

Red Queen Evolution by Cycles of Evolutionary Branching and Extinction

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We review mechanisms that lead to cyclic evolution with alternating levels of diversity. Such cycles involve directional evolution towards a so-called evolutionary branching point, where selection becomes disruptive and splits the population into two strategies. Coevolution of these strategies eventually leads to the extinction of one of them. The remaining strategy evolves back to the evolutionary branching point, and a new cycle begins. There are a number of different evolutionary mechanisms that can produce this kind of cycles including chance extinction, switching between population dynamical attractors, and coevolution with an ecologically distinct species. We also present an example for branching-extinction cycles where the direction of evolution changes between monomorphic and dimorphic populations solely due to the different levels of diversity. The latter cycles exhibit a novel feature: Even though extinction is deterministic in the sense that it is unavoidable and always occurs at the same trait values, it is random which of the two coexisting strategies goes extinct. As a result, long and short cycles alternate in a random sequence.

Keywords: Adaptive dynamics, coevolution, evolutionary cycles, evolutionary branching, extinction, Lotka–Volterra model, Red Queen dynamics

1. 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 sys-

tems (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, 2000), 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).

Khibnik and Kondrashov (1997) classified the different mechanisms leading to cyclic 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. If different trait values are favoured at different densities, then the fluctuations in population density cause small-amplitude

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fluctuations in the relatively slowly evolving traits. With increasing separation between the ecological and the evolutionary time-scales (making the customary assumption that evolution is much slower than population dynamics), 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 present 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 switching between different population dynamical attractors such that the direction of evolution changes when the population densities settle on a different attractor [see Doebeli and Ruxton (1997) and Khibnik and Kondrashov (1997) for examples].

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 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 that exhibit changing levels of diversity.

The simplest scenario for such cycles is the following. A monomorphic population evolves to an evolutionary branching point, where it experiences disruptive selection and splits into two strategies (phenotypes) separated by a widening gap. After evolutionary branching gave rise to a dimorphic population, the two coexisting strategies either continue to diverge or undergo parallel coevolution opposite to the direction of monomorphic evolu-

tion until one strategy goes extinct. The remaining strategy then evolves to the branching point and the cycle starts again.

Evolutionary branching appears to be a ubiquitous phenomenon in models of adaptive dynamics (e.g. Metz et al., 1992, 1996; Van der Laan and Hogeweg, 1995; Doebeli, 1996; Doebeli and Ruxton, 1997; Meszéna et al., 1997; Geritz et al., 1998, 1999; Boots and Haraguchi, 1999; Jansen and Mulder, 1999; Kisdi, 1999; Kisdi and Geritz, 1999; Koella and Doebeli, 1999; Parvinen, 1999; Day, 2000; Doebeli and Dieckmann, 2000; Mathias et al., 2001; Mathias and Kisdi, 2002 in press; etc.). Even though in many models the diversity produced by branching is preserved on the evolutionary time-scale, deterministic extinction is also common. Extinction happens if the evolution of coexisting strategies leads out of the domain of trait values where the strategies are able to coexist. In order to close the branching-extinction cycle, it is further necessary that after extinction, the remaining strategy is in the basin of attraction of the branching point. If this last condition is violated, then the monomorphic population left after extinction does not evolve back to the original branching point but for example attains a monomorphic ESS (see Geritz et al., 1999; Kisdi, 1999 for examples).

In this paper, we review mechanisms that can lead to branching-extinction cycles under the assumption of separate ecological and evolutionary time-scales. In addition, we construct an example with two novel features: (i) the direction of evolution reverses between monomorphic and dimorphic populations solely due to different levels of diversity, and (ii) extinction is deterministic in the sense that it occurs with certainty and at definite trait values, but it is random which of the two strategies goes extinct. As a result, two kinds of cycles (one shorter, one longer) occur in a random sequence.

Throughout this paper we assume clonal inheritance, and use the word 'species' for ecologically distinct entities (such as predator and prey) whereas 'strategies' stand for ecologically similar individuals that differ only in the trait value that undergoes evolution. Under appropriate conditions, these models also generalise to diploid sexual populations (see Discussion).

2. Cycles of evolutionary branching and extinction

Repeated evolutionary branching and extinction have been found in several published models (Van der Laan and Hogeweg, 1995; Doebeli and Ruxton, 1997; Koella and Doebeli, 1999; Doebeli and Dieckmann, 2000; Mathias and Kisdi, in press). Unfortunately, most studies provided only simulations, and often the precise evolutionary mechanism cannot be ascertained without a more detailed analysis. Here we review various mechanisms underlying cycles of evolutionary branching and extinction in published models. We also describe potential mechanisms of branching-extinction cycles that are analogous to the causes of cycles with constant number of coexisting strategies (Khibnik and Kondrashov, 1997).

2.1. *Chance extinction*

Consider a population that undergoes evolutionary branching and then evolves to an evolutionarily stable dimorphism. 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 at the stable dimorphism, then in a population of finite size, this strategy will be prone to extinction due to demographic stochasticity. In many simple models with no deterministic extinction, the branching point is the only attractor of monomorphic evolution. In this case the remaining monomorphic population necessarily evolves back to the branching point, and repeated cycles of evolutionary branching and chance extinction follow.

As evolution proceeds towards the evolutionarily stable dimorphism 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 stable dimorphism, but in other cycles the rare resident may avoid chance extinction longer and thus the population evolves nearer to the evolutionarily stable dimorphism before falling back to monomorphism. (In simplified deterministic simulations, however, where strategies are considered extinct

once their density becomes lower than some arbitrary extinction threshold, extinction occurs always at the same trait values, and the cycles have approximately the same length.) If chance extinction occurs only rarely, then the population can reach the evolutionarily stable dimorphism 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 after branching, the population evolved towards an evolutionarily stable dimorphism. The strategy with higher germination rate, however, fast declined in number during a series of years with unfavourable above-ground conditions. In large populations, the high-germination strategy died out only after a long run of bad years; since this occurred with only low probability, extinction happened after a period of stasis at the evolutionarily stable coalition. In smaller populations, however, a shorter run of unfavourable years could kill the high-germination strategy, and the population could not reach the evolutionarily stable coalition before falling back to monomorphism. Chance extinction may easily happen also in populations with nonequilibrium dynamics without external fluctuations, if the density of a strategy sometimes becomes very low such that extinction occurs due to demographic stochasticity (or, in simplified models, density crosses the extinction threshold).

In general, cycles of variable length and extinction at variable trait values suggest chance extinction. Extinction after stasis at the evolutionarily stable dimorphism (or polymorphism), found for example in the individual-based simulations of Doebeli and Dieckmann (2000), may also be the consequence of chance events.

2.2. *Multiple attractors of population dynamics*

A resident population with the same trait value may have multiple population dynamical attractors, for example alternative stable equilibria with low and high density (e.g. May, 1977; Matsuda and Abrams, 1994) or in-phase and out-of-phase cycles in coupled subpopulations (Gyllenberg et al., 1993;

Hastings, 1993). Populations with the same resident strategies but at different population dynamical attractors may provide very different biotic environments. The success of invasion by a new mutant thus depends not only on the trait value of the resident but also on the population dynamical attractor at which the resident population is found (Rand et al., 1994). In particular, the direction of evolution may change if the population switches from one population dynamical attractor to another (Matsuda and Abrams, 1994; Doebeli and Ruxton, 1997; Khibnik and Kondrashov, 1997; Parvinen, 1999).

When can a population switch between alternative population dynamical attractors? With small mutations, the population remains on the same attractor during directional evolution as long as the attractor exists (see Geritz et al., in press), and switches to a new attractor only if, in the course of evolution, the original attractor disappears through a “catastrophic” (e.g. saddle-node or “fold”) bifurcation. Evolutionary branching also preserves the population dynamical attractor in the sense of continuous change in the biotic environment: At the very beginning of dimorphic divergence, the two coexisting strategies are both still very similar to the preceding monomorphic population, and moreover the sum of their densities nearly equals the preceding monomorphic equilibrium density. This implies that the biotic environment set by the dimorphic population is close to the preceding monomorphic population, and in this sense the population tracks its attractor even after branching (Geritz et al., in press). Similarly, extinction through a transcritical bifurcation (i.e. when density declines to zero in a continuous way) does not imply discontinuous change in the biotic environment: If, in a dimorphic population, the density of one strategy gradually decreases, then the density of the other strategy converges to the monomorphic equilibrium, which is attained at the moment of extinction. Extinction, however, can cause attractor switching if it occurs through a “catastrophic” bifurcation (see also Gyllenberg and Parvinen, 2001).

To see first how attractor switching can lead to cyclic evolution of a single strategy, assume, for example, that a 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 $x_1 < x_2$).

The population dynamics are thus bistable for resident trait values $x_1 < x < x_2$. If on attractor A_1 directional evolution proceeds towards smaller trait values, then the population evolves down 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 larger trait values up to strategy x_2 , where it switches back to attractor A_1 and starts to evolve downwards again. The switching between population dynamical attractors results in cyclic evolution of the monomorphic population (Doebeli and Ruxton, 1997; Khibnik and Kondrashov, 1997).

Essentially the same type of cycles may involve an ‘excursion’ to dimorphic populations followed by extinction. Consider the scenario described in the previous paragraph, but assume that while on attractor A_1 , the population undergoes evolutionary branching, which is later followed by the extinction of the large strategy through a transcritical bifurcation such that the population is still on attractor A_1 . As it often happens after deterministic extinction (Geritz et al., 1999; Kisdi, 1999), assume that the monomorphic population of the remaining small strategy continues to evolve on A_1 towards even smaller trait values. When evolution eventually reaches x_1 , where attractor A_1 ceases to exist, the population switches to the alternative attractor A_2 . The cycle is closed by directional evolution on A_2 upwards to x_2 , switching back to A_1 , and convergence back to the branching point on A_1 . Notice that even though this scenario features recurrent branching and extinction, it is essentially similar to the monomorphic cycles based on attractor switching (hence to the second type of ecogenetically driven cycles of Khibnik and Kondrashov, 1997). In particular, the entire excursion to dimorphism (branching and extinction) happens on one attractor, and the catastrophic bifurcations that are essential for reversing the direction of evolution both occur in monomorphic populations (at x_1 and x_2 , respectively).

In other scenarios, however, the dimorphic phase may play an essential role in attractor switching. For example, the dimorphic population may undergo a catastrophic bifurcation whereby one strategy goes extinct, and the remaining strategy falls directly on the monomorphic attractor A_2 . In this case cyclic evolution results even if A_1 exists for all monomorphic populations: Since the

boundary x_j is never encountered, its existence is not necessary for cycles.

We are not aware of any example where attractor switching have been rigorously proved to be the underlying cause for cycles of evolutionary branching and extinction. Although chance extinction cannot be ruled out, the cycles found in numerical simulations by Doebeli and Ruxton (1997) seem to be due to attractor switching; alternative attractors are known to exist in their model and invading mutants can cause attractor switching (see also Doebeli 1998). The abrupt changes in population dynamics associated with extinction found by Koella and Doebeli (1999, Fig. 7a–b) may hint to possible attractor switching.

2.3. *Coevolution with another species*

Evolutionary cycles often occur in coevolving species such as predator and prey [‘genetically driven’ systems of Khibnik and Kondrashov (1997); see e.g. Marrow et al. (1992, 1996), Dieckmann et al. (1995), Abrams and Matsuda (1997), Doebeli (1997), Gavrillets (1997) and Law et al. (1997) for examples]. Similarly to the case of attractor switching, these coevolutionary cycles may also include an ‘excursion’ to dimorphism such that e.g. the prey evolves two distinct strategies, and exhibits repetitive evolutionary branching and extinction.

Coevolutionary cycles of branching and extinction might also emerge if an interacting species exerts alternating levels of disruptive selection on the focal species depending on how diverse the strategies within the focal species are. Here we propose this possibility only as a highly speculative verbal argument: This kind of coevolutionary cycles has not yet been tested or encountered in concrete models. As a possible example, one can envisage a predator–prey system where predators may evolve broad (generalist) or narrow (specialist) utilisation capabilities. If predation is independent of the strategy of the prey, as in case of a very generalist predator, the prey evolves to an ESS such that it can best consume the most abundant resource from a continuous resource distribution. The monomorphic prey favours a specialist predator that matches the prey. The specialist predator exerts disruptive selection on the prey

such that the prey undergoes evolutionary branching (Brown and Vincent, 1992; Doebeli and Dieckmann, 2000). As the two prey strategies diverge, they select for a more generalist predator. In turn, disruptive selection on the prey weakens, and the two prey strategies converge back towards the monomorphic ESS; the population eventually falls back to monomorphism when the ESS (or a very similar strategy) takes over the population. Alternatively, two prey strategies and the predator utilisation width may also stabilise at a joint equilibrium; cycles might result if the predator’s evolution is lagged behind the prey.

Van der Laan and Hogeweg (1995) found coevolutionary cycles of branching and extinction in predator–prey systems where the strategy space is circular. For example, the strategy of both species may be the circadian timing of their activity (very late night is indeed very early morning). Predators evolve to match the time of activity of the prey, whereas the prey tries to avoid matching. One possible evolutionary scenario is the following. Disruptive selection from the predator initiates evolutionary branching in the prey, as in case of ordinary linear strategy spaces. Branching in the prey then leads to branching in the predator as well (Brown and Vincent, 1992; Doebeli and Dieckmann, 2000). On the circular strategy space, the initially diverging strategies ultimately converge at the opposite position of the circle. Both species fall back to monomorphism and the cycle starts over again [Van der Laan and Hogeweg, 1995, Fig. 1a case (i)]. Another possible cycle involves branching and extinction in only the predator. Initially two prey and two predator strategies occupy alternating positions on the circle. This configuration is the best for the prey, but the predators are at fitness minima and both predator strategies undergo branching. One branch from each diverging fork converge upon each prey, approaching matching strategies that is best for the predator. Upon convergence, one of the two converging predator strategies goes extinct, and the prey finds an escape by evolving away from the remaining predator strategy. This restores the initial pattern with alternating strategies [Van der Laan and Hogeweg, 1995, Fig. 1b (i)]. Still other scenarios are possible if the predator is more generalist; e.g. cyclic convergence and divergence of two prey strategies chased by two predator strategies may also occur

without extinctions and branching events [Van der Laan and Hogeweg, 1995, Fig. 1a (ii, iii)]. In all of these intriguing patterns, the circularity of the strategy space plays an essential role in creating closed evolutionary cycles.

Among the three main types of branching-extinction cycles reviewed above, the first (chance extinction) has no clear analogue in the classification of Khibnik and Kondrashov (1997). Cycles based on chance extinction occur only in finite populations and are stochastic in nature. Concerning the deterministic cycles, those relying on multiple population dynamical attractors belong to the class of ecogenetically driven cycles, whereas the coevolutionary cycles are genetically driven. (In this paper, we assume strict separation between ecological and evolutionary time-scales, hence we do not consider purely ecologically driven cycles.)

A single monomorphic species with a single evolving trait can exhibit cyclic evolution only if switching between population dynamical attractors (ecogenetically driven cycles). Purely genetically driven cycles are not possible in one-dimensional evolution (i.e. with a single trait in a monomorphic species). Indeed, all genetically driven cycles included by Khibnik and Kondrashov (1997) involve at least two ecologically different species (such as a predator and a prey).

Could a purely genetically driven branching-extinction cycle occur in only one species, without attractor switching and without the periodically changing influence of a separate coevolving species? The two strategies emerging from evolutionary branching represent two dimensions of evolution, hence the limitations of one-dimensional evolutionary dynamics do not apply. To obtain cyclic evolution, the direction of evolution of at least one strategy of the dimorphic population must be opposite to monomorphic evolution; in absence of attractor switching or coevolving species, this reversal in the direction of evolution must be brought about solely by the changing level of polymorphism in the focal species. Second, extinction must occur in a deterministic way and such that the remaining monomorphic population can evolve back to the branching point. Below we argue that this is indeed possible, and show an example in a simple Lotka–Volterra competition model. Unfortunately, our example has no mechanistic underpinning, but nevertheless it enables us to investigate the dy-

namical properties of this type of branching-extinction cycles in detail.

3. Genetically driven cycles of evolutionary branching and extinction in a single species

In this section, we show that cycles of evolutionary branching and extinction within a single species represent a generic evolutionary pattern. We use the framework of mutation-limited adaptive dynamics as developed by Metz et al. (1996) and Geritz et al. (1997, 1998). Throughout we assume that for each resident strategy x the 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 specifies the invasion fitness of the mutant.

We start with constructing a pairwise invasibility plot (PIP) that indicates which mutant strategy y can invade the established population of strategy x (Fig. 1). There is no *a priori* constraint on the shape of a PIP other than the resident strategy must have zero long-term growth in its established population, and therefore the main diagonal $y = x$ of the PIP is a border line between ‘invasion’ and ‘noninvasion’ parts. In the example shown in Figure 1, directional evolution proceeding by succes-

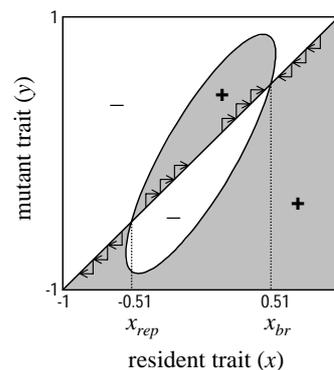


FIG. 1. Pairwise invasibility plot (PIP). Shaded area: the mutant can invade; clear area: the mutant cannot invade; arrows: directional evolution by invasions and substitutions. The lower evolutionary singularity (x_{rep}) is a repeller whereas the higher singularity (x_{br}) is an evolutionary branching point (convergence stable but evolutionarily unstable, see Geritz et al., 1998). The Lotka–Volterra model yields this PIP with parameter values $\alpha = 4.5$, $\beta = 12.12$, $\gamma = 11.5$ and $\delta = 1$

sive invasions and fixations of mutants with small phenotypic effect leads to an evolutionary branching point (x_{br}) provided that the initial trait value is in the basin of attraction (i.e. above x_{rep} ; see e.g. Geritz et al., 1998).

Having approached x_{br} , the population undergoes evolutionary branching that gives rise to two distinct strategies. In order to investigate the evolution of the dimorphic population, we need a two-dimensional trait evolution plot (TEP; Fig. 2). Assuming that all dimorphisms are protected, two strategies can coexist if both can invade the established population of the other. Accordingly, the set of strategy pairs that can form dimorphisms is constructed from the PIP as the overlapping parts of ‘invasion’ areas of the PIP itself and of its mirror image taken along the main diagonal (shaded area in Fig. 2; see Geritz et al., 1998). The overlapping parts of ‘noninvasion’ areas represent strategy pairs where neither strategy can invade the other, i.e. the rare type always goes extinct (dotted area in Fig. 2). Since the labelling of the resident strategies (x_1, x_2) is arbitrary, the TEP is always symmetric

along the main diagonal. Without loss of generality, we shall assume that $x_1 < x_2$, i.e. we restrict the analysis to the upper left half of the TEP.

Within the area of coexistence (shaded part of Fig. 2), the two coexisting strategies undergo directional evolution (indicated by arrows in Fig. 2b). In the vicinity of the branching point ($x_1 = x_2 = x_{br}$) selection is always disruptive (Eshel et al., 1997; Geritz et al., 1998), and the two strategies diverge from each other. When evolution has left the neighbourhood of the branching point, however, the direction of evolution may change. The area of coexistence 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).

The possible structure of the TEP is constrained since the isoclines cannot connect to the boundary of the area of coexistence at arbitrary points, but at specific points such a connection must exist (see Geritz et al., 1999, Appendix for proof). The x_1 -isocline must connect to the boundary where x_2 goes extinct vertically above the monomorphic singularity (point P_1 in Fig. 2). By mirroring, 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). Moreover, 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).

Curiously, the TEP shown in Figure 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 strategies have exactly zero fitness as mutants in each other’s established population, 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

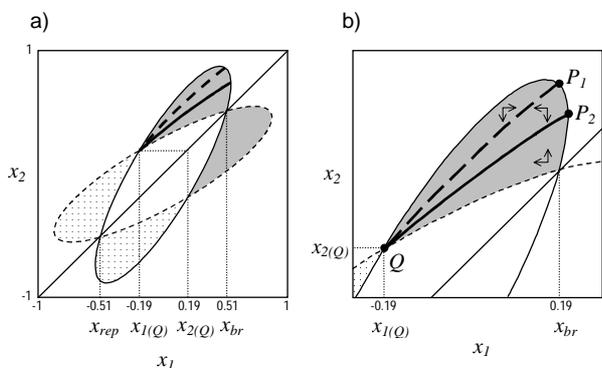


FIG. 2. Trait evolution plot (a), and the area of coexistence enlarged (b). Shaded area: the area of coexistence (x_1 and x_2 coexists in a protected dimorphism); dotted area: the rare strategy goes extinct whichever it is; thin dashed line: x_1 -extinction boundary; thin continuous line: x_2 -extinction 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 Figure 1

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, the fitness of a rare mutant 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 Lotka–Volterra example below).

Inside the area of coexistence, the shape of the isoclines cannot be derived from general constraints. For example, the isoclines may intersect such that the population converges to a dimorphic evolutionary singularity. However, it is also possible that the isoclines do not intersect and thus there is no dimorphic singularity in the area of coexistence (Fig. 2). In this case, the dimorphic population evolves as follows. After evolutionary branching, when the two strategies are still near to $x_1 = x_2 = x_{br}$, disruptive selection drives the evolution of the smaller strategy (x_1) downwards whereas the larger strategy (x_2) evolves upwards. As the population approaches the x_2 -isocline, the evolution of x_2 slows down because 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 evolution 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. 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 (Fig. 1), starting a new cycle of evolutionary branching and extinction.

It may also 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, monomorphic evolution leads back to the branching point. Since $x_{2(Q)}$ is nearer to the branching point than $x_{1(Q)}$, it takes less time to reach the branching point and complete the cycle. Depending on the emergence of mutants near Q , it is random which strategy goes extinct. As a consequence, long and short cycles follow in random order according to which strategy was left after extinction.

4. A specific example based on a Lotka–Volterra competition model

In this section, we construct a specific example for the cycles of evolutionary branching and extinction described above. 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

$$a(x_i, x_j) = 1 - (x_j - x_i)$$

$$(\alpha x_i^2 - \beta x_i x_j + \gamma x_j^2 - \delta). \quad (2)$$

For a given set of resident strategies, the Lotka–Volterra model always has a unique population dynamical equilibrium (setting the right-hand side of Eq. 1 equal to zero, there is a single solution for the equilibrium densities), and consequently all polymorphisms are protected (unprotected polymorphisms are possible only if there is a second, unstable fixed point of population dynamics). 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

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

The PIP corresponding to Eq. 3 with parameters $\alpha=4.5$, $\beta=12.12$, $\gamma=11.5$ and $\delta=1$ is identical to the one shown in Figure 1. The structure of the PIP, and hence the qualitative features of the evolutionary process, are robust with respect to changing the parameters.

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,

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

where the equilibrium densities of the two resident strategies are

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

and

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

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, $s_{x_1,x_2}(x_i + \varepsilon) \approx$

$$\approx s_{x_1,x_2}(x_i) + \left. \frac{\partial s_{x_1,x_2}(y)}{\partial y} \right|_{y=x_i} \varepsilon, \text{ is positive. Since the}$$

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 posi-

tive; if the fitness gradient is negative, then a greater mutant ($\varepsilon > 0$) can invade. The direction of evolution of strategy x_i ($i=1,2$) in the dimorphic population of strategies x_1, x_2 is thus given by the sign of the fitness gradient

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

as indicated by horizontal ($i=1$) and vertical ($i=2$) arrows in Figure 2b.

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. 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. 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 $k N_{x_1} s_{x_1, \dots, x_n}(x_i + \varepsilon)$ (with $k=0.333$) if $s_{x_1, \dots, x_n}(x_i + \varepsilon) > 0$. Strategies were considered extinct and were removed from the simulation if their frequency dropped below the (arbitrarily chosen) extinction threshold of 0.005. This simulation

algorithm is the same as in Geritz et al. (1998) except that here we took the demographic stochasticity of rare mutants into account.

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 co-existing strategies undergo parallel evolution 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.

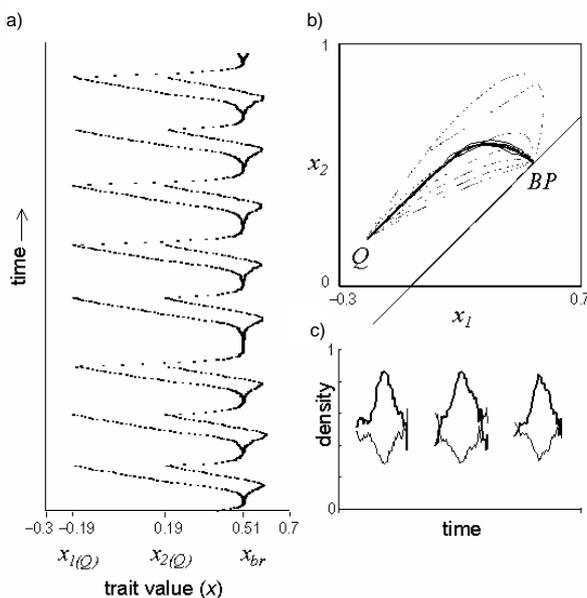


FIG. 3. (a) Simulated evolutionary tree (Lotka–Volterra model, parameters as in Fig. 1). Strategies present were recorded each $2 \cdot 10^5$ years; total time span is $1.2 \cdot 10^9$ years. (b) Evolutionary trajectory in the area of coexistence superimposed on the contour lines of the equilibrium density of strategy x_1 (for clarity, the density of x_2 is not shown). Dashed lines: contour lines of \hat{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

In this example, directional evolution in the monomorphic population is so fast that the difference in length between “long” cycles (when the smaller strategy is left after extinction) and “short” cycles (when the larger strategy is left) 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. A different 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).

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

TABLE 1

The speed of evolution during monomorphic directional evolution, evolutionary branching, and dimorphic directional evolution

Evolutionary time (10^5 years)				
	Monomorphic evolution		Evolutionary branching	Dimorphic evolution
	in short cycles	in long cycles		
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

Data from the simulation shown in Figure 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)

results in wide random changes in the densities at the beginning of dimorphic evolution in each cycle (Fig. 3c). 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. These random fluctuations of population densities foreshadow the random extinction to follow. Since there is only one population dynamical attractor, there is no isolated abrupt change in population densities as in case of attractor switching.

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.

5. Discussion

Cycles of evolutionary branching and extinction may occur due to a number of different underlying mechanisms including random extinction, switching between population dynamical attractors (ecogenetically driven cycles), coevolution with another, ecologically distinct species such as predator and prey (genetically driven cycles), and even solely due to changing evolution at different levels of polymorphism within a species or different levels of diversity within a guild containing ecologically very similar species (genetically driven cycles). A number of different scenarios have been considered within each category; we do not claim the list of mechanisms to be exhaustive.

The example we showed for the last mechanism in this paper also exhibits the peculiar feature that even though extinction occurs deterministically at specific trait values, it is random which of the two strategies goes extinct, and consequently short and long cycles occur in random order. Our example is not mechanistic (i.e. Eq. 2 is not derived from underlying ecological assumptions), but it demonstrates that these cycles are possible under frequency-dependent selection.

Throughout the paper we considered examples where cycles involve monomorphic and dimorphic stages. Similar cycles are conceivable between higher levels of diversity as well, perhaps even with repeated branching building up a high level of diversity followed by mass extinction.

Most models of evolutionary branching assume clonal inheritance, but the results can be generalised 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 analysed similarly to the adaptive dynamics of clonal strategies (Kisdi and Geritz, 1999). In particular, evolutionary branching in allele space results in two distinctly different alleles, 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 be-

tween 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; Geritz and Kisdi, 2000) 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.

Most quantitative traits of course are controlled by many, more or less independent loci with small allelic effects in each. Multi-locus 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, however, strongly hindered by recombination between loci such that in randomly mating populations, evolution gets stuck at the branching point (Abrams et al., 1993b).

Evolutionary branching happens readily in multi-locus simulations if mating is assortative (Doebeli, 1996; Dieckmann and Doebeli, 1999; Doebeli and Dieckmann, 2000). There is a growing number of empirical studies that demonstrate disruptive natural selection on traits that are ecologically relevant and that also provide cues for mate choice (e.g. Ratcliffe and Grant, 1983; Schluter and Nagel, 1995; Wood and Foote, 1996; Macnair and Gardner, 1998; Feder, 1998; Nagel and Schluter, 1998; Grant et al., 2000). Whenever mating is assortative with respect to the ecological trait, evolutionary branching splits the population into two reproductively at least partially isolated groups, i.e. incipient species. Moreover, assortative mating often evolves in the multi-locus simulations if not yet in place when the population arrives at the branching point (Doebeli, 1996; Dieckmann and Doebeli, 1999; Doebeli and Dieckmann, 2000). 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 within a guild of species that are ecologically very similar except for the trait under selection.

In many aspects, cycles of evolutionary branching and extinction are related to taxon cycles (Rummel and Roughgarden, 1985; Taper and Case, 1992, 1993). In taxon cycles, the first species evolves to a trait value where evolution stops, but the population can be invaded by a second species that has a different trait value but is otherwise ecologically very similar to the first species. Such a trait value may be an evolutionary branching point if assortative mating does not evolve and thus evolutionary branching is prevented by multi-locus inheritance (Abrams et al., 1993b), or may be a local (but not global) ESS. Following invasion, the coevolution of the two species leads to extinction and the remaining species eventually evolves to the trait value where the cycle started. Invasion-extinction cycles may be very variable if the invading species is different each time or if invasion happens before the population has reached the branching point or local ESS. If, however, invasions are rare on an evolutionary time-scale, and always the same species invades (that is evolutionarily stable in some source area), then regular cycles of invasion and extinction follow.

Might cycles of evolutionary branching and extinction be ubiquitous not only in models but also in the fossil record? Unfortunately, this question is not easy to answer. On a geological time-scale, directional evolution is often very fast (Hendry and Kinnison, 1999). Simple models of mutation-limited evolution (such as Fig. 3a) are misleading with respect to the real evolutionary time scale: Selection operating on standing genetic variation proceeds orders of magnitude faster than mutation-limited evolution. Due to the haphazard nature of fossilisation, cycles of branching and extinction may appear in the fossil record merely as trait values scattered over a range in a seemingly random fashion, and thus may be indistinguishable from a rather wide, temporally constant within-species distribution of the trait.

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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

$$\begin{aligned} \tilde{S}_{x_1, x_2}(y) = & D(x_1, x_2) - a(y, x_1)s_{x_2}(x_1) \\ & - a(y, x_2)s_{x_1}(x_2). \end{aligned} \tag{A1}$$

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

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

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_i -isocline ($i=1,2$) are given by

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

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_i -isocline inside the area of coexistence and extends the isocline to the extinction boundary. From Eq. (A1) we get

$$\begin{aligned} \left. \frac{\partial \tilde{S}_{x_1, x_2}(y)}{\partial y} \right|_{y=x_i} &= \\ &= - \left. \frac{\partial a(y, x_1)}{\partial y} \right|_{y=x_i} s_{x_2}(x_1) - \left. \frac{\partial a(y, x_2)}{\partial y} \right|_{y=x_i} s_{x_1}(x_2). \end{aligned} \tag{A4}$$

Since in point Q both $s_{x_1(Q)}(x_2(Q))=0$ and $s_{x_2(Q)}(x_1(Q))=0$, for $i=1,2$. This point thus belongs to both isoclines extended to the closure of the area of coexistence.

$$\left. \frac{\partial \tilde{S}_{x_1(Q), x_2(Q)}(y)}{\partial y} \right|_{y=x_i(Q)} = 0$$

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