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Evolution by natural selection to extinction

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ABSTRACT

Question: How does the mechanistic underpinning of a discrete-time model affect the possibility for evolutionary suicide?

Mathematical methods: Adaptive dynamics. Relevant theory on attractor families and bifurcations.

Features of model: A discrete-time population model derived from a continuous-time resource-consumer model with processes of harvesting resource, mate finding, and egg production.

Results: A population-level multiplicative parameter is affected both by the probability of egg survival and harvest effort. Higher survival probability is selected for, which can result in a period-doubling cascade to chaos, and in evolutionary suicide through a global bifurcation. Also, higher harvest effort is selected for, but it becomes a scaling factor for the model without qualitatively affecting its dynamics, and demographically stochastic extinction occurs.

Conclusion: Evolutionary predictions should be based on individual-level traits.

Keywords: adaptive dynamics, evolutionary suicide, evolution to extinction,
first-principles derivation, mechanistic modelling.

INTRODUCTION

In *On the Origin of Species*, Darwin (1859, p. 201) wrote: ‘Natural selection will never produce in a being anything injurious to itself, for natural selection acts solely by and for the good of each.’ At first sight this statement seems to be at odds with evolution to extinction. Note, however, the scale of events: for any population, there is a significant environmental feedback loop. The behaviour of individuals in a population will inevitably affect the availability of relevant resources, which again affects the growth of the population. In particular, if the investigated species is involved in a food web with many species, these effects can be complicated to model. However, in a large population, a single individual has a very small, almost insignificant, impact on the relevant resources. Therefore, an individual deviating from the common behaviour of the population may perform better than others in the present environment, but the environment will be affected only after the new strategy becomes common enough in the population, to the extent that this strategy is no longer

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beneficial in the altered environment. This effect was noted also by Darwin: ‘After the lapse of time, under changing conditions of life, if any part comes to be injurious, it will be modified; or if it be not so, the being will become extinct, as myriads have become extinct.’ As natural selection operates on the level of individuals, evolution does not necessarily proceed to benefit the whole population, and it can even result in the extinction of the evolving population. Such a phenomenon has been called evolutionary suicide (Ferrière, 2000) or Darwinian extinction (Webb, 2003).

Selfish behaviour against the common good has a central role also in the tragedy of the commons (Hardin, 1968, 1998). In a famous example, an individual sheep-owner has to decide whether or not to put one more sheep to graze on common land of the village. The sheep-owner will benefit from the increment of one sheep, but the cost of decreased land quality will be shared among all sheep-owners. It is thus always beneficial for an individual sheep-owner to increase the number of sheep on the commons, and this will lead to the over-exploitation of the commons. In this example, it is relatively straightforward to recognize the selfish behaviour of an individual sheep-owner, and restrictions can be imposed to avoid over-exploitation. In many other cases, harmful behaviour may not be so easily recognized, maybe only after extinction or other harmful consequences. Mathematical modelling may provide tools for preventing such phenomena.

THEORY

Principles of building mathematical models

There are, in general, two principles according to which one can construct a mathematical model. In the phenomenological, top-down approach, one chooses a convenient mathematical structure so that it contains relevant features on the population level. In the mechanistic, bottom-up approach, one describes the behaviour of individuals in detail, after which the population-level model is a straightforward consequence of bookkeeping. This approach is also called ‘first-principles derivation’.

Both modelling approaches have their advantages. A phenomenological model can contain all relevant population-level behaviour, and can be chosen to be simple enough so that detailed mathematical analysis is possible without the need for numerical analysis or stochastic simulations. On the other hand, in phenomenological models, parameters can only be interpreted as features on the population level, not on the individual level. This is a major problem if one wants to study evolution by natural selection using mathematical models. Mutations affect the behaviour of individuals, and it is the individual benefits and costs that determine whether a mutation can spread in a population. Therefore, evolutionary predictions should be based on individual-level traits (Rueffler *et al.*, 2006). For examples of mechanistic derivations of population models, see Sumpter and Broomhead (2001), Geritz and Kisdi (2004), Brännström and Sumpter (2005), Rueffler *et al.* (2006), Eskola and Geritz (2007), Eskola and Parvinen (2007, 2010), and Anazawa (2009).

Invasion fitness and singular strategies

Evolution by natural selection has been studied using various mathematical methods and notations (Eshel, 1983; Matsuda, 1985; Van Tienderen and De Jong, 1986; Taylor, 1989; Christiansen, 1991), including the fitness generating function (*G*-function) approach (Vincent *et al.*, 1993; Cohen *et al.*, 1999) and adaptive dynamics (Metz *et al.*, 1992, 1996; Dieckmann and Law, 1996; Geritz *et al.*, 1997, 1998). Here I have chosen to use the notation of adaptive dynamics.

Invasion fitness (Metz *et al.*, 1992) is the long-term exponential growth rate $r(s_{\text{mut}}, E_{\text{res}})$ of a rare mutant with strategy s_{mut} in an environment E_{res} set by the resident population. Usually, it is assumed that the resident has been around long enough for a population-dynamical attractor to be reached. The set of all possible strategies is called the strategy space. To distinguish proper residents from cases with a population size of zero, I call the viability set V that set of strategies to which there corresponds at least one population-dynamical attractor that is not the extinction equilibrium.

Originally in adaptive dynamics the strategy was assumed to be a real number, but vector-valued strategies and function-valued strategies also have been investigated. Only if a mutant has positive fitness may the corresponding mutation spread in the population. This can result in the mutant substituting the resident, thus becoming a new resident itself. Mutations are typically assumed to be small, but a trait-substitution sequence can substantially alter the strategy composition of the evolving population.

Eventually, the population may reach an uninvadable strategy – also called an evolutionarily stable strategy, or ESS (Maynard Smith and Price, 1973; Maynard Smith, 1976). With such a strategy as resident, all mutants different from the resident have negative fitness, which means that the resident strategy is a (local) fitness maximum. Therefore, the selection gradient (i.e. the derivative of invasion fitness with respect to the strategy of the mutant) vanishes at such points,

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

In general, strategies for which the selection gradient is zero are called evolutionarily singular strategies (Geritz *et al.*, 1998). A (singular) strategy s^* is an evolutionary attractor (convergence stable) if the repeated invasion of nearby mutant strategies into resident strategies leads to the convergence of resident strategies towards s^* (Christiansen, 1991). One should note that an uninvadable strategy does not have to be an evolutionary attractor, and an evolutionary attractor does not have to be uninvadable. In the latter case, a monomorphic population may become dimorphic, i.e. to consist of individuals of two different strategies, and these two strategies evolve away from each other. This phenomenon is called evolutionary branching (Geritz *et al.*, 1998). If reproductive isolation also emerges, evolutionary branching can result in sympatric speciation (Dieckmann and Doebeli, 1999), and thus increase biodiversity. In contrast, evolutionary suicide causes biodiversity losses.

Defining evolutionary suicide

Ferrière (2000) defined evolutionary suicide as a trait-substitution sequence driven by mutation and selection taking a population towards and across a boundary in the population's trait space beyond which that population cannot persist. This means that evolution can (with small mutational steps) take the strategy of the population close to the boundary of the viability set ∂V (extinction boundary). Finally, a 'kamikaze' mutant with a strategy not in V can invade, moving the dynamics away from the resident attractor and resulting in the extinction of the whole population (Parvinen, 2005).

According to the definition above, evolutionary suicide can be (at least) of two forms. Deterministic evolutionary suicide occurs when all trait-substitution sequences starting from a specific strategy s result in the extinction of the considered population. In mutationally stochastic evolutionary suicide, some trait-substitution sequences result in extinction while others do not.

The definition of evolutionary suicide does not cover evolution to demographically stochastic extinction ['gradual Darwinian extinction' *sensu* Webb (2003)] in which evolution leads to population densities that become so small that chance extinction becomes increasingly likely. Matsuda and Abrams (1994a) called this process 'runaway selection to self-extinction'; but note that the demographic stochasticity that eventually causes extinction is not explicitly included in their model.

Bifurcations and attractor families

One of the original assumptions of adaptive dynamics (Geritz *et al.*, 1998, p. 36) is that '[t]he strategies in a given resident population can be considered as a set of model parameters that implicitly specify a unique attractor for the resident population dynamics.' Since many models do have several population-dynamical attractors even in a monomorphic population (e.g. Parvinen, 1999), adaptive dynamics theory has been developed further to deal with such situations (Geritz *et al.*, 2002; Geritz, 2005). Such theory is especially important for understanding evolutionary suicide because it necessarily involves two population-dynamical attractors: a non-extinct state of the resident before the invasion of a kamikaze-mutant, and the extinction equilibrium.

Geritz *et al.* (2002) studied so-called attractor families: consider a population-dynamical attractor $A(s)$ for all $s \in \hat{S}$, where $\hat{S}$ is a compact subset of the strategy space S. (When $S \subset \mathbb{R}^n$, the set $\hat{S}$ is closed and bounded.) This means that for each s, $A(s)$ is a subset of the community state space – the space including all feasible states of its population dynamics. If $A(s)$ varies continuously as a function of s on $\hat{S}$, then $(A, \hat{S})$ is called an attractor family [definition 3.2 of Geritz *et al.* (2002) provides more details]. The type of the attractor within an attractor family may change, such as in a period-doubling bifurcation, but the attractor cannot disappear. Furthermore, the area 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 is called the tube.

Figure 1 illustrates the situation in which the mutant can invade the resident on a specific attractor and the resident cannot invade the mutant on the corresponding attractor. Since the mutant is initially rare, the resident-mutant population is at least initially inside the tube. Without knowing more of the specific system, various events could occur after the initial increase of the mutant population. The following cases correspond to those illustrated in Fig. 1.

A. Attractor inheritance: the mutant replaces the resident and stays in the same attractor family.
B. Attractor switching: the mutant replaces the resident, but does not stay in the same attractor family.
C. Co-existence inside the tube.
D. Co-existence outside the tube.
E. Resident strikes back: after the initial increase of the mutant population, the mutant population decreases, and the system reaches another resident attractor (Mylius and Diekmann, 2001).

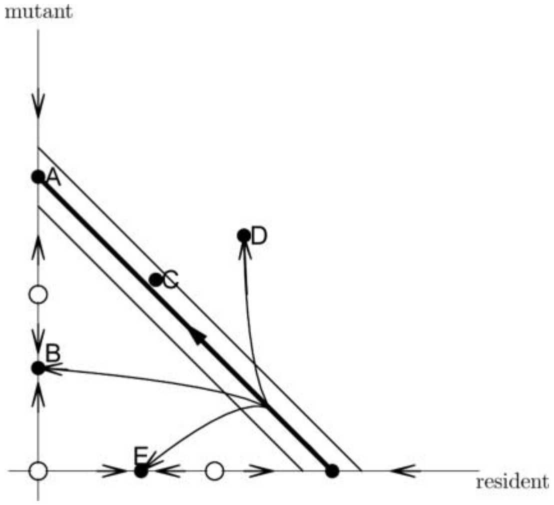

Fig. 1. There are several potential outcomes of mutant invasion (the initial increase of the mutant population) in the case of several population-dynamical attractors (solid circles). Open circles correspond to repellors of population dynamics. *Source*: Parvinen (2005).

Based on the results of Geritz *et al.* (2002), several of these possibilities can be ruled out. Under rather general conditions, according to the so-called Tube Theorem, for small mutations ($s_{\mathrm{mut}} \approx s_{\mathrm{res}}$) the resident-mutant dynamics will remain inside the tube. This rules out options B, D, and E. Furthermore, Geritz (2005) has shown that the co-existence of similar strategies is possible only when they are close to a singular strategy. For small mutations, attractor inheritance (A) is thus the general event away from specific population-dynamical bifurcations. A kamikaze-mutant essentially means attractor switching to the extinction equilibrium, which can thus only take place close to population-dynamical bifurcations, in which the present attractor disappears, or otherwise changes in a discontinuous way.

The results of Geritz *et al.* (2002) and Geritz (2005) provide the theoretical basis of why, in the definition of evolutionary suicide, it is stated that strategies first need to approach the extinction boundary. At that boundary, a population-dynamical bifurcation occurs, so that non-extinct attractors no longer exist. In general, such bifurcations can be of two different types. In a continuous transition to extinction (Fig. 2a), the population-dynamical attractor smoothly approaches an extinction equilibrium, whereas in the opposite case the transition is discontinuous (Fig. 2b).

In a continuous transition to extinction, in addition to the population density, the effect of the resident population on the environment also goes to zero (at least in well-constructed models). Therefore, at the extinction boundary, the environment corresponds to the virgin environment. In such an environment, precisely those mutants can invade that are viable in the absence of the resident, and therefore evolutionary suicide is not possible (Gyllenberg *et al.*, 2002; see also Gyllenberg and Parvinen, 2001; Webb, 2003). A discontinuous transition to extinction is therefore a necessary, but not sufficient, condition for evolutionary suicide.

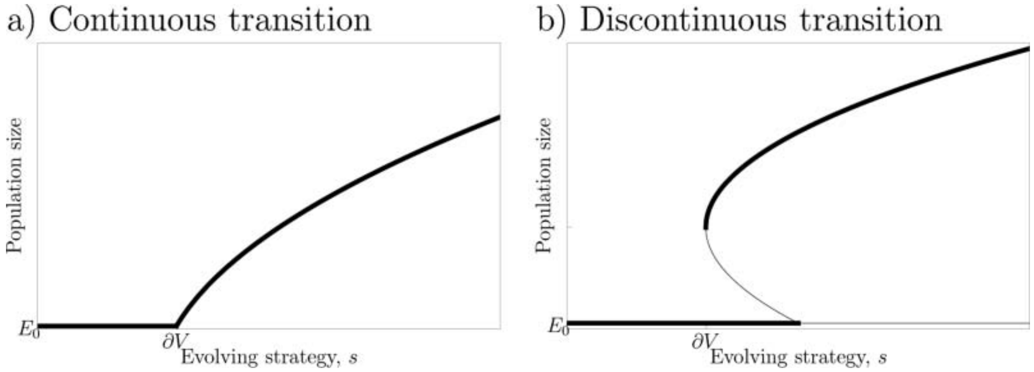

Fig. 2. At the extinction boundary ∂V, the transition to extinction can be continuous (a) or discontinuous (b). In the former case, mutants will grow as if they were in the virgin environment E_0, so that a mutant can invade if and only if it is viable, which prevents evolutionary suicide.

A DISCRETE-TIME POPULATION MODEL

First-principles derivation of the model

Following Geritz and Kisdi (2004), let $R_n(t)$ denote the resource population density, and $x_n(t)$ the consumer population density within season n at time t. In the absence of consumers, the resource population is assumed to grow according to $\dot{R}_n(t) = \alpha R_n(t) f(R_n(t))$, in which the function f is assumed to be continuous and monotonically decreasing on $(0, \infty)$ such that $\lim_{R \to 0} Rf(R)$ is finite. Furthermore, I assume that for some given positive K the function f satisfies the condition $f(R) > 0$ if $R < K$ and $f(R) < 0$ if $R > K$. Therefore, K is the unique asymptotically stable positive equilibrium density for the resource dynamics in the absence of consumers.

All consumers harvest the resource with effort β according to the law of mass action (linear functional response). Geritz and Kisdi (2004) assumed that each individual produces eggs at a rate proportional to the food intake. Here, instead, I follow the approach of Eskola and Parvinen (2007), and assume that reproduction requires two individuals, resulting in the Allee effect (Allee *et al.*, 1949). The Allee effect is one mechanism that can result in a discontinuous transition to extinction at the extinction boundary (Fig. 2b). At the beginning of each season, all consumers are individual adults U, which search for mates at rate c in order to form a pair P. Pairs produce eggs (the species is assumed to be isogamous) at a per capita rate proportional to the food intake. I use $E_n(t)$ to denote the density of eggs accumulated since the beginning of the reproductive season. Overall, the following differential equations for the within-year dynamics are obtained:

$$\begin{aligned}
&\dot{R}_n(t) = \alpha R_n(t) f(R_n(t)) - R_n(t)\beta\overbrace{(U_n(t) + 2P_n(t))}^{x_n(t) = x_n(0)} && \\
&\dot{E}_n(t) = \gamma P_n(t)\beta R_n(t), && E_n(0) = 0 \qquad (2)\\
&\dot{U}_n(t) = -cU_n(t)^2, && U_n(0) = x_n(0)\\
&\dot{P}_n(t) = \tfrac{1}{2}cU_n(t)^2, && P_n(0) = 0
\end{aligned}$$

All adults die at the end of the season (time $t = 1$). Those eggs that survive to the next season and hatch, which happens with probability σ, constitute the population in the beginning of the next season.

I assume that resource dynamics is fast, so that it is always in the stable quasi-equilibrium $\hat{R}_n(t)$:

$$\hat{R}_n(t) = \begin{cases} f^{-1}\left(\frac{\beta}{\alpha} x_n(t)\right) & \text{if } 0 \leq x_n(t) \leq x^* \\ 0 & \text{if } x_n(t) > x^*, \end{cases} \tag{3}$$

where $x^* = \frac{\alpha}{\beta} \lim_{R \to 0} f(R)$. Since there is no within-season mortality, the equality $x_n(t) = U_n(t) + 2P_n(t) = U_n(0) = x_n(0)$ holds, and thus $\hat{R}_n(t) = \hat{R}_n(0)$ throughout the season. The solution of the differential equations for $U_n(t)$ and $P_n(t)$ is

$$U_n(t) = \frac{x_n(0)}{1 + cx_n(0)t} \quad \text{and} \quad P_n(t) = \frac{\frac{1}{2}cx_n(0)^2 t}{1 + cx_n(0)t}. \tag{4}$$

Now the right-hand side of the differential equation for egg density is known, and the solution is obtained by integration:

$$E_n(t) = \gamma\beta\hat{R}_n(0)\,\frac{cx_n(0)\,t - \ln(1 + cx_n(0)\,t)}{2c}. \tag{5}$$

Finally, the discrete-time population model $x_{n+1}(0) = \sigma E_n(1)$ becomes

$$x_{n+1}(0) = \begin{cases} \lambda x_n(0)\left[1 - \dfrac{1}{cx_n(0)}\ln(1 + cx_n(0))\right] f^{-1}\left(\frac{\beta}{\alpha} x_n(0)\right), & \text{if } 0 \leq x_n(0) \leq x^* \\ 0 & \text{if } x_n(0) > x^* \end{cases} \tag{6}$$

where $\lambda = \dfrac{\sigma\gamma\beta}{2}$ and $x^* = \frac{\alpha}{\beta} \lim_{R \to 0} f(R)$. See Fig. 3 for an illustration.

Population dynamics for a mutant

A mutant is an individual with different behaviour from the resident. A mutant population is initiated when a mutation occurs in a single resident individual. Therefore, the mutant population is necessarily initially rare. Consider now a rare mutant population with size y_n in the environment set by a resident population with size x_n. In this model the mutants may differ in their survival probability (σ_{mut}) and harvest effort (β_{mut}) from the resident. Unlike harvest effort, survival probability is not a direct behavioural trait, but some specific behaviour of individuals may affect the survival probability without affecting other model parameters.

Since the mutant is rare, it will not affect the resource dynamics, which thus will be at the stable quasi-equilibrium given by (3). Furthermore, almost all individual adults encountered by a mutant will be residents. Let $Y_n(t)$ be the probability that a focal mutant has not formed a (mating) pair until time t. It will satisfy the differential equation

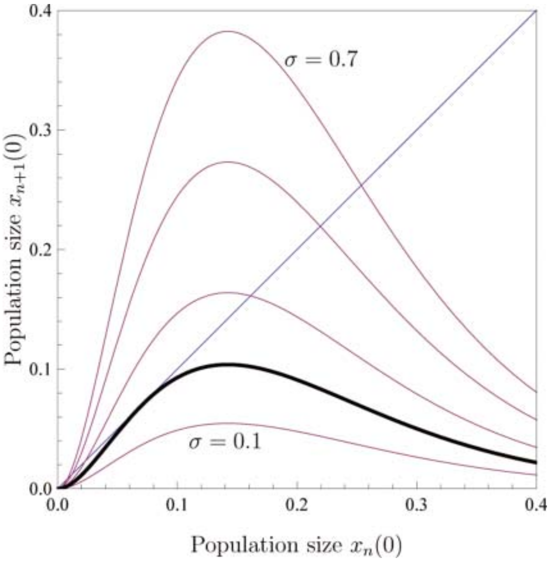

Fig. 3. Illustration of the discrete-time population model (6) for different values of σ (0.1, 0.19, 0.3, 0.5, and 0.7). Resource grows according to the Gompertz equation resulting in Ricker-type dynamics (14). Parameter values: $K = 1000$, $\gamma = 1$, $c = 0.4$, $\alpha = 1$, $\beta = 2$.

$\dot{Y}_n(t) = -c\,Y_n(t)U_n(t)$ with the initial condition $Y_n(0) = 1$ and $U_n(t)$ given by (4). This differential equation has the solution

$$Y_n(t) = \frac{1}{1 + cx_n(0)t}\cdot \tag{7}$$

The probability that a mutant has formed a (mating) pair with a resident is $1 - Y_n(t)$. Half of the offspring of such pairs are mutants. This holds true even for true sexual reproduction: since the mutant is rare, it will almost always be a heterozygote (one mutant allele, one resident allele), and the resident a homozygote (two resident alleles). In such circumstances, half of the offspring will be heterozygotes and half resident homozygotes. The expected per capita amount of mutant eggs $\tilde{E}$ produced until time t satisfies the differential equation

$$\frac{d}{dt}\tilde{E}_n(t) = \gamma\tfrac{1}{2}(1 - Y_n(t))\frac{\beta_{\mathrm{res}} + \beta_{\mathrm{mut}}}{2}\hat{R}_n(0), \quad \tilde{E}_n(0) = 0, \tag{8}$$

which has the solution

$$\tilde{E}_n(t) = \gamma\frac{\beta_{\mathrm{res}} + \beta_{\mathrm{mut}}}{2}\frac{1}{2}\left[t - \frac{1}{cx_n(0)t}\ln(1 + cx_n(0))\right]\hat{R}_n(0). \tag{9}$$

Overall, the following population dynamics for the mutant is obtained:

$$y_{n+1} = y_n\sigma_{\mathrm{mut}}\,\gamma\frac{\beta_{\mathrm{res}} + \beta_{\mathrm{mut}}}{2}\frac{1}{2}\left[1 - \frac{1}{cx_n}\ln(1 + cx_n)\right]\hat{R}_n, \tag{10}$$

in which, for simplicity, x_n is a shorthand notation for $x_n(0)$, etc.

Invasion fitness and the fitness gradient

Based on the mutant population dynamics (10), the invasion fitness for a mutant with strategy $s_{\text{mut}} = \{\sigma_{\text{mut}}, \beta_{\text{mut}}\}$ becomes

$$\begin{aligned} R(s_{\text{mut}}, E_{\text{res}}) &= \lim_{T \to \infty} \sqrt[T]{y_{T+1}/y_1} \\ &= \sigma_{\text{mut}}\, \gamma \frac{\beta_{\text{res}} + \beta_{\text{mut}}}{2} \lim_{T \to \infty} \sqrt[T]{\prod_{n=1}^{T} \frac{1}{2}\left[1 - \frac{1}{cx_n}\ln(1 + cx_n)\right] \hat{R}_n} \end{aligned} \tag{11}$$

The evolutionary analysis of (11) is straightforward. For an extant resident, $R(s_{\text{res}}, E_{\text{res}}) = 1$, so that the limit of the root term must be finite and positive. Furthermore, this implies

$$R(s_{\text{mut}}, E_{\text{res}}) = \frac{\sigma_{\text{mut}}}{\sigma_{\text{res}}} \frac{\beta_{\text{res}} + \beta_{\text{mut}}}{2\beta_{\text{res}}}. \tag{12}$$

Therefore,

$$\begin{aligned} \frac{\partial}{\partial \sigma_{\text{mut}}} R(s_{\text{mut}}, E_{\text{res}})\bigg|_{s_{\text{mut}} = s_{\text{res}}} &= \frac{1}{\sigma_{\text{res}}} > 0 \\ \frac{\partial}{\partial \beta_{\text{mut}}} R(s_{\text{mut}}, E_{\text{res}})\bigg|_{s_{\text{mut}} = s_{\text{res}}} &= \frac{1}{2\beta_{\text{res}}} > 0, \end{aligned} \tag{13}$$

and thus both strategy components are expected to increase by natural selection for any resource growth function.

This result is not surprising, since mutants with higher survival probability will naturally have on average more surviving offspring than residents will. Furthermore, a mutant with higher harvest effort will produce more offspring than a resident, and the diminishing effect to resources will be observed only after the mutant is not rare anymore.

Numerical example

I will next investigate a numerical example, in which the resource is assumed to grow according to the Gompertz equation, $f(R) = 1 - \frac{\ln R}{\ln K}$ in which $K > 1$. Now $x^* = \frac{\alpha}{\beta} \lim_{R \to 0} f(R) = \infty$, and the inverse function of f is $f^{-1}(x) = Ke^{-x \ln K}$. In the Geritz and Kisdi (2004) setting, this results in the Ricker (1954) model for the consumer population, and under the assumptions used here, in a Ricker-type model (Eskola and Parvinen, 2007) for a monomorphic resident:

$$x_{n+1} = \underbrace{\frac{\sigma\gamma\beta}{2}}_{=\lambda} \left[x_n - \frac{1}{c}\ln(1 + cx_n)\right] Ke^{-\frac{\beta}{\alpha} x_n \ln K}. \tag{14}$$

Parvinen and Dieckmann (2013) showed in a similar kind of model, $x_{n+1} = \lambda x_n^2 e^{-kx_n}$, that if the compound parameter λ increases because of natural selection, the type of the non-extinct population dynamical attractor can change from an equilibrium to a cycle, and further to chaos. Furthermore, the chaotic attractor can collide with an unstable equilibrium, beyond which the population is no longer viable, resulting in evolutionary suicide (see their figure 3). Parvinen and Dieckmann (2013) did not specify which individual-level trait they considered to affect the compound parameter λ. Here, the survival probability σ affects the compound parameter λ, and that alone. Figure 4a shows the above-described pattern in population dynamics, and thus selection for increasing σ results in evolutionary suicide in this case.

Also, harvest effort β affects the compound parameter λ. By increasing β, each individual will receive more resources, if the amount of resources were to remain the same, but when all individuals harvest more intensively, the quasi-equilibrium $\hat{R}_n(0)$ of the resource will decrease. Since β affects other parts of the model as well as λ (14), the effect of β on population dynamics can be expected to be different from that observed in Fig. 4a. Indeed, in the case illustrated in Fig. 4b, parameter β does not qualitatively affect the population dynamics: the positive population-dynamical attractor is a two-cyclic orbit (at least for all values of β shown), so evolutionary suicide, contrary to the case of evolving σ, is not expected to occur. Instead, the population size will decline until it is so small that stochastic events will cause extinction ['runaway selection to self-extinction' (Matsuda and Abrams, 1994a)].

This observation can be further analysed as follows. When x_n is small, $x_n - \frac{1}{c}\ln(1 + cx_n) = c\frac{1}{2}x_n^2 + O(x_n^3)$, and thus (14) becomes approximately

$$x_{n+1} = \frac{\sigma\gamma\beta}{4} x_n^2 K e^{-\frac{\beta}{\alpha} x_n \ln K}, \tag{15}$$

so that by denoting $z_n = \beta x_n$, for the scaled variable the following equation holds:

$$z_{n+1} = \frac{\sigma\gamma}{4} z_n^2 K e^{-\frac{1}{\alpha} z_n \ln K}, \tag{16}$$

which does not depend on β. This means that the parameter β is only a scaling factor, and has no qualitative effect on the dynamics, when x_n is small. The same result applies for any resource growth function.

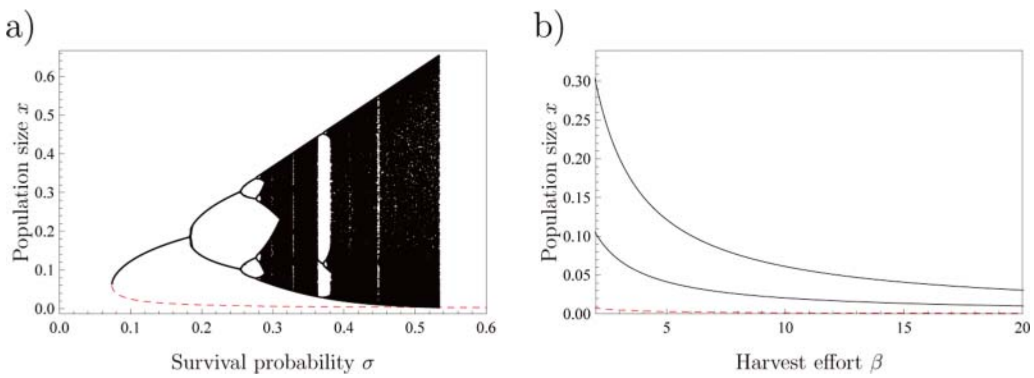

Fig. 4. Population-dynamical attractors (black points) of the model (14) as a function of (a) survival probability σ and (b) harvest effort β. The dashed curve illustrates an unstable equilibrium. Common parameter values: $K = 3000$, $\gamma = 1$, $c = 0.4$, $\alpha = 1$. Panel (a) $\beta = 2$, (b) $\sigma = 0.25$.

Trade-off between harvesting effort and survival probability

It is possible that survival probability σ and harvest effort β do not evolve independently. There can thus be a trade-off between the strategy components. Consider the case $\beta = h(\sigma)$, where h is a decreasing, non-negative function. In this case, the fitness gradient (13) becomes

$$\frac{\partial}{\partial \sigma_{\text{mut}}} R(s_{\text{mut}}, E_{\text{res}}) \bigg|_{s_{\text{mut}} = s_{\text{res}}} = \frac{1}{\sigma_{\text{res}}} + h'(\sigma_{\text{res}}) \frac{1}{2h(\sigma_{\text{res}})} \cdot \tag{17}$$

The benefit of increased survival probability σ comes with a cost in the form of reduced harvest effort. If this cost is strong enough, the fitness gradient may become negative. This occurs if

$$\frac{h'\,(\sigma_{\text{res}})}{h(\sigma_{\text{res}})} < -\frac{2}{\sigma_{\text{res}}}. \tag{18}$$

For example, trade-off functions of the form $h(\sigma) = \theta\sigma^{-\xi}$ satisfy this condition, when $\xi > 2$. In that case, selection will cause σ to decrease. However, the population is not viable when σ is too low, and evolutionary suicide occurs. For low σ, the transition to extinction is caused by the collision and disappearance of a stable equilibrium and an unstable equilibrium (see, for example, Fig. 4a, which is qualitatively correct even in the presence of the trade-off).

In conclusion, by choosing different mechanisms affecting the compound parameter λ, qualitatively different scenarios, both in an ecological and evolutionary sense, can be obtained. This observation supports the premise that evolutionary predictions should be based on individual-level traits (Rueffler *et al.*, 2006).

DISCUSSION

Evolutionary suicide has been found in models describing many different situations, including dispersal in metapopulations, cooperation, asymmetric competition, and resource use. [See, for example, Parvinen (2005), Rankin and López-Sepulcre (2005), and Parvinen and Dieckmann (in press) for reviews, and Fiegna and Velicer (2003) for an experiment in which it is observed.]

In those metapopulation models in which evolution of dispersal has been shown to result in evolutionary suicide (Cadet, 1998; Gyllenberg *et al.*, 2002; Parvinen, 2007), dispersal typically evolves to be too infrequent for the metapopulation to be viable. In that case, there is not enough immigration for the population size in sparsely populated patches to reach sustainable sizes. Such a metapopulation-level Allee effect can be caused, for example, by demographic stochasticity, by an Allee effect in local growth in patches, or by catastrophe rates decreasing with the local population size. In the observed cases, by dispersing less, a mutant may better take advantage of good local growth conditions. Eventually this results in the collapse of the metapopulation.

Cooperation can also be considered as a quantitative trait (e.g. Doebeli *et al.*, 2004). The conflict between population-level benefits of cooperation and individual-level benefits of defection is well known, and evolution against cooperation can result in evolutionary suicide (Parvinen, 2010, 2011).

The conflict between individual- and population-level benefits can be present also in asymmetric competition models. By behaving more aggressively or by becoming bigger, for example, one can perform better than others, but this can have negative effects on the population (Matsuda and Abrams, 1994a; Gyllenberg and Parvinen, 2001). Analogous effects can be observed in some resource-consumer models. For an individual, it may be beneficial to harvest the resource more intensively, but this may result in the collapse of the resource, and extinction of the evolving consumer population (Matsuda and Abrams, 1994b; Parvinen and Dieckmann, 2013).

Here, a discrete-time population model of type

$$x_{n+1} = \lambda x_n z(x_n) f^{-1}(kx_n), \qquad \text{where } z(x_n) = \left[1 - \frac{1}{cx_n}\ln(1 + cx_n)\right] \tag{19}$$

derived from a continuous-time resource-consumer model has been investigated. When the compound parameter λ is increased, the population dynamics experiences a period-doubling cascade to chaos, after which the chaotic attractor collides with an unstable equilibrium, beyond which the population is no longer viable. As illustrated by Parvinen and Dieckmann (2013) for this kind of model (with $z(x_n) = x_n$), if some mechanism affects the compound parameter λ only, evolution for increasing λ can cause evolutionary suicide. In this article, I have addressed the mechanistic underpinning in detail. If an individual-level trait directly affects the overwinter survival probability of eggs, the above-described process is indeed expected to occur. However, although the harvest effort of consumers does affect λ, it affects also other compound parameters of the model (k), so that for values of λ large enough, the harvest effort becomes essentially a scaling factor for the model without qualitatively affecting its dynamics. Instead of a sudden collapse of the population, it gradually decreases, so that eventually demographic stochasticity will cause the extinction of the evolving population. Note, however, that such demographic stochasticity is not explicitly included in the model. In conclusion, different individual-level traits can have different effects on population-level parameters, so that ecological scenarios and evolutionary predictions differ.

Morris *et al.* (2016) performed experiments on meadow voles, and investigated a related asymmetric competition model. In their model, when experiencing identical resource levels, despotic individuals have better productivity than individuals using resources according to the ideal-free distribution. Despotic behaviour can thus be selected for, but can also cause population sizes occasionally to be dangerously low, so that demographic stochasticity may cause extinction. By adding a threshold population density below which population extinction is assumed to be certain, extinction can be observed in finite time.

Many species that once lived on Earth have gone extinct. Potential explanations include dramatic changes in the environment, to which the species has not been able to adapt. Evolutionary suicide provides a potential explanation for species extinctions, but is of a very different type: by not evolving, the species could persist, but natural selection itself causes extinction. Understanding the possibility for such processes may help to prevent species extinctions in the future.

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