generating new singularities is by means of a fold bifurcation. Two singular strategies can simultaneously appear (or, equivalently, annihilate one another if the parameter is changed in the opposite direction) either as a pair of a non-ESS repeller and a branching point or as a pair of a convergence stable ESS and an ESS that lacks convergence stability. The first possibility is illustrated for the present model in Fig. 6. The second possibility (which does not occur in the model) arises if the pattern of shading in Fig. 6 is reversed.

The model-independent results described above may point the way to a more general evolutionary bifurcation theory describing how the number and stability properties of evolutionary singularities change as a consequence of changes in model parameters. Such an evolutionary bifurcation theory will be different from classical bifurcation theory (see, e.g., Kuznetsov, 1995) in that two independent stability concepts are involved, that is, evolutionary stability and convergence stability. Geritz *et al.* (1997, 1998) consider two additional stability concepts

concerning the invading ability of the singular strategy and the possibility of polymorphisms occurring near the singularity. Bifurcation of evolutionary singularities, therefore, may yield both novel and potentially more intricate patterns than in the classical theory.

With mutation-limited evolution and small evolutionary steps, an initially monomorphic population can reach an evolutionarily stable dimorphism only by means of evolutionary branching. Higher levels of polymorphism are reached through a series of successive branching events interspersed by stretches of directional selection. Evolutionary branching is possible (and will occur) only near evolutionary singularities that are convergence stable but lack evolutionary stability (Metz *et al.*, 1996; Geritz *et al.*, 1997, 1998). If more than one evolutionarily stable outcome is possible, it depends on the initial resident strategies to which the population will eventually evolve (Fig. 4). If after branching there are no convergence stable singularities, the population eventually falls back again to a lower level of polymorphism by extinction of one or more branches (Figs. 12 and 13).

Since by assumption all offspring have the same seed size as their mother, the model would apply only to apomictic or strictly selfing plant species. Branching in a monomorphic population of sexual plants with additive genetics on a single locus or a group of tightly linked loci occurs in the same ecological circumstances as for the present clonal model (Van Dooren, 1998; Kisdi and Geritz, 1998). In a genetically polymorphic population, however, the evolutionary dynamics may be quite different, and more complex, due to the occurrence of phenotypically intermediate heterozygotes resulting from crosses between different branches. Application of our results to sexual plants, therefore, requires the additional assumption that plants from different branches do not interbreed. Geritz *et al.* (1997, 1998) argue that branching is likely to favor the evolution of reproductive isolation of branches, because during branching the phenotypically intermediate offspring from parents in different branches have low fitness, so that mating within the same branch is selectively advantageous. Specific models for the evolution of assortative mating and reproductive isolation driven by evolutionary branching support this view (Doebeli, 1996; Doebeli and Dieckmann, 1999; Kisdi and Geritz, 1998).

In the model each plant by assumption produces seeds of one size only. The evolutionarily stable seed size distributions, however, can be interpreted more generally as the result of different plant types producing seeds of one specific size each, or one plant type producing seeds of different sizes in the corresponding frequencies, or any combination of these two (Geritz, 1995). Moreover,

while the model was formulated for annual plants, the evolutionarily stable outcomes apply to perennials as well if R is interpreted as the expected amount of resources that becomes available in a site during a plant's lifetime (Geritz *et al.*, 1988; Geritz, 1995). Finally, while in the model all germination sites have the same amount of resources, the results apply more generally if R is interpreted as the average over all germination sites (Geritz, 1995). The evolutionary dynamics (as opposed to the final evolutionary outcomes), however, may be different for the different generalizations of the model.

We are not aware of any empirical data that directly support the particular functional form relating seed size to competitive ability. The reason why we have used the form given in Eq. (4) is that it has the desired property that plants from larger seeds are better competitors and have a disproportionately large advantage over plants from smaller seeds (Stanton, 1985; Wulff, 1986b). A less realistic property, however, may be that in the model competitive asymmetry could become arbitrarily large for sufficiently large differences in seed size. In reality, relative germination date and plant spacing, which were not included in the model, also affect plant competition (Black and Wilkinson, 1963; Ross and Harper, 1972; Ford and Diggle, 1981; Howell, 1981), and limit the maximum possible degree of competitive asymmetry due to differences in seed size.

Most models of competitive asymmetry in plants address the issue of self-thinning and the emerging size hierarchy in plant populations (Aikman and Watkinson, 1980; Ford and Diggle, 1981; Benjamin, 1988; Bonan, 1988), or the issue of biodiversity and limiting similarity (Fagerström and Ågren, 1979; Tilman, 1994; Abrams, 1996). In an evolutionary context, Rees and Westoby (1997) consider the possibility of evolutionarily stable coalitions of plants with different seed sizes depending on the strength of competitive asymmetry. Although they use a different approach and do not consider evolutionary branching, their results are largely consistent with ours.

Matsuda and Abrams (1994) argue that strong competitive asymmetry can lead to runaway evolution to self-extinction if large trait values have an associated cost (such as a lower per capita seed number in the present model), resulting in smaller populations. Although in deterministic models populations may never actually reach zero density, in reality they may become sufficiently small that eventually stochastic factors cause their extinction. Self-extinction may in turn lead to taxon cycles if, on a larger timescale, the habitat is periodically recolonized by small seeds produced elsewhere. (For related examples of taxon cycles, see, e.g., Maynard Smith and

Brown, 1986; Taper and Case, 1992; Abrams and Matsuda, 1994; Matsuda and Abrams, 1994.) Evolutionary cycles found by Law *et al.* (1997) in a model with competitive asymmetry are of a different type and are driven by differences in competitive asymmetry within species, and do not occur in the present model.

APPENDIX

Isoclines and Their Connection to the Boundary of the Area of Coexistence

Isoclines connect to the boundary of the area of coexistence only at specific places (Metz *et al.*, 1996). These places depend on the positions of the monomorphic singularities and on the shape of the area of coexistence. Moreover, the direction of the fitness gradient on either side of the isocline close to its connection to the boundary, and also whether the isocline corresponds to a local fitness maximum or fitness minimum, follows from the monomorphic singularities and the shape of the area of coexistence. As a consequence, there is an intimate relationship between monomorphic and dimorphic singularities that can be used to understand various outcomes of the present model. The theory given below applies more generally, however, and is not just confined to the present model. Moreover, similar arguments apply to higher levels of polymorphisms as well, although a graphical representation becomes troublesome.

Figure 14 shows the area of coexistence for $\alpha R = 6$ and $\beta R = 25$ with the m_1 -isoclines and arrows that indicate the direction of evolution in m_1 . (We here consider only the m_1 -isocline, because the m_2 -isocline is obtained by simply taking the mirror image of the m_1 -isocline along the main diagonal.) The boundary of the area of coexistence is made up of two curves defined by $W_{m_1}(m_2) = 1$ or $W_{m_2}(m_1) = 1$. The m_1 -isocline connects to segments of the boundary defined by $W_{m_1}(m_2) = 1$ at any point that is vertically above a singular strategy on the m_1 -axis (Fig. 14; solid circles). The reason for this can be seen intuitively as follows. Inside the area of coexistence m_2 is protected against extinction by an annual growth rate that is larger than one when m_2 happens to be rare. On the boundary where $W_{m_1}(m_2) = 1$ this is no longer the case, so that if we approach the boundary from the inside of the area of coexistence, the frequency of m_2 at the demographic equilibrium gradually dwindles to zero. Near the boundary, therefore, the effect of m_2 on the evolution of m_1 is negligible, and the direction of evolution in m_1 must be the same as if the population were

monomorphic. In particular, if m_1 coincides with a singular strategy in a monomorphic population, then any point on the boundary vertically above m_1 will also have a fitness gradient that is zero and thus must lie on the m_1 -isocline (Fig. 14; solid circles). Moreover, if m_1 is evolutionarily stable or lacks evolutionary stability, then on the boundary the isocline corresponds also to, respectively, a local fitness maximum (Fig. 14; points q and r) or a local fitness minimum (Fig. 14; points o, p, t, and u).

The m_1 -isocline connects to segments of the boundary defined by $W_{m_2}(m_1) = 1$ at any point where the boundary has a horizontal tangent (Fig. 14; open circles). The reason for this can be seen intuitively as follows. For a population virtually on the boundary of the area of coexistence, only mutants of m_1 further into the interior of the area of coexistence can invade, whereas mutations directed toward the outside cannot. In other words, along the boundary, the local fitness gradient with respect to m_1 points to the inside of the area of coexistence. At each point where the boundary has a horizontal tangent, therefore, the fitness gradient changes direction, so that the point of contact with the tangent must lie on the m_1 -isocline (Fig. 14; open circles). If at the point of contact the boundary is locally convex, the fitness gradient points toward the isocline (Fig. 14; point v). Moreover, since any change in m_1 at the point of contact brings the population outside the area of coexistence, no mutant can invade, and hence the isocline corresponds to a fitness maximum with respect to mutations in m_1 . If the

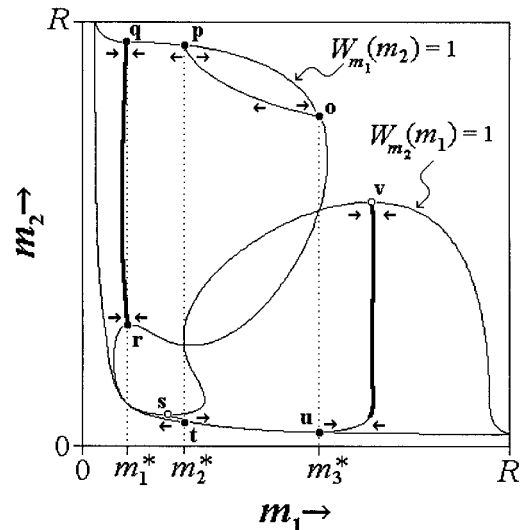


FIG. 14. Connections of the m_1 -isocline to the boundary of the area of coexistence for $\alpha R = 6$ and $\beta R = 25$. The monomorphic ESS, the repeller, and the branching point are denoted by, respectively, m_1^* , m_2^* , and m_3^* . Arrows indicate the direction of evolution of m_1 inside the area of coexistence.

boundary of the area of coexistence at the point of contact is locally concave, however, then the fitness gradient points away from the isocline (Fig. 14; point s). Moreover, any change in m_1 at the point of contact brings the population inside the area of coexistence, so that any mutant could invade, and the isocline thus represents a local fitness minimum with respect to mutations in m_1 .

Loss of Global Evolutionary Stability and the Emergence of New Singularities

An ESS loses its global evolutionary stability when in the pairwise invasibility plot the set of potential invading mutants extends above the point on the horizontal axis representing the ESS (e.g., Fig. 5; $\alpha R = 5.0$, $\beta R = 25$). For a population already settled at the ESS this has no consequences if evolution proceeds by small steps only and the potentially invading mutants are too dissimilar from the resident type to be generated by a single mutation. However, if the extension of the set of potentially invading mutants also leads to an extension of the area of coexistence, then a new, evolutionarily stable dimorphic singularity appears at the very same moment the ESS loses its global evolutionary stability. This is a direct consequence of the way isoclines are connected to the boundary of the area of coexistence. Similar arguments apply to higher levels of polymorphism although a graphical representation may no longer be possible.

Figure 15 shows the area of coexistence with isoclines and invasion cones before, during, and after the ESS, m^* , loses its global evolutionary stability at, respectively, $\alpha R = 4.40$, 4.45 , and 4.50 , and for fixed $\beta R = 15$. When the ESS is still globally evolutionarily stable (Fig. 15a), the isoclines do not intersect, and hence there are no

dimorphic singularities. The m_1 -isocline connects points q and r where the boundary of the area of coexistence has horizontal tangents. Its mirror image, the m_2 -isocline, connects points o and p. When the ESS is about to lose its global evolutionary stability (Fig. 15b), point o has moved to a position directly above the ESS, and therefore now also coincides with a point on the m_1 -isocline. At this stage, however, the m_1 -isocline exists in a collapsed state consisting only of one point on the boundary. Moreover, as point o belongs to both the m_1 -isocline and the m_2 -isocline, it also represents a dimorphic singularity. Once the ESS has lost its global evolutionary stability (Fig. 15c), there are two points (s and t) on the boundary of the area of coexistence that lie directly above the ESS. The m_1 -isocline is therefore no longer a single point, but has expanded into a curve with endpoints s and t, while at the same time the dimorphic singularity has moved from the boundary into the interior of the area of coexistence. Just after the ESS has lost its global evolutionary stability, the dimorphic singularity is necessarily evolutionarily stable: both the m_1 -isocline (which inherits its stability properties from the ESS) and the m_2 -isocline in the neighborhood of its endpoint o (where the area of coexistence is locally convex) correspond to fitness maxima.

The dimorphic singularity in its primordial stage consists of two seed types (i.e., on the boundary of the area of coexistence when the ESS is just about to lose its global evolutionary stability; Fig. 15b). The smaller seed type has the same size as the monomorphic ESS, while the other represents the first of mutants that can invade the ESS at slightly higher values of αR , but has still a zero frequency itself. This explains why in Fig. 10b it is the lower and not the upper branch of the dimorphism that connects to the thin dotted line representing the

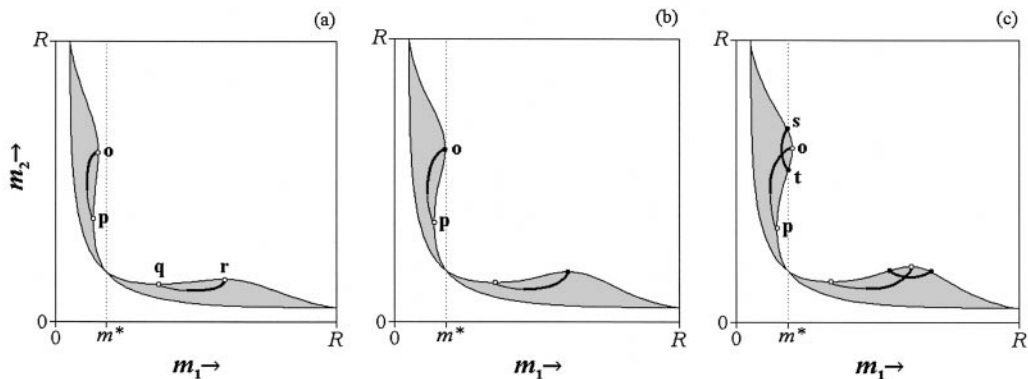


FIG. 15. Loss of global evolutionary stability of an ESS and the simultaneous appearance of an evolutionarily stable and convergence stable dimorphic singularity. (a) $\alpha R = 4.40$, (b) $\alpha R = 4.45$, and (c) $\alpha R = 4.50$ and fixed $\beta R = 15$. The monomorphic ESS is denoted by m^* .

monomorphic singularities. For values of βR below point P in Fig. 10a, the situation is the reverse, because then the first of mutants that can invade the ESS has a seed size smaller than that of the ESS (Fig. 10c).

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