



Red Queen Evolution by Cycles of Evolutionary Branching and Extinction

Kisdi, E., Jacobs, F.J.A. and Geritz, S.A.H.

**IIASA Interim Report
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Interim Report

IR-00-030

**Red Queen Evolution by Cycles
of Evolutionary Branching and Extinction**

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The Adaptive Dynamics Network at IIASA fosters the development of new mathematical and conceptual techniques for understanding the evolution of complex adaptive systems.

Focusing on these long-term implications of adaptive processes in systems of limited growth, the Adaptive Dynamics Network brings together scientists and institutions from around the world with IIASA acting as the central node.

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THE ADAPTIVE DYNAMICS NETWORK

The pivotal role of evolutionary theory in life sciences derives from its capability to provide causal explanations for phenomena that are highly improbable in the physico-chemical sense. Yet, until recently, many facts in biology could not be accounted for in the light of evolution. Just as physicists for a long time ignored the presence of chaos, these phenomena were basically not perceived by biologists.

Two examples illustrate this assertion. Although Darwin's publication of "The Origin of Species" sparked off the whole evolutionary revolution, oddly enough, the population genetic framework underlying the modern synthesis holds no clues to speciation events. A second illustration is the more recently appreciated issue of jump increases in biological complexity that result from the aggregation of individuals into mutualistic wholes.

These and many more problems possess a common source: the interactions of individuals are bound to change the environments these individuals live in. By closing the feedback loop in the evolutionary explanation, a new mathematical theory of the evolution of complex adaptive systems arises. It is this general theoretical option that lies at the core of the emerging field of adaptive dynamics. In consequence a major promise of adaptive dynamics studies is to elucidate the long-term effects of the interactions between ecological and evolutionary processes.

A commitment to interfacing the theory with empirical applications is necessary both for validation and for management problems. For example, empirical evidence indicates that to control pests and diseases or to achieve sustainable harvesting of renewable resources evolutionary deliberation is already crucial on the time scale of two decades.

The Adaptive Dynamics Network has as its primary objective the development of mathematical tools for the analysis of adaptive systems inside and outside the biological realm.

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Abstract

We use the theory of adaptive dynamics to construct and analyse a generic example of cycling evolution with alternating levels of polymorphism. A monomorphic population evolves towards larger trait values until it reaches a so-called evolutionary branching point. Disruptive selection at the branching point splits the population into two strategies. In the dimorphic population the strategies undergo parallel coevolution towards smaller trait values. Finally one of the two strategies goes extinct, and the remaining single strategy evolves upwards again to the branching point. The reversal of the direction of evolution is brought about by the changing level of polymorphism. Extinction is deterministic, i.e., it occurs inevitably and always at the same trait values; which of the two strategies goes extinct is, however, random. The present model is discussed in relation to other mechanisms for evolutionary cycles involving branching and extinction.

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Red Queen Evolution by Cycles of Evolutionary Branching and Extinction

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Introduction

Continual evolution under constant external conditions, called Red Queen dynamics, intrigued biologists ever since Van Valen (1973) raised the possibility of sustained evolutionary changes. Early lag-load models of Red Queen evolution (Stenseth and Maynard Smith, 1984) soon gave place to models with explicit trait dynamics (Rosenzweig et al., 1987). Since most continuous traits are bounded, Red Queen dynamics usually take the form of evolutionary cycles. Many examples of cyclic evolution are known, for example in predator-prey systems (Abrams, 1992, 1997; Marrow et al., 1992, 1996; Dieckmann et al., 1995; Van der Laan and Hogeweg, 1995; Abrams and Matsuda, 1997; Doebeli, 1997; Gavrillets, 1997; Doebeli and Dieckmann, in press), in competitive coevolution (Pease, 1984; Law et al., 1997), in the evolution of dispersal in metapopulations (Doebeli and Ruxton, 1997) or in sexual selection (Iwasa and Pomiankowski, 1995, 1999; Pomiankowski and Iwasa, 1998).

A customary approach to model coevolution in ecological systems is to assume that evolution (i.e., changes in trait values of the coexisting strategies or species) is much slower than population dynamics (changes in the densities of the coexisting strategies). Under the separation of ecological and evolutionary time scales, Khibnik and Kondrashov (1997) classified the different mechanisms leading to Red Queen evolution into the categories of ecologically, genetically, and ecogenetically driven systems. In ecologically driven systems, the population densities of the coexisting strategies settle on a nonequilibrium attractor, and the fluctuations in population densities cause small-amplitude fluctuations in the relatively slowly evolving traits. With increasing time scale separation, however, these trait fluctuations disappear. Most examples of cyclic evolution cited above fall in the category of genetically driven systems, i.e., the coevolution of trait values has nonequilibrium dynamics while population densities track equilibrium values corresponding to the momentary trait values. The

ecogenetically driven systems may simply exhibit a superposition of ecologically and genetically driven cycles (and hence become genetically driven cycles if ecological and evolutionary time scales are truly separated). In some cases, however, coupling of the ecological and evolutionary time scales is essential for sustaining the evolutionary cycles (Abrams, 1992) or even for the persistence of the community (Van der Laan and Hogeweg, 1995; Doebeli, 1997). Other ecogenetically driven cycles involve switches between different population dynamical attractors such that the direction of evolution changes when the population densities settle on another attractor (see Doebeli and Ruxton (1997) for an example).

In their classification, Khibnik and Kondrashov (1997) assumed that the number of coevolving strategies (or species) is constant. This, however, need not be the case. Strategies may go extinct during coevolution. New strategies may also arise through the process of evolutionary branching, when a single ancestral strategy gradually splits up into two distinct strategies under disruptive selection (Metz et al., 1996; Geritz et al., 1997, 1998). If evolutionary branching and extinction alternate, then evolutionary cycles may result with changing levels of polymorphism.

In this paper, we use the theory of adaptive dynamics as developed by Dieckmann and Law (1996), Metz et al. (1996) and Geritz et al. (1997, 1998, 1999) to demonstrate that cycles of evolutionary branching and extinction indeed represent a generic evolutionary pattern. The simplest case of such cycles is the following. A monomorphic population evolves towards larger trait values until it reaches an evolutionary branching point, where it experiences disruptive selection and splits into two phenotypes separated by a widening gap. After evolutionary branching gave rise to a dimorphic population, the two coexisting strategies undergo parallel coevolution towards smaller trait values. Finally one of the two strategies goes extinct, and the remaining strategy evolves up again to the branching point. In the first part of the paper, we show that this scenario can be obtained as a generic outcome in the framework of adaptive dynamics. (For easy reference, we also recapitulate the necessary theoretical elements of adaptive dynamics using the graphical approach of Geritz et al. 1998, 1999.) In the second part, we construct an example based on a Lotka-Volterra competition model; this example allows us to verify the conclusions by a direct simulation of the evolutionary process.

Repeated evolutionary branching and extinction have been found in several models, most of them using simulation experiments only (Van der Laan and Hogeweg, 1995; Doebeli and Ruxton, 1997; Koella and Doebeli, 1999; Doebeli and Dieckmann, in press; Mathias and Kisdi, in press). There are several mechanisms which can lead to such cycles. Reversal of the direction of evolution may be caused not only by the changing level of polymorphism but also by a periodic change in the biotic environment

due to coevolution with another species, or by switching between multiple population dynamical attractors. Extinction can occur either deterministically or due to demographic stochasticity when population size is relatively small. It is often difficult to identify the cause of cycles in the simulations without an analytical investigation of the model. In this paper, we focus on the conceptually simplest case, where the changing level of polymorphism alone produces evolutionary cycles in a fully deterministic way. In order to exclude the alternative mechanisms of coevolution and multiple population dynamical attractors, we construct a model with a single species that always has a unique population dynamical attractor. Population size is assumed to be infinite such that extinction is deterministic. We compare the alternative mechanisms for cycles of evolutionary branching and extinction in the Discussion.

Cycles of evolutionary branching and extinction

Let us start with a monomorphic resident population of strategy x . A new, rare mutant strategy, y , may invade the population only if its long-term logarithmic growth rate (or "fitness"), $s_x(y)$, is positive (Metz et al., 1992). The mutant's growth rate depends on the resident strategy because the resident population sets the biological environment of the mutant (e.g., the abundance of resources or the satiation of predators) as well as on the mutant's own strategy. We assume that for each strategy x the resident population has a unique population dynamical attractor and that mutations occur infrequently such that the resident population has settled on its population dynamical attractor before the next mutant appears. In this case the resident strategy (or strategies) fully specify the biological environment of the mutant.

We can represent which mutants are able to invade populations with different resident strategies graphically on a so-called pairwise invasibility plot (PIP): In the space of strategy pairs (x, y) , the parts where $s_x(y) > 0$ correspond to strategy pairs such that the mutant can invade, whereas in the parts where $s_x(y) < 0$ the mutant goes extinct (Fig. 1; Geritz et al., 1998 gives a more detailed account on the methods used). There is no *a priori* constraint on the functional form of $s_x(y)$, and consequently on the shape of the PIP other than the resident strategy must have zero long-term growth, i.e., $s_x(x) = 0$ and the main diagonal $y = x$ of the PIP is always a border line between 'invasion' and 'noninvasion' parts. Hence the PIP shown in Fig. 1 is generic (a specific ecological example yielding this PIP will be presented in the next section).

If mutations have only small phenotypic effect ($|y - x| < \delta$, where δ is a small positive number called the mutation radius), then only a narrow band along the main diagonal of

the PIP is of immediate interest. If mutants somewhat above the diagonal ($y > x$) can invade, then smaller mutants ($y < x$) go extinct for almost every resident x . By successive invasions and substitutions, the population undergoes directional evolution towards larger trait values. In the reverse case, directional evolution proceeds towards smaller trait values (Fig. 1).

Directional evolution stops at the so-called evolutionarily singular strategies, where the main diagonal and the second border line between 'invasion' and 'noninvasion' areas intersect. An evolutionarily singular strategy is convergence stable (Eshel, 1983; Christiansen, 1991) if directional evolution starting from its neighbourhood approaches it. In Fig. 1, x_{br} is convergence stable; x_{rep} , in contrast, is convergence unstable and hence acts as an evolutionary repeller.

An evolutionarily singular strategy is a local ESS if no mutant within the mutation radius can invade it. The convergence stable singularity x_{br} in Fig. 1, however, is not evolutionarily stable: Both larger and smaller mutants are able to invade the resident population of x_{br} . Convergence stable strategies that nevertheless lack evolutionary stability are evolutionary branching points, where two distinct strategies evolve in the population (Metz et al., 1996; Geritz et al., 1997, 1998).

In order to see what happens after the population has reached the branching point x_{br} , we need to construct a two-dimensional trait evolution plot (TEP), which allows us to investigate the simultaneous evolution of two coexisting strategies. First we have to establish which strategy pairs can coexist in a dimorphic resident population. Assume that all dimorphisms are protected. Then x_1 and x_2 can coexist if and only if both x_1 and x_2 can spread when rare, i.e., if both $s_{x_1}(x_2)$ and $s_{x_2}(x_1)$ are positive. The pairs of coexisting strategies thus can be obtained by superimposing the PIP and its mirror image taken along the main diagonal: The overlapping parts of the 'invasion' areas on the original ($s_{x_1}(x_2) > 0$) and on the mirror image ($s_{x_2}(x_1) > 0$) correspond to the strategy pairs (x_1, x_2) that can coexist (Fig. 2). The overlapping parts of 'noninvasion' areas represent strategy pairs where neither strategy can invade the other, i.e., the rare type always goes extinct ($s_{x_1}(x_2) < 0$) and ($s_{x_2}(x_1) < 0$).

Notice that the area of coexistence reaches the main diagonal only near the branching point (x_{br}). As the monomorphic population evolves along the diagonal and approaches x_{br} , then sooner or later a mutant and its progenitor resident strategy will fall inside the area of coexistence. The mutant then does not substitute the resident, but instead the two very similar strategies form a protected dimorphism.

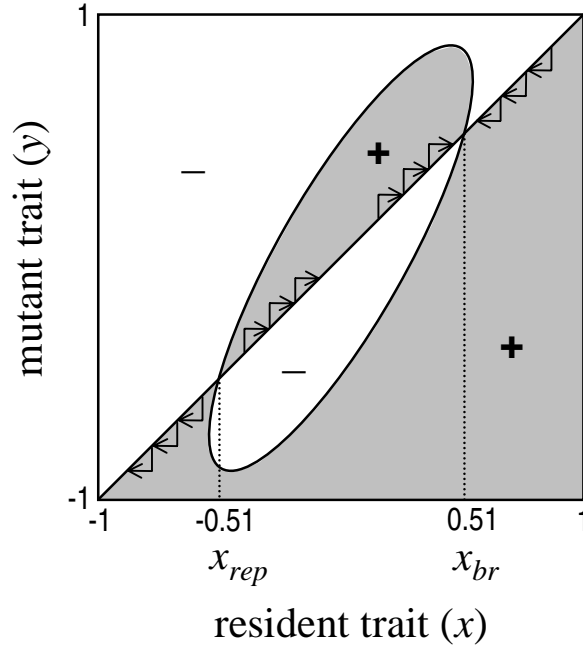


Fig. 1. Pairwise invasibility plot (PIP). Shaded area: the mutant can invade ($s_x(y) > 0$); clear area: the mutant cannot invade ($s_x(y) < 0$); arrows: directional evolution by invasions and substitutions. The lower evolutionary singularity (x_{rep}) is convergence unstable and hence a repellor (directional evolution leads away from it), whereas the higher singularity (x_{br}) is an evolutionary branching point (convergence stable but evolutionarily unstable, i.e., can be invaded by both smaller and larger mutants and thus is not a final state of evolution). - The Lotka-Volterra model yields this PIP with parameter values $\alpha = 4.5, \beta = 12.12, \gamma = 11.5$ and $\delta = 1$.

The two resident strategies of a dimorphic population undergo directional coevolution. Similarly to the monomorphic case, let $s_{x_1, x_2}(y)$ denote the long-term logarithmic growth rate of mutant y in the resident population of x_1 and x_2 . Since the resident strategies have zero long-term growth, $s_{x_1, x_2}(x_1)$ and $s_{x_1, x_2}(x_2)$ must be zero. If $s_{x_1, x_2}(y)$ is positive for y somewhat larger than x_1 (and thus generically negative for y somewhat lower than x_1), then larger mutants of x_1 can invade the population and substitute x_1 , therefore x_1 undergoes directional evolution towards larger trait values. Directional evolution of x_2 can be established analogously. In the TEP (Fig. 2), horizontal and vertical arrows indicate the direction of evolution for x_1 and x_2 , respectively. Since the labelling of the resident strategies is arbitrary, the TEP is always

symmetric along the main diagonal. For convenience, we assume that $x_1 < x_2$, i.e., we restrict the analysis to the upper left half of the plot.

In the vicinity of the branching point $x_1 = x_2 = x_{br}$ the two strategies always undergo divergent coevolution, i.e., x_1 evolves downwards while x_2 evolves upwards (see Eshel et al., 1997 and Geritz et al., 1998 for proof). As a consequence, the initially very similar coexisting strategies become phenotypically clearly distinct. When coevolution has left the neighbourhood of the branching point, however, the direction of evolution may change. The area of coexistence thus consists of parts with different directions of evolution of $x_1(x_2)$; the lines separating these parts, on which directional evolution in $x_1(x_2)$ ceases, we call the x_1 - (x_2 -) isoclines (Fig. 2).

There is one more constraint on the function $s_{x_1, x_2}(y)$, and consequently on the possible structure of a TEP (Geritz et al., 1999). To investigate this, first consider the boundary of the area of coexistence. The boundary consists of two parts: One part is derived from the ‘invasion-noninvasion’ boundary of the original PIP where $s_{x_1}(x_2) = 0$, and the other part is derived from the ‘invasion-noninvasion’ boundary of the mirrored PIP where $s_{x_2}(x_1) = 0$. On the first part of the boundary the frequency of x_2 is zero, therefore we refer to this part as the x_2 -extinction boundary; the second part is the x_1 -extinction boundary. As we approach, say, the x_2 -extinction boundary from inside the area of coexistence, the frequency of x_2 decreases to zero, and on the boundary it undergoes a transcritical bifurcation (i.e., it remains zero outside the area of coexistence). [Other types of bifurcations through which the dimorphism could be lost, such as a fold or a Hopf-bifurcation, imply that zero frequency of x_2 is a population dynamical attractor already inside the area of coexistence, and thus they are excluded by the assumption that all dimorphisms are protected.]

Since on the x_2 -extinction boundary the frequency of x_2 is zero, we have that $s_{x_1, x_2}(y) \rightarrow s_{x_1}(y)$ as we approach the boundary, with the two becoming equal on the boundary itself. If x_1 coincides with the monomorphic evolutionary singularity, then directional evolution of x_1 ceases in a population monomorphic for x_1 , and therefore also in the ‘dimorphic’ population on the x_2 -extinction boundary. The x_1 -isocline thus must connect to the x_2 -extinction boundary vertically above the monomorphic singularity (point P_1 in Fig. 2). By the same argument, the x_2 -isocline connects to the x_1 -extinction boundary horizontally to the left of the monomorphic singularity (no such point exists in Fig. 2).

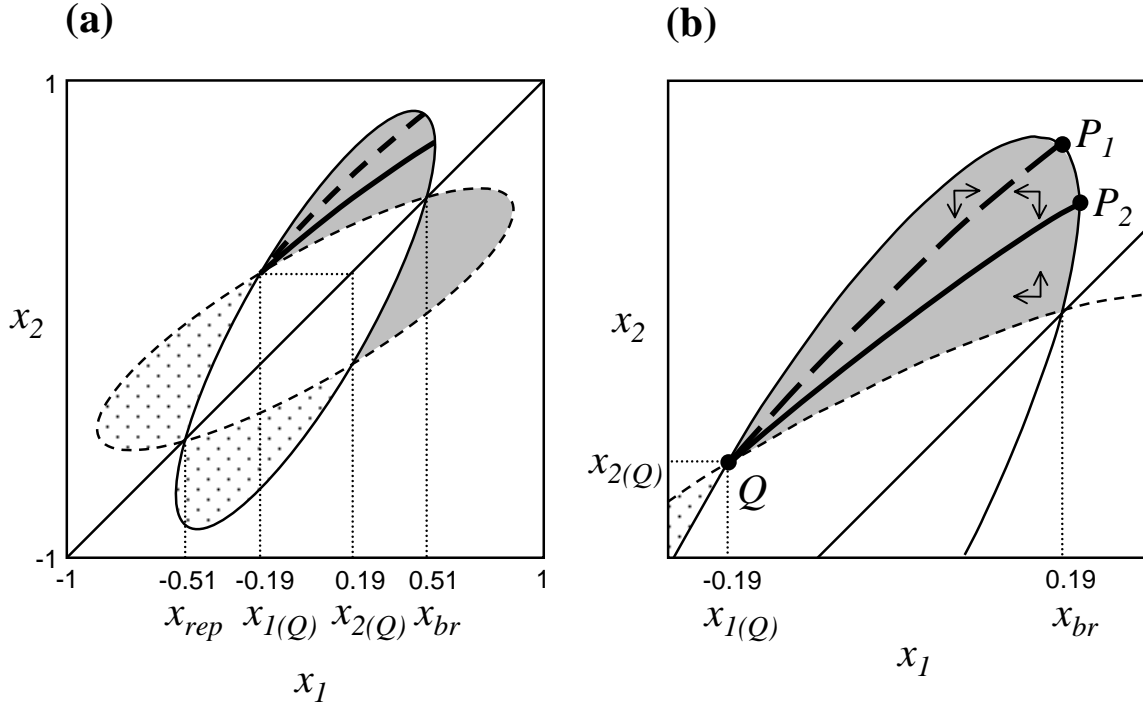


Fig. 2. Trait evolution plot (a), and the area of coexistence enlarged (b). Shaded area: the area of coexistence, where x_1 and x_2 can coexist in a protected dimorphism (both $s_{x_1}(x_2) > 0$ and $s_{x_2}(x_1) > 0$); dotted area: the rare strategy goes extinct whichever it is (both $s_{x_1}(x_2) < 0$ and $s_{x_2}(x_1) < 0$); thin dashed line: x_1 -extinction boundary; thin continuous line: x_2 -extinction boundary; thick dashed line: x_1 -isocline; thick continuous line: x_2 -isocline; horizontal and vertical arrows: direction of evolution in x_1 and in x_2 , respectively; P_1 and P_2 : connection of the x_1 - and x_2 -isoclines to the boundary of the area of coexistence; Q : intersection of the extinction boundaries. By evolutionary branching the population enters the area of coexistence near x_{br} . Dimorphic evolution first proceeds in the direction up and to the left until the population gets inbetween the two isoclines; then it goes down and to the left. At point Q , one of the two residents dies out and the population falls back to monomorphism either at $x_{1(Q)}$ or at $x_{2(Q)}$. - The Lotka-Volterra model yields this TEP with parameter values as in Fig. 1.

Directional evolution of x_2 always leads away from the x_2 -extinction boundary: On the boundary the population is equivalent with a monomorphic population of x_1 , and such a population can be invaded by a mutant of x_2 that is inside the area of coexistence. As a consequence, the evolution of x_2 must change its direction, and thus the x_2 -isocline

must connect to the x_2 -extinction boundary where the x_2 -extinction boundary has a vertical tangent point (P_2 in Fig. 2). Analogously, the x_1 -isocline connects to the x_1 -extinction boundary where it has a horizontal tangent point (no such point in Fig. 2; see the Appendix of Geritz et al., 1999 for a more elaborated demonstration of these assertions).

Curiously, the TEP shown in Fig. 2 has only one regular connection point to the boundary of the area of coexistence for each isocline: The isoclines must go through these points, but then they must stay within the area of coexistence as they may not connect to any other regular point of the boundary. The intersection of the two extinction boundaries (point Q in Fig. 2) is, however, an exceptional point. Here both $s_{x_1}(x_2) = 0$ and $s_{x_2}(x_1) = 0$, and the two strategies $x_{1(Q)}$ and $x_{2(Q)}$ can coexist in a neutrally stable equilibrium at any frequency. To see this, consider different paths leading to Q within the area of coexistence. The frequencies of the two resident strategies in population dynamical equilibrium are different along different paths and they also converge to different limiting values as the paths approach Q . For example, the frequency of x_1 is low along a path near the x_1 -extinction boundary whereas it is almost one along a path near the x_2 -extinction boundary. Provided that the equilibrium frequency is a continuous function of the trait values, any resident frequency is a limiting value for some path when it approaches Q . In the point Q thus all frequencies represent neutrally stable equilibria of the population dynamics.

Since the resident dimorphic population of $x_{1(Q)}$ and $x_{2(Q)}$ does not have a unique population dynamical attractor, $s_{x_1, x_2}(y)$ is not defined in Q . As the extinction boundaries intersect in Q and the isoclines must stay between them, the isoclines also converge to Q but are undefined in point Q ; in other words, Q belongs to the closure of both isoclines (see the Appendix for a formal proof in the example below). Despite the exceptional nature of point Q , its existence is generic because it depends only on the shape of the arbitrary ‘invasion-noninvasion’ border line of the PIP.

Inside the area of coexistence, the shape of the isoclines cannot be derived from generic constraints on $s_{x_1, x_2}(y)$. For example, the isoclines may intersect. At the intersection of the two isoclines directional evolution ceases in both resident strategies; analogously to the monomorphic singularity, the population has either attained a dimorphic evolutionarily stable coalition or undergoes evolutionary branching again (Metz et al., 1996; Geritz et al., 1998). However, it is also a generic possibility that the isoclines do

not intersect and thus there is no dimorphic singularity in the area of coexistence (Fig. 2).

The PIP and TEP shown in Figs. 1 and 2, respectively, conform only with the universal constraints described above, and therefore represent an evolutionary scenario fully generic in the framework of adaptive dynamics. Let us now deduce the expected course of evolution starting with a monomorphic population inbetween the two monomorphic singularities. As we have seen in Fig. 1, the monomorphic population undergoes directional evolution towards the branching point x_{br} , where it becomes dimorphic. Initially, the two coexisting strategies undergo divergent coevolution (Fig. 2). However, as the population approaches the x_2 -isocline, the evolution of x_2 slows down. The reason for this is that in the vicinity of the x_2 -isocline the invading mutants of x_2 have only slightly positive growth rate, and therefore are easily lost due to demographic stochasticity while rare (Dieckmann and Law, 1996). The prevailing direction of evolution is thus to the left, whereby the population crosses the x_2 -isocline. Once the population is inbetween the two isoclines, both strategies evolve towards smaller trait values. Slow evolution of $x_1(x_2)$ near the $x_1(x_2)$ -isocline keeps the population inbetween the two isoclines as coevolution continues towards the intersection of the extinction boundaries (point Q).

Extinction happens when the population has arrived at the neighbourhood of Q such that the distance to the extinction boundaries is comparable to the size of mutations (δ). The next invading mutant of x_1 , for example, may ‘overshoot’ the x_2 -extinction boundary, i.e., x_2 may not be able to coexist with the invading mutant. As the mutant substitutes x_1 , it drives x_2 extinct. The remaining monomorphic population is near $x_{1(Q)}$ and therefore is inbetween the monomorphic repeller singularity, x_{rep} , and the branching point, x_{br} (Fig. 2). The monomorphic population thus will undergo directional evolution towards larger trait values until it reaches the branching point again, starting a new cycle of evolutionary branching and extinction (cf. Fig. 1).

It also may happen that an invading mutant of x_2 overshoots the x_1 -extinction boundary such that x_1 goes extinct, and the remaining monomorphic population is near $x_{2(Q)}$. Similarly to the previous case, the monomorphic population evolves upwards to the branching point. The difference between these two possibilities is that $x_{2(Q)}$ is nearer the branching point than $x_{1(Q)}$, hence it takes less time to complete the cycle. The invariable pattern of evolution is (i) directional evolution towards larger trait values in

the monomorphic population, (ii) evolutionary branching, (iii) parallel coevolution towards smaller trait values in the dimorphic population, and (iv) falling back to monomorphism by the extinction of one of the strategies. Which strategy goes extinct is, however, random, and there is a difference in the length of the cycle depending on which strategy remained in the monomorphic population after extinction.

A specific example based on a Lotka-Volterra competition model

In this section, we construct a specific example that exhibits cycles of evolutionary branching and extinction. Consider the Lotka-Volterra competition model

$$\frac{1}{N_{x_i}} \frac{dN_{x_i}}{dt} = r(x_i) \left[1 - \frac{\sum_j a(x_i, x_j) N_{x_j}}{K(x_i)} \right] \quad (1)$$

where N_{x_i} is the population density of strategy x_i . For simplicity, we assume that the intrinsic growth rate and the carrying capacity are independent of the trait value such that (after appropriate scaling of time and density) $r(x) \equiv 1$ and $K(x) \equiv 1$. Let the competitive coefficient between strategy x_i and x_j be of the cubic form

$$a(x_i, x_j) = 1 - (x_j - x_i)(\alpha x_i^2 - \beta x_i x_j + \gamma x_j^2 - \delta) \quad (2)$$

Since the growth rate of a particular strategy is a linear function of all densities (cf. Eq. 1), for a given set of resident strategies the population dynamics always have a unique fixed point, and all polymorphisms are protected (i.e., each strategy increases in frequency when rare). As $a(x, x) = 1$, the equilibrium density of a monomorphic resident population of any strategy x is $\hat{N}_x = K(x) = 1$. From Eq. 1, the growth rate of a rare mutant strategy y in the equilibrium population of strategy x is given by

$$s_x(y) = \frac{1}{N_y} \frac{dN_y}{dt} = r(y) \left[1 - \frac{a(y, x) \hat{N}_x}{K(y)} \right] = 1 - a(y, x) \quad (3)$$

With parameter values $\alpha = 4.5$, $\beta = 12.12$, $\gamma = 11.5$ and $\delta = 1$, the PIP corresponding to Eq. 3 is identical to the one shown in Fig. 1.

For obtaining the TEP (Fig. 2), we need the growth rate of a rare mutant y in the dimorphic resident population of strategies x_1 and x_2 . Analogously to Eq. 3,

$$s_{x_1, x_2}(y) = 1 - \left[a(y, x_1) \hat{N}_{x_1} + a(y, x_2) \hat{N}_{x_2} \right] \quad (4)$$

where the equilibrium densities of the two resident strategies are

$$\hat{N}_{x_1} = \left[1 - a(x_1, x_2) \right] / \left[1 - a(x_1, x_2) a(x_2, x_1) \right] \quad (5a)$$

and

$$\hat{N}_{x_2} = \left[1 - a(x_2, x_1) \right] / \left[1 - a(x_1, x_2) a(x_2, x_1) \right], \quad (5b)$$

respectively. The resident strategy $x_i (i=1,2)$ can be substituted by its mutant

$y = x_i + \varepsilon$ if the mutant's growth rate, $s_{x_1, x_2}(x_i + \varepsilon) \approx s_{x_1, x_2}(x_i) + \left. \frac{\partial s_{x_1, x_2}(y)}{\partial y} \right|_{y=x_i} \varepsilon$, is

positive. Since the resident strategies have zero growth rate in equilibrium

($s_{x_1, x_2}(x_i) = 0$), a larger mutant ($\varepsilon > 0$) can invade if the fitness gradient $\left. \frac{\partial s_{x_1, x_2}(y)}{\partial y} \right|_{y=x_i}$

is positive; if the fitness gradient is negative, then a smaller mutant ($\varepsilon < 0$) can invade.

The direction of evolution of strategy ($i=1,2$) in the dimorphic population of strategies x_1, x_2 is thus given by the sign of the fitness gradient

$$\left. \frac{\partial s_{x_1, x_2}(y)}{\partial y} \right|_{y=x_i} = - \left[\left. \frac{\partial a(y, x_1)}{\partial y} \right|_{y=x_i} \hat{N}_1 + \left. \frac{\partial a(y, x_2)}{\partial y} \right|_{y=x_i} \hat{N}_2 \right] \quad (6)$$

The TEP derived from Eq. 6 supplemented with Eqs. 2 and 5 with the parameter values as above is shown in Fig. 2. The horizontal and vertical arrows in Fig. 2 indicate the sign of the fitness gradient for x_1 and x_2 , and hence their direction of evolution, respectively. On the x_1 -, x_2 -isocline the corresponding fitness gradient is zero; across the isocline, the sign of the fitness gradient reverses.

Having a specific example enables us to perform a direct simulation of the evolutionary process independent of the adaptive dynamic analysis presented above. The simulation provides a numerical test of the predictions made by the theory. In the simulation, we did not constrain the population to be strictly monomorphic or dimorphic. Instead, we iterated the population dynamics of all strategies present by Eq. 1.

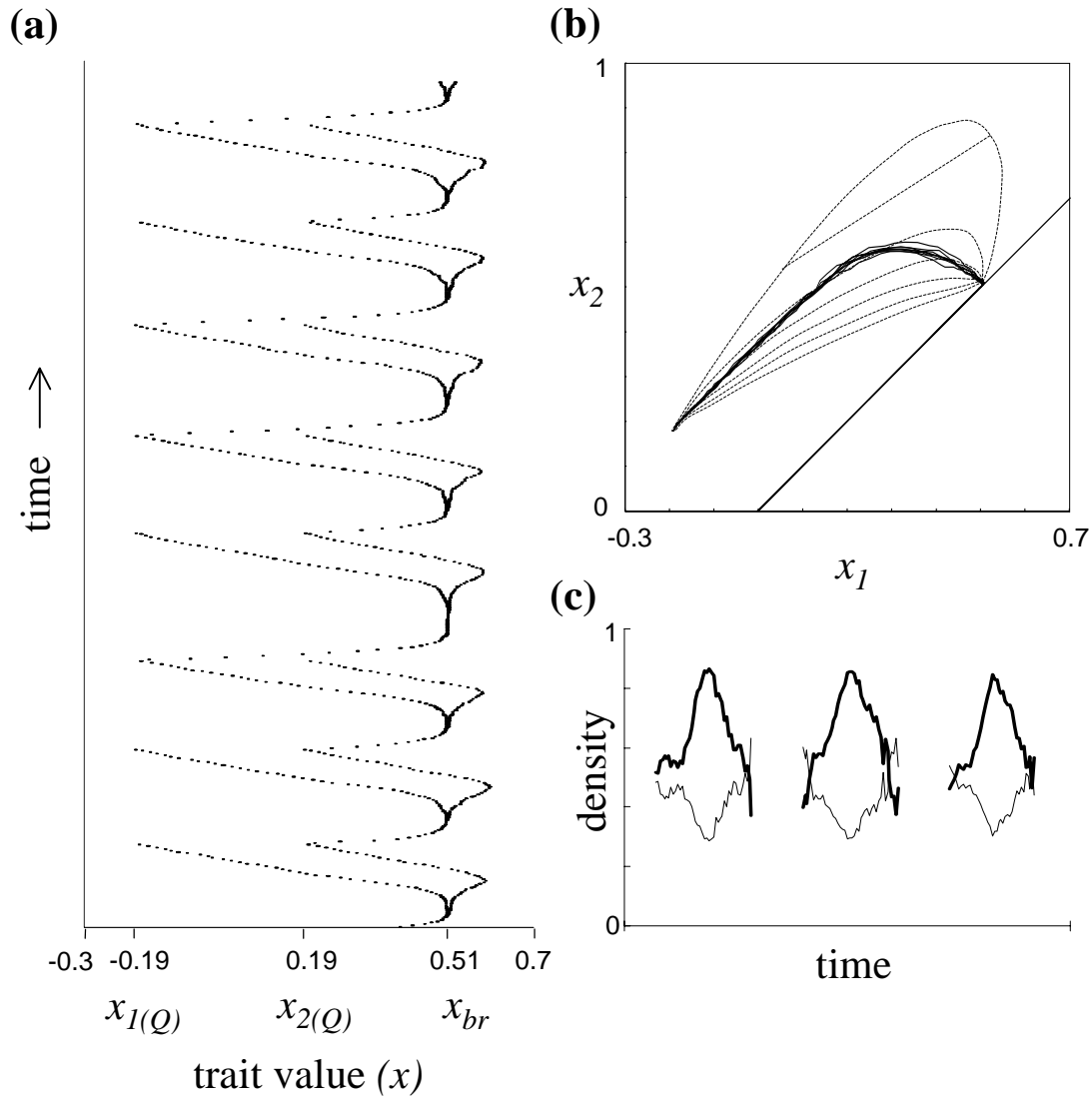


Fig. 3. (a) Simulated evolutionary tree (parameters as in Fig. 1). Strategies present were recorded each $2 \cdot 10^5$ years; total time span is $1.2 \cdot 10^9$ years. (b) Evolutionary trajectory in the area of coexistence superimposed on the contourlines of the equilibrium density of strategy x_1 (density of x_2 is not shown for clarity). Dashed lines: contourlines of N_{x_1} at 0, 0.2, 0.4, 0.6, 0.8, and 1; continuous lines: evolutionary trajectories in eight cycles (data from the simulation shown in (a)). Dimorphic evolution proceeds from the branching point (BP) to point Q . (c) Changes in population densities \hat{N}_{x_1} (thick line) and \hat{N}_{x_2} (thin line) during the dimorphic part of the first three cycles of the simulation.

New strategies were generated by small mutations of the residents. Adding new strategies to the population involves two kinds of stochastic processes (Dieckmann and Law, 1996). First, each strategy was allowed to produce a mutant with a probability

proportional to its population density. The mutant differed from the resident by a small mutation stepsize $\varepsilon = \pm 0.002$ with equal probability in either direction. Second, since the mutant is present initially in low numbers, it is subject to demographic stochasticity. The probability of avoiding extinction due to demographic stochasticity is proportional to the growth rate of the mutant provided that the growth rate is positive; otherwise the mutant dies out with probability 1. In the simulation, the mutant $x_i + \varepsilon$ was added to the population at a low initial density with probability $\max[kN_{x_i, s_{x_1}, \dots, x_n}(x_i + \varepsilon), 0]$, with $k = 0.333$. Strategies were considered extinct and were removed from the simulation if their frequency dropped below the (arbitrarily chosen) extinction threshold of 0.005.

During the simulation, we periodically recorded which strategies were present in the population. The resulting evolutionary tree (Fig. 3a) shows the predicted cycles of evolutionary branching and extinction. The initial monomorphic population first evolves to the branching point at $x_{br} = 0.51$ (cf. Fig. 1). After evolutionary branching, the two coexisting strategies undergo parallel coevolution towards smaller trait values until they reach the vicinity of point Q in the TEP (Fig. 2), i.e., $x_{1(Q)} = -0.19$ and $x_{2(Q)} = 0.19$. Here one of the two strategies dies out (the smaller one in the first, second, fourth, and seventh cycle in Fig. 3a, and the larger one in the remaining cycles). After extinction, the remaining monomorphic population evolves fast towards larger trait values until it reaches the branching point again.

Since either of the two residents may go extinct, there are two kinds of randomly alternating cycles with short and with long monomorphic periods, respectively, depending on whether the resident nearer to or further away from the branching point remained in the population after extinction. In this example, however, directional evolution is so fast in the monomorphic population that the difference in length between the two kinds of cycles is barely noticeable. Another source of variability in cycle length is the stochastic occurrence of successful mutants. The speed of evolution is slowest as well as most variable during evolutionary branching (Table 1). This is so because fitness differences are small near the evolutionary branching point such that the advantageous mutants have only a slightly positive growth rate and are often lost due to demographic stochasticity. The waiting time for the next successfully invading mutant has thus both a large expected value and a large variance. Another cause for low speed (but not for variable speed) near the branching point is that the substitution of the resident by the invading mutant is slow due to the small fitness differences, such that it takes a long time before the spreading mutant itself becomes the source of a new mutation. In monomorphic populations the fitness differences are large when the population is away from evolutionary singularities: Monomorphic evolution is the

fastest between $x_{1(Q)}$ and $x_{2(Q)}$, the range covered by long cycles but missing from short cycles. This explains why the average speed of monomorphic evolution is greater in the long cycles than in the short cycles (Table 1).

Evolutionary time (10^5 years)				
	Monomorphic evolution		Evolutionary	Dimorphic
	in short cycles	in long cycles	branching	evolution
average	14	24	54	69
standard deviation	0	1	12	4
Time / unit trajectory length				
average	43	27	468	84
standard deviation	4	1	111	5

Table 1. The speed of evolution during monomorphic directional evolution, evolutionary branching, and dimorphic directional evolution. Data from the simulation shown in Fig. 3, time resolution $2 \cdot 10^5$ years. Trajectory length is measured on the TEP; branching includes evolution within a distance of 0.05 from the branching point on the main diagonal of the TEP (monomorphic evolution, $x = x_1 = x_2$) or inside the area of coexistence (dimorphic evolution).

This example was constructed such that population density is constant throughout monomorphic evolution. In dimorphic populations, however, the equilibrium densities of the two residents change in a characteristic way as the trait values evolve (Fig. 3b,c). Dimorphic evolution proceeds along a stochastic broken-line trajectory within the area of coexistence: Each invading mutant brings the population further by a small but finite step into horizontal or vertical direction, depending on which resident is being substituted. Stochasticity stems from the random order in which the two residents produce successful mutants (and, in general, from the random size of mutations; in the present simulation, however, mutation size was constant). Near the branching point the equilibrium densities of the two residents are very sensitive to the exact trait values (Fig. 3b), therefore the small-scale stochasticity of the evolutionary trajectory results in wide random changes in the densities at the beginning of dimorphic evolution in each cycle (Fig. 3c). When the population has evolved away from the branching point but is still evolving roughly perpendicularly to the density contourlines (Fig. 3b), population

density changes in a smooth way. Next, the evolutionary trajectory turns to a much smaller angle with the density contourlines. In this phase of the cycle the stochastic variation of the trajectory is perpendicular to the contourlines, which results in more variation in the equilibrium densities. Shortly before extinction, when the population is near point Q , the densities are again sensitive to the exact trait values such that they vary strongly along the stochastic evolutionary trajectory (Fig. 3c).

A tenfold increase in mutation stepsize (from $\varepsilon = 0.002$ to $\varepsilon = 0.02$) makes directional evolution hundred times faster (simulation data not shown). This is due to two effects. First, each substitution brings about ten times as large change in phenotype. Second, the favourable mutants have larger fitness advantage and therefore a higher chance to escape extinction due to demographic stochasticity. The latter effect is also approximately proportional to the size of mutations as long as mutations are small and the population is away from evolutionary singularities. The effect of increasing mutation stepsize on the speed of evolutionary branching is even larger, because at the branching point the fitness of a mutant attains a minimum as a function of the mutant phenotype (see Geritz et al. 1998) and due to the curvature of the fitness function larger mutants have an a proportionally larger fitness advantage. Besides the quantitative effect on the speed of evolution, increasing the size of mutations also causes a qualitative change in evolution: In five out of twenty cycles, the smaller strategy of the dimorphic population underwent a second branching event yielding three distinct strategies in the population. Secondary branching is possible near the x_1 -isocline (Geritz et al., 1998, 1999). Two factors may promote secondary branching when mutations are large enough. First, the deviations of the stochastic evolutionary trajectory from the expected mean path laying inbetween the two isoclines increase when the individual mutational steps are larger, and hence there is a higher probability that the actual trajectory comes near to the x_1 -isocline. Second, when the size of mutations is increased, evolutionary branching speeds up relative to directional evolution, which makes it more likely that branching can take place before the evolution of x_2 moves the population away from the x_1 -isocline (cf. Fig. 2). After the detour to trimorphic states, the population falls back to monomorphism and cyclic evolution continues.

Discussion

In this paper we demonstrated evolutionary cycles with alternating levels of polymorphism. There are two key factors necessary to obtain such cycles. First, the direction of evolution must reverse between different levels of polymorphism: For example when monomorphism is alternating with dimorphism, directional evolution in at least one strategy of the dimorphic population must be opposite to directional

evolution in the monomorphic population. Second, the monomorphic population must have an evolutionary branching point where it becomes dimorphic, and directional evolution in the dimorphic population must lead to extinction whereby the population falls back to monomorphism again. If the monomorphic population that remains after extinction is in the basin of attraction of the branching point where dimorphism evolved in the first place, then repeated branching and extinction results in sustained evolutionary cycles.

Our model exhibits cycles of evolutionary branching and extinction under the conceptually simplest circumstances. The direction of evolution switches solely due to the different levels of polymorphism. Extinction of one of the two strategies happens with certainty when the evolutionary trajectory leaves the set of strategy pairs that are able to coexist. There exist, however, other mechanisms as well that may cause changes in the direction of evolution or may lead to extinction, and therefore may result in evolutionary cycles phenomenologically similar to the one we demonstrate. Below we review these alternative mechanisms.

(1) *Chance extinction*. Consider a population that undergoes evolutionary branching and then evolves towards a singular coalition (an intersection of the isoclines) inside the area of coexistence, where directional evolution ceases. In a deterministic model, this population would not fall back to monomorphism. If, however, one of the two resident strategies has only a low equilibrium frequency when the trait values are near the singular coalition, then in a population of finite size, this strategy will be prone to extinction due to demographic stochasticity. Provided that the remaining monomorphic population evolves back to the branching point, repeated cycles of evolutionary branching and chance extinction follow.

As evolution proceeds towards the singular coalition and the equilibrium density of one resident declines, the probability of extinction increases. Due to the random nature of extinction by demographic stochasticity, the cycles have variable length: Extinction may happen when the population is still relatively far from the singular coalition, but in other cycles the rare resident avoids chance extinction longer and thus the population evolves nearer the dimorphic singularity before falling back to monomorphism. (In simplified deterministic simulations where strategies are considered extinct once their frequency becomes smaller than a low extinction threshold, extinction occurs always at the same pair of trait values, and the cycles have approximately the same length. A small variation in length may occur due to variable waiting time for successful new mutations; but with small mutations and therefore many mutational steps, or when mutations are not limiting the speed of evolution, total evolutionary time will be very near its expected value.) If chance extinction occurs only rarely, then the population can

reach an evolutionarily stable coalition of strategies and spend a variable length of time there before extinction restarts the cycle.

In stochastic environments, fluctuating population numbers can result in chance extinction. In a model exhibiting evolutionary cycles of germination rate with repeated branching and extinction, Mathias and Kisdi (in press) found that the population evolved towards a dimorphic evolutionarily stable coalition after evolutionary branching. The strategy with higher germination rate, however, fast declined in number if a series of years occurred with unfavourable above-ground conditions. In large populations, the high-germination strategy died out only after a long run of bad years; since such a long series of bad years occurred only with low probability, extinction happened after a period of stasis at the evolutionarily stable coalition. In a smaller population, however, the high-germination strategy went extinct after a shorter run of unfavourable years, and the population could not reach the evolutionarily stable coalition before falling back to monomorphism.

(2) *Multiple attractors of population dynamics*. The direction of evolution may change due to a switch in the population dynamical attractor. Assume, for example, that the monomorphic population has two attractors, A_1 and A_2 , such that A_1 exists for trait values $x < x_1$ and A_2 exists for $x > x_2$ with $x_2 < x_1$. For $x_2 < x < x_1$ the population dynamics are bistable, and the growth rate of a mutant depends not only on the trait values of the resident strategy but also on the specific population dynamical attractor of the resident population (cf. Rand et al., 1994). With small mutations, the population remains on the same attractor during directional evolution as long as the attractor exists (see Geritz et al., in prep. for proof). Thus if on attractor A_1 directional evolution proceeds towards larger trait values, then the population evolves up to strategy x_1 where A_1 ceases to exist and the population switches to attractor A_2 . If on A_2 the direction of evolution is opposite, then the population evolves towards smaller trait values down to strategy x_2 where it switches back to attractor A_1 and starts to evolve upwards again, resulting in cyclic evolution of the monomorphic population (Khibnik and Kondrashov, 1997; Doebeli and Ruxton, 1997).

Essentially the same cycles may involve an ‘excursion’ to dimorphic populations. Assume that while on attractor A_1 , the population undergoes evolutionary branching. The evolution of the dimorphic population leads to the extinction of the smaller strategy, and the monomorphic population of the remaining larger strategy continues to evolve towards larger trait values still on attractor A_1 . The cycle is closed by switching to A_2 , directional evolution downwards, and switching back to A_1 as before.

Alternatively, extinction through a ‘catastrophic’ bifurcation (e.g. when the dimorphic attractor is lost at a fold bifurcation) may bring the population to attractor A_2 immediately when it falls back to monomorphism. Though monomorphic and dimorphic population states are alternating in these cycles, switching the attractors is essential in reversing the direction of evolution and hence in producing closed cycles.

(3) *Coevolution with another species.* Evolutionary cycles often occur in coevolving monomorphic species (‘genetically driven’ systems of Khibnik and Kondrashov; see e.g. Marrow et al., 1992, 1996; Dieckmann et al., 1995; Abrams and Matsuda, 1997; Doebeli, 1997; Gavrillets, 1997; Law et al., 1997 for examples). Similarly to the case of attractor switching, these coevolutionary cycles may also include an ‘excursion’ to dimorphism, and thus exhibit repetitive evolutionary branching and extinction.

In a dimorphic population, divergent and convergent evolution may alternate due to cyclic coevolution with another species. During divergent evolution, the two strategies become more and more widely separated. This evokes an evolutionary change in the interacting species, which in turn switches the dimorphic population from divergent to convergent evolution. Convergent evolution then reverses the direction of evolution in the interacting species as well, which after some time causes divergent evolution again in the dimorphic species.

During convergent evolution, the two strategies approach a single evolutionarily stable strategy. If convergent evolution continues long enough such that the two strategies are within the mutation radius from the ESS, then the population falls back to monomorphism as the ESS (or a very similar strategy) takes over the population (Geritz et al., 1998). When selection becomes disruptive again, then the ESS bifurcates into a branching point and dimorphism is restored. Monomorphism is thus alternating with dimorphism during the cycle. This scenario, however, is not essentially different from a cycle where the two strategies approach each other but no extinction occurs: The population of two similar strategies closely resembles a population with a single strategy. Evolutionary cycles of this type (involving two prey and two predator species and a circular phenotype space) were found by Van der Laan and Hogeweg (1995).

Without the analysis of adaptive dynamics, it is often not possible to ascertain the cause(s) leading to evolutionary cycles of branching and extinction in simulations. Nevertheless, the simulations may provide hints for the underlying mechanisms. Cycles of stochastic length may be due to chance extinction. Extinction after stasis at the evolutionarily stable coalition, found for example in the individual-based simulations of Doebeli and Dieckmann (in press), also suggests chance extinction; the same could be suspected if extinction occurs at different trait values as the cycle repeats. The abrupt

changes in population dynamics found by Koella and Doebeli (1999) hint to possible attractor switches.

The cycles described in this paper involve deterministic extinction in the sense that extinction happens with certainty and always at the same trait values. Which resident strategy goes extinct is, however, random. Consequently, short and long cycles occur in random order (although the probability of extinction of one or the other resident may be unequal, and a short simulation may show the same cycle each time). Apart from the two kinds of cycles, and apart from some variability due to the stochastic occurrence of successful mutants, the cycles are regular. There is no isolated abrupt change in population density as in case of an attractor switch. Shortly before extinction, however, the equilibrium population densities show characteristic random fluctuations during evolution (Fig. 3c).

Throughout this paper we assumed clonal inheritance, but our results can be generalized to diploid sexual populations as well. Consider first a trait controlled by a single locus with a continuum of potential alleles or by a number of tightly linked loci inherited effectively as a single locus. Though in sexual populations phenotypes are not transmitted from parents to offspring as in case of clonal inheritance, alleles are: The adaptive dynamics of alleles can be analyzed similarly to the adaptive dynamics of clonal strategies (Kisdi and Geritz, 1999). In particular, evolutionary branching in allele space results in two distinctly different allele, and hence in genetic polymorphism, in an initially monomorphic population. When evolutionary cycles of branching and extinction occur in allele space, then the population is alternating between genetic polymorphism and genetic monomorphism.

If heterozygotes are intermediate in phenotype, then they are selected against during evolutionary branching (Geritz et al., 1998). This favours the evolution of assortative mating between the emerging branches (Dieckmann and Doebeli, 1999; Kisdi and Geritz, in press; Geritz and Kisdi, in prep.) or the evolution of dominance (Van Dooren, 1999). With reproductive isolation between the branches or with full dominance (e.g. if alleles for larger trait values are always dominant over alleles for smaller trait values) adaptive dynamics exactly coincide with the clonal model.

Multi-locus quantitative genetic models of trait evolution are largely compatible with the clonal models of adaptive dynamics as long as directional evolution is concerned (Taper and Case, 1992; Abrams et al., 1993a; Dieckmann and Law, 1996). Evolutionary branching is strongly hindered by recombination between loci such that the evolution of randomly mating populations gets stuck at the branching point (Abrams et al., 1993b). With assortative mating, however, evolutionary branching happens readily in multi-locus simulations; moreover, assortative mating does evolve in these simulations if not

yet in place when the population arrives at the branching point (Doebeli, 1996; Dieckmann and Doebeli, 1999; Doebeli and Dieckmann, in press). The evolution of reproductive isolation by assortative mating converts within-species genetic polymorphism arisen by branching in allele space into two separate species. Evolutionary cycles of branching and extinction thus represent cycles with alternating level of species diversity.

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Appendix

In this Appendix we show that the intersection of the two extinction boundaries (point Q in Fig. 2) necessarily belongs to both the x_1 - and x_2 -isoclines extended to the closure of the area of coexistence in the Lotka-Volterra competition model with an arbitrary smooth function $a(x_i, x_j)$.

For (x_1, x_2) in the closure of the area of coexistence let us define

$$\tilde{S}_{x_1, x_2}(y) = D(x_1, x_2) - a(y, x_1)s_{x_2}(x_1) - a(y, x_2)s_{x_1}(x_2). \quad (\text{A1})$$

where $D(x_1, x_2) = 1 - a(x_1, x_2)a(x_2, x_1)$ denotes the determinant of the matrix of competitive coefficients. Using Eqs. 3, 4 and 5 we can rewrite the growth rate of a mutant in a dimorphic population in the form

$$\begin{aligned} s_{x_1, x_2}(y) &= 1 - a(y, x_1)\hat{N}_{x_1} - a(y, x_2)\hat{N}_{x_2} = \\ &= 1 - a(y, x_1)\frac{s_{x_2}(x_1)}{D(x_1, x_2)} - a(y, x_2)\frac{s_{x_1}(x_2)}{D(x_1, x_2)} = \\ &= \frac{\tilde{S}_{x_1, x_2}(y)}{D(x_1, x_2)} \end{aligned} \quad (\text{A2})$$

Inside the area of coexistence $D(x_1, x_2)$ is positive; at the intersection of the two extinction boundaries (point Q in Fig. 2), however, $D(x_{1(Q)}, x_{2(Q)}) = 0$. To see this, notice that $\tilde{S}_{x_1, x_2}(x_1) = \tilde{S}_{x_1, x_2}(x_2) = 0$ for all (x_1, x_2) in the closure of the area of coexistence because $s_{x_1, x_2}(x_1) = s_{x_1, x_2}(x_2) = 0$ for all (x_1, x_2) inside the area of coexistence and $\tilde{S}_{x_1, x_2}(y)$ as defined by (A1) is smooth. At point Q , which is on the extinction boundary of both x_1 and x_2 , $s_{x_1(Q)}(x_{2(Q)}) = 0$ and $s_{x_2(Q)}(x_{1(Q)}) = 0$; taking either $y = x_{1(Q)}$ or $y = x_{2(Q)}$ in Eq. (A1) implies that $D(x_{1(Q)}, x_{2(Q)}) = 0$.

The points of the x_1 -isocline ($i = 1, 2$) are given by

$$\left. \frac{\partial s_{x_1, x_2}(y)}{\partial y} \right|_{y=x_i} = \frac{1}{D(x_1, x_2)} \left. \frac{\partial \tilde{S}_{x_1, x_2}(y)}{\partial y} \right|_{y=x_i} = 0 \quad (\text{A3})$$

i.e., the line that satisfies $\left. \frac{\partial \tilde{S}_{x_1, x_2}(y)}{\partial y} \right|_{y=x_i} = 0$ coincides with the x_1 -isocline inside the area of coexistence and extends the isocline to the extinction boundary. From Eq. (A1) we get

$$\left. \frac{\partial \tilde{S}_{x_1, x_2}(y)}{\partial y} \right|_{y=x_i} = - \left. \frac{\partial a(y, x_1)}{\partial y} \right|_{y=x_i} s_{x_2}(x_1) - \left. \frac{\partial a(y, x_2)}{\partial y} \right|_{y=x_i} s_{x_1}(x_2) \quad (\text{A4})$$

Since in point Q both $s_{x_1(Q)}(x_{2(Q)}) = 0$ and $s_{x_2(Q)}(x_{1(Q)}) = 0$, $\left. \frac{\partial \tilde{S}_{x_1(Q), x_2(Q)}(y)}{\partial y} \right|_{y=x_i(Q)} = 0$ for

$i = 1, 2$. This point thus belongs to both isoclines extended to the closure of the area of coexistence.