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Remarks on Branching-Extinction Evolutionary Cycles

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Contents

Abstract

We show in this paper that the evolution of cannibalistic consumer populations can be a never ending story involving alternating levels of polymorphism. More precisely, we show that a monomorphic population can evolve toward high levels of cannibalism until it reaches a so-called branching point, where the population splits into two sub-populations characterized by different, but initially very close, cannibalistic traits. Then, the two traits coevolve until the more cannibalistic subpopulation undergoes evolutionary extinction. Finally, the remaining population evolves back to the branching point, thus closing an evolutionary cycle. The model on which the study is based is purely deterministic and derived through the adaptive dynamics approach. Evolutionary dynamics are investigated through numerical bifurcation analysis, applied both to the ecological (resident-mutant) model and to the evolutionary model. The general conclusion emerging from this study is that branching-extinction evolutionary cycles can be present in wide ranges of environmental and demographic parameters, so that their detection is of crucial importance when studying evolutionary dynamics.

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Remarks on Branching-Extinction Evolutionary Cycles

Fabio Dercole

1 Introduction

Red Queen dynamics are evolutionary dynamics that do not converge to an equilibrium (Van Valen, 1973, see also Rosenzweig and Schaffer, 1978, Stenseth and Maynard Smith, 1984, Futuyma, 1986 and Rosenzweig *et al.*, 1987). The name was inspired by the book "Through the Looking-Glass and What Alice Found There" (Carroll, 1871), where the Red Queen says: "Now, here, you see, it takes all the running you can do, to keep in the same place." As remarked by the Red Queen, the most intriguing case of Red Queen dynamics is that of evolutionary cycles, where natural selection keep (periodically) the system in the same evolutionary state. This is in contrast with the (wrong) idea that an evolutionary change always implies some sort of improvement.

Evolutionary cycles have captured the attention of theoretical ecologists and geneticists in the last decades (see e.g. Abrams, 1992; Marrow *et al.*, 1992; Dieckmann *et al.*, 1995; Iwasa and Pomiankowski, 1995, 1999; Marrow *et al.*, 1996; Abrams and Matsuda, 1997; Gavrilets, 1997; Dercole *et al.*, 2003). In all the above cited works, the adaptive traits vary cyclically while the population densities track the equilibrium corresponding to the current trait values. Other kinds of evolutionary cycles involve populations which are not at equilibrium at ecological timescale (at least during part of the evolutionary cycle) (Khibnik and Kondrashov, 1997; Dercole *et al.*, 2002b), or switch between different attractors begetting evolutionary reversals (Khibnik and Kondrashov, 1997; Doebeli and Ruxton, 1997; Dercole *et al.*, 2002a). Finally, there is also the possibility of evolutionary cycles due to alternating levels of *polymorphism*. Such cycles, called *branching-extinction evolutionary cycles*, are characterized by recurrent *evolutionary branching* and *extinction*, which periodically add and remove a population (or morphs) to and from the system.

At a *branching point* (Metz *et al.*, 1996; Geritz *et al.*, 1997, 1998) one of the *resident* populations, characterized by a particular trait value, coexists with a population of *mutants* characterized by a slightly different trait value. Moreover, the two initially similar traits are under opposite selection pressures, so that the mutant population becomes a new resident population and the number of coevolving traits increases. At evolutionary extinction (Matsuda and Abrams, 1994; Ferrière, 2000) the trait of a population reaches a critical value at which the corresponding equilibrium density vanishes or catastrophically collapses to zero, thus reducing the number of coevolving traits. Therefore, in the simplest branching-extinction evolutionary cycle the evolutionary dynamics of a monomorphic population are characterized by a globally stable branching point and the dimorphic evolutionary trajectories originating close to the branching point end with the evolutionary extinction of one of the two sub-populations.

Branching-extinction evolutionary cycles have been observed in several models (Van der Laan and Hogeweg, 1995; Doebeli and Ruxton, 1997; Koella and Doebeli, 1999; Doebeli and Dieckmann, 2000) through stochastic simulations. However, from a stochastic simulation it is hard to say if extinction is produced by demographic stochasticity, when the population density is relatively small, or by the deterministic mechanism of evolutionary extinction described above. Only Kisdi *et al.* (2001) presented an example of branching-extinction evolutionary cycle where extinction occurs deterministically. Such an example is based on a Lotka-Volterra population competition model (Lotka, 1920; Volterra, 1926). As is well known, these models are rather degenerate both biologically (the per capita growth rates are unbounded) and mathematically (their bifurcations are non-generic (Kuznetsov, 1998)). Moreover, the particular model analyzed in Kisdi *et al.* (2001) uses a very peculiar dependence of the competition coefficients upon the traits. Such a dependence, which is hardly defendable biologically, seems to be adopted simply in view of obtaining a branching-extinction cycle. Finally, mathematically speaking, the long-term evolutionary behavior of the model is not captured by a true cycle. In fact, the dimorphic trajectories originating close to the branching point converge to a point in trait space where both sub-populations go extinct, thus virtually determining the halt of evolutionary dynamics. However, stochastically, one sub-population goes extinct first. Then, the remaining (very scarce) monomorphic population evolves back to the branching point. Of course, which sub-population goes extinct first is a matter of chance and, depending upon this random event, different monomorphic transients lead back to the branching point. Thus, a stochastic simulation would show long-term evolutionary dynamics in which two different periods (from the branching point back to it) alternate randomly.

In this paper we present the first fully deterministic example of branching-extinction evolutionary cycle, using the model for the evolution of cannibalistic traits in consumer populations recently described in Dercole and Rinaldi (2002). We show that any monomorphic population converges to an intermediate level of cannibalism where it branches into two sub-populations. Then, assuming that body size of adult individuals and cannibalism are positively correlated (as it is often the case (Fox, 1975; Polis, 1981, 1988)), we show that during the dimorphic evolutionary phase the two sub-populations evolve into a weakly cannibalistic *dwarf* population and a highly cannibalistic *giant* population, until the giant population undergoes an evolutionary extinction. The key point of our result is that the giant population density does not vanish gradually at evolutionary timescale, but rather collapses suddenly (Gyllenberg and Parvinen, 2001). Such a discontinuous extinction event reverses the selection pressure on the dwarf population, which then begins to enhance its cannibalistic attitude.

As in Kisdi *et al.* (2001), we follow the approach of *adaptive dynamics theory* developed by Metz *et al.* (1996); Geritz *et al.* (1997, 1998). This approach is based on the assumption that small and rare random mutations are followed by natural selection and allows one to describe the dynamics of the traits in a purely deterministic way, through an ODE called the *canonical equation* (Dieckmann and Law, 1996; Champagnat *et al.*, 2001), which is capable of explaining evolutionary branching and extinction.

The paper is organized as follows. In the next section we sketch the derivation of the monomorphic and dimorphic canonical equations. In the third section we derive the branching-extinction evolutionary cycle for a particular parameter setting. A discussion of the mechanisms necessary for this kind of evolutionary cycles to exists and some comments on the robustness of the results close the paper.

2 The model

Assume that a cannibalistic consumer population is characterized by a positive phenotypic trait from now on called *cannibalism*, indicated by x and positively correlated with the size of adult individuals. This assumption is not necessary for our result but it facilitates its interpretation. In fact, x can be simply identified with a suitable measure of adult body size (like length or weight, but see e.g. Mittelbach and Persson (1998) for other examples in cannibalistic fish populations), so that the coexistence of two sub-populations, one with low and one with high cannibalism, should be revealed by the presence of dwarfs and giants in the same environment.

The derivation of the canonical equation of adaptive dynamics requires three things: (i) the knowledge of the interactions occurring at ecological time scale between all sub-populations; (ii) the dependence of the demographic parameters of the sub-populations upon the traits; (iii) the frequency and distribution of the mutations. All this is specified in the next two sub-sections.

2.1 Ecological model

The interactions between N cannibalistic consumer sub-populations with biomass densities n_i and traits x_i, $i = 1, \ldots, N$, are described by the following ODE:

$$\dot{n}_i = n_i f_i(n, x) \tag{1a}$$

where

$$f_i(n, x) = \left(\frac{\sum_{j=0}^{N} e_{ij}\, a_{ij}\, n_j}{1 + \sum_{j=0}^{N} h_{ij}\, a_{ij}\, n_j} - \sum_{j=1}^{N} \frac{a_{ji}\, n_j}{1 + \sum_{k=0}^{N} h_{jk}\, a_{jk}\, n_k} - \sum_{j=1}^{N} c_{ij}\, n_j \right) \tag{1b}$$

$n = (n_1, \ldots, n_N)$, $x = (x_1, \ldots, x_N)$, n_0 is the density of a common resource, a_{ij} and h_{ij} are the attack rate and the handling time of the i-th sub-population associated with the food source of type j, e_{ij} is a conversion factor transforming food intake of type j into new biomass of type i and c_{ij} specifies the extra-mortality due to competition.

The parameters n_0, e_{ij} and c_{ij} are assumed to be constant, while the attack rates a_{ij} and the handling times h_{ij} depend upon the traits as follows:

$$a_{i0} = \frac{2\, A_{i0}}{\left(\dfrac{x_i}{x^0}\right)^{\alpha} + \left(\dfrac{x^0}{x_i}\right)^{\alpha}} \tag{2a}$$

$$a_{ij} = A_{ij} \left[\frac{2}{\left(\dfrac{p\, x_i}{x_j}\right)^{\beta} + \left(\dfrac{x_j}{p\, x_i}\right)^{\beta}} \right] \left(\frac{x_i^{\gamma}}{\underline{x}^{\gamma} + x_i^{\gamma}} \right) \left(1 - \frac{x_i^{\delta}}{\bar{x}^{\delta} + x_i^{\delta}} \right) \tag{2b}$$

$$h_{ij} = w_1\, x_i^{-w_2} \tag{2c}$$

where A_{ij} is the maximum attack rate, x^0 is the trait value at which a population is best adapted to the common resource (see eq. (2a)) and $\alpha > 1$, $\beta > 1$, $\gamma > 1$, $\delta > 1$, $p < 1$, $\underline{x}$, $\bar{x}$, w_1 and w_2 are suitable positive parameters which specify the shape of the functions (2) (see Dercole and Rinaldi, 2002, for a more detailed description). In particular, the cannibalistic attack rate a_{ij} is higher when the body size of the victim is in a suitable ratio with that of the predator, i.e. when $x_j = p\, x_i$, $p < 1$ (see eq. (2b)). Moreover, small values of β imply high values of the cannibalistic attack rate a_{ii} (see eq. (2b) with $x_i = x_j$), i.e. great possibilities for individuals of trait x_i to predate individuals of the same trait. In the real world such a population would be characterized by a substantial change in size from juvenile to adult, so that adult individuals can easily predate young ones (Polis, 1981, 1988). However, an explicit description of the age/size distribution, which naturally calls for relatively complex age/size structured models (see e.g. Bosch van den *et al.*, 1988; Diekmann *et al.*, 1986; Metz and Diekmann, 1986a,b,c; Briggs *et al.*, 2000; Claessen *et al.*, 2000), poses some problems in the derivation of the canonical equation of adaptive dynamics. In fact, as we shall see in Section 2.2, the canonical equation captures the evolutionary dynamics under the assumptions that an invading mutant generically substitutes its former resident. Unfortunately, as far as we know, this property is not yet proved for structured population models. Moreover, for such models, the canonical equation can hardly be determined in closed form. For these reasons, our choice has been to hide the size-structure of the population, thus describing each population with a first order ODE (see eq. (1)) where the parameter $(1/\beta)$ is a sort of surrogate for the *size range* of the individuals in the population. As discussed above, $(1/\beta)$ gives an indication of the level of intra-trait cannibalism, which is enhanced by factors such as, among others, the size range in the population.

2.2 Evolutionary model

We now use model (1, 2) with $N = 2$ and 3 to derive the monomorphic and dimorphic evolutionary models. The first $(N - 1)$ populations are considered to be the resident populations while the last population is considered to be the mutant population. Consistently with the adaptive dynamics approach, we assume that mutations are rare events, so that the resident populations are at equilibrium when a mutation occurs and are never challenged by more than one mutation at a time. Moreover, we also assume that the trait x_N of the mutant is only slightly different from one of the resident traits, say x_i (i.e. $x_N = x_i + \epsilon$, with ϵ small) and that the mutant population density n_N is initially very small. Under the above conditions, model (1, 2) can be used to establish the fate of the mutant and resident populations. Generically, an invading mutant replaces the former resident (see Dercole, 2002, for detailed conditions and proofs) so that, in the end, the system is composed of new set of $(N - 1)$ resident populations with i-th trait given by $x_i + \epsilon$. In the opposite case, i.e. when the mutant population does not invade, it goes extinct so that the traits of the resident populations remain unchanged. This process of mutation and selection can be further specified by making suitable assumptions on the frequency and distribution of small mutations (Dieckmann and Law, 1996; Champagnat *et al.*, 2001). The conclusion for $N = 2$ is that the rate at which the trait x_1 varies at evolutionary time scale is given by the following monomorphic canonical equation:

$$\dot{x}_1 = k\,\bar{n}_1(x_1)\frac{\partial \bar{f}_2(x_1, x_2)}{\partial x_2}|_{x_2=x_1} \tag{3}$$

where k is proportional to the frequency and variance of small mutations, $\bar{n}_1(x_1)$ is the resident population equilibrium density in the absence of mutants (see Dercole and Rinaldi, 2002, for a proof of existence and uniqueness) and $\bar{f}_2(x_1, x_2)$ is the *fitness of the mutant*, i.e.

$$\bar{f}_2(x_1, x_2) = f_2(\bar{n}_1(x_1), 0, x_1, x_2) \tag{4}$$

Geritz *et al.* (1997, 1998) showed that a stable monomorphic equilibrium $\bar{x}_1$ is a *branching point* if

$$\frac{\partial^2 \bar{f}_2(\bar{x}_1, x_2)}{\partial x_2^2}|_{x_2=\bar{x}_1} > 0 \tag{5}$$

At a branching point a mutant population invades but does not replace the former resident, thus it becomes a new resident itself. Moreover, the two initially very similar traits x_1 and x_2 differentiate in accordance with the dimorphic canonical equation (see the forthcoming eq. (6)).

The numerical bifurcation analysis (Kuznetsov, 1998; Doedel *et al.*, 1997; Kuznetsov and Levitin, 1997) of model (3, 4) carried out in Dercole and Rinaldi (2002) reveals that a globally stable branching point $\bar{x}_1$ characterizes the monomorphic dynamics of a population with wide size range living in a rich environment (i.e. for sufficiently high values of the parameters $1/\beta$ and n_0). Thus, for such a population, we now focus on the dimorphic evolutionary dynamics, namely the evolution of the cannibalistic traits x_1 and x_2 of two coexisting sub-populations with densities n_1 and n_2.

As explained in Dercole and Rinaldi (2002), the study of dimorphic evolutionary dynamics must be limited to the *coexistence region*, which is the region of all pairs (x_1, x_2) for which model (1, 2), for $N = 2$, has a stable and strictly positive equilibrium. Such a region can be

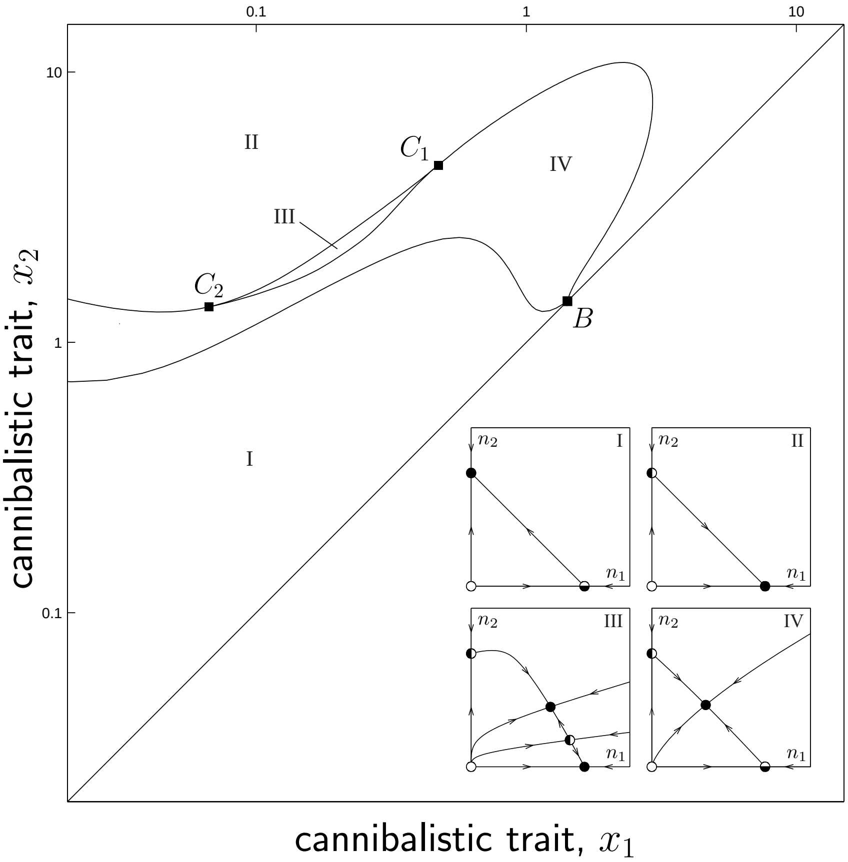

Figure 1: Bifurcation diagram of model (1, 2) ($N = 2$) with respect to cannibalistic traits x_1 and x_2. Upper triangle: bifurcation curves and regions I-IV (squares indicate codimension-2 bifurcation points). Lower triangle: state portraits of model (1, 2) ($N = 2$) for each region I-IV (circles indicate equilibria). Parameter values: $n_0 = 500$, $\beta = 1.9$, $A_{i0} = 1$, $A_{ij} = 10$, $x^0 = 0.1$, $\underline{x} = 0.5$ $\bar{x} = 5$, $p = 0.2$, $\alpha = 2$, $\gamma = 8$, $\delta = 2$, $c = 1$, $e = 0.6$, $w_1 = 0.1$, $w_2 = 0.25$, $i, j = 1, 2$. Region III has been horizontally stretched for purpose of illustration.

computed by performing the bifurcation analysis of model (1, 2) ($N = 2$) with respect to the traits x_1 and x_2 interpreted as constant parameters. Since the trajectories in the space (x_1, x_2) are symmetric with respect to the diagonal $x_2 = x_1$, we limit the analysis to the region $x_1 < x_2$ and call populations 1 and 2 dwarf and giant populations, respectively. An example of this bifurcation analysis is shown in Fig. 1, where the upper part reports all bifurcation curves which identify four regions (I-IV), while the lower part reports the corresponding state portraits of model (1, 2) ($N = 2$). Since only in the state portraits III and IV there is a stable and strictly positive equilibrium, the region of coexistence is the union of regions III and IV. Point B on the diagonal $x_2 = x_1$ corresponds to the monomorphic branching point, i.e. $B \equiv (\bar{x}_1, \bar{x}_1)$. The nature of a bifurcation curve separating two nearby regions can be understood by comparing the two corresponding state portraits. For example, the bifurcation curve separating region II from region IV is characterized (see state portraits II and IV) by the collision of a stable and strictly positive node with a saddle on the n_1-axis (so-called *transcritical bifurcation*). Thus, if a dimorphic trajectory in region IV moves toward this bifurcation curve, the giant population density vanishes and the giant population eventually goes extinct when the dimorphic trajectory hits the curve. By contrast, the bifurcation curve separating region II from region III is characterized (see state portraits II and III) by the collision of a stable and strictly positive node with a strictly positive saddle (so-called *fold bifurcation*). Thus, if a dimorphic trajectory in region III moves toward this bifurcation curve, the giant population density does not vanish, but catastrophically collapses (at ecological timescale) as soon as the dimorphic trajectory crosses the curve.

Let now $N = 3$ and denote by $\bar{n}_1(x_1, x_2)$ and $\bar{n}_2(x_1, x_2)$ the densities of the stable and strictly positive equilibrium of model (1, 2) ($N = 2$) in the region of coexistence. The dimorphic canonical equation reads:

$$\begin{aligned} \dot{x}_1 &= k_1\, \bar{n}_1(x_1, x_2) \frac{\partial \bar{f}_3(x_1, x_2, x_3)}{\partial x_3}|_{x_3 = x_1} \\ \dot{x}_2 &= k_2\, \bar{n}_2(x_1, x_2) \frac{\partial \bar{f}_3(x_1, x_2, x_3)}{\partial x_3}|_{x_3 = x_2} \end{aligned} \tag{6}$$

where k_1 and k_2 are proportional to the frequency and variance of small mutations in the two resident populations and $\bar{f}_3(x_1, x_2, x_3)$ is the fitness of the mutant, i.e.

$$\bar{f}_3(x_1, x_2, x_3) = f_3(\bar{n}_1(x_1, x_2), \bar{n}_2(x_1, x_2), 0, x_1, x_2, x_3) \tag{7}$$

3 The branching-extinction evolutionary cycle

The dimorphic evolutionary dynamics defined by model (6, 7) within the coexistence region shown in Fig. 1 are sketched in Fig. 2. The coexistence region is partitioned in white, light gray and dark gray sub-regions. Trajectories starting in the white region tend toward a dimorphic equilibrium D (which can be either a branching point or not, see Geritz *et al.* (1998) or Dercole (2002) for the specific conditions). Trajectories starting in the light gray region hit the boundary of the coexistence region where a catastrophic evolutionary extinction occurs, namely between points C_1 and C_2 (see Fig. 1). Notice that points C_1 and C_2 are equilibria of equation (6, 7). In fact, $\bar{n}_2(x_1, x_2) = 0$ (i.e. $\dot{x}_2 = 0$, see the second equation of model (6)) at such points and $\dot{x}_1$ has opposite sign at opposite sides of C_1 and C_2 along the boundary of the coexistence region. Thus, a so-called x_1-*nullcline* (i.e. a curve in the (x_1, x_2) trait space where $\dot{x}_1 = 0$) passes through points C_1 and C_2. Finally, dark gray regions are those in which the giant [dwarf] population density smoothly vanishes when the evolutionary trajectory approaches the extinction boundary separating region II [I] from region IV (see Fig. 1).

Since the branching point B, where dimorphism originates, lies on the boundary of the light gray region the long-term evolutionary attractor of models (3, 4) and (6, 7) is the branching-extinction evolutionary cycle represented by the thick trajectory in Fig. 2. In words, when dwarf and giant traits become sufficiently different, the giant population is not capable of sustaining itself by harvesting on the dwarf population and is driven extinct by natural selection (see point $X^* \equiv (x_1^*, x_2^*)$ in Fig. 2). After that (i.e. after the sudden transition from X^* to X^{**} in Fig. 2) the dwarf population evolves back to the branching point B, starting with a trait $x_1 = x_1^*$, in accordance with the monomorphic canonical equation (3, 4). Thus, starting from any ancestral monomorphic condition the final outcome of evolution is the branching-extinction evolutionary cycle of Fig. 2, characterized by two distinct evolutionary phases: a monomorphic evolution toward the branching point (from X^{**} to B) and a dimorphic evolution marked by the temporary presence of a highly cannibalistic population of giants (from B to X^*).

4 Discussion and conclusions

An evolutionary cycle characterized by alternating levels of polymorphism has been shown to be the evolutionary attractor of cannibalistic consumer populations with wide size range living in rich

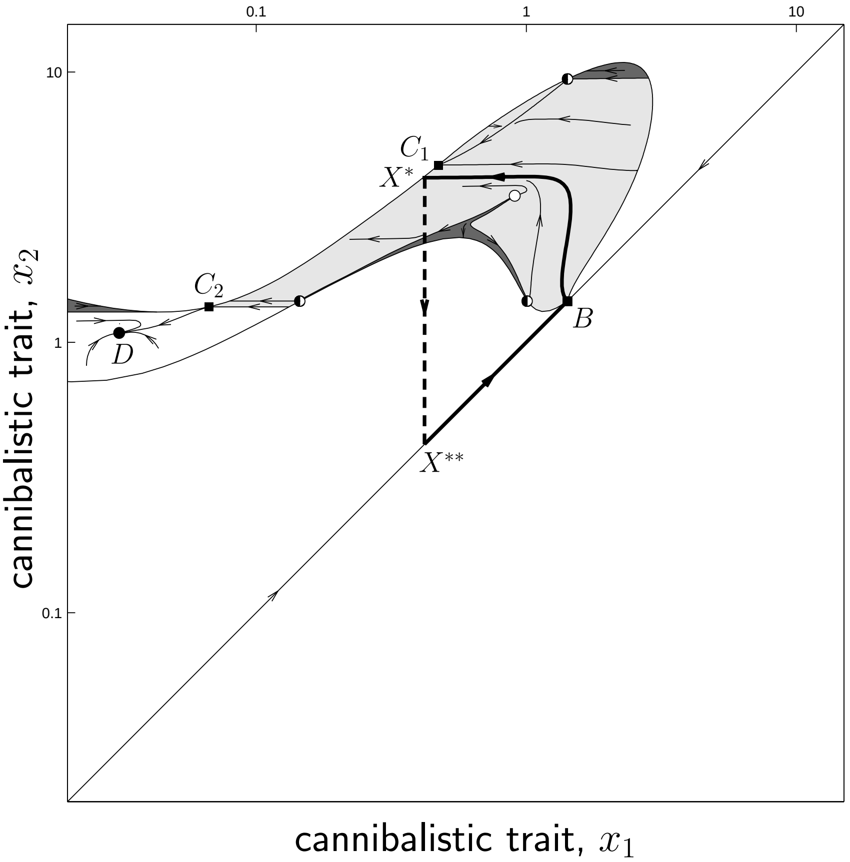

Figure 2: Dimorphic evolutionary dynamics (circles indicate dimorphic equilibria) and the branching-extinction evolutionary cycle (thick trajectory). Parameter values as in Fig. 1 ($k_1 = k_2$).

environments. The deterministic mechanisms that lead to such evolutionary cycles have been first addressed by Kisdi *et al.* (2001) and require the following three properties: (i) the monomorphic population has an evolutionary branching point where it becomes dimorphic; (ii) the dimorphic evolution originating at the branching point leads to the evolutionary extinction of one of the two morphs, say morph 2; (iii) the post-extinction monomorphic population (i.e. morph 1) is in the basin of attraction of the branching point.

Condition (iii) implies that the direction of evolution of trait 1 reverses during the transition from dimorphism to monomorphism. This is not possible if the evolutionary extinction occurs through a transcritical bifurcation of the dimorphic population equilibrium $(\bar{n}_1(x_1, x_2), \bar{n}_2(x_1, x_2))$. In fact, in such a case, the population density $\bar{n}_2(x_1, x_2)$ vanishes when approaching the bifurcation curve, so that only population 1 is present. This implies, by continuity, that $\dot{x}_1$ cannot have different values just before and after the bifurcation.

Thus, the key point of our result is that the evolutionary extinction of the giant population occurs through a fold bifurcation, which, being catastrophic, allows the evolutionary reversal of the dwarf population. More precisely, just before the bifurcation, $\dot{x}_1$ is negative and given by equation (6) evaluated at point X^* (see Fig. 2), where $\bar{n}_2(x_1, x_2)$ is strictly positive (and equal to the limit of $\bar{n}_2(x_1, x_2)$ along the evolutionary trajectory approaching X^*). By contrast, when the evolutionary trajectory crosses the bifurcation curve, the giant population suddenly collapses (i.e. $\bar{n}_2(x_1, x_2)$ converges to zero at ecological timescale, see state portraits II and III in Fig. 1) and $\dot{x}_1$ is positive and given by equation (3) evaluated at point X^{**}.

Kisdi *et al.* (2001) have considered a Lotka-Volterra ecological model in which only transcritical bifurcations are possible. Thus, in order to reverse the selection pressure on the remaining population they have been forced to consider a quite peculiar situation in which the evolutionary extinction of both sub-populations occurs simultaneously. This is why in their case the dimorphic evolutionary trajectories converge to a codimension-2 bifurcation point, namely the point of intersection of two transcritical bifurcation curves.

In closing this paper we like to comment on the robustness of the result. In principle, a complete bifurcation analysis of models (3, 4) and (6, 7) with respect to all couples of strategic parameters (like the environmental richness (n_0) and the size range ($1/\beta$)) would answer all possible questions concerning the robustness of our conclusions. In particular, a complete bifurcation analysis would allow us to determine all possible qualitative evolutionary scenarios and the regions in parameter space where such scenarios occur. However, such an analysis poses nontrivial technical problems, since the dimorphic population equilibrium is not known in closed form, so that model (6, 7) is actually a *differential algebraic system*, for which algorithms for the numerical solution of boundary-value problems are not yet fully developed (Ascher and Spiteri, 1994). Such algorithms are needed for the continuation of heteroclinic bifurcations (saddle to saddle connections) like those present in our model. Indeed, if one would like to determine the boundary of the region in parameter space where the branching-extinction evolutionary cycle exists, one should produce through numerical continuation the parameter combinations for which the unstable manifold of the saddle point B (trajectory BX^*) coincides with the stable manifold of the saddle point C_2 (see Fig. 2).

Despite these technical difficulties, we checked, by means of extensive numerical integration of model (6, 7) for various parameter settings, that the branching-extinction evolutionary cycle of Fig. 2 is structurally stable and present in wide ranges of environmental and demographic parameters. Thus, our conclusion is that branching-extinction evolutionary cycles are robust evolutionary attractors and their detection is of crucial importance for fully understanding evolutionary dynamics.

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