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## Self-extinction through optimizing selection

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## 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.

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## 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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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,  $r(s, E) = \ln R_0(s, E)$  when  $|r|$  is small. This concept was originally defined for constant environments (Dieckmann 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

$$p_{1,t+1} = \frac{v_t p_{1,t}}{v_t p_{1,t} + p_{2,t}}, \quad (3)$$

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  $t = 1, \dots, T$ , is

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

with  $E = (X_1, X_2, \dots)$ . 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.

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