

Chapter Seven

Branching-Extinction Evolutionary Cycles

We show in this chapter that evolving communities can have a quite peculiar evolutionary attractor, called a branching-extinction evolutionary cycle. First, an adaptive trait characterizing a monomorphic species evolves toward a branching point, where the species turns dimorphic by splitting into two resident populations. Then, the two resident traits coevolve until one of the two populations goes extinct. Finally, the remaining population evolves back to the branching point, thus closing the evolutionary cycle. All this is shown by studying the evolution of cannibalistic traits in consumer populations and by focusing on the role of environmental richness. The evolution of “dwarf” (weakly cannibalistic) and “giant” (highly cannibalistic) coexisting morphs and the possibility of periodic evolutionary extinction of highly cannibalistic populations in rich environment is established among other evolutionary scenarios. Parts of this chapter are taken from Dercole and Rinaldi (2002) and Dercole (2003).

7.1 INTRODUCTION

Evolutionary cycles have captured the attention of theoretical ecologists and geneticists in the last decades (see, e.g., Abrams, 1992a; Marrow et al., 1992; Dieckmann et al., 1995; Iwasa and Pomiankowski, 1995, 1999; Marrow et al., 1996; Abrams and Matsuda, 1997; Gavrilets, 1997; see also Chapter 5). In all these cited works, the adaptive traits cyclically vary while the abundances of the resident populations track the demographic equilibrium corresponding to the current trait values. Other kinds of evolutionary cycles involve populations that switch between different demographic attractors, begetting evolutionary reversals (Doebeli and Ruxton, 1997; Khibnik and Kondrashov, 1997; see also Chapter 8), or characterized by wilder demographic dynamics (at least during part of the evolutionary cycle; see Khibnik and Kondrashov, 1997, and Chapter 9). Finally, there is also the possibility of evolutionary cycles due to alternating levels of polymorphism. Such cycles, called branching-extinction evolutionary cycles (see Section 1.8), are characterized by recurrent evolutionary branching and extinction, which periodically add and remove a population (or morph) to and from the community.

As we have seen in Chapter 3, at a branching point one of the resident populations, characterized by a particular trait value, coexists with a conspecific population of mutants characterized by a slightly different trait value. The two initially similar traits are under opposite selection pressures, so that the mutant population becomes a new resident population and the polymorphism of the species
increases. Moreover, in sexual species, as remarked in Section 1.7, if the force of disruptive selection is strong enough and mechanisms of assortative mating induce individuals to mate with phenotypically similar partners, then interbreeding between the two resident populations ceases and two reproductively isolated sub-species actually evolve. At evolutionary extinction (see Section 1.8) an adaptive trait of a resident population reaches a critical value at which the corresponding population abundance vanishes or catastrophically collapses to zero, thus reducing the species polymorphism or even the number of coevolving species. Thus, in the simplest branching-extinction evolutionary cycle the evolutionary dynamics of a monomorphic species are characterized by a globally stable branching point, and the dimorphic evolutionary trajectory originating at the branching point ends with the evolutionary extinction of one of the two resident populations.

Branching-extinction evolutionary cycles have been observed by several authors (van der Laan and Hogeweg, 1995; Doebeli and Ruxton, 1997; Koella and Doebeli, 1999; Doebeli and Dieckmann, 2000) through stochastic simulations and individual-based models (see Chapter 2). However, it is hard to say if in these cases extinction is produced by demographic stochasticity, modeling accidental extinctions when the population abundances are relatively small, or by the deterministic mechanism of evolutionary extinction. Kisdi et al. (2001) presented a first example of branching-extinction evolutionary cycle where extinction occurs deterministically, but the trait dependence of the demographic parameters of their model is hardly defendable biologically and seems to be adopted simply in view of obtaining a branching-extinction cycle. Moreover, mathematically speaking, the long-term evolutionary behavior obtained by Kisdi et al. (2001) is not captured by a true cycle. In fact, the dimorphic evolutionary trajectory originating at the branching point converges to a critical point in trait space where the two resident populations coexist at one among an infinite number of neutrally stable demographic equilibria, ranging from the extinction of one population to that of the other, with high sensitivity with respect to the dimorphic initial condition. However, at this degenerate demographic equilibrium, small mutations cause the extinction of one of the two populations, while the remaining population evolves back to the branching point. Of course, which population goes extinct at the critical point is a matter of chance and, depending upon this random event, different monomorphic evolutionary 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) randomly alternate.

In this chapter we present an example of fully deterministic branching-extinction evolutionary cycle (first discussed in Dercole, 2003) concerning the evolution of cannibalistic traits in consumer populations. We show that a consumer monomorphic species evolves to an intermediate level of cannibalism at which it branches into two initially similar resident populations. Then, assuming that body size of adult individuals and cannibalism are positively correlated (as it is often the case; see Fox, 1975; Polis, 1981, 1988), we show that during the dimorphic evolutionary phase the two resident populations evolve into a weakly cannibalistic “dwarf” population and a highly cannibalistic “giant” population, until the giant population undergoes an evolutionary extinction. As we will see, the key point is that the gi-
ant population abundance does not gradually vanish on the evolutionary timescale while approaching extinction, but rather suddenly collapses (a case of so-called evolutionary suicide, as discussed in Sections 1.8 and 3.6). Such a discontinuous extinction event reverses the selection pressure on the dwarf population, which then begins to enhance its cannibalistic attitude.

The chapter is organized as follows. In the next two sections we describe the demographic dynamics of a polymorphic cannibalistic community and sketch the derivation of the corresponding monomorphic and dimorphic AD canonical equations. In Section 7.4 we derive the branching-extinction evolutionary cycle for a particular parameter setting. A discussion of the mechanisms leading to evolutionary attractors characterized by alternating levels of polymorphism and some comments on their robustness close the chapter.

7.2 A MODEL OF CANNIBALISTIC DEMOGRAPHIC INTERACTIONS

Cannibalism, defined as intraspecific predation, is a behavioral trait found in a wide variety of animals, ranging from protozoa and rotifers to birds and mammals (Fox, 1975). The most important studies based on field and laboratory data have been surveyed by Polis (1981, 1988), who has shown that pronounced cannibalism is a frequent feature in species that grow through a wide size range. Often cannibalism develops at a demographic timescale as a reaction of adult individuals to food scarcity (Fox, 1975). However, besides the evidence for dietary induction, several types of data and theoretical studies indicate that, for many species, there is a strong genetic component to cannibalism (see Polis, 1981, and references therein; Henson, 1997; Getto et al., 2005).

Cannibalistic consumer populations naturally call for relatively complex age- and/or size-structured demographic models (see, e.g., Diekmann et al., 1986; van den Bosch et al., 1988; Cushing, 1991; Claessen and de Roos, 2003; Claessen et al., 2004). However, to easily derive the AD canonical equation we use a strongly simplified model. In particular, we hide the size-structure of the population as well as all environmental heterogeneity and seasonalities, which are known to enhance cannibalism in many species (Fox, 1975). Thus, both resident and mutant populations are described with a first-order ODE with constant parameters. Although the model is only a caricature of the real world, it contains the basic ingredients for a sound discussion of the evolutionary emergence of cannibalism. In fact, the cannibalistic predation rate and the searching efficiency of common resources are described by trait-dependent demographic parameters. Moreover, the functional form of the model and the ranges of its admissible parameter values have been carefully selected to fit a paradigmatic case, namely that of the Eurasian perch (Perca fluviatilis), described in great detail in Claessen et al. (2000).

Assume that a cannibalistic consumer population is characterized by an adaptive trait \( x \) related to its cannibalistic attitude. Since we do not want to refer to a particular species, we cannot specify what \( x \) is. However, to facilitate the interpretation of the results, we take the liberty of assuming that the size of adult individuals is positively correlated with the cannibalistic trait. Thus, \( x \) can be simply identified
with a suitable measure of body size, so that the coexistence of two populations, one with low and one with high cannibalism, should be revealed by the presence of dwarf and giant individuals in the same environment.

We now consider $P$ consumer populations, characterized by abundances $n_i$ and traits $x_i$, $i = 1, \ldots, P$, and assume that their demographic interactions are described by the following ODE system:

$$
\dot{n}_i = n_i \left( \sum_{j=0}^{P} e_{ij} a_{ij} n_j \left( 1 + \sum_{j=0}^{P} a_{ij} \tau_{ij} n_j \right) \right) - \sum_{j=1}^{P} a_{ji} n_j - \sum_{j=1}^{P} c_{ij} n_j ,
$$

(7.1)

$i = 1, \ldots, P$, where the index 0 refers to a common resource available to all populations at constant abundance $n_0$ (from now on called *environmental richness*). The three terms on the right-hand side of equation (7.1) are natality due to food intake, mortality due to cannibalism, and mortality (or reduced natality) due to intraspecific competition. The first term is written in the form of a type II functional response (see Section 3.3) and takes into account that each individual has two alternative food sources: the common resource and its own conspecifics. In the case of the Eurasian perch, the common resource is zooplankton on which all perch feed, at least in the first stages of their life (Holcik, 1977). Thus, rich environments are those in which young perch have more access to food. The parameter $e_{ij}$ is a conversion factor transforming food intake of type $j$ into new biomass of type $i$, $\tau_{ij}$ is the handling time of the $i$th population associated with the food source of type $j$, and $c_{ij}$ specifies the strength of intraspecific competition. Although all demographic parameters might depend upon various traits, to obtain a tractable problem we limit the analysis to the case in which the parameters $e_{ij}$ and $c_{ij}$ are constant ($e_{ij} = e$ and $c_{ij} = c$ for all $i, j = 1, \ldots, P$), while the attack rates $a_{ij}$ and the handling times $\tau_{ij}$ are trait-dependent. As usual at this stage, other choices would be justifiable.

The attack rate $a_{i0}$ specifies the consumption of the common resource and is assumed to be given by the same bell-shaped function of the trait $x_i$, for all $i = 1, \ldots, P$, because a consumer performs better when its body size is well tuned with the size of the local resource. In the analysis we use the following function:

$$
a_{i0}(x_i) = a_i(x_i) = \frac{2a_{r0}}{\left( \frac{x_i}{a_{r1}} \right)^{\alpha_{r2}} + \left( \frac{a_{r1}}{x_i} \right)^{\alpha_{r2}}},
$$

(7.2)

where $a_{r0}$ is the maximum attack rate, achieved for $x_i = a_{r1}$, and $\alpha_{r2}$ controls the sharpness of the bell shape.

As for the cannibalistic attack rate $a_{ij}$, we assume it is shaped as in Figure 7.1. Along each ray at constant $x_j/x_i$ ratio, the attack rate is bell-shaped and vanishes for $x_i$ tending to both zero and infinity. Similarly, $a_{ij}$ is a bell-shaped function of $x_j/x_i$, since the predation rate is higher when the body size of the victim is in a suitable ratio with that of the predator.
Figure 7.1 The cannibalistic attack rate $a_{ij}$ as a function of the traits $x_i$ and $x_j$ (see equation (7.3)). The thick line indicates the restriction of $a_{ij}$ on the ray $x_j = a_{c1} x_i$. Parameter values: $a_{c0} = 1, a_{c1} = 0.4, a_{c2} = 2, a_{c3} = 4, a_{c4} = 2, a_{c5} = 0.3, a_{c6} = 0.9$.

The function we use in our analysis is

$$a_{ij}(x_i, x_j) = a_{c}(x_i, x_j) = \frac{2a_{c0}}{a_{c1} x_i + x_j} a_{c2} x_i a_{c3} \left(1 - \frac{x_i^{3a_{c4}}}{a_{c6} x_i^{a_{c4}} + x_j^{a_{c4}}}ight), \quad (7.3)$$

where $a_{c0}$ is the maximum attack rate, $a_{c1} < 1$ is the optimum victim-predator body size ratio, $a_{c2} > 1, a_{c3} > 1, a_{c4} > 1$ control the sharpness of the bell shapes, while $a_{c5}$ and $a_{c6}$ are sort of thresholds indicating the body sizes at which cannibalism becomes physiologically significant and limited by habitat morphology, respectively (see Figure 7.1). To allow the survival of populations with negligible cannibalism ($x_i < a_{c5}$), we assume in the following $a_{c1} < a_{c5}$. Moreover, small values of $a_{c2}$ imply high values of the cannibalistic attack rate $a_{ii}$ (see equation (7.3) 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). For this reason the parameter $(1/a_{c2})$ is a sort of surrogate for the size range of the individuals in the population and will, indeed, be called size range in the following.

Finally, the handling times $\tau_{ij}$, which can be estimated from feeding experiments performed under excessive food conditions (Byström and Garcia-Berthou, 1999), are assumed to depend mainly upon the consumer trait $x_i$, through the function

$$\tau_{ij}(x_i) = \tau(x_i) = \tau_1 x_i^{-\tau_2},$$

taken from Claessen et al. (2000).
7.3 COEVOLUTION OF DWARFS AND GIANTS

We now study the evolution of cannibalism starting from a single monomorphic consumer species, i.e., a single resident population characterized by abundance \( n \) and trait \( x \). As we will see, the species can turn dimorphic through evolutionary branching, so that weakly cannibalistic dwarfs and highly cannibalistic giants coevolve during the dimorphic evolutionary phase.

Monomorphic Evolutionary Dynamics

Using model (7.1), with \( P = 1 \), one can easily show that its equilibrium \( \bar{n}(x) \) is unique, stable, and given by the positive root of the second-order equation

\[
0 = e a_c(x, x) \tau(x) \bar{n}(x)^2 + (c(1 + a_r(x) \tau(n_0) + (1 - e)a_c(x, x)) \bar{n}(x) - e a_c(x) n_0.
\]

Then, consistently with the AD approach, we assume that the resident population is settled at its equilibrium \( \bar{n}(x) \) when a mutant appears, that the trait \( x' \) of the mutant is only slightly different from \( x \), and that the mutant population abundance \( n'_0 \) is initially very small. Under these conditions, model (7.1), with \( P = 2 \), can be written in the standard form of a resident-mutant model:

\[
\frac{d n}{d t} = n f(n, n_0, x, x'), \\
\frac{d n_0}{d t} = n_0 f(n_0, n, x', x),
\]

from which, in accordance with definition (3.19) in Chapter 3, the invasion fitness of the mutation is obtained as

\[
\lambda(x, x') = f(0, \bar{n}(x), x, x) - \frac{e(a_t(x') n_0 + a_r(x', x) \bar{n}(x))}{1 + a_t(x') \tau(x') n_0 + a_r(x', x) \tau(x) \bar{n}(x)} - e\bar{n}(x).
\]

The resulting one-dimensional AD canonical equation is therefore given by

\[
\dot{x} = k \bar{n}(x) \left. \frac{\partial}{\partial x'} \lambda(x, x') \right|_{x' = x},
\]

where \( k \) is a constant parameter proportional to the frequency and variance of small mutations (the so-called mutational rate).

Equation (7.4) always admits the trivial solution \( x = 0 \), because both \( \bar{n}(x) \) and \( \partial \lambda / \partial x'|_{x' = x} \) are zero for \( x = 0 \) (as one can easily see by taking into account that \( a_t(x) \) vanishes with \( x \), see equation (7.2)). Moreover, the trivial solution \( x = 0 \) is always unstable (i.e., \( \dot{x} > 0 \) for small \( x > 0 \)), since \( \bar{n}(x) \) and \( \partial \lambda / \partial x'|_{x' = x} \) are positive for small and positive values of \( x \). In generic conditions, the nontrivial equilibria of (7.4) are either one or three, as shown in Figure 7.2 for three different combinations (see caption) of environmental richness \( (n_0) \) and size range \( (1/a_{c2}) \).
Figure 7.2 The equilibrium abundance $\bar{x}(x)$ of the resident population and the monomorphic evolutionary dynamics (on the horizontal axis in logarithmic scale), where circles indicate evolutionary equilibria (filled [empty] circles: stable [unstable] equilibria). (A) Evolution toward a weakly cannibalistic population of dwarfs ($n_0 = 10$, $a_{c2} = 2.5$). (B) Evolution toward a highly cannibalistic population of giants ($n_0 = 500$, $a_{c2} = 1.5$). (C) Evolutionary bistability ($n_0 = 10$, $a_{c2} = 1.5$). Other parameter values: $c = 1$, $e = 0.6$, $a_{r0} = 1$, $a_{r1} = 0.1$, $a_{r2} = 2$, $a_{r6} = 10$, $a_{c3} = 8$, $a_{c4} = 2$, $a_{c5} = 0.5$, $a_{c6} = 5$, $\tau_1 = 0.1$, $\tau_2 = 0.25$.

In the case of Figure 7.2C, two stable evolutionary equilibria $\bar{x}^{(1)}$ and $\bar{x}^{(2)}$ (filled circles on the $x$ axis) are separated by an unstable equilibrium $\bar{x}^{(u)}$ (empty circle), so that cannibalism can evolve toward either a low value $\bar{x}^{(1)}$, corresponding to a dense population of dwarfs, or a high value $\bar{x}^{(2)}$, corresponding to a scarce population of giants. In the other two cases there is only one stable equilibrium: a low trait value ($\bar{x}^{(1)}$) with high population abundance in case A, and a high trait value ($\bar{x}^{(2)}$) with low population abundance in case B. The transition from C to A [B] corresponds to a saddle-node bifurcation (see Appendix A) of the canonical equation (7.4), characterized by the collision of $\bar{x}^{(u)}$ with $\bar{x}^{(2)}$ [$\bar{x}^{(1)}$].

Once monomorphic evolutionary dynamics have found a halt at a stable equilibrium ($\bar{x}^{(1)}$ or $\bar{x}^{(2)}$), one must establish if the equilibrium is a terminal point (TP) or a branching point (BP). For this, we use the test presented in Chapter 3 (Section 3.7), i.e.,

$$\frac{\partial^2}{\partial x^2} \lambda(\bar{x}^{(i)}, x') \bigg|_{x' = \bar{x}^{(i)}} \begin{cases} < 0, & \bar{x}^{(i)} \text{ is a TP} \\ > 0, & \bar{x}^{(i)} \text{ is a BP}, \end{cases} \quad i = 1, 2.$$

For example, the low equilibria $\bar{x}^{(1)}$ in Figure 7.2 are TPs, while the high equilibria $\bar{x}^{(2)}$ are BPs, but other combinations are possible for other values of environmental richness ($n_0$) and size range ($1/a_{c2}$).

The study of monomorphic evolutionary dynamics is completed by performing the bifurcation analysis of the canonical equation (7.4) with respect to ($n_0$) and ($1/a_{c2}$), thus producing the diagram shown in Figure 7.3. The two saddle-node bifurcation curves merging at the cusp point $C$ are the combinations of parameter values ($n_0, 1/a_{c2}$) for which the unstable equilibrium $\bar{x}^{(u)}$ collides with either $\bar{x}^{(1)}$ or $\bar{x}^{(2)}$. By contrast, the remaining curve represents the ($n_0, 1/a_{c2}$) combinations separating $\bar{x}^{(2)}$-terminal points from branching points (branching bifurcation). The parameter space ($n_0, 1/a_{c2}$) is subdivided into four regions, characterized by dif-
Figure 7.3 Bifurcation diagram of the monomorphic AD canonical equation (7.4) with respect to $n_0$ and $1/a_{1,2}$. The curves identify four regions characterized by one or two stable evolutionary equilibria, which can be either evolutionarily terminal points (TP) or branching points (BP). Parameter values as in Figure 7.2.

Different mixes of terminal and branching points. In particular, Figure 7.3 shows that in poor environments a TP always exists and that species dimorphism is a possible evolutionary option only in populations with wide size range. Moreover, dimorphism is the only option in populations with wide size range living in very rich environments.

**Dimorphic Evolutionary Dynamics**

We now focus on the coevolution of two coexisting populations, characterized by abundances $n_1$ and $n_2$ and cannibalistic traits $x_1$ and $x_2$. Recall that in sexual species, as is the Eurasian perch, which motivated the present study, dimorphic evolutionary dynamics describe the coevolution of two reproductively isolated resident populations, so that the analysis that follows assumes that individuals mate with partners of similar body size, so that population interbreeding practically stops as soon as the two traits $x_1$ and $x_2$ diversify.

Of course, the study of dimorphic evolutionary dynamics must be limited to the region of all pairs $(x_1, x_2)$ for which model (7.1), with $P = 2$, has a stable and strictly positive equilibrium, i.e., to the so-called evolution set of the dimorphic community. Such a region can be computed by performing the bifurcation analysis of model (7.1) ($P = 2$) with respect to the traits $x_1$ and $x_2$ interpreted as constant.
Figure 7.4 Bifurcation analysis of model (7.1) \((P = 2)\) with respect to cannibalistic traits \(x_1\) and \(x_2\). Upper triangle: bifurcation diagram and regions 1–4 (filled circles indicate codimension-2 (cusp) bifurcation points; in particular, point \(B\) corresponds to the monomorphic branching point). Lower triangle: demographic state portraits of model (7.1) \((P = 2)\) corresponding to regions 1–4 (filled circles: stable equilibria; half-filled circle: saddles; empty circles: repellors). The evolution set of the dimorphic community is the union of regions 1 and 4 where demographic state portraits display a strictly positive equilibrium. Parameter values as in Figure 7.2 except for \(n_0 = 500\) and \(a_{c2} = 1.9\). Region 4 has been stretched for purpose of illustration.

parameters. Since the evolutionary 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 a dimorphic evolution set obtained for wide size range and rich environments (i.e., for high values of environmental richness, \(n_0\), and size range, \(1/a_{c2}\), for which monomorphic evolutionary dynamics halt at a globally stable branching point, see Figure 7.3) is shown in Figure 7.4. Four qualitatively different demographic behaviors are identified (see the demographic state portraits in the lower part of the figure), corresponding to regions 1–4 of the bifurcation diagram (upper part of the figure). Since only in regions 1 and 4 is there a stable and strictly positive demographic equilibrium, the dimorphic evolution set is the union of regions 1 and 4.

The nature of a bifurcation curve separating two nearby regions in Figure 7.4 can be understood by comparing the two corresponding demographic state portraits.
For example, the bifurcation curve separating region \( \mathcal{R}_1 \) from region \( \mathcal{R}_2 \) is characterized by the collision of a stable and strictly positive equilibrium with a saddle on the \( n_1 \)-axis (transcritical bifurcation, see Appendix A). Thus, if a dimorphic evolutionary trajectory in region \( \mathcal{R}_1 \) moves toward this boundary of the evolution set, the giant population vanishes and goes extinct when the trajectory hits the bifurcation curve (a case of so-called evolutionary murder, see Sections 1.8 and 3.6: what is ultimately responsible for the giants’ evolutionary extinction is the evolution of the dwarf population). By contrast, the bifurcation curve separating region \( \mathcal{R}_3 \) from region \( \mathcal{R}_4 \) is characterized by the collision of a stable and strictly positive equilibrium with a strictly positive saddle (a saddle-node bifurcation that leaves the stable equilibrium on the \( n_1 \)-axis as the only demographic attractor). Thus, if a dimorphic evolutionary trajectory in region \( \mathcal{R}_4 \) moves toward this boundary of the evolution set, the giant population abundance does not vanish, but catastrophically collapses (on the demographic timescale) at the bifurcation (evolutionary suicide: the giant population evolves to its self-destruction).

Let us now denote by \( \tilde{n}_1(x_1, x_2) \) and \( \tilde{n}_2(x_1, x_2) \) the resident population abundances at the stable and strictly positive equilibrium of model (7.1) \((P = 2)\), for \((x_1, x_2)\) in the dimorphic evolution set. The dimorphic AD canonical equation then reads

\[
\dot{x}_1 = k\tilde{n}_1(x_1, x_2) \frac{\partial \lambda_1(x_1, x_2, x'_i)}{\partial x'_1} \bigg|_{x'_i = x_1}, \quad (7.5a)
\]

\[
\dot{x}_2 = k\tilde{n}_2(x_1, x_2) \frac{\partial \lambda_2(x_1, x_2, x'_i)}{\partial x'_2} \bigg|_{x'_i = x_2}, \quad (7.5b)
\]

where \( \lambda_i(x_1, x_2, x'_i) \) is the fitness of the \( i \)-th mutant population (abundance \( n'_i \), trait \( x'_i \), \( i = 1, 2 \)), which can be easily obtained from model (7.1) with \( P = 3 \). In fact, by writing model (7.1) \((P = 3)\) in the form

\[
\begin{align*}
\dot{n}_1 &= n_1 f_1(n_1, n_2, n'_1, x_1, x_2, x'_1), \\
\dot{n}_2 &= n_2 f_2(n_1, n_2, n'_2, x_1, x_2, x'_2),
\end{align*}
\]

plus

\[
\begin{align*}
\dot{n}'_1 &= n'_1 f_1(n'_1, n_2, n_1, x'_1, x_2, x_1) \\
\dot{n}'_2 &= n'_2 f_2(n'_1, n'_2, n_1, x'_1, x_2, x_2)
\end{align*}
\]

for \( i = 1 \) and

for \( i = 2 \), it follows that

\[
\begin{align*}
\lambda_1(x_1, x_2, x'_1) &= f_1(0, n_2(x_1, x_2), \tilde{n}_1(x_1, x_2), x'_1, x_2, x_1), \\
\lambda_2(x_1, x_2, x'_2) &= f_2(n_1(x_1, x_2), 0, \tilde{n}_2(x_1, x_2), x_1, x'_2, x_2).
\end{align*}
\]

Notice that the resident demographic equilibrium \((\tilde{n}_1(x_1, x_2), \tilde{n}_2(x_1, x_2))\) is not known in closed form, but only implicitly through its definition

\[
\begin{align*}
f_1(\tilde{n}_1(x_1, x_2), \tilde{n}_2(x_1, x_2), 0, x_1, x_2, \cdot) &= 0, \\
f_2(\tilde{n}_1(x_1, x_2), \tilde{n}_2(x_1, x_2), 0, x_1, x_2, \cdot) &= 0
\end{align*}
\]
The dimorphic evolutionary dynamics defined by model (7.5) within the evolution set shown in Figure 7.4 (the union of regions $1$ and $4$) are sketched in Figure 7.5. The evolution set is partitioned into white, light gray, and dark gray regions. Trajectories starting in the white region tend toward a dimorphic evolutionary equilibrium $D$ (which can be either a branching or terminal point, but this distinction is not investigated here). Trajectories starting in the light gray region hit the boundary of the evolution set between points $C_1$ and $C_2$, where the evolutionary suicide of the
giant population takes place (see Figure 7.4). Notice that points $C_1$ and $C_2$ are evolutionary equilibria (saddles). In fact, $\dot{n}_2(x_1, x_2) = 0$ (i.e., $\dot{x}_2 = 0$) at such points (they lie on the intersection of regions 1, 2, and 3, see corresponding demographic state portraits in Figure 7.4) and $\dot{x}_1$ has opposite sign at opposite sides of $C_1$ and $C_2$ along the boundary of the evolution set. Finally, dark gray regions are those in which the dwarf [giant] population abundance smoothly vanishes when the evolutionary trajectory approaches the extinction boundary separating region 2 from region 1 (see Figure 7.4).

Since the branching point $B$, where dimorphism originates, lies on the boundary of the light gray region, the evolutionary attractor of the community is the branching-extinction evolutionary cycle represented in Figure 7.5 by the thick trajectory. In words, when the dwarf and giant cannibalistic attitudes become sufficiently distinct, the giant population is not capable of sustaining itself by harvesting on the dwarf population. However, more cannibalistic mutants are at advantage and drive the population to self-extinction (see point $E_2(x_1^{(E)}, x_2^{(E)})$ in Figure 7.5). After the giant extinction (i.e., after the sudden (dashed) transition from $E$ to $M$ in Figure 7.5) the dwarf population evolves back to the branching point $B$, starting with a trait value $x_1 = x_1^{(E)}$, in accordance with the monomorphic canonical equation (7.4). Thus, starting from any ancestral monomorphic condition the final outcome of the mutation-selection process is the branching-extinction evolutionary cycle of Figure 7.5, characterized by two distinct evolutionary phases: a monomorphic evolution toward the branching point (from $M$ to $B$) and a dimorphic evolution characterized by the temporary presence of a highly cannibalistic population of giants (from $B$ to $E$).

### 7.5 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 environments. The deterministic mechanisms that lead to such evolutionary cycles have been first addressed by Kisdi et al. (2001) and require the following minimal ingredients: (i) a monomorphic species that can turn dimorphic through an evolutionary branching; (ii) a dimorphic evolutionary phase originating at the branching point that leads to the evolutionary extinction of one of the two morphs, say morph 2; (iii) a postextinction monomorphic species (i.e., morph 1) in the basin of attraction of the branching point.

In the present study, condition (iii) forces the rate of evolutionary change of trait 1 ($\dot{x}_1$) to reverse in the transition from dimorphism to monomorphism. This is not possible if population 2 is murdered by population 1. In fact, in such a case, the abundance $\dot{n}_2(x_1, x_2)$ vanishes while approaching the boundary of the evolution set (transcritical bifurcation of the dimorphic demographic equilibrium), so that only population 1 is actually present at the boundary. This implies that just before and just after the extinction of population 2, population 1 feels the same biotic (and abiotic) environment, hence the same selection pressure, so that the extinction of
population 2 cannot trigger a discontinuity of \( \dot{x}_1 \).

Thus, the key point of our branching-extinction evolutionary cycle is that population 2 undergoes an evolutionary suicide (saddle-node bifurcation of the dimorphic demographic equilibrium). Being present at nonvanishing abundances along the whole dimorphic evolutionary phase, population 2 has a relevant impact on the biotic environment felt by population 1, and its sudden disappearance abruptly changes the selection pressure on population 1. More precisely, in the case of Figure 7.5, just before the extinction of population 2, \( \dot{x}_1 \) is negative and given by equation (7.5a) evaluated at point \( E \), where \( n_2(x_1, x_2) \) is strictly positive (and equal to the limit of \( n_2(x_1, x_2) \) along the dimorphic evolutionary trajectory approaching \( E \)). By contrast, after the sudden disappearance of the giant population, \( \dot{x}_1 \) is positive and given by the monomorphic canonical equation (7.4) evaluated at point \( M \).

Kisdi et al. (2001) have considered a demographic model in which only transcritical bifurcations are possible (they used a bilinear competition model). Thus, to reverse the selection pressure on the postextinction population, they have been forced to consider a quite peculiar situation in which the dimorphic evolutionary trajectories converge to a codimension-2 bifurcation point, namely the point of intersection of two transcritical bifurcation curves. At this codimension-2 bifurcation point the dimorphic demographic equilibrium is neutrally stable and depends sensitively upon the dimorphic initial conditions. Moreover, further mutations determine the random extinction of one of the two populations.

In closing this chapter we would like to comment on the robustness of the result. In principle, a complete bifurcation analysis of the AD canonical equations (7.4) and (7.5) with respect to all couples of strategic parameters (like the environmental richness, \( n_0 \), and the size range, \( 1/a_{\alpha_2} \)) would allow us to determine all possible qualitative evolutionary scenarios and their corresponding regions in parameter space. In particular, a measure of the region giving rise to branching-extinction evolutionary cycles would be indicative of the robustness of our conclusions. However, the bifurcation analysis of model (7.5) poses nontrivial technical problems, since the dimorphic demographic equilibrium \( (n_1(x_1, x_2), n_2(x_1, x_2)) \) is not known in closed form. The differential-algebraic system (7.6) should therefore be used in the analysis, though appropriate numerical techniques for the continuation of global bifurcations (see Appendix A) are not yet fully developed (Ascher and Spiteri, 1994).

A particular global bifurcation indeed characterizes the appearance/disappearance of the branching-extinction evolutionary cycle of Figure 7.5, namely the saddle-saddle connection \( B-C_2 \) (so-called heteroclinic bifurcation). In fact, the evolutionary dynamics of the community are trapped by the branching-extinction evolutionary cycle when the unstable manifold of the saddle point \( B \) reaches the boundary of the evolution set between points \( C_1 \) and \( C_2 \). However, if point \( E \) were below point \( C_2 \), the dimorphic evolutionary equilibrium \( D \) would be the evolutionary attractor reached by the community.

Despite technical difficulties, we checked, by means of extensive simulations of model (7.6) for various parameter settings, that the branching-extinction evolutionary cycle of Figure 7.5 is present in a relatively broad region of parameter space characterized by high environmental richness and size range. Moreover, a partial analysis carried out in Dercole and Rinaldi (2002) has shown that stable
dimorphic evolutionary equilibria, possibly leading to higher polymorphism, and monomorphic low cannibalistic terminal points, perhaps reached after temporary dimorphic phases, represent alternative evolutionary scenarios when the conditions for branching-extinction evolutionary cycles are not matched.

Thus, our conclusion is that branching-extinction evolutionary cycles are robust evolutionary attractors and that their detection is of crucial importance for fully understanding evolutionary dynamics. Of course, in the case of cannibalistic communities, one should check if evolutionary cycles of the same kind are supported by more realistic age- and/or size-structured demographic models. However, the derivation of the AD canonical equation in such a case would be problematic. Well-organized simulations of a suitable individual-based model (see Section 2.3) may provide the best framework in which to answer this question.