International Institute for
Applied Systems Analysis
Schlossplatz 1
A-2361 Laxenburg, Austria

Tel: +43 2236 807 342
Fax: +43 2236 71313
E-mail: publications@iiasa.ac.at
Web: www.iiasa.ac.at

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Self-extinction through optimizing selection

Kalle Parvinen (parvinen@iiasa.ac.at)
Ulf Dieckmann (dieckmann@iiasa.ac.at)

Approved by

Pavel Kabat
Director General and Chief Executive Officer

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Self-extinction through optimizing selection

Kalle Parvinen [a,b,*], Ulf Dieckmann [b]

[a] Department of Mathematics and Statistics, FIN-20014 University of Turku, Finland
[b] Evolution and Ecology Program, International Institute for Applied Systems Analysis, A-2361 Laxenburg, Austria

AUTHOR-HIGHLIGHTS

- In evolutionary suicide, selection drives a viable population to extinction.
- Evolutionary suicide is akin to the Tragedy of the Commons.
- Evolutionary suicide would thus appear to be incompatible with optimizing selection.
- We show that, contrary to intuition, optimizing selection can cause self-extinction.
- Even frequency-independent selection can cause self-extinction.

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ABSTRACT

Evolutionary suicide is a process in which selection drives a viable population to extinction. So far, such selection-driven self-extinction has been demonstrated in models with frequency-dependent selection. This is not surprising, since frequency-dependent selection can disconnect individual-level and population-level interests through environmental feedback. Hence it can lead to situations akin to the tragedy of the commons, with adaptations that serve the selfish interests of individuals ultimately ruining a population. For frequency-dependent selection to play such a role, it must not be optimizing. Together, all published studies of evolutionary suicide have created the impression that evolutionary suicide is not possible with optimizing selection. Here we disprove this misconception by presenting and analyzing an example in which optimizing selection causes self-extinction. We then take this line of argument one step further by showing, in a further example, that selection-driven self-extinction can occur even under frequency-independent selection.

1. Introduction

Darwin (1859, p. 228) believed that natural selection "will never produce in a being anything injurious to itself, for natural selection acts solely by and for the good of each." While modern evolutionary theory (Lawlor and Maynard Smith, 1976; Metz et al., 1992, 1996; Dieckmann and Law, 1996; Geritz et al., 1997) long since left behind such Panglossian views, mechanisms by which natural selection causes the extinction of an evolving population have only recently been discovered in models of life-history evolution (Matsuda and Abrams, 1994a,b; Ferrière, 2000; Gyllenberg and Parvinen, 2001; Gyllenberg et al., 2002; Webb, 2003; Parvinen, 2007, 2010). Such processes of selection-driven self-extinction have become referred to as "evolutionary suicide" (Ferrière, 2000; Gyllenberg and Parvinen, 2001; Gyllenberg et al., 2002) or "Darwinian extinction" (Webb, 2003), and have been observed also in various other models (Rousset and Ronce, 2004; Zayed and Packer, 2005; Dercole et al., 2006; Hedrick et al., 2006; Parvinen, 2007; Gandon and Day, 2009) and experiments (Fiegna and Velicer, 2003). For recent reviews of the phenomenon, see Dieckmann and Ferrière (2004), Parvinen (2005), and Rankin and López-Sepulcre (2005).

The processes resulting in extinction through evolutionary suicide are conceptually closely related to the "tragedy of the commons" (Hardin, 1968; see also Rankin et al., 2007) in which consumers accessing a public good overexploit it to their own detriment. Selection operates at the level of individuals: those genotypes accruing more offspring in a given environment will increase in frequency. However, what is good for an individual is not necessarily good for its population. "Selfish" strategies that are beneficial to individuals when rare, and which can thus invade populations, may result in a deteriorating environment and smaller population size once they become common (e.g., Wright, 1969, p. 127). This feature is also central to the modern interpretation of Fisher's so-called fundamental theorem of natural

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[*] Corresponding author at: Department of Mathematics and Statistics, FIN-20014 University of Turku, Finland. Tel.: +358 2 333 5623; fax: +358 2 231 0311.
E-mail addresses: kalparvi@utu.fi (K. Parvinen), dieckmann@iiasa.ac.at (U. Dieckmann).

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selection (Frank and Slatkin, 1992; Okasha, 2008), which describes only the direct effects of natural selection on average fitness, but not indirect effects occurring through the change caused by evolution to the environment. These indirect effects can go as far as causing population extinction. Already Haldane (1932, p. 119) noted that in a rare and scattered species, natural selection will make an organism fitter in its struggle with the environment, but “as soon as a species becomes fairly dense matters are entirely different. Its members inevitably begin to compete with one another.” For example, competition for light may result in tall plants, although this implies high physiological costs that may severely undermine the evolving population's viability.

Extinction of an evolving population is the exact opposite of what one would expect from optimizing selection. Therefore it would seem that evolutionary suicide cannot possibly occur for evolutionary dynamics governed by an optimization principle (Metz et al., 1996; Heino et al., 1998; Metz et al., 2008). In fact, a possible outcome in such cases is that the population size of the evolving population will be maximized (Roughgarden, 1976). Contrary to this expectation, here we show that natural selection can cause self-extinction even when evolution proceeds according to an optimization principle. The new mechanism for evolutionary suicide results from global bifurcations; its harbingers are strong population fluctuations.

2. Methods

To establish the basis for our analyses below, we first recall salient distinctions between different types of selection. The following distinctions come on top of the more familiar distinctions among directional, stabilizing, and disruptive selection, and are independent of those:

- *Frequency-dependent selection*. Selection is frequency-dependent, if a strategy's advantage varies with its overall frequency within a population (Ayala and Campbell, 1974; Hartl and Clark, 2007). For a sample of alternative formulations, see Heino et al. (1998).
- *Optimizing selection*. Selection is optimizing, if it will result in the maximization of a measure of fitness (Metz et al., 2008).

These notions lead to three types of selection, which are not always clearly separated in the literature: frequency-independent optimizing selection, frequency-dependent optimizing selection, and frequency-dependent non-optimizing selection. This highlights that frequency-independent selection is always optimizing (Appendix A.1), whereas frequency-dependent selection can be either optimizing or non-optimizing.

Below, we define frequency-dependent selection and optimizing selection in more technical detail. Naturally, those definitions must rely on a definition of fitness. For this purpose, we use the general definition of invasion fitness (Metz et al., 1992), as the long-term exponential growth rate $r(s,E)$ of a rare strategy (phenotype) s in the environment E set by the resident(s).

2.1. Frequency-dependent selection

Some textbooks only give a verbal definition of frequency-dependent selection, such as “the direction of selection is […] dependent on the gene frequency” (Falconer and Mackay, 1996, p. 43) or “the fitness of phenotypes depends on their frequency distribution” (Bürger, 2000, p. 289), while other textbooks (Crow and Kimura, 1970; Ewens, 2004; Barton et al., 2007) have given analogous definitions.

Wright (1932) famously suggested that adaptive evolution can be seen as a hill-climbing process on a fitness landscape. According to the modern interpretation of Fisher's fundamental theorem of natural selection (Frank and Slatkin, 1992; Okasha, 2008), natural selection has a direct increasing effect on a population's average fitness, whereas the evolutionary change in its strategy composition affects fitness indirectly, by causing changes to the environment. The latter effect is typically only implicitly included in the traditional hill-climbing metaphor, whereas it is explicitly taken into account in the definition of the invasion fitness $r(s,E)$. Under this definition, frequency-dependent selection manifests itself through the dependence of the environment E on a population's strategy composition. To formalize the verbal definition of frequency-dependent selection, we need to consider a strategy's advantage relative to another strategy. Specifically, the fitness advantage of strategy s_1 relative to strategy s_2 in the environment E is measured by $r(s_1,E)-r(s_2,E)$. Therefore, a natural definition of frequency-independent selection is as follows:

For all realizable environments E and strategies s_1,s_2,
the difference $r(s_1,E)-r(s_2,E)$ does not depend on E. (1)

By realizable environments, we mean all values of E that can result from a population-dynamical attractor of an arbitrary set of resident strategies.

For some models it is convenient to measure population growth between generations by the basic reproduction ratio $R_0(s,E)$, which is related to invasion fitness through the natural logarithm, $r(s,E)\propto \ln R_0(s,E)$ when $|r|$ is small. This concept was originally defined for constant environments (Diekmann et al., 1990). (For extensions to fluctuating environments, see Bacaër and Guernaoui, 2006; Bacaër and AitDads, 2012; Inaba, 2012; Bacaër and Khaladi, 2013.) Furthermore, in discrete-time models, population growth is often measured by discrete-time fitness $R(s,E)$, which is also related to invasion fitness through the natural logarithm, $r(s,E)=\ln R(s,E)$. For R, and analogously for R_0, condition (1) can thus be expressed as follows:

For all realizable environments E and strategies s_1,s_2,
the fraction $R(s_1,E)/R(s_2,E)$ does not depend on E. (2)

Let us now see how this definition relates to the dynamics of the strategy frequencies p_1 and p_2 of the strategies s_1 and s_2, respectively. In unstructured discrete-time population models, the dynamics of the population density $x_{i,t}$ of strategy s_i can in general be written as $X_{t+1}=F(s_1,s_2,X_t)$, using the vector $X_t=(x_{1,t},x_{2,t})$. In the special case $x_{i,t+1}=f(s_i,X_t)x_{i,t}$, only the strategy s_i affects the population dynamics of x_i. For the strategy frequencies $p_{1,t}=x_{1,t}/(x_{1,t}+x_{2,t})$ and $p_{2,t}=1-p_{1,t}$, this yields

$$p_{1,t+1}=\frac{v_t p_{1,t}}{v_t p_{1,t}+p_{2,t}}, \tag{3}$$

with $v_t=f(s_1,X_t)/f(s_2,X_t)$. The discrete-time fitness of a rare strategy s, when the resident population is on a population-dynamical attractor characterized by the time series X_t for $t=1,\ldots,T$, is

$$R(s,E)=\lim_{T\to\infty}\sqrt[T]{x_{T+1}/x_1}=\lim_{T\to\infty}\sqrt[T]{\prod_{t=1}^{T}f(s,X_t)}, \tag{4}$$

with $E=(X_1,X_2,\ldots)$. For fixed-point equilibria, this quantity thus reduces to $R(s,E)=f(s,X)$. Therefore, condition (2) results in a constant v_t in Eq. (3), which is the formal definition of frequency-independent selection usually found in textbooks of population genetics (e.g., table 6.1 on page 214 of Hartl and Clark, 2007). Condition (3) is thus a special case of the more general conditions (1) and (2). In particular, an important advantage of conditions (1) and (2) is that they can be applied also to structured populations.

2.2. Optimizing selection

As illustrated by the definition of invasion fitness above, the environmental interaction variable E contains all information necessary for determining the fitness of a strategy (phenotype) s. The variable E can be a scalar, vector, or function, and its dimension characterizes the dimension of the environment (Heino et al., 1998). However, the definition of invasion fitness only requires that E contain enough information to calculate fitness, but not that this information be represented in maximally compact form. Therefore, the dimension of an environment is that of its minimal description. In the appendix we present a practical method for determining this dimension.

In exceptional (and biologically unrealistic) cases without density dependence, no information about the environment is needed for determining fitness, but in any realistic model, 1 is the smallest possible dimension of the environment. The main point to appreciate is that selection is optimizing if and only if the dimension of the environment is 1: according to Metz et al. (2008), “It is necessary and sufficient for the existence of an optimization principle that the strategy affects fitness in an effectively monotone one-dimensional manner, or equivalently, that the environment affects fitness in an effectively monotone one-dimensional manner.” Formally, this is equivalent to

$$r(s,E) \sim z(f(s),g(E)), \tag{5}$$

where f and g are scalar functions, the function z is increasing with respect to both arguments, and the ~ sign denotes sign-equivalence (Metz et al., 1996). Although E may be multi-dimensional, if (5) holds, E affects a strategy's fitness only through the one-dimensional $g(E)$, so the dimension of E is (at most) 1, and the following optimization principle exists:

$$r(s',E(s))>0 \text{ if and only if } f(s')>f(s). \tag{6}$$

In that case, strategies s' with $f(s')>f(s)$ can invade a population with strategy s. Consequently, evolution will maximize $f(s)$. When any strategy s has reached a population-dynamical attractor, bringing about the environment $E(s)$, the invasion fitness of this strategy s in the environment $E(s)$ equals zero, $r(s,E(s))=z(f(s), g(E(s))=0$. Therefore the fact that evolution maximizes $f(s)$ implies that $g(E)$ is simultaneously minimized (Metz et al., 2008).

Intuitively, if selection is optimizing, one would expect that evolutionary suicide cannot happen. Below we disprove this tempting misconception.

3. Results

We now show that selection-driven self-extinction is possible under frequency-dependent optimizing selection (Example 1) and even under frequency-independent optimizing selection (Example 2).

3.1. Example 1: Self-extinction under frequency-dependent optimizing selection

The first model we study is a simple consumer–resource model with an Allee effect (Allee et al., 1949) in the resource. An Allee effect means that individuals benefit from the presence of conspecifics, and these benefits are lost as population densities decline. Here the Allee effect implies that the resource population can no longer sustain itself when it becomes too small. We assume that in the absence of consumers, the density N of the resource population changes according to $\dot{N}=N(aN/(1+N)-d-\tilde{d}N)$, where $\dot{N}$ denotes the time derivative of N. The component $aN/(1+N)$ is the resource's per capita birth rate, which decreases through an Allee effect from a at very high resource density to 0 at zero resource density; for a discussion of possible mechanistic underpinnings, see Boukal and Berec (2002). The density-independent and density-dependent components of the resource's per capita death rate are d and $\tilde{d}N$, respectively.

To cover all aspects of frequency-dependent selection, we consider several strategies $i=1,2,\ldots,n$ of consumers with harvest intensities s_i and densities C_i, which convert resource intake into offspring with an efficiency $e>0$. Consumers die because of competition with other consumers (at a rate proportional to $\tilde{m}$) and also for intrinsic causes (at rate m). Altogether, we obtain the following differential equations for the resource and a polymorphic consumer population,

$$\dot{N}=N\left(\frac{aN}{1+N}-d-\tilde{d}N\right)-N\sum_{j=1}^{n}s_jC_j,$$

$$\dot{C}_i=es_iNC_i-\left(m+\tilde{m}\sum_{j=1}^{n}C_j\right)C_i. \tag{7}$$

Notice that even for $\tilde{m}=0$, all consumer densities remain bounded.

We use this model to illustrate and to show how models with non-optimizing and optimizing frequency-dependent selection can drive a population to extinction. According to Eq. (7), the invasion fitness (Metz et al. 1992) for the harvesting intensity s evolving in Example 1 is

$$r(s',E)=es'\overline{N}-m-\tilde{m}\overline{C}, \tag{8}$$

where s' is the harvesting intensity of the mutant, $\overline{C}$ is the time-averaged resident consumer population density, and $\overline{N}$ is the corresponding time-averaged resource population density. The environmental interaction variable $E=(\overline{N},\overline{C})$ is at most two-dimensional. In the appendix we show that it is two-dimensional when $\tilde{m}>0$, and one-dimensional when $\tilde{m}=0$. In the latter case, there is frequency-dependent optimizing selection.

Since fitness is an increasing function of s', for an individual consumer it is always advantageous to harvest resources more intensively, so the intensification of harvesting is always favored by natural selection (Fig. 1a). This, however, inevitably leads to decreased resource availability, which is harmful to all consumers. Therefore, when selection drives harvesting intensity beyond a threshold, both resource and consumers go extinct (Fig. 1a–c). This is a typical example of self-extinction caused by non-optimizing selection. Fig. 2 illustrates the population-dynamical bifurcation resulting in extinction. As long as the harvesting intensity is low, consumer–resource dynamics can attain a stable equilibrium (yellow circle), allowing for sustainable exploitation of the resource by the consumer (Fig. 2a). This is shown by the set of trajectories (thin curves) ending up at the stable equilibrium. Other trajectories lead to the origin, implying that certain initial conditions lead to extinction. Isoclines (red curves) separate ranges of increasing resource or consumer density from those in which these densities decrease. Notice that, in addition to the equilibrium at the origin, the stable interior equilibrium coexists with an unstable one (a saddle point, blue circle). Natural selection drives up the harvesting intensity until these two equilibria collide (Fig. 2b), resulting in their mutual annihilation and thus in the inevitable collapse of the consumer–resource system (Fig. 2c). It is not accidental that the transition to extinction seen in Fig. 2a–c is discontinuous, with gradual evolutionary change leading to sudden extinction. In fact, it has been shown that evolutionary suicide cannot occur if the transition to extinction is continuous (Gyllenberg et al., 2002). In other words, a discontinuous transition to extinction is a necessary condition for selection-driven self-extinction.

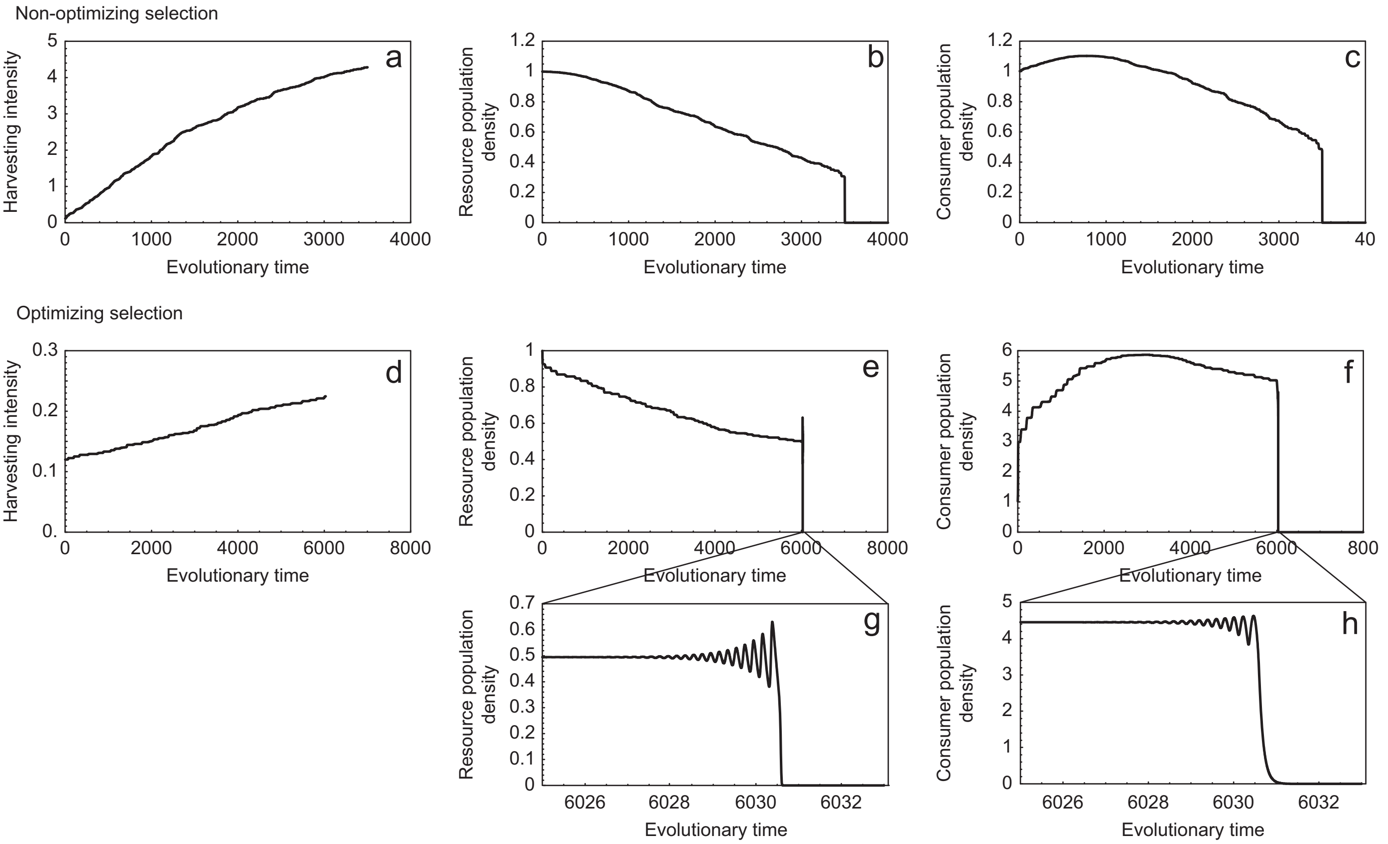

Fig. 1. Evolutionary suicide through non-optimizing selection ($\tilde{m}=6$), panels a–c, and through optimizing selection ($\tilde{m}=0$), panels d–h (Example 1). Evolving harvesting intensities (a, d) increase over time until evolutionary suicide occurs. Other panels illustrate corresponding changes in resource densities (b, e, g) and consumer population densities (c, f, h). Whereas in the non-optimizing case (a–c) population densities monotonically decrease prior to sudden extinction, evolutionary suicide in the optimizing case (d–h) is preceded by characteristic density fluctuations (g, h). Parameters: $a=18$, $d=1$, $\tilde{d}=8$, $e=0.9$, and $m=0.1$.

More in general, it has been shown (Gyllenberg and Parvinen, 2001) that, in models with one-dimensional environmental interaction variables, and thus with optimizing selection, evolutionary suicide cannot occur through the collision of two equilibria. This precludes evolutionary suicide under optimizing selection through the route shown in Fig. 2a–c. Nevertheless, we will show below that even optimizing selection can cause self-extinction. For this purpose, we consider the consumer–resource model introduced above with $\tilde{m}$ equal to zero, thus neglecting the effects of direct competition between consumers. Under these conditions selection continues to favor the intensification of harvesting. Can this then still lead to evolutionary suicide? Surprisingly, the answer is yes: again, resource and consumer go extinct, once the evolving harvesting intensity becomes too high (Fig. 1d–h).

What kind of population-dynamical bifurcation can allow for evolutionary suicide under optimizing selection? Bifurcations as the one in Fig. 2a–c are called local, because the full bifurcation structure can be understood simply by considering a small neighborhood around the collision point. By contrast, a stable limit cycle or a chaotic attractor can disappear through a global bifurcation (see Bazykin et al., 1998; Kooi, 2003 for detailed analyses), and through such a bifurcation evolutionary suicide can occur even if selection is optimizing. Fig. 2d–g illustrate this for the case $\tilde{m}=0$: at low harvesting intensity (Fig. 2d) the situation is akin to the previous case with $\tilde{m}>0$ (Fig. 2a). However, we see that now the population-dynamical attractor is not always an equilibrium, but instead changes from a stable equilibrium (Fig. 2d) to a stable limit cycle (Fig. 2e). A global bifurcation occurs when the unstable manifold of the right saddle at (1, 0) (thick yellow curve) and the stable manifold of the left saddle at (0.125, 0) (thick blue curve) collide (thick green curve). Before the bifurcation (Fig. 2e), the yellow curve connects to the limit cycle and the blue curve acts as a separatrix (separating initial conditions from which the dynamics converge either to the limit cycle or to the origin). At the bifurcation (Fig. 2f), the two curves coincide, forming a so-called heteroclinic orbit. After the bifurcation (Fig. 2g), the yellow curve connects to the origin and the blue curve to the unstable equilibrium such that all trajectories now lead to extinction. Webb (2003) observed a similar phenomenon in another consumer–resource model, see her Eqs. (5) and (6), and her Figs. 9 and 10 (although one can show that selection on mean predator mortality is optimizing in the model (Webb, 2003), the types of selection causing self-extinction were not examined in her model).

We thus conclude that even optimizing selection can result in evolutionary suicide.

3.2. Example 2: Self-extinction under frequency-independent optimizing selection

As another example of evolutionary suicide under optimizing selection we present a modified Ricker (1954) model in which the population's growth rate is evolving. In addition, this model shows that evolutionary suicide is possible under frequency-independent selection. The model is defined in discrete time, with a population's density x_{t+1} in the next time step being dependent on its current density x_t according to $x_{t+1}=h(x_t)x_t$. The original Ricker (1954) model is given by $h(x)=ae^{-kx}$, where a is the fecundity at low population densities and k measures the strength of density regulation. Discrete-time models with an Allee effect can be

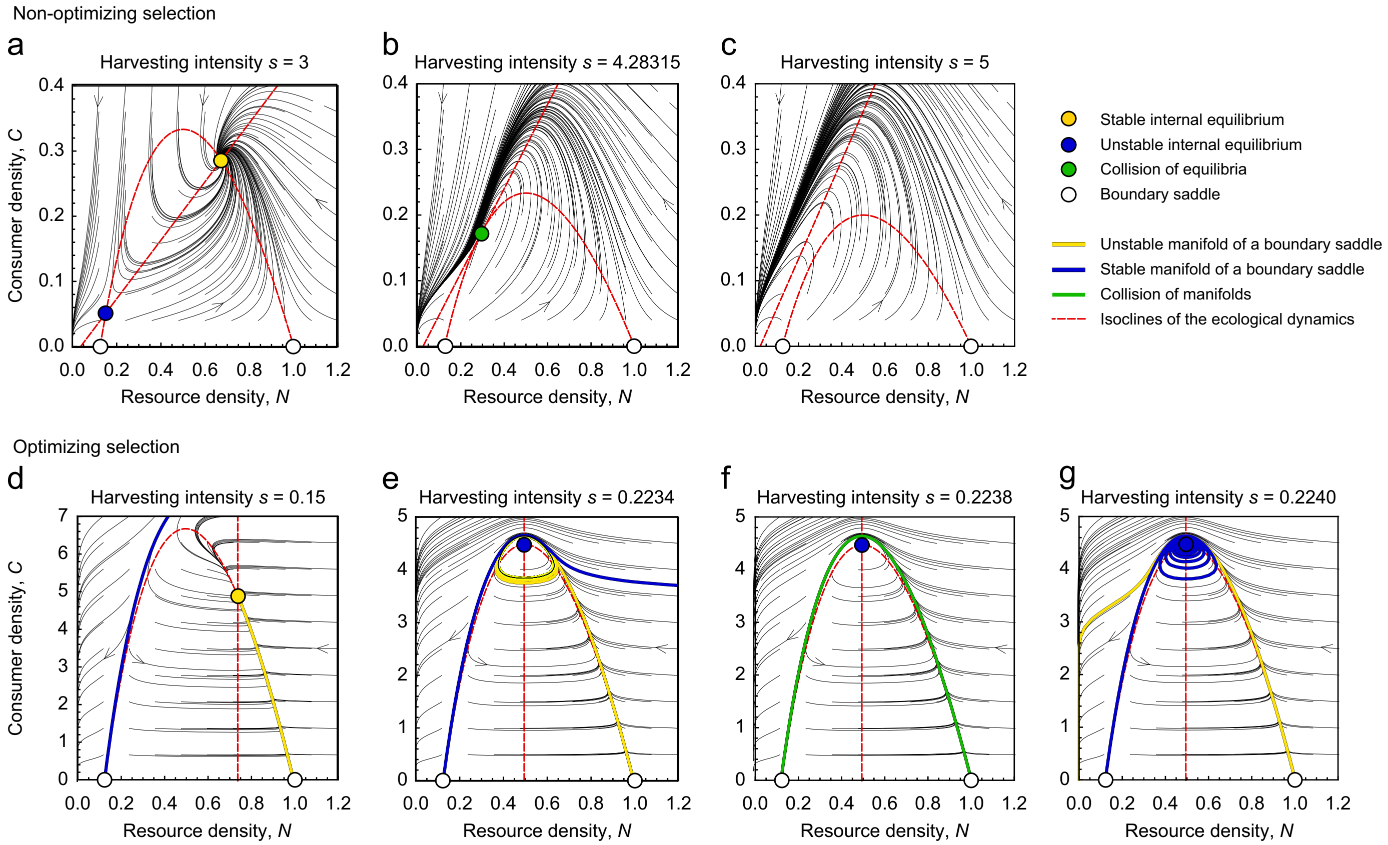

Fig. 2. Evolutionary suicide through non-optimizing selection (a–c) and optimizing selection (d–g) proceed along fundamentally different routes (Example 1). A first route (a–c) leads through a local bifurcation, in which a stable equilibrium (yellow circle) collides with an unstable one (a saddle point, blue circle). Evolutionary suicide through optimizing selection requires a different route (d–g), involving a global bifurcation, in which the unstable manifold of the right saddle at (1, 0) (thick yellow curve) and the stable manifold of the left saddle at (0.125, 0) (thick blue curve) collide (thick green curve). Parameters as in Fig. 1. (For interpretation of the references to color in this figure caption, the reader is referred to the web version of this paper.)

derived from first principles in many ways: our choice of $h(x) = sxe^{-kx}$ can be motivated, for example, with difficulties in mate finding (Eskola and Parvinen, 2007). For several strategies $i = 1, 2, \ldots, n$ with different growth rates s_i, the population dynamics are given by

$$x_{i,t+1} = s_i x_{i,t} N_t e^{-kN_t} \quad \text{with } N_t = \sum_{j=1}^{n} x_{j,t}. \tag{9}$$

This implies that the discrete-time invasion fitness of a mutant with growth rate s' is

$$R(s', E) = \lim_{T\to\infty} \sqrt[T]{x_{T+1}/x_1} = s' \lim_{T\to\infty} \sqrt[T]{\prod_{t=1}^{T} N_t e^{-kN_t}}, \tag{10}$$

where N_t is the total population size at time t. The dynamics of the modified Ricker model is rich and can even be chaotic. Even though the full time-course of densities therefore is needed in Eq. (10), and the dimension of the environmental interaction variable $E = (N_1, N_2, \ldots)$ hence is infinite, this is not the minimal description of the environment. In the appendix we show that individuals only perceive the environment through a one-dimensional variable. The environment is thus one-dimensional and the invasion fitness (10) can be written as in (5). Therefore, selection is optimizing. In the appendix we also show that selection in this model is frequency-independent.

The invasion fitness (10) is an increasing function of the growth rate s'. Thus, natural selection always favors increases in this strategy, taking the population through a period-doubling route to chaos. Similar to the first example, there is a threshold value for the growth rate s at which natural selection abruptly drives the population to extinction by way of evolutionary suicide (Fig. 3). When s exceeds this threshold (for $k = 1$, this happens at $s \approx 19.6316$), a global bifurcation occurs, in which the population's stable chaotic attractor collides with an unstable equilibrium. As a result, the chaotic attractor disappears and the population goes extinct.

We have thus confirmed that evolutionary suicide can occur even in models with frequency-independent optimizing selection.

4. Discussion

Although it may seem paradoxical at first sight, in this paper we have shown that evolutionary suicide is possible under frequency-dependent optimizing selection (Example 1) and even under frequency-independent optimizing selection (Example 2). Evolutionary suicide means that selection forces strategies to evolve towards and beyond an extinction boundary. The population-dynamical bifurcation through which viability is lost can be of fairly simple type in models with non-optimizing selection. In the simplest case, a stable equilibrium collides with an unstable one and thus disappears. However, this bifurcation does not allow for evolutionary suicide under optimizing selection (Gyllenberg and Parvinen, 2001). Nevertheless, as illustrated here, more complicated bifurcations involving non-equilibrium attractors or repellors can allow for evolutionary suicide also under optimizing selection.

Broadly speaking, we can thus conclude that evolutionary suicide can occur via two mechanisms. In the first one, there is a clear dissociation of individual and common good, like in the

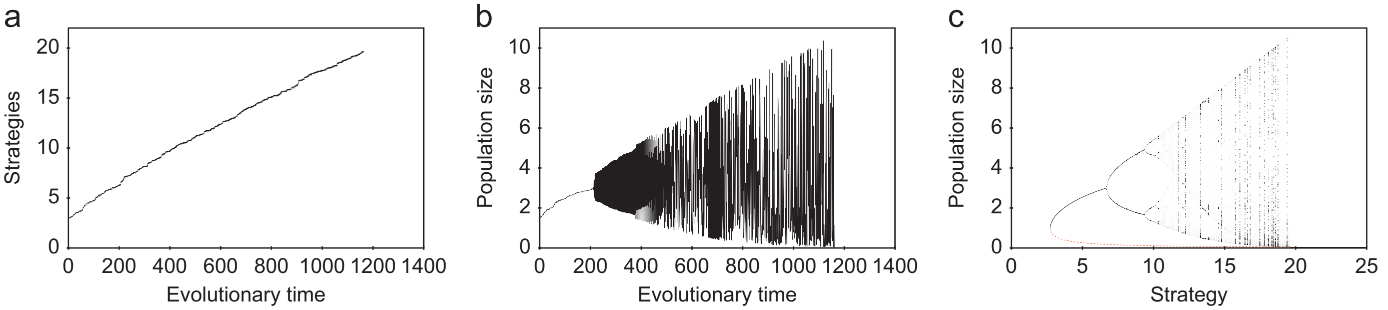

Fig. 3. Evolutionary suicide through frequency-independent optimizing selection (Example 2). Evolutionary dynamics of growth rates s (a) and corresponding population sizes N (b). (c) Population-dynamical attractor and unstable equilibrium (dashed curve) as a function of the growth rate s. Parameters: $k=1$.

“tragedy of the commons” (Hardin, 1968), mentioned already in the introduction. This situation is traditionally linked with frequency-dependent selection, and there are close conceptual similarities with the emergence of selfish strategies in studies addressing the evolution of cooperation (Nowak and Sigmund, 2005; Nowak, 2006; Hauert et al., 2007; Parvinen, 2010, 2011).

Here we have identified a second mechanism for evolutionary suicide. Even under optimizing selection, evolutionary suicide can occur, provided that population viability is lost through a global bifurcation (defined by the fact that the full bifurcation structure cannot be understood simply by considering a small neighborhood in the state space around a collision point). We have presented two prototypical models in which the new mechanism operates. Note that this novel class of evolutionary phenomena may not have been detected before because models of optimizing selection are often so simple in their population dynamics that they do not allow for cyclic or chaotic dynamics, such that global bifurcations are excluded. In systems of ordinary differential equations, simplicity in population dynamics coincides at least partly with the number of equations: for one-dimensional differential equation, all attractors are fixed-point equilibria, whereas two dimensions are needed for cycles, and three dimensions for chaos. In discrete time, however, even simple-looking models can have complex population dynamics, such as those illustrated in our Example 2. Against this background and in the context of evolutionary suicide, it might thus be worthwhile to consider ecological mechanisms enhancing or preventing complex dynamics. For example, Ruxton (1995) suggested that sexual reproduction may reduce a population's likelihood to exhibit chaos. Note also, that under complex dynamics, seemingly viable population dynamics may just be on a chaotic transient, eventually resulting in population extinction (Mc Cann and Yodzis, 1994).

Naturally, the presence of an extinction boundary does not guarantee that evolutionary suicide occurs. This is because in addition, selection must force strategies to evolve towards and beyond such an extinction boundary. In case extinction is brought about by a global bifurcation, complex dynamics precede extinction. Therefore, the question under what circumstances natural selection favors traits that result in more complex (chaotic) dynamics or less complex (equilibrium) dynamics (Gatto, 1993; Doebeli and Koella, 1995; Ebenman and Johansson, 1996; Johst et al., 1999) is relevant in the study of evolutionary suicide. Already without natural selection, a population experiencing chaotic dynamics can repeatedly reach very low densities, which exposes it to chance extinction. With natural selection towards an extinction boundary, such exposure is especially fatal, like in our Example 2, in which the chaotic attractor collides with an unstable equilibrium.

As mentioned earlier, selection is optimizing if it will result in the maximization of some measure of fitness (Metz et al., 2008). As explained in the Methods section, a measure of environmental quality will always be minimized under optimizing selection. A special case of such pessimization is Tilman's R^* principle (Tilman, 1982, p. 47; Tilman, 1988, p. 21), according to which, among several consumers limited by a single resource, the one consumer that engenders the lowest equilibrium resource level R^* competitively excludes all the others. From this observation one may get the impression that, under optimizing selection, the best strategy is selected for, and because it can survive in the worst environment, optimizing selection cannot result in extinction. A more careful look at this matter makes the observed phenomenon of evolutionary suicide under optimizing selection understandable. In order to appreciate what happens in our Example 1, a consumer–resource model, we only need to restate the R^* principle as “the consumer that is most efficient in the use of the resource will displace all others”, and notice that the most efficient consumer may indeed be too efficient: overharvesting may then result in the collapse of the resource population. In our model, no consumers can survive in such a situation, so evolutionary suicide happens. This may help to understand, at a more intuitive level, why evolutionary optimization and suicide do not exclude each other.

The observation that evolutionary suicide can result from common evolutionary phenomena, such as selection for higher harvesting intensity or for higher growth rate, raises a fundamental question. If this phenomenon is widespread, then why does life generally persist? Answers are many fold. First, evolutionary suicide may actually be rather common, resulting in relatively frequent extinctions. According to the fossil record, an enormous amount of species is known to have gone extinct, and it is difficult to assess whether their extinctions have resulted from evolutionary suicide or from other causes. Second, there are many mechanisms that can potentially prevent evolutionary suicide. In the context of avoiding the tragedy of the commons (Hardin, 1968), various behavioral and regulatory mechanisms have been proposed, including “mutual coercion, mutually agreed upon” by Hardin (1968, 1998). Evolutionary suicide in natural populations, however, is not a phenomenon that can be avoided through regulatory interventions. The simplest natural ecological mechanisms for preventing evolutionary suicide are additional costs or benefits implied by the evolving traits, such as a cost of harvesting in our Example 1 or a cost of growth in our Example 2. Also joint evolutionary dynamics can prevent extinction. For example, the joint evolution of female resistance and male harassment can prevent evolutionary suicide occurring through excessive male harassment (Rankin et al., 2011). Spatial structure, such as in a metapopulation, can also prevent selection-driven extinction: for example, dispersing individuals may escape unfavorable situations, such as excessive harassment (Eldakar et al., 2009). Furthermore, the relatedness between individuals in small local populations can be high, which may select for more cooperative strategies (Fletcher and Doebeli, 2009; Parvinen, 2011) and thus prevent evolutionary suicide. This requires low dispersal, which in turn may be the outcome of evolution (Parvinen, 2013).

Can evolutionary suicide be anticipated? When it occurs through the collision of a stable and an unstable equilibrium in a one-dimensional model, population densities smoothly decrease to a finite value before the extinction takes place (Gyllenberg and Parvinen, 2001). For examples, see Gyllenberg and Parvinen (2001, Fig. 3), Gyllenberg et al. (2002, Figs. 1c and 7b), Webb (2003, Fig. 4), Parvinen (2005, Fig. 8), and Parvinen (2010, Fig. 3). Whatever the reason for a population decline is, they receive the attention of managers. Such a decline can then be interpreted as an early warning signal for triggering management actions. By contrast, when evolutionary suicide occurs under non-equilibrium population dynamics, a gradual decline cannot be relied upon as a warning signal. Instead, changes in the fluctuations of population density (Fig. 1g and h), either of oscillatory or chaotic nature, precede the transition to extinction, see also Webb (2003, Figs. 6, 8, and 10), Parvinen (2010, Fig. 6). Such fluctuations, and changes in the period of the oscillations, can thus herald the danger of imminent evolutionary suicide.

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Appendix A

A.1. Testing for optimizing selection

A first operational method of testing for optimizing selection requires finding the dimension of an environment's minimal description, with respect to a given fitness function. This dimension is defined by the rank of the fitness function $r(s,E)$ with regard to the environmental interaction variable E. In many models, this rank is independent of E, but when it depends on E, it suffices to investigate this rank around $r(s,E)=0$. Mathematically (e.g., Tu, 2008), said rank is given by the rank of the derivative of r with respect to $E=(E_1,\ldots,E_n)$, where the n components of E are independent. Thus, the sought dimension equals the maximum number, for all feasible s_i and E, of linearly independent vectors

$$\nabla_E r(s_i,E)=\left(\frac{\partial}{\partial E_1},\ldots,\frac{\partial}{\partial E_n}\right)r(s_i,E), \tag{A.1}$$

for $i=1,\ldots,n$. Hence, we can simply construct the matrix M with rows given by the vectors in (A.1) and then evaluate its rank. This implies that the sought dimension equals n, if and only if M has full rank, i.e., if its determinant is not vanishing. A similar construction was already considered by Meszéna et al. (2006).

Sometimes, a model's (not necessarily minimal) representation of the environmental interaction variable is infinite-dimensional. The infinite-dimensional version of the gradient (A.1) may then consist of zero elements only: This happens if each element of E changes r only infinitesimally. In such cases, it will be helpful to study a finite-dimensional approximation.

We can prove that, under frequency-independent selection, the number of linearly independent vectors $\nabla_E r(s_i,E)$ always exactly equals 1: From (1) it follows that for all s_1 and s_2 the derivative $(\partial/\partial E_k)(r(s_1,E)-r(s_2,E))=0$ for $k=1,\ldots,n$, and therefore $\nabla_E r(s,E)$ does not depend on s. Hence, the dimension of the environment in models with frequency-independent selection always equals 1, meaning that selection in such models is always optimizing.

Based on the results of Gyllenberg and Service (2011), a second operational condition for the presence of an optimization principle exists. First, it is straightforward to see that an optimization principle (6) excludes mutual invadability,

$$r(s_1,E(s_2))\geq 0 \text{ if and only if } r(s_2,E(s_1))\leq 0, \tag{A.2}$$

and also that the invasibility relation is transitive,

$$r(s_1,E(s_2))\geq 0 \text{ and } r(s_2,E(s_3))\geq 0 \text{ together implies } r(s_1,E(s_3))\geq 0, \tag{A.3}$$

which means that if the strategy s_1 can invade the strategy s_2, and the strategy s_2 can invade the strategy s_3, then necessarily the strategy s_1 will be able to invade the strategy s_3. In other words, there are no rock-paper-scissors triples of strategies. Gyllenberg and Service (2011) proved that under rather general conditions, conditions (A.2) and (A.3) together are equivalent to condition (6), which provides another method for testing for optimizing selection.

A third operational method has been discussed by Metz et al. (2008) and Gyllenberg et al. (2011). This method is based on the visual inspection of the sign-structure of pairwise invasibility plots (PIPs). Condition (A.2) corresponds to skew-symmetry, which means that a PIP does not change when it is mirrored across its diagonal and the signs of invasion fitness are inverted. Furthermore, the transitivity condition (A.3) implies that for any resident strategy s, strategies s_i that satisfy $r(s_i,E(s))=0$ are equivalent to the strategy s in the sense that they must have the same sign structure, $r(s',E(s_i))\sim r(s',E(s_{\mathrm{res}}))$ for all s, which is also readily inspected visually.

Here we have listed various methods of testing for optimizing selection. The first method, which is based on (A.1), is relatively easy to apply, if invasion fitness can be written in explicit form. Concerning the second method, transitivity (A.3) cannot be verified in finitely many operations. The third method is easy to apply numerically, but a rigorous test requires that the curves satisfying $r(s',E(s))=0$ be expressed analytically.

A.2. Selection in Example 1

We can see from Eq. (8) that the fitness difference (1) in Example 1 equals

$$r(s_1,E)-r(s_2,E)=eN(s_1-s_2), \tag{A.4}$$

which does depend on the component N of the environmental interaction variable $E=(N,\overline{C})$, so selection in this model is frequency-dependent. The gradient of the fitness function (8) with respect to $E=(N,\overline{C})$ is $\nabla_E r(s,E)=(es,-\tilde{m})$. For any two strategies $s_1\neq s_2$, these vectors are linearly independent if the determinant

$$\begin{vmatrix} es_1 & -\tilde{m} \\ es_2 & -\tilde{m} \end{vmatrix}=e\tilde{m}(s_2-s_1) \tag{A.5}$$

does not vanish. For $\tilde{m}>0$ the environment is thus two-dimensional and selection is not optimizing, whereas for $\tilde{m}=0$ the environment is one-dimensional and selection is optimizing.

A.3. Selection in Example 2

From Eq. (10), we see that the fitness ratio (2) in Example 2 equals

$$R(s_1,E)/R(s_2,E)=s_1/s_2, \tag{A.6}$$

and thus never depends on the environmental interaction variable E. Furthermore, we observe that Eq. (3) holds with a constant $v=s_1/s_2$. Therefore, selection in this model is frequency-independent. When the population-dynamical attractor $(N_1, N_2, \ldots)$ of the resident is cyclic, $N_{T+1} = N_1$, the invasion fitness (10) is

$$R(s', E) = s' \sqrt[T]{\prod_{t=1}^{T} N_t e^{-kN_t}} \tag{A.7}$$

The gradient of the fitness function (A.7) with respect to the environmental interaction variable $E = (N_1, N_2, \ldots, N_T)$ is

$$\nabla_E R(s, E) = \frac{s}{T} \sqrt[T]{\prod_{t=1}^{T} N_t e^{-kN_t}} \left(\frac{1-kN_1}{N_1}, \frac{1-kN_2}{N_2}, \ldots, \frac{1-kN_T}{N_T} \right). \tag{A.8}$$

We observe that upon variation of s, this vector remains the same, except for a changing multiplication factor in front. Therefore, all vectors $\nabla_E R(s_i, E)$, for $i = 1, \ldots, n$, are linearly dependent, and the dimension of the environment is 1. This implies optimizing selection. Using the notion of Eq. (5), the optimized function g is given by

$$R(s', E) = s' g(N_1, N_2, \ldots) \text{ with } g(N_1, N_2, \ldots) = \overline{N}_{\text{g}} e^{-k\overline{N}_{\text{a}}}, \tag{A.9}$$

involving the geometric mean $\overline{N}_{\text{g}}$ and the arithmetic mean $\overline{N}_{\text{a}}$ of densities in a population with strategy s. For non-cyclic resident attractors, i.e., in the limit $T \to \infty$, the effect of each single element of the environmental interaction variable on fitness, and therefore also all elements of the vector (A.8), approach zero. Nevertheless, also in this case, invasion fitness can be written with a one-dimensional environmental interaction variable according to Eq. (A.9). To conclude, in this model selection is both optimizing and frequency-independent.

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