REVIEW ARTICLE

EVOLUTIONARY SUICIDE

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ABSTRACT

The great majority of species that lived on this earth have gone extinct. These extinctions are often explained by invoking changes in the environment, to which the species has been unable to adapt. Evolutionary suicide is an alternative explanation to such extinctions. It is an evolutionary process in which a viable population adapts in such a way that it can no longer persist. In this paper different models, where evolutionary suicide occurs are discussed, and the theory behind the phenomenon is reviewed.

1. INTRODUCTION

Modern evolutionary theory has been widely used to understand phenotypic evolution because of natural selection. One interesting phenomenon is evolutionary branching (Metz *et al.*, 1996a; Geritz *et al.*, 1997, 1998), where strategies first approach monomorphically a singular strategy, but then divide into two groups, and evolve further away from each other. The question whether evolutionary branching can lead to sympatric speciation, has raised a lot of interest (Dieckmann and Doebeli, 1999; Dieckmann *et al.*, 2004). The enormous number of different living species gives motivation for such studies. However, an even larger number of species are known to have gone extinct. These extinctions are often explained by invoking changes in the environment, to which the species has been unable to adapt. This paper concentrates on another possible explanation, which is a kind of reverse evolutionary branching. In some occasions, the species in question could persist with its current strategy, but natural selection forces the species to change its strategy resulting in extinction. This phenomenon is called evolutionary suicide (Ferrière, 2000), but it is also called Darwinian extinction (Webb, 2003), and evolution to extinction (Dieckmann *et al.*, 1995).

The word evolution suggests itself that it would act for the good of the population. For this reason, evolutionary suicide may seem counterintuitive. However, evolution operates at the level of individuals. Those individuals who get most offspring in the current environment will increase in frequency. As a result, the environment experienced by the individuals will change. This change is not necessarily a good one for the population. Already Darwin (1859, 1871) observed that natural selection may favour traits that eventually, through a feedback to the environment, turn out to be harmful to the individuals. The peacock's tail is a typical example of this. This topic was later discussed in detail by Haldane (1932). Evolutionary suicide is an extreme example of such a harmful event.

In Section 2 the modelling framework used in this paper is presented, including the framework of adaptive dynamics (Metz *et al.*, 1992, 1996a; Dieckmann and Law, 1996;

Geritz *et al*., 1997, 1998). After that, a mathematical definition of different types of evolutionary suicide will be given, together with some simple examples.

In Section 3 the theory behind evolutionary suicide will be studied. It is discovered that a bifurcation in population dynamics is a necessary condition for evolutionary suicide. More precisely, it has to be a discontinuous transition to extinction (Gyllenberg *et al*., 2002). The classification by Webb (2003) of different bifurcations allowing for evolutionary suicide is also presented. In some special cases, there exist even necessary and sufficient conditions (Gyllenberg and Parvinen, 2001). The relation between frequency-dependent selection and evolutionary suicide is also discussed.

In Section 4 different models where evolutionary suicide occurs are discussed. In addition to the two asymmetric competition models studied in Section 2, the following models are investigated: a so called common good model, dispersal in a metapopulation, a resource-consumer model, and a simple model defined in discrete time. The paper ends with a discussion (Section 5).

2. MODELLING FRAMEWORK AND SIMPLE EXAMPLES

It is assumed that the behaviour of individuals depends on their strategy s. In most studies, the strategy s is a real number, and thus the set of possible strategies is one-dimensional. More generally, the strategy s can be an n-dimensional vector, or even infinite-dimensional (Dieckmann *et al*., subm; Parvinen *et al*., 2006). The set of possible strategies is often called the *strategy space*. The evolving population is not necessarily viable for all possible strategies. The *viability set V* is the set of all strategies to which there corresponds at least one non-extinct population dynamical attractor. Furthermore, the boundary ∂V of the viability set V will be called the *extinction boundary*.

2.1. Adaptive dynamics

After the introduction of the original concept of an evolutionarily stable strategy (ESS; Maynard Smith, 1976; Maynard Smith and Price, 1973), ESS-theory has been applied to a wide variety of models, and has resulted in various concepts and techniques of modern ESS-theory (e.g. Eshel, 1983; Matsuda, 1985; Van Tienderen and De Jong, 1986; Taylor, 1989; Christiansen, 1991). A fair fraction of these concepts and techniques have been integrated and extended into a single mathematical framework for modelling the dynamics of long-term phenotypic evolution, called adaptive dynamics (Metz *et al*., 1992, 1996a; Dieckmann and Law, 1996; Geritz *et al*., 1997, 1998).

It is assumed that a resident population has reached its population dynamical attractor. Then an initially rare mutant with a slightly different strategy appears. If the invasion fitness $r(s_{\mathrm{mut}}, E_{\mathrm{res}})$ of a rare mutant s_{mut} in an environment E_{res} set by the resident is positive, the mutant is able to grow in population size. Therefore, the mutant can invade and possibly replace the old resident and become the new resident itself. Mutations are assumed to happen rarely, so that the population dynamics has settled to an attractor before the next mutation happens. These mutation-invasion events result in the change of the strategy of the individuals constituting the population. These events define a trait-substitution sequence, a sequence of mutants each one replacing the phenotype that was previously present.

Usually invasion fitness is defined as the long-term exponential growth rate of a rare mutant in an environment set by the resident (Metz *et al.*, 1992). In constant environments it is possible to use the basic reproduction ratio $R(s_{\mathrm{mut}}, E_{\mathrm{res}})$, the expected number of offspring produced by an individual during its entire life (Diekmann *et al.*, 1990). Generally, $r(s_{\mathrm{mut}}, E_{\mathrm{res}}) > 0$ if and only if $R(s_{\mathrm{mut}}, E_{\mathrm{res}}) > 1$. In case the basic reproduction ratio in a virgin environment $R_0(s) > 1$, the extinction equilibrium is unstable, and the strategy s is viable.

If no mutant can invade the resident, then the strategy s_{res} of the resident is unbeatable, and it is called an evolutionarily stable strategy (ESS; Maynard Smith, 1976). When a resident population has reached an evolutionarily stable strategy, the fitness of mutants in the environment set by such a resident may be considered. As no mutant can invade, all mutants necessarily have lower fitness than the resident, i.e., $r(s_{\mathrm{mut}}, E(s_{\mathrm{res}})) < 0$ for all $s_{\mathrm{mut}} \neq s_{\mathrm{res}}$. Therefore, the resident strategy is a (local) fitness maximum and the selection gradient, i.e., the derivative of invasion fitness with respect to the strategy of the mutant, vanishes at such points,

$$\left. \frac{\partial}{\partial s_{\mathrm{mut}}} r(s_{\mathrm{mut}}, E_{\mathrm{res}}) \right|_{s_{\mathrm{mut}}=s_{\mathrm{res}}} = 0 \tag{1}$$

More generally, strategies for which the selection gradient is zero, are called evolutionarily singular strategies (Metz *et al.*, 1996a; Geritz *et al.*, 1998).

A (singular) strategy s^* is convergence stable or an evolutionary attractor if the repeated invasion of nearby mutant strategies into resident strategies will lead to the convergence of resident strategies towards s^* (Christiansen, 1991). If an evolutionary attractor is also evolutionarily stable, it is called a continuously stable strategy (CSS; Eshel, 1983) and it is a feasible final outcome of an evolutionary process. In case a monomorphically attracting strategy is not unbeatable, evolution will not stop there, but evolutionary branching can occur because of disruptive selection. The monomorphic population will then divide into two groups, and the strategies of these groups will evolve further away from each other. An evolutionary branching point is thus an evolutionarily singular strategy that is monomorphically attracting and dimorphically repelling.

A useful graphical tool in the analysis of the evolutionary dynamics of one-dimensional strategies is a pairwise invasibility plot (Matsuda, 1985; Van Tienderen and De Jong, 1986). In these plots, the sign of the invasion fitness $r(s_{\mathrm{mut}}, E(s_{\mathrm{res}}))$ is displayed in dependence on resident and mutant strategies. As the resident population is on an attractor, the fitness function necessarily satisfies $r(s_{\mathrm{res}}, E(s_{\mathrm{res}})) = 0$. Therefore, the diagonal $s_{\mathrm{mut}} = s_{\mathrm{res}}$ is a zero-contour of the invasion fitness. Singular strategies lie at those points, where other zero-contours cross the diagonal. In the pairwise invasibility plots in this paper, dark gray regions correspond to combinations of resident and mutant strategies, s_{res} and s_{mut}, that allow for mutant invasion. For these combinations, the invasion fitness $r(s_{\mathrm{mut}}, E(s_{\mathrm{res}}))$ is positive. In contrast, light gray regions correspond to negative signs and therefore to deleterous mutants.

2.2. Definitions of evolutionary suicide

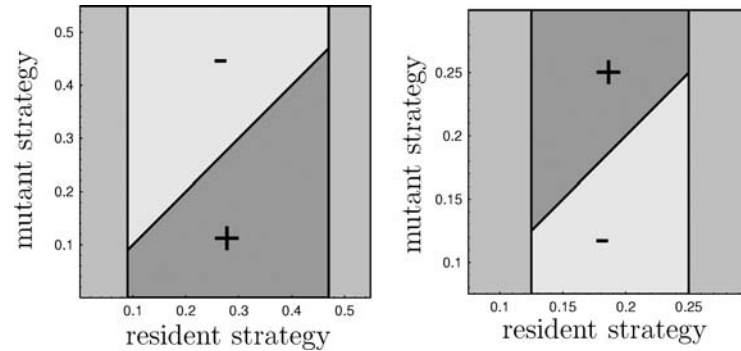Now a definition of evolutionary suicide can be given:

Figure 1. Typical pairwise invasibility plots in the case of evolutionary suicide. The medium gray rectangles on the left and right side of each panel corresponds to values of the resident strategy for which the population is not viable.

Evolutionary suicide:
There exists a strategy $s \in V$ such that if the initial strategy of the population is s, evolution can (with small mutations) take the strategy of the population sufficiently close to the extinction boundary ∂V that a mutant with a strategy not in V can invade, moving the dynamics out of the resident attractor with as a result in the extinction of the whole population, resident and mutant alike.

The definition above covers both deterministic and mutationally stochastic evolutionary suicide. In *deterministic evolutionary suicide* all possible trait substitution sequences will result in the extinction of the populations described above. This is typical in one-dimensional strategy spaces, in which case the possibility of evolutionary suicide can be easily seen from pairwise invasibility plots (Figure 1). The situation where some trait substitution sequences result in extinction and others do not, will be called *mutationally stochastic evolutionary suicide*, to indicate that it depends on chance whether extinction happens or not, and to distinguish from demographically stochastic evolutionary suicide, which will be defined below. Mutationally stochastic evolutionary suicide is typical in the case of multidimensional strategy spaces (see Section 3.5).

A weaker phenomenon than what has been defined as evolutionary suicide, is *demographically stochastic evolutionary suicide*. In this phenomenon evolution leads to so small population size that extinction by chance becomes possible. Webb (2003) called this phenomenon gradual Darwinian extinction. This phenomenon was first observed in a mathematical model by Matsuda and Abrams (1994a), and will be presented next.

2.3. Runaway evolution to self-extinction

Matsuda and Abrams (1994a) studied a model where consumers with linear functional responses compete for logistically growing resources. The strategy of an individual describes the mean size (or position on a gradient) of the resources it uses. In this model,

the invasion fitness of a mutant is equal to

$$r(s_{\mathrm{mut}}, s_{\mathrm{res}}) = r_0 \left(1 - \alpha(s_{\mathrm{mut}}, s_{\mathrm{res}}) \frac{N}{K(s_{\mathrm{mut}})} \right), \tag{2}$$

where r_0 is the population's intrinsic rate of increase, N is the total population density, $K(s_{\mathrm{mut}})$ is the carrying capacity, and α is the competition coefficient. Matsuda and Abrams (1994a) assumed that it is of form

$$\alpha(s_{\mathrm{mut}}, s_{\mathrm{res}}) = \exp\left(-\beta(s_{\mathrm{mut}} - s_{\mathrm{res}}) - \frac{(s_{\mathrm{mut}} - s_{\mathrm{res}})^2}{4\sigma^2} \right). \tag{3}$$

The carrying capacity is written in form $K(s) = K_0 \exp(-f(s))$.

With these assumptions, the fitness gradient is equal to

$$\frac{\partial}{\partial s_{\mathrm{mut}}} r(s_{\mathrm{mut}}, s_{\mathrm{res}})|_{s_{\mathrm{mut}} = s_{\mathrm{res}}} = r_0(\beta - f'(s_{\mathrm{res}})). \tag{4}$$

If $f'(s_{\mathrm{res}}) < \beta$ for all strategies s_{res}, the fitness gradient is positive for all s_{res}. Therefore, the strategy value will increase indefinitely. For example, if $f(s_{\mathrm{res}}) = \frac{[\log(s_{\mathrm{res}}/s_0)]^2}{2w^2}$, this happens if $\frac{1}{w^2 e s_0} < \beta$. As $K(s_{\mathrm{res}}) \to 0$ as $s_{\mathrm{res}} \to \infty$, the population density will continuously decrease and approach zero. Eventually, the population will thus become extinct because of demographic stochasticity. Matsuda and Abrams (1994a) called this phenomenon "runaway evolution to self-extinction". In our terminology, this is demographically stochastic evolutionary suicide. In contrast with deterministic evolutionary suicide, the population remains viable (although small), since the extinction equilibrium is unstable. In demographically stochastic evolutionary suicide it thus takes an infinite trait substitution sequence to approach population size zero, while in deterministic evolutionary suicide extinction happens after finitely many trait substitutions.

2.4. Asymmetric competition model with an Allee effect

Next an example by Gyllenberg and Parvinen (2001) of evolutionary suicide in a modification of the asymmetric Lotka-Volterra competition model is presented. The strategy s describes body size or length of horns etc. Individuals of the population engage in competitive interactions, where a trait value larger than that of the other contestant gives an advantage. Higher trait value results, however, in decreased fecundity or survival. In the asymmetric Lotka-Volterra competition model, the population densities N_i of the phenotypes $i = 1, 2, \ldots, n$ grow according to

$$\frac{dN_i}{dt} = N_i \left[\rho(s_i) - c \sum_{j=1}^{n} \alpha(s_i - s_j) N_j \right],$$

where $\bar{N} = \sum_{i=1}^{n} N_i$ is the total population density and $\rho(s_i)$ is the intrinsic growth rate of a contest-free population consisting of individuals with trait s_i. The competition coefficient $\alpha(s_i - s_j)$ describes the effect of strategy s_j on s_i. The function $\alpha(s)$ is usually a decreasing function, and $\rho(s)$ is decreasing at least with high values of s.
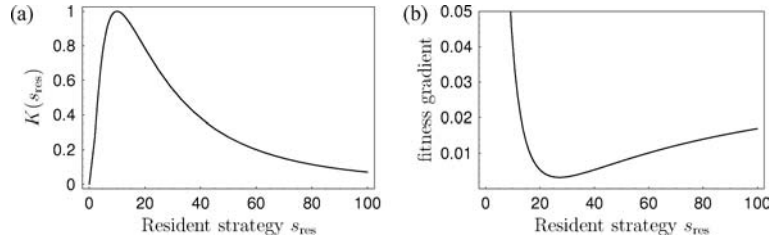
Figure 2. Runaway evolution to self-extinction: Carrying capacity (a) and fitness gradient (b) as functions of the resident strategy s_{res}. Parameters: $\beta = 0.04$, $r = 1$, $s_0 = 10$, $w = 1$. Source: Matsuda and Abrams (1994a).

The modification of Gyllenberg and Parvinen (2001) to the asymmetric Lotka-Volterra competition model is to incorporate an Allee effect (Allee *et al.*, 1949), i.e., a negative per capita growth rate at low population sizes.

$$\frac{dN_i}{dt} = N_i \left[\rho(s_i) \frac{a\bar{N}}{1 + \bar{N}} - b - c \sum_{j=1}^{n} \alpha(s_i - s_j) N_j \right], \quad i = 1, 2, \ldots, n. \quad (5)$$

The chosen competition coefficient is the same as in the previous example (Section 2.3, equation (3)), thus $\alpha(s_j - s_i) = \exp\left[-\beta(s_j - s_i) - (s_j - s_i)^2 / (4\sigma^2)\right]$. The chosen growth rate ρ is Gaussian: $\rho(s) = \exp\left[-(s - m)^2 / (2\sigma_\rho^2)\right]$.

Consider now the situation with a resident population of density N with strategy s_{res}. The state $N = 0$ which corresponds to extinction is always a stable equilibrium. If $\rho(s_{\text{res}})$ is large enough, there exist two positive equilibria, of which one is stable and one is unstable. When $\rho(s_{\text{res}})$ reaches a critical value, a bifurcation occurs, where the two positive equilibria collide and disappear. Beyond that value, the extinct equilibrium $N = 0$ is the only stable equilibrium (see Figure 3a).

The fitness of the mutant equals

$$r(s_{\text{mut}}, s_{\text{res}}) = \rho(s_{\text{mut}}) \frac{aN(s_{\text{res}})}{1 + N(s_{\text{res}})} - b - c\alpha(s_{\text{mut}} - s_{\text{res}}) N(s_{\text{res}}). \quad (6)$$

The fitness gradient in this model is equal to

$$\frac{\partial}{\partial s_{\text{mut}}} r|_{s_{\text{mut}}=s_{\text{res}}} = \rho'(s_{\text{res}}) \frac{aN(s_{\text{res}})}{1 + N(s_{\text{res}})} + \beta c N(s_{\text{res}}). \quad (7)$$

When β is large enough, the fitness gradient is always positive. An example of a pairwise invasibility plot in such a case is illustrated in Figure 3b. Larger strategy values s are favoured in selection. Therefore, strategies will reach the upper boundary of viability. In such a situation, the fitness gradient is still positive, and thus mutants with a larger strategy value than that of the resident, have positive fitness. These mutants cannot, however, persist. As a result, the population will become extinct. A simulation of such occurrence of deterministic evolutionary suicide is plotted in Figures 3c and d.
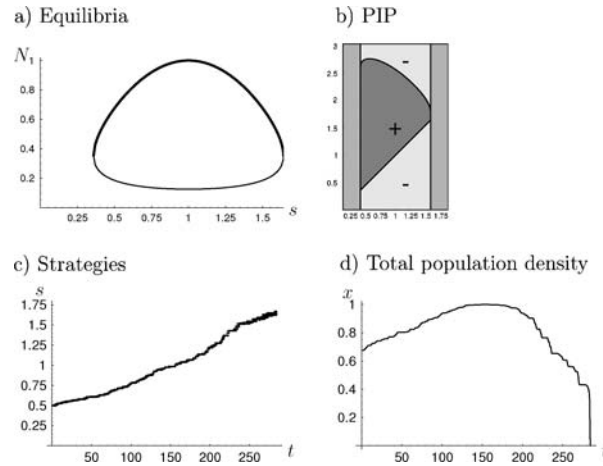
Figure 3. Asymmetric competition model: (a) Equilibrium population densities. Stable equilibria lie on the thick curve, unstable ones on the thin curve. (b) Pairwise invasibility plot. (c) and (d) Evolutionary simulation. Part (c) contains the strategies s present in the system at time t. and part (d) the total population density. Parameters for growth: $a = 18$, $b = 1$, $c = 8$, $m = 1$, $\sigma_\rho = 1$ and competition: $\beta = 1$, $\sigma = 5$. Source: Gyllenberg and Parvinen (2001).

3. THEORY

So far two examples have been studied, which have given some insight into evolutionary suicide. Next the theory behind it will be studied in detail.

3.1. Attractor inheritance and attractor switching

In the basic framework of adaptive dynamics it is assumed that the resident population has a unique attractor. However, if evolutionary suicide is observed, there are necessarily at least two attractors for a resident population, one positive attractor and the extinction equilibrium. In the case of several attractors, another basic assumption that a mutant with a positive fitness will either coexist with the resident or replace the resident, does not necessarily hold either (Doebeli, 1998; Mylius and Diekmann, 2001). It is thus necessary to know how to handle a situation with several resident attractors.

Assume that $A(s)$ is a population dynamical attractor for all $s \in S$, where S is a compact subset of the strategy space. For each s, $A(s)$ is thus a subset of the population state space. $A(s)$ is called an *attractor family*, if $A(s)$ varies continuously as a function of s on S (see definition 3.2 of Geritz *et al.* (2002) for a precise definition).

Assume that the mutant can invade the resident on a specific attractor and the resident cannot invade the mutant on the corresponding attractor. Initially, the mutant population is small, and therefore the resident-mutant population is inside a narrow tube in the resident-mutant population state space where the sum of the population densities of the resident and the mutant are close to the resident densities of the monomorphic resident attractor.
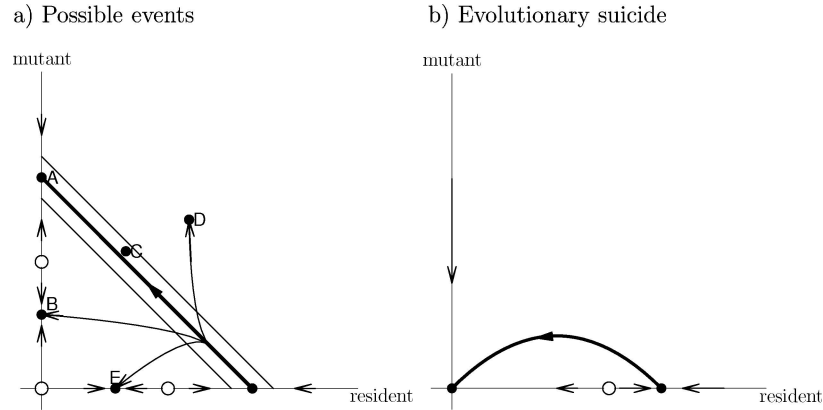
a) Possible events   b) Evolutionary suicide

Figure 4. (a) Possible events after the initial increase of the mutant population in the case of several attractors. Evolutionary suicide (b). Black circles illustrate attractors and white circles repellors of population dynamics.

In Figure 4a possible events happening after the initial increase of the mutant population are illustrated. The mutant can replace the resident and stay in the same attractor family (attractor inheritance, (A)). The mutant can replace the resident, but does not stay in the same attractor family (attractor switching, (B)). The resident and mutant populations can coexist in an intermediate attractor inside the tube (C). There can be coexistence in an intermediate attractor outside the tube (D). The mutant population can initially increase, but then decrease again, and the system reaches another resident attractor (E). This phenomenon is called the resident strikes back scenario (Mylius and Diekmann, 2001).

At first sight it seems that the case with multiple attractors is too hard to analyze using the invasion fitness function only. However, under rather general conditions, it has been shown (Geritz *et al.*, 2002, Tube Theorem) that if $s_{\mathrm{mut}} \approx s_{\mathrm{res}}$, the mutant will remain in the same attractor family, and thus attractor inheritance occurs. Other events, such as attractor switching, are possible only if the resident strategy is close to a bifurcation point. Based on this result, the following situation is necessary for a mutant to take the whole population to the extinction equilibrium:

- For the resident population with strategy s_{res} there exist at least two monomorphic attractors, of which one is the extinction equilibrium, and the other is a nontrivial attractor.
- The mutant with strategy $s_{\mathrm{mut}} \approx s_{\mathrm{res}}$ has positive fitness in the environment set by the resident (in a non-trivial attractor).
- The same non-trivial attractor does not exist for the mutant, and the extinction equilibrium is a monomorphic attractor for the mutant.

Such a situation is illustrated in Figure 4b.

3.2. Ecological bifurcations

It has now become clear that in order to evolutionary suicide to happen, there has to happen a bifurcation, where a non-extinct resident attractor disappears. (Note, however, that demographically stochastic evolutionary suicide does not require any bifurcations.)
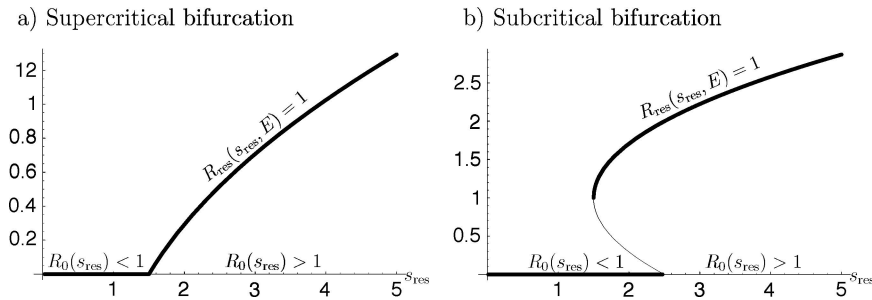
a) Supercritical bifurcation   b) Subcritical bifurcation

Figure 5. (a) Continuous and (b) discontinuous transition to extinction. Stable equilibria lie on the thick curve, unstable ones on the thin curve. In both cases the extinction boundary is at $s^* = 1.5$.

Such bifurcations happen at the boundary ∂V of the viability set. Note that this is only a necessary condition. In addition, it must be possible for the strategy to evolve to the boundary of viability, and a mutant must have positive fitness in such a resident environment. This section will concentrate on the different types of bifurcations. Not all of them allow for evolutionary suicide, as will be shown below.

3.2.1. *A continuous transition to extinction does not allow for evolutionary suicide*

The change of the population dynamical attractor from viability to extinction at the boundary ∂V can happen through several different types of bifurcations. If the attractor goes continuously to zero, this is called a continuous transition to extinction. A typical example is the situation in which the solution corresponding to population extinction loses its stability through a supercritical bifurcation (see Figure 5a).

Consider an attractor family $A(s)$. In this case specially, it is assumed that at a point s_{ext} on the extinction boundary ∂V, the attractor $A(s_{\mathrm{ext}})$ is the extinction equilibrium. For this reason, when the strategy s approaches s_{ext}, the population size of the resident goes continuously to zero. In well constructed models, the effect of the resident population on the environment also goes then to zero. For this reason, if the resident is at the extinction boundary, the mutant population will grow as if it were in a virgin environment. Therefore the mutant's fitness is the same as fitness in the virgin environment. That means that exactly those mutants that are viable in the absence of the resident can invade. Mutants that are not viable cannot invade. Evolutionary suicide is therefore not possible. This proves the following theorem.

Theorem 1 (Gyllenberg et al., 2002). *Let s be an evolving parameter, V the viability region and A(s) an attractor family. If $\lim_{s \to \partial V} A(s)$ is equal to the extinction equilibrium, then the extinction boundary ∂V is evolutionarily repelling. Therefore, if the strategy of the resident would be almost at the extinction boundary, selection would take the strategy into the interior of the viability region, and evolutionary suicide is not possible.*

Another proof of the same phenomenon has later been presented by Webb (2003). As a corollary, a discontinuous transition to extinction (catastrophic bifurcation) is a necessary (but not sufficient) condition for evolutionary suicide.

Table 1. Simple codimension 1 bifurcations (in 2-dimensional space) that may underlie Darwinian extinction and their classification as dangerous or safe. Source: Webb (2003).

Bifurcation	Classification
Saddle-node bifurcation of equilibria	Dangerous
Transcritical bifurcation of equilibria	Safe
Supercritical Hopf bifurcation	Safe
Subcritical Hopf bifurcation	Dangerous
Saddle-node bifurcation of limit cycles	Dangerous*
Saddle-node bifurcation on a limit cycle	Safe
Homoclinic bifurcation	Dangerous
Heteroclinic bifurcation	Dangerous
Transcritical bifurcation of limit cycles	Safe

*Exceptional case in two dimensions

3.2.2. *Classification of bifurcations*

Webb (2003) studied the possibility of occurrence of evolutionary suicide (sudden Darwinian extinction) in an ecological subsystem with n populations and several evolving strategies. However, most of her results concern a simplified system of one population x or two populations x and y, and one evolving strategy α. Table 1 contains her classification of bifurcations happening in this system. Bifurcations potentially corresponding to evolutionary suicide are labelled dangerous, others safe. This classification essentially repeats the fact that one needs a discontinuous transition to extinction (catastrophic bifurcation) in order to observe evolutionary suicide.

In the specific examples of Webb (2003), x is the prey population density, y the predator population density, and α is the predator attack rate, and they are expected to satisfy the following system of differential equations

$$\frac{dx_1}{dt} = xf_1(x, y, \alpha)$$
$$\frac{dx_2}{dt} = yf_2(x, y, \alpha) \qquad (8)$$
$$\frac{d\alpha}{dt} = \frac{\partial f_2}{\partial \alpha}.$$

In this formulation of Webb (2003), there is no time-scale separation between ecological and evolutionary dynamics, and mutations are assumed to be infinitesimally small.

Concerning the bifurcations in the models presented in this paper, a saddle-node bifurcation of equilibria happens in the asymmetric competition model with an Allee effect (1-dimensional, see Section 2.4), in the common good model (2-dimensional, see Section 4.1) and in the structured metapopulation model. A heteroclinic bifurcation happens in the resource-consumer model (Section 4.3), see also Figure 9 of Webb (2003). All these bifurcations are discontinuous transitions to extinction.

As Webb (2003) studied only models defined in continuous time, the bifurcation in the simple discrete-time model (Section 4.4) is not listed in Table 1. In this model, there

happens a catastrophic bifurcation, where a chaotic attractor collides with an unstable equilibrium (Figure 12).

3.3. One-dimensional environmental interaction variable and direct competitive interactions

So far it has been assumed that the invasion fitness of a mutant can be written in the form $r(s_{\text{mut}}, E_{\text{res}})$, where E_{res} is the environment set by the resident. Usually the environment consists of factors such as the availability of food, quality of habitat, predation pressure on the population etc. The resident population affects these factors *indirectly*. After the environment has been set, it is no longer necessary to know the actual resident strategy to calculate the fitness of the mutant.

In some occasions, however, individuals of the population engage in *direct* competitive interactions. This is the case in the two simple examples (Sections 2.3 and 2.4), which are both asymmetric competition models. In such a situation, the basic reproduction ratio (as proxy for invasion fitness) can be written as

$$R(s_{\text{mut}}, E_{\text{res}}, s_{\text{res}}) \tag{9}$$

Gyllenberg and Parvinen (2001) studied the conditions for evolutionary suicide in the case when both the strategy s and the environmental interaction variable E are one-dimensional. Without loss of generality, it can be assumed that the value $E = 0$ corresponds to the extinction equilibrium (in many models E is simply the population size). Gyllenberg and Parvinen (2001) assumed that all attractors are equilibria. Now, the resident equilibrium is determined by the condition $R_{\text{res}}(s_{\text{res}}, E_{\text{res}}) = R(s_{\text{res}}, E_{\text{res}}, s_{\text{res}}) = 1$. As evolutionary suicide is impossible with transcritical bifurcations (Figure 5a), the only possible bifurcation that allows evolutionary suicide, is a one-dimensional saddle-node bifurcation (Figure 5b). Assume that such a bifurcation happens for strategy s^*, for which the corresponding environmental interaction variable is E^*. As is easily seen from Figure 5b, $R_{\text{res}}(s^*, E) < 1$ for all $E \neq E^*$ in a neighborhood of E^*. This means that E^* is a local maximum point for the function $R_{\text{res}}(s^*, E)$. As the function R_{res} is smooth, equivalently

$$\left.\frac{d}{dE} R_{\text{res}}(s^*, E)\right|_{E=E^*} = 0 \tag{10}$$

and

$$\left.\frac{d^2}{dE^2} R_{\text{res}}(E, s^*)\right|_{E=E^*} < 0. \tag{11}$$

Gyllenberg and Parvinen (2001) defined the direction of the extinction boundary in the following way: the direction of the extinction boundary is positive if strategies $s > s^*$ are viable, and strategies $s < s^*$ are nonviable. Otherwise the direction is negative. The direction of the extinction boundary is determined by $\text{sign}[\frac{d}{ds} R_{\text{res}}(s, E^*)|_{s=s^*}]$. In order to have evolutionary suicide, the strategies $s > s^*$ must be viable, and strategies $s < s^*$ nonviable and mutants with $s_{\text{mut}} < s^*$ must be able to invade (or the other way round). This happens if and only if the fitness gradient and the direction of the extinction boundary have opposite signs. This proves the theorem by Gyllenberg and Parvinen (2001)

Theorem 2 (Gyllenberg and Parvinen, 2001). *Assume that to each strategy $s \in \mathbb{R}$ in the viability set V corresponds a unique nontrivial population dynamical equilibrium with corresponding environment $E(s)$. Evolutionary suicide occurs if and only if there exists an $s^* \in \partial V$ and $E^* = \lim_{s \to s^*} E(s)$ such that the conditions (10) and (11) and the following condition hold:*

$$\text{sign}\left[\frac{d}{ds}R_{\text{res}}(s, E^*)\Big|_{s=s^*}\right] \neq \text{sign}\left[\frac{\partial}{\partial s_{\text{mut}}}R_{\text{mut}}(s_{\text{mut}}, E^*, s_{\text{res}})\Big|_{s_{\text{mut}}=s_{\text{res}}=s^*}\right]. \qquad (12)$$

The conditions (10)–(12) guarantee that if the resident strategy s_{res} is close to the bifurcation point s^*, then evolution will take the resident strategy closer and closer to s^*. When $|s_{\text{res}} - s^*|$ is small enough, a mutant with a strategy outside the domain of the resident attractor can invade, moving the dynamics out of the resident attractor. In this situation $R_{\text{res}}(s_{\text{mut}}, E^*) < 1$, and thus the new attractor will have $E < E^*$. Evolutionary suicide occurs if and only if this new attractor has $E = 0$, which corresponds to extinction. This certainly happens if the attractor $E(s)$ is the only nontrivial attractor. The above mentioned conditions will anyway guarantee attractor switching.

It is easy to show (Gyllenberg and Parvinen, 2001) that if the environmental interaction variable E is one-dimensional and there are no direct competitive interactions, the quantities in equation (12) are equal, and have thus the same sign. This means that evolutionary suicide cannot occur. This is an intuitive result, because selection is frequency-independent in such a situation. Next frequency-independent selection will be discussed in more detail, and a counterintuitive observation made that in some occasions, evolutionary suicide can still occur. This, however, requires other attractors than equilibria.

3.4. Frequency-independent selection and evolutionary suicide

Assume again, that the invasion fitness $r(s_{\text{mut}}, E_{\text{res}})$ depends on the strategy s_{mut} of the mutant, and the environment E_{res} set by the resident. Assume now, that $s_{\text{mut}} \in \mathbb{R}$ and $E_{\text{res}} \in \mathbb{R}$, and thus the environment is one-dimensional. Such a situation is usually called *frequency-independent selection* (Metz *et al.*, 1996b; Heino *et al.*, 1998).

More generally, the trait vector s and environment E act one-dimensionally when the invasion fitness can be written as

$$r(s_{\text{mut}}, E_{\text{res}}) = z\left[f(s_{\text{mut}}), g(E_{\text{res}})\right], \qquad (13)$$

where the functions $f \in \mathbb{R}$ and $g \in \mathbb{R}$, and the function z is increasing with respect to both arguments. (Actually the sign-equivalence $\text{sign}(r) = \text{sign}(z)$ is enough.) Metz *et al.* (1996b) showed that this leads to a optimization principle of evolution maximizing $f(s_{\text{mut}})$ and to a pessimization principle of evolution minimizing $g(E)$.

In many cases this optimization means the maximization of the evolving population size, which should clearly prevent extinction. In optimizing evolution, the best strategy is selected for, and it is the only one which can survive in the worst environment – the situation with maximal population. It seems reasonable that evolutionary suicide cannot occur in such a situation. Actually, Gyllenberg and Parvinen (2001) proved it in the case that the extinction boundary results from a local bifurcation of two colliding equilibria (saddle-node bifurcation).

Counterintuitively, it is possible to have evolutionary suicide and an optimization principle at the same time! In the resource-consumer-model (Section 4.3) the fitness of the mutant (17) can be written as a function $f s \bar{S} - \mu$ of the search effort strategy $s \in \mathbb{R}$ and the average resource level $\bar{S} \in \mathbb{R}$. Therefore both the trait vector and the environment act one-dimensionally. This leads to an optimisation principle of maximising s, and to a pessimisation principle of minimising $\bar{S}$ (see Figure 11). However, a catastrophic bifurcation happens and evolutionary suicide occurs. This is not against the result of Gyllenberg and Parvinen (2001) because they assumed that all attractors are equilibria.

Another example, where evolutionary suicide occurs with frequency-independent selection, is the simple discrete-time model (Section 4.4). Also in this model a catastrophic bifurcation occurs allowing for evolutionary suicide. It is concluded that the existence of an optimisation principle in the sense of Metz *et al.* (1996b) does not prevent evolutionary suicide, although in simple models catastrophic bifurcations are not usual.

3.5. Multi-dimensional strategy spaces

When the strategy space is one-dimensional, it is necessary and sufficient for suicide to have a point at the extinction boundary, where the fitness gradient points out of the viability region (Gyllenberg and Parvinen, 2001). When the dimension of the strategy space larger than one this is no longer the case. Take a resident with a strategy s_{res} at the extinction boundary. With most directions of the fitness gradient, it is possible to find a mutant with positive fitness both inside and outside the viability region (Figure 6a). This is in some cases possible even if the fitness gradient is perpendicular to the tangent of the extinction boundary (Figure 6b), although the probability of finding both types of mutants goes to zero when the mutation step size goes to zero.

The fitness gradient tells the direction in strategy space in which the fitness of the mutant increases most. This is not necessarily the most probable direction in which evolution will proceed. In multi-dimensional strategy spaces one has to take into account
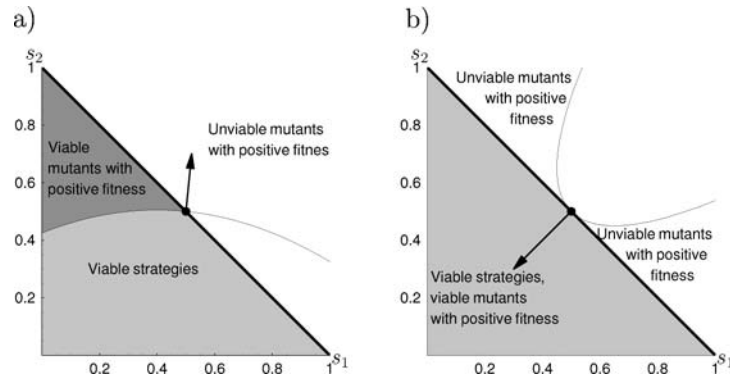

Figure 6. Illustration of two-dimensional strategy space. The viable strategies are assumed to be (s_1, s_2) satisfying $s_1 + s_2 \leq$. This area is shaded with gray. The extinction boundary is plotted with a thick line. The zero contour of the fitness function, when the resident strategy is $(\frac{1}{2}, \frac{1}{2})$ is plotted with a thin curve. In the case (b) the fitness gradient is perpendicular to the extinction boundary.

differences in the mutational variance of each component of the strategy vector, as well as the possible covariance between the mutations in these components. Evolutionary analysis in multi-dimensional strategy spaces (Marrow *et al.*, 1996; Leimar, 2001; Meszéna *et al.*, 2001) is thus more difficult than in one-dimensional strategy spaces.

When evolutionary suicide is observed in a one-dimensional strategy space, typically all trait substitution sequences result in extinction (deterministic evolutionary suicide). Based on the reasoning above, in the multi-dimensional case some trait substitution sequences result in extinction while others do not (mutationally stochastic evolutionary suicide). However, the probability of extinction may still be almost equal to one.

3.6. Extinction of one branch of a dimorphic population

Evolutionary branching (Geritz *et al.*, 1998) is a phenomenon, where strategies first approach monomorphically a singular strategy, but then divide into two groups, and evolve further away from each other. In some occasions it is possible, that one of the branches goes extinct, and the population becomes monomorphic again. This phenomenon has been observed for example in the context of the evolution of dispersal (Parvinen, 1999, the case $F = 0.75$ in Figure 8), asymmetric competition (Geritz *et al.*, 1999; Kisdi *et al.*, 2001) and the evolution of cannibalism (Dercole, 2003). In the case described by Dercole (2003), after the extinction of one of the branches, the remaining strategy evolves again to the branching point, resulting in a branching-extinction cycle. As can be easily seen from the Figure 1 of Dercole (2003), there happens a saddle-node bifurcation which results in the extinction of the branch with a strategy more geared towards cannibalism. For a review of branching-extinction cycles, see Kisdi *et al.* (2001). In addition, Kisdi *et al.* (2001) presented an example, where dimorphic evolution leads to a degenerate point where extinction of one of the branches is sure, but which of the two branches goes extinct depends on mutational stochasticity.

Since one branch of the dimorphic population remains viable, this phenomenon is not called evolutionary suicide. Furthermore, in the case of two evolving populations, it is not clear that the branch of the population that goes extinct actually itself causes the extinction. It may be that the surviving branch forces the other branch to extinction, which could perhaps be called "evolutionary murder".

4. EXAMPLES

Evolutionary suicide has been observed in many different types of models, ranging from simple models to structured metapopulation models, and in models defined in continuous and discrete time. This rich variety of different ecological scenarios and model types shows that evolutionary suicide is not a strange phenomenon happening in specifically adjusted models only.

Evolutionary suicide in an asymmetric competition model has already been discussed in Section 2.4. Next other models will be discussed. The first one of them is a chemostat model with an inflow of poison. In this model the cleaning effort is the evolutionary variable (Section 4.1). This model is named a "common good model" because the situation is very close to the tragedy of the commons (Hardin, 1968).

After that the evolution of dispersal in a structured metapopulation model will be studied (Section 4.2) and some results of Gyllenberg *et al.* (2002) will be presented.

Also Cadet (1998) has found evolutionary suicide in a different metapopulation model. In Gyllenberg *et al.* (2002) local populations are large, and a differential equation describes the dynamics of the population density of an individual patch. In Cadet (1998) local populations are small, and a Markov chain is used to describe the local population dynamics. Both discovered that an Allee effect in growth conditions can lead to evolutionary suicide. These models serve as examples of evolutionary suicide in structured models.

Further on, the evolution of consumer search effort in a resource-consumer model, and growth rate in a simple discrete-time model will be investigated. These models are examples of evolutionary suicide occurring with frequency-independent selection.

4.1. Common good model (Chemostat)

Consider a population living in a river (Parvinen, unpublished). Upstream there is a factory with a flow of pollution into the water. Depending on the concentration S of pollutant in the water, individuals experience different living conditions. An increased pollution level decreases fecundity. An individual living in the river may choose to clean water with a rate s with a cost of increased mortality $b(s)$. Normal quality in the river without cleaning is S_0. The change in the pollution level S and population density x is assumed to satisfy the following system of differential equations.

$$\begin{cases} \dot{S} = D(S_0 - S) - sxS \\ \dot{x} = \left[\dfrac{1}{1 + S} \dfrac{ax}{1 + x} - b(s) - cx \right] x. \end{cases} \tag{14}$$

Because of the Allee effect, the extinct equilibrium $(S_0, 0)$ is always stable. For other equilibria there are the following possibilities:

- There are two nonzero equilibria, from which one is stable and one unstable (Figure 7c).
- There is one nonzero equilibrium which is non-hyperbolic (Figure 7b and d).
- There is only the extinct equilibrium (Figure 7a and e).

When the resident population is at an equilibrium (S, x), the fitness of the mutant is

$$r(s_{\mathrm{mut}}, S, x) = \left[\frac{1}{1 + S} \frac{ax}{1 + x} - b(s_{\mathrm{mut}}) - cx \right]. \tag{15}$$

The fitness gradient is $\frac{\partial}{\partial s_{\mathrm{mut}}} r(s_{\mathrm{mut}}, S, x) = -b'(s_{\mathrm{mut}}) < 0$, because the mortality function $b(s)$ is assumed to be increasing. Because the fitness gradient is negative, lower cleaning effort is always favored by selection. It may be so that the population is not viable in normal water quality S_0. In such a case, the cleaning effort in the population will decrease, until it reaches the boundary of viability (Figure 8). A mutant with a lower strategy can still invade but not persist. This invasion will, however, take the resident away from its attractor. The population goes extinct and evolutionary suicide has happened.
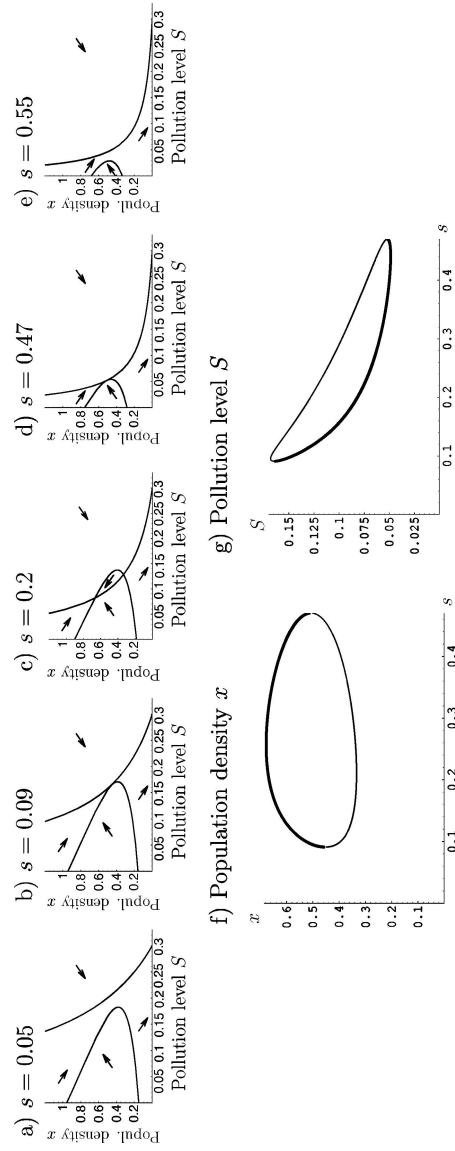
Figure 7. Common good model: (a)–(e) Phase-plane figure with different values of the cleaning effort strategy s. (f) Population density and (g) pollution level in an equilibrium. Thick line corresponds to a stable equilibrium, thin to unstable. Parameters $a = 18$, $c = 8$, $S_0 = 0.3$.
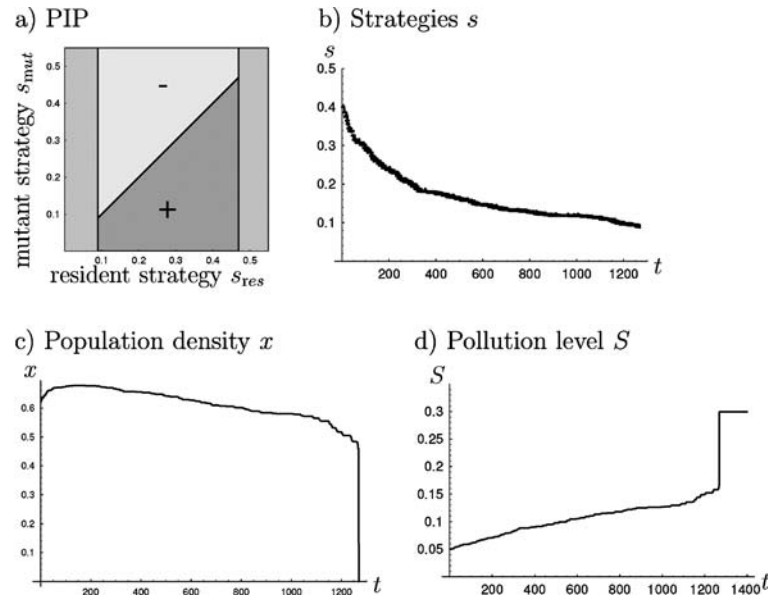
Figure 8. Common good model: The cleaning effort strategy s (b), population density (c) and pollution level (d) in an evolutionary simulation. The corresponding pairwise invasibility plot is in panel (a). Parameters $a = 18$, $c = 8$, $S_0 = 0.3$.

4.2. Dispersal in metapopulations

In the models described so far, the population dynamics of one phenotype occurred in a one or two-dimensional space. As an example of ecologically more complicated model, evolution of dispersal in a structured metapopulation model will be studied. It serves also as an example of an evolutionary bifurcation from an ESS to evolutionary suicide. The results presented here are from Gyllenberg *et al*. (2002).

The basic model was presented by Gyllenberg and Metz (2001) and Metz and Gyllenberg (2001) (these two papers did not discuss evolutionary suicide). It consists of an infinite number of ecologically identical habitat patches. Each patch can support a local population. Local population growth due to birth and death events is described by a per capita growth function $g(x)$, where x is the local population density. Patches are connected by dispersal: individuals leave their patch at a rate s and enter a disperser pool. Individuals in the disperser pool experience mortality at a per capita rate ν and they leave the pool and immigrate into a patch at a per capita rate α. The dispersal risk $\rho = \nu/(\alpha + \nu)$ is the probability that a disperser will not survive migration. Local populations may go extinct as a result of catastrophes, which are assumed to occur at a size-specific rate $\mu(x)$. After a catastrophe, the patch remains habitable, and is immediately recolonized by migrants from the disperser pool. For details of the model, see (Gyllenberg and Metz, 2001; Metz and Gyllenberg, 2001; Gyllenberg *et al*., 2002).

Gyllenberg *et al*. (2002) found two ecological mechanisms, which can result in evolutionary suicide in this model. One mechanism involves catastrophe rates that increase
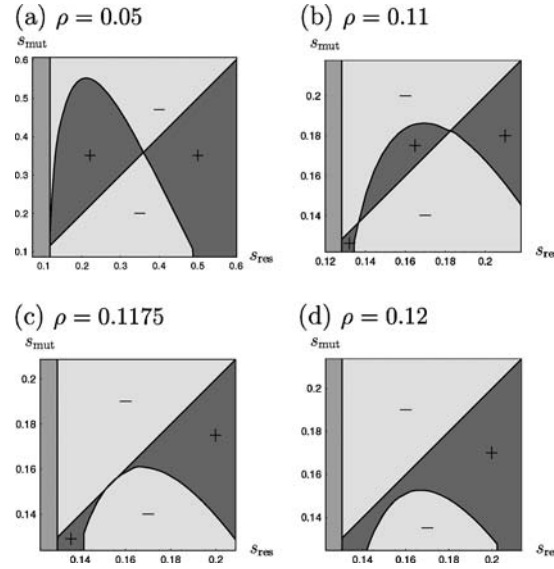
Figure 9. Structured metapopulation model: Pairwise invasibility plots illustrating the route to evolutionary suicide. Local growth is logistic with $g(x) = (1 - x)$. Parameters: $\alpha = 0.5$. The catastrophe function $\mu(x)$ is decreasing. Source: Gyllenberg *et al.* (2002).
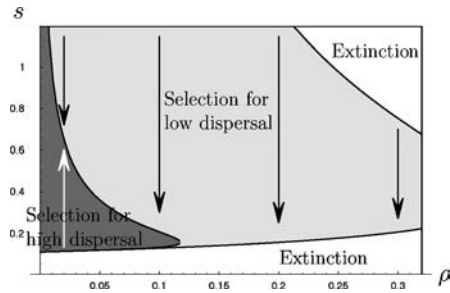

Figure 10. Structured metapopulation model: Dispersal rates at which selection favors lower dispersal rates are plotted in light gray; selection for higher dispersal rates is indicated by dark gray. In the white area the metapopulation is not viable. Parameters are the same as in Figure 9. Source: Gyllenberg *et al.* (2002).

with decreasing local population size. The other mechanism involves an Allee effect in the growth function $g(x)$. The first one will be presented as an example. In Figure 9 pairwise invasibility plots with different values of the dispersal risk ρ are illustrated. See also Figure 10.

For low dispersal risk ρ, there exists one evolutionary attractor, which is an ESS (Figure 9a). When the risk increases, the viable region decreases and the CSS dispersal rate approaches the lower boundary of viability. When the risk is high enough, there appears another evolutionarily stable strategy that, however, is not convergence stable, i.e., it is an evolutionary repellor (Figure 9b). When the dispersal risk increases even more, these two singular strategies collide (Figure 9c) and thereby disappear (Figure 9d). Evolutionary suicide can happen for some initial conditions already in the cases b and c.

For larger values of the dispersal risk, evolutionary suicide happens for all initial values of the dispersal strategy s.

4.3. Resource-consumer model

Already Rosenzweig (1973, 1977) stated that predators may endanger themselves and their victims by increasing their proficiency, especially if there is an Allee effect present. Let us next analyze such a model (Parvinen, unpublished).

Assume that the resource population S grows, in the absence of the consumer population x, according to $\dot{S} = S[\frac{aS}{1+S} - b - cS]$, which includes an Allee effect. The resource population has two positive equilibria $S_{1,2} = \frac{a-b-c\pm\sqrt{D}}{2c}$ if $D = (a - b - c)^2 - 4bc > 0$. The equilibria are numbered such that $S_1 \leqslant S_2$. The consumer (predator) searches for resource (prey) with an effort s. The consumer converts caught resource to offspring with efficiency f. The consumer has a death rate μ. The resource-consumer dynamics is thus

$$\begin{cases} \dot{S} = S\left[\dfrac{aS}{1+S} - b - cS\right] - sSx \\ \dot{x} = fsSx - \mu x. \end{cases} \tag{16}$$

If the search effort strategy s is small, the consumer cannot maintain itself and the only attractors are the stable equilibria $(0, 0)$ and $(S_2, 0)$. When s increases, a stable internal equilibrium (S^*, x^*) appears. Then there happens a Hopf bifurcation where the internal equilibrium loses its stability and a limit cycle appears. The limit cycle disappears in a catastrophic bifurcation, in which it collides with a saddle (heteroclinic bifurcation). After that, the only attractor is the extinct equilibrium $(0, 0)$.

The evolutionary variable is the consumer search effort s. In an environment S set by the resident population, the fitness of a mutant population with a search effort s_{mut} is

$$r(s_{\text{mut}}, S) = \frac{1}{T}\int_0^T fsS(t) - \mu dt = fs\bar{S} - \mu, \tag{17}$$

where $\bar{S}$ is the average resource population density. The fitness gradient $\frac{\partial}{\partial s_{\text{mut}}}r(s_{\text{mut}}, s_{\text{res}})|_{s_{\text{mut}}=s_{\text{res}}} = f\bar{S}$ is always positive. Therefore, a mutant with a larger s than that of the resident can always invade. The search effort s will therefore increase until it reaches the upper boundary of viability, where a catastrophic bifurcation, in which the limit cycle disappears, will occur. When the resident search effort has reached the boundary of viability, a mutant with even higher s can invade, but this will take the resident out of the limit cycle, and the resource and consumer populations will both go to zero, thus evolutionary suicide occurs (see Figure 11).

Note that the fitness function in equation (17) satisfies the conditions of frequency-independent selection by Metz *et al.* (1996b), given in equation (13). However, a catastrophic bifurcation allows for evolutionary suicide.
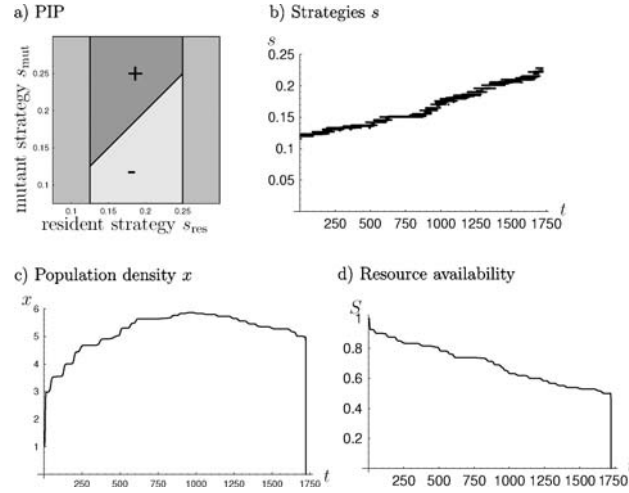
Figure 11. Resource-consumer model: Pairwise invasibility plot (a) and an evolutionary simulation (b–d). Parameters $a = 18$, $b = 1$, $c = 8$, $f = 0.9$, and $\mu = 0.1$.

4.4. Simple discrete-time model

All the previous examples have been defined in continuous time. Here a simple discrete-time model, where evolutionary suicide happens, is given (Parvinen and Dieckmann, unpublished). Actually, it is not surprising that evolutionary suicide can happen also in discrete-time models, because every continuous time model can be rewritten in discrete time.

Most one-dimensional models in discrete-time are of form

$$x_{t+1} = f(x_t)x_t. \tag{18}$$

If $f(x) = re^{-kx}$, then this is the famous Ricker (1954) model. This model is modified by adding an Allee effect, and the resulting function is

$$f(x) = sxe^{-kx}, \tag{19}$$

where s is the evolving parameter. With small values of s, the population is not viable and all trajectories converge to 0. When $s = e$, there appear two equilibria, from which the smaller one is always unstable. The larger one is first stable, but then experiences the period-doubling route to chaos similarly as in the original Ricker model. However, approximately at $s \approx 19.6316$ the chaotic attractor collides with the lower unstable equilibrium. This is a catastrophic bifurcation beyond which all trajectories go to zero (see Figure 12).

If $x_i, i = 1, \ldots, \infty$ is a dense orbit in the resident attractor, the fitness of the mutant is

$$r(s_{\text{mut},(x_1,x_2,\ldots)}) = \ln\left(\lim_{n\to\infty} \sqrt[n]{\prod_{i=1}^{n} s_{\text{mut}} x_i e^{-kx_i}}\right) \tag{20}$$

$$= \ln\left(s_{\text{mut}} \bar{x}_{\text{geom}} e^{-k\bar{x}_{\text{arithm}}}\right) = \ln\left(\frac{s_{\text{mut}}}{s_{\text{res}}}\right). \tag{21}$$
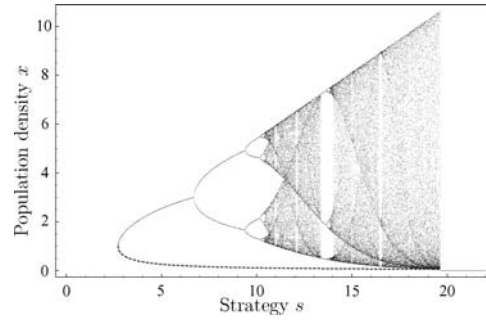
Figure 12. Simple discrete-time model: Period-doubling route to chaos and the collision of the chaotic attractor with the lower unstable equilibrium (drawn as a dashed curve).

The fitness gradient $\frac{\partial}{\partial s_{\text{mut}}} r(s_{\text{mut}}, s_{\text{res}})|_{s_{\text{mut}}=s_{\text{res}}} = \frac{1}{s_{\text{res}}} > 0$, and larger strategy values are therefore always favoured by selection. The strategy values s will thus increase until the upper boundary of viability is reached, and evolutionary suicide happens. Also in this model, the fitness function in equation (20) satisfies the conditions of frequency-independent selection by Metz *et al.* (1996b), given in equation (13). More precisely, $f(s_{\text{mut}}) = s_{\text{mut}}$, $g(x_1, x_2, \ldots) = \bar{x}_{\text{geom}} e^{-k\bar{x}_{\text{arithm}}}$, and $z(f, g) = \log(fg)$. Also here a catastrophic bifurcation allows for evolutionary suicide.

5. DISCUSSION

In this paper I have given an overview of evolutionary suicide, which is an evolutionary process during which a viable population adapts in such a way that it can no longer persist (Ferrière, 2000). Mathematical definitions of different types of evolutionary suicide, including deterministic evolutionary suicide, mutationally stochastic evolutionary suicide and demographically stochastic evolutionary suicide were given.

Because of the results by Geritz *et al.* (2002), it is clear that a bifurcation, in which the present nontrivial ecological attractor disappears, is a necessary condition for evolutionary suicide. Furthermore, if this bifurcation is a continuous transition to extinction, then evolutionary suicide cannot occur (Gyllenberg *et al.*, 2002). As a corollary, a discontinuous transition to extinction is a necessary condition for evolutionary suicide. The Allee effect (Allee *et al.*, 1949) is one possible way to get such a bifurcation, but other ways have been found as well, such as a nonlinear functional response in Matsuda and Abrams (1994b). There are many different types of bifurcations possibly allowing for evolutionary suicide already in a two-dimensional ecological model. Webb (2003) has given a complete classification of bifurcations in one and two-dimensional ecological models in continuous time. Dangerous bifurcations are saddle-node bifurcations of equilibria, subcritical Hopf bifurcations, saddle-node bifurcations of limit cycles, homoclinic bifurcations, and heteroclinic bifurcations. In this paper models with some of these bifurcations were presented. In addition, a model defined in discrete time was studied, in which a chaotic attractor collides with an unstable equilibrium.

The existence of a discontinuous transition to extinction is not enough for evolutionary suicide to happen. In addition, evolution must take the resident to the extinction boundary,

and an unviable mutant must be able to invade the resident, and take the whole population to extinction. Such a mutant could actually be called a kamikaze mutant. In the case of one-dimensional strategies, the possibility of evolutionary suicide is easily seen from a pairwise invasibility plot. Also, in some special cases, it is possible to formulate analytical conditions for evolutionary suicide to happen (Gyllenberg and Parvinen, 2001).

In the case of frequency-independent selection, evolution acts according to an optimization principle (Metz *et al.*, 1996b). In many cases this optimization means the maximization of the evolving population size, which should clearly prevent extinction. Nevertheless, a global catastrophic bifurcation can allow evolutionary suicide in such a situation.

As Webb (2003) stated, Darwinian extinction (evolutionary suicide) is difficult to study in nature simply because it is difficult to observe anything about extinct populations. Some methods exist, however. Already Haldane (1932) noted that the geological record is full of cases were enormous horns and spines has been the prelude to extinction and then wrote that "... in some of the cases the species literally sank under the weight of its own armaments." From an experimental point of view, the topic is also difficult, because one usually does not want to set up a situation, in which the species under study goes extinct, especially not in a field experiment. However, understanding the possible mechanisms behind evolutionary suicide may help us to prevent the extinction of some endangered species. The author hopes that this paper will raise discussion, and result in a better understanding of the phenomenon in the future.

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