When Does Evolution Optimize?
On the relationship between evolutionary stability, optimization and density dependence

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1 Introduction

Many basic principles in ecology and life-history theory are derived from the maximization of ‘fitness’. The two measures of fitness, or optimization criteria, that are most widely used for his purpose, are the population growth rate, r_0, and the basic reproduction number, R_0. r_0 Is also called the intrinsic rate of natural increase, or the Malthusian parameter, and is defined as the exponential population growth rate on a continuous time basis. R_0 is also known as the expected life-time production of offspring, and is defined as the multiplicative population growth rate on a discrete, generation basis. (See, *e.g.*, Roughgarden 1979; Yodzis 1989; Diekmann *et al.* 1990.) Other possible fitness measures include reproductive value v, minimum required resource level, carrying capacity, and several others (see Caswell, 1989; Roff, 1992; Stearns, 1992; Charlesworth, 1994, and the references therein).

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However, results may differ, depending on which fitness measure is used. For example, the prediction of reaction norms for age and size at maturity depends on whether R_0 (Stearns & Koella, 1986) or r_0 (Kozłowski & Wiegert, 1987) is used as a fitness measure. The question which function is the Holy Grail of fitness measures has led to much discussion (see Roff, 1992; Stearns, 1992; Charnov, 1993; Kozłowski, 1993, for an overview).

The problem boils down to the fact that the role of the environment is missing in this discussion. Fitness necessarily depends both on the individual trait value and on the environment perceived by the individual, whereas fitness measures, used as optimization criteria, are functions of only one variable, the trait. Evolutionarily stable strategies (ESS's, or non-invasible strategies; see Maynard Smith & Price, 1973; Maynard Smith, 1982; Eshel, 1996) can very well be characterized by an optimization criterion, but this is restricted to the environment set by the resident phenotype. Only under very special conditions, there exist stand-in fitness measures (not to be confused with fitness itself) that are maximized by evolution, independent of the environment (Michod, 1979; Mylius & Diekmann, 1995; Pásztor *et al.*, 1996).

We start our argumentation with a general definition of fitness, derived from invasion analysis. Then we survey the relationship between evolutionarily stable strategies and optimization criteria. It turns out that the population dynamical embedding, in particular density dependence, plays a crucial role in shaping this relationship.

Our analysis leads to the derivation of necessary and sufficient conditions for the special case that the eventual outcome of the evolutionary process is characterizable by some optimization principle. In (still more) special cases, such a principle happens to reduce to maximization of r_0 or R_0. We use these results to analyse an example, showing that the details of the population dynamical embedding may influence evolutionary predictions to an unexpected extent. Finally, we survey the relationship between optimization principles and the shape of pairwise invasibility plots (PIPs).

2 Setting the stage

We characterize individuals by their type X, which can be a vector consisting of several variables. X is a member of the set of all individual strategies $\mathbb{X}$. Depending on whether one is interested in taxonomy, life-history theory, or (behavioural) ecology, one can imagine X as one or more trait values, life-history variables, or behavioural strategies, specifying all relevant aspects in which individuals may differ. Unless stated otherwise, we will assume that the population is *monomorphic*: *i.e.*, all individuals have the same trait value. The world in which they live is fully characterized by an (also possibly multi-dimensional) *environment* E. The only constraint we put on the environment is that it should be *ergodic*. This is a technical condition which in practice amounts to the absence of long-lasting trends. We denote the set of all possible environments by $\mathbb{E}$.

Ecological embedding

We assume that there exists a population-dynamical feedback loop, such that the population affects the environment and, in its turn, the environment influences population dynamics. The exact nature of the population-dynamical feedback loop depends on the ecology, but one can think of crowding or food availability as possible mechanisms. Due to the feedback loop between a population of individuals of type X and the environment, the population density as well as the environment converge to some *attractor*. We confine our considerations to environments that can occur as an attractor for some X, which we denote as $E_{\text{attr}}(X)$. (Notice that we do not need to explicitly consider the non-biotic and other components of the environment that are not dynamically coupled to the trait under study.)

Often, it is useful to consider a special, fixed environment as *reference environment*. As a special case of a reference environment, one can imagine the *virgin environment*, which corresponds to the situation where individual organisms experience no effect (yet) from the presence of other individuals. For example, studying the evolution of parasitoid virulence in a host-parasitoid model, the virgin environment for parasitoid individuals would encompass the host population undepressed by parasitoid influence. We refer to the virgin environment as E_{V}.

In the following, we will use the phrase *eco-evolutionary model* to describe combinations of life history, ecological embedding, and a trait under the force of evolution.

Fitness

Our evolutionary argument is based upon the following fitness concept: Consider a thought experiment, in which we let a clone of type X grow in a constant environment E. We define *fitness*, denoted by $\rho(X,E)$, as the hypothetical average rate of exponential growth of the clone

$$\rho(X,E) \;:=\; \lim_{t\to\infty} \frac{\ln[N(t)]}{t}\,, \tag{1}$$

where $N(t)$ is the overall size of the clone at time t. (See Charlesworth 1980, 1994; Caswell 1989; Tuljapurkar 1989, 1990; Metz *et al.* 1992; Rand *et al.* 1994; Ferrière & Gatto 1995; Metz *et al.* 1996[a].) Notice that this definition, and we emphasize this by writing $\rho(X,E)$ as a function of two variables, expresses that fitness necessarily depends both on the type X of the clone and the environment E in which it supposedly lives (see also Michod, 1979; Pásztor, 1988; Metz *et al.*, 1992; Diekmann & Metz, 1994; Mylius & Diekmann, 1995; Geritz *et al.*, 1997).

As a special case, we have

$$\text{in constant environments} \qquad \rho(X,E) \;=\; r(X,E)\,, \tag{2}$$

where r is the exponential growth rate (see, *e.g.*, Roughgarden, 1979; Yodzis, 1989). For later reference we note that on a population dynamical attractor corresponding to trait value (or strategy parameter) X, necessarily

$$\rho(X,E_{\text{attr}}(X)) \;=\; 0 \tag{3}$$

because on average no growth occurs; in constant environments, the population is in steady state.

Note that $\rho(X,E)$ [from (1)] is the fundamental concept of fitness. The performance of any optimization criterion, *i.e.* a function of X, purportedly maximized by evolution, has to be judged relative to its capability to predict the evolutionary endpoints calculated from a complete invasibility analysis, based on ρ.

Evolutionary invasibility and attainability

The trait values $\hat{X}$, brought forth by evolution, should be non-invasible as well as attainable. The first adjective expresses that $\hat{X}$ is an evolutionary trap in the sense that if $\hat{X}$ is adopted by the whole population, any invasion by individuals with a different strategy will fail. This is equivalent to the definition of an *Evolutionarily Stable Strategy* (ESS; see Maynard Smith & Price, 1973; Maynard Smith, 1982). An ESS corresponds to an equilibrium point (or singular point) of the adaptive dynamics, but despite the tempting "Stable" in its name it is not necessarily an attractor of the adaptive dynamics. The second adjective, 'attainable', is to ascertain that $\hat{X}$ is an attractor; that is, there should exist evolutionary pathways leading to the ESS. These pathways one can imagine as all feasible sequences of strategies, with each strategy invasible by its successor, and the non-invasible $\hat{X}$ as the final, absorbing one.

In the special case of a one-dimensional trait space, the attainability condition is to require that, in a population of individuals with trait value x' which is slightly different from $\hat{x}$, local mutants on the $\hat{x}$ side be more fit and local mutants on the non-$\hat{x}$ side be less fit than $\hat{x}$-individuals.

The problem of attraction or attainability as an incompleteness in the definition of an ESS, and the resulting need for further classification was recognized early (*e.g.* Eshel & Motro, 1981; Eshel, 1983; Taylor, 1989), but has never really pervaded the evolutionary biological literature. (See also Lessard 1990; Eshel 1996; Metz *et al.* 1996^b; Geritz *et al.* 1997, 1998; Geritz & Kisdi to appear.)

Depending on the context, we will use the names *non-invasible strategy* (which is the name we prefer because it is an exact description of the concept) as well as 'ESS' (for historical reasons) and 'evolutionarily stable life history' (when we are dealing with life-history problems), and indicate non-invasible trait values by an asterisk (*). Non-invasible strategies or trait values that are also attainable we will generally refer to as *evolutionary stops*, in the spirit of the "streetcar theory of evolution" metaphor put forward by Hammerstein & Selten (1994) and Hammerstein (1996). We will indicate variables corresponding to an evolutionary stop by a hat ($\hat{}$). Notice that for the historical reasons mentioned above, we have to refrain from using the adjective 'stable' for the last category because this has been used already for what we call non-invasible strategies (ESS's). This is especially unfortunate from a mathematical point of view because in dynamical systems theory, a singular point which combines non-invasibility and attainability would be called a 'stable equilibrium'.

Notice that we unscrupulously sweep all genetic constraints under the carpet, which is only partially defendable (see, *e.g.*, Liberman, 1988; Hammerstein & Selten, 1994; Hammerstein, 1996; Weissing, 1996; Matessi & Di Pasquale, 1996).

We define the evolutionary stops by the following algorithm:

I. Determine for each trait value X the environment which it generates as a resident, $E_{\text{attr}}(X)$;

II. Maximize, for each possible environment, the fitness $\rho(X, E)$ over all trait values X, resulting in a function $X_{\mathrm{opt}}(E)$;

III. The set of non-invasible strategies is now given by all X for which the following equation holds:

$$X_{\mathrm{opt}}(E_{\mathrm{attr}}(X)) \;=\; X\,; \tag{4}$$

IV. To ascertain attainability, verify that the set of trait values X_0 from which $\hat{X}$ is approximated with positive probability through a sequence $X_0, X_1, \ldots, \hat{X}$, such that $\rho(X_{i+1}, E_{\mathrm{attr}}(X_i)) > 0$, is sufficiently large.

This may not be the most practical way to find evolutionary stops. Especially step IV (where genetic constraints make themselves felt) is troublesome and therefore often ignored. However, this way of defining them will prove to be useful in the next sections.

3 Optimization principles

A posteriori optimization criteria

Consider any eco-evolutionary model. If X^* is an ESS, it follows directly from the definition of non-invasibility that

$$\rho(X, E_{\mathrm{attr}}(X^*)) \;<\; 0 \qquad \text{for all } X \neq X^* \tag{5}$$

or, in words, all trait values different from the ESS value have negative fitness in the environment that is set by the ESS value. Because $\rho(X^*, E_{\mathrm{attr}}(X^*)) = 0$ this means that the function $X \mapsto \rho(X, E_{\mathrm{attr}}(X^*))$ has a maximum at X^*. [We use the notation '$x \mapsto f(x, y)$' to indicate that we temporarily consider f as a function of one variable, x, and keep y fixed.] Hence, we can conclude that if X^* is a non-invasible strategy, then the function

$$X \;\mapsto\; \rho(X, E_{\mathrm{attr}}(X^*)) \tag{6}$$

is an optimization criterion.

It is very important to realize that (5) does generally not hold for other values of the environment than $E_{\mathrm{attr}}(X^*)$. Only in an environment characterized by a population dynamical attractor that is set by an evolutionarily stable resident, it is necessarily the case that fitness is zero for the resident clone and less than zero for all others. This restriction makes the optimization criterion (6) only useful with the hindsight that X^* is indeed an ESS. Hence, we call (5) an *a posteriori* optimization criterion. If we do not know the ESS value X^* then we cannot determine the proper environmental condition $E_{\mathrm{attr}}(X^*)$. On the other hand, as soon as we know the ESS, and the corresponding environmental condition, we can construct arbitrary optimization criteria: any function of the strategy set $\mathbb{X}$ to the real numbers $\mathbb{R}$ which has a maximum at X^* will do the job.

Fitness measures

From the discussion about *a posteriori* optimization criteria, we may conclude that we should concentrate on optimization criteria that are independent of that part of the environmental condition that corresponds to the population dynamical attractor produced by the resident population. That is, we want to address the question:

> *Can we find a function of the trait, which allows us to determine which trait value has the highest fitness, independent of the choice of the environment?*

We define a *fitness measure* as a function ξ of the strategy set $\mathbb{X}$ to the real numbers $\mathbb{R}$, which allows us to determine which trait value has higher fitness, independent of the choice of the environment, in the sense that $\xi(X_1) > \xi(X_2)$ implies $\rho(X_1, E_0) > \rho(X_2, E_0)$ for all $E_0 \in \mathbb{E}$.

If there is a unique trait value (say $\hat{X}$) maximizing ξ, independent of E, then it will surely outperform all others when it is a resident (*i.e.*, in the environment set by itself), and hence it will be an ESS. In addition, if another trait value X' that is not too different from $\hat{X}$ is adopted by the population (and provided the fitness function satisfies some continuity properties; see, *e.g.*, Taylor 1989; Geritz *et al.* 1997) then clones with trait values closer to $\hat{X}$ will be able to invade whereas clones with trait values more different from $\hat{X}$ than X' will die out after an invasion attempt. So at least locally $\hat{X}$ is also an attractor of the adaptive dynamics. More precisely: ξ acts as a Lyapunov function for any adaptive dynamics on the trait space. (A Lyapunov function, for a dynamical system on a state space $\mathbb{X}$, is a function $L : \mathbb{X} \to \mathbb{R}$, which can be interpreted as a contour map of the state space. The evolution of the system can then be described as a steady uphill movement, and the final state of the system can be found by maximizing L.) Those adaptive dynamics can still differ with respect to the production of mutants. If the probability that a mutant ends up in a set $\{ X \in \mathbb{X} \mid |\xi(X) - \xi(\hat{X})| < \varepsilon \}$ is positive for all ε and all parents X close enough to $\hat{X}$, then $\hat{X}$ is an attractor of the adaptive dynamics. If this probability is positive for all parents X then $\hat{X}$ attracts globally.

If we know the ecological conditions for the existence of fitness measures, and we have an algorithm to find them, we can circumvent the complicated procedure I–IV and calculate ESS's by simply maximizing appropriate fitness measures, at least in all cases where those conditions are fulfilled.

We feel that the above definition of a fitness measure is the explication of the intuitive meaning people give to that term. However, as it turns out this definition is stronger than needed: What really matters is (i) whether we are able to calculate the ESS by optimizing some function ξ, and, preferably but not necessarily, (ii) whether ξ also is a Lyapunov function of the adaptive dynamics for the eco-evolutionary models under consideration.

A priori optimization- and pessimization principles

An *optimization principle* for an eco-evolutionary model is a function $\xi : \mathbb{X} \to \mathbb{R}$ with the property that the ESS can be calculated by maximizing $\xi(X)$, for all possible constraints on $\mathbb{X}$. And a *pessimization principle* or *Verelendungs principle* we define analogously as: a function $\eta : \mathbb{E} \to \mathbb{R}$ with the property that the ESS can be calculated by minimizing $\eta(E_{\text{attr}}(X))$, for all possible constraints on $\mathbb{X}$.

The rationale behind those definitions derives from the following observation: In the literature, putative optimization (or pessimization) principles are generally introduced before the trait space, or, more frequently, before the constraints on that space are introduced. Such a procedure only makes sense under the implicit assumption that the principle under consideration is independent of the particular choice of trait space and constraints. (The rules of logic tell us that a general statement about some proposition with a free variable in it, in this case the unspecified domain of the function ξ, should always be interpreted as if it were preceded by the universal quantor: 'for all possible values of that variable'.)

Being an optimization principle is a weaker property than being a fitness measure. A fitness measure allows the comparison of two trait values for any possible environment, whereas an optimization principle only allows the comparison of two trait values on their corresponding environments. To see this, just constrain the trait space to two values: $\{X_1, X_2\}$. In that case, $\xi(X_1) > \xi(X_2)$ means that X_1 is the ESS, which is the case if and only if $\rho(X_2, E_{\text{attr}}(X_1)) < 0$, and X_2 is not an ESS, which is the case if and only if $\rho(X_1, E_{\text{attr}}(X_2)) > 0$.

The last statement also tells us that, biologically, an optimization principle is a one-dimensional measure which tells for any pair of trait values who will win in an invasion contest. Therefore, if an optimization principle exists, it also acts as a Lyapunov function for any adaptive dynamics on the eco-evolutionary model.

[Only one optimization principle known to us from the literature does not satisfy the above comparison property. This exception is the MacArthur product rule from sex-ratio theory: $\xi(X) = f(X)\,m(X)$, with f and m the basic female and male fitnesses (see Charnov, 1982). This principle only allows calculating the ESS for constraints corresponding to *convex* sets in the (f, m)-plane. MacArthur's ξ is not a Lyapunov function either: X_1 and X_2 may be mutually invasible, even when $\xi(X_2) > \xi(X_1)$. This happens if, on the straight line connecting $(f(X_1), m(X_1))$ and $(f(X_2), m(X_2))$ in the (f, m)-plane, there are values of fm larger than $\xi(X_2)$.]

A pessimization principle η can be interpreted as an ecological measure of the quality of the environment as perceived by the individuals: If $\eta(E_{\text{attr}}(X_1)) > \eta(E_{\text{attr}}(X_2))$ then $\rho(X_2, E_{\text{attr}}(X_1)) > 0$, while by definition $\rho(X_2, E_{\text{attr}}(X_2)) = 0$. That is, X_2 perceives $E_{\text{attr}}(X_1)$ as better than $E_{\text{attr}}(X_2)$. The same holds for X_1, since $\rho(X_1, E_{\text{attr}}(X_1)) = 0$, while the η-inequality tells that $\rho(X_1, E_{\text{attr}}(X_2)) < 0$.

Remains to find necessary and sufficient conditions telling when an eco-evolutionary model will allow an optimization- or a pessimization principle.

One-dimensional action

The crucial condition for the existence of fitness measures as well as optimization- and pessimization principles is that the trait or the environment works in a so-called one-dimensional manner. Before defining this precisely, we shall give a simple example.

Box 1 Example 0

Assume that the environment is really one-dimensional and can be represented as a linearly ordered set, like (a subset of) the real numbers $\mathbb{R}$, and the ecological dynamics converges to a point equilibrium. Additionally, suppose that fitness $\rho(X, E)$ is monotonic, say increasing, in its second argument. Imagine, as a biological example, that we are interested in predator evolution, and the environmental variable is prey density. In this case, E_{attr} is completely specified by the equation $\rho(X, E_{\mathrm{attr}}(X)) = 0$ because the monotonicity of $E \mapsto \rho(X, E)$ guarantees that this equation has only one solution.

Now it is easy to see that X^* is an ESS if, and only if, $E_{\mathrm{attr}}(X)$ has its minimum at X^*. First consider the case that $E_{\mathrm{attr}}(X)$ is minimal at X^*. Then we have by definition

$$E_{\mathrm{attr}}(X^*) \quad < \quad E_{\mathrm{attr}}(X) \qquad \text{for all } X \neq X^* \tag{7}$$

and consequently, because $\rho(X, E)$ is supposed to be increasing in its second argument,

$$\rho(X, E_{\mathrm{attr}}(X^*)) \quad < \quad \rho(X, E_{\mathrm{attr}}(X)) \quad = \quad 0 \qquad \text{for all } X \neq X^* \,. \tag{8}$$

Hence in this case X^* is an ESS. On the other hand, if $E_{\mathrm{attr}}(X)$ is not minimal at X^* then there is some X' such that $E_{\mathrm{attr}}(X^*) > E_{\mathrm{attr}}(X')$ from which we conclude that

$$\rho(X', E_{\mathrm{attr}}(X^*)) \quad > \quad \rho(X', E_{\mathrm{attr}}(X')) \quad = \quad 0 \,. \tag{9}$$

Hence X^* is invasible by X' and we conclude that in this case X^* is not an ESS.

If $E \mapsto \rho(X, E)$ is not increasing but decreasing then exactly the same argument applies, but with 'minimum' replaced by 'maximum' and the corresponding inequalities reversed.

The conclusion we may draw from example 1 is that if $E_{\mathrm{attr}}(X)$ can be parameterized one-dimensionally and fitness is monotonic in that parameter then that parameter is a pessimization principle.

When the environment is multi-dimensional there is no such thing as monotonicity of fitness in its environmental argument, because monotonicity of a function is only defined in relation to a one-dimensional argument. However, when the effect of the environment (or the trait) on fitness is such that we can map $\mathbb{E}$ (or $\mathbb{X}$) onto some one-dimensional set, and if fitness is increasing or decreasing on this set, we can still with some right say that the environment (or the trait) acts in a one-dimensional way. With this picture in mind, we now generalize the one-dimensional action from the previous example to multi-dimensional environments and trait vectors.

We say that a *trait acts strictly one-dimensionally* whenever there exists a function $\xi : \mathbb{X} \to \mathbb{R}$ as well as a function $\mathcal{X} : \mathbb{R} \times \mathbb{E} \to \mathbb{R}$ which increases in its first argument, such that

$$\rho(X, E) \quad = \quad \mathcal{X}(\xi(X), E) \,. \tag{10}$$

Analogously, we say that the *environment acts strictly one-dimensionally* whenever there exists a function $\eta : \mathbb{E} \to \mathbb{R}$ and a function $\mathcal{E} : \mathbb{X} \times \mathbb{R} \to \mathbb{R}$ which increases in its second argument, such that

$$\rho(X,E) \;=\; \mathcal{E}(X,\eta(E))\;. \tag{11}$$

However, if we are just hunting for optimization- or pessimization principles, then we can be less strict: Because the invasion success of a rare mutant is determined solely by the question whether the mutant fitness is positive or negative, it is sufficient to find mappings ξ or η that preserve the *sign* of $\rho(X,E)$.

We say that the *trait acts one-dimensionally* (this is just an abbreviation; the more precise expression would be 'qualitatively or weakly one-dimensionally') whenever there exists a function $\xi : \mathbb{X} \to \mathbb{R}$ as well as a function $\mathcal{X} : \mathbb{R} \times \mathbb{E} \to \mathbb{R}$ which increases in its first argument, such that

$$\operatorname{sign}\Big[\,\rho(X,E)\,\Big] \;=\; \operatorname{sign}\Big[\,\mathcal{X}(\xi(X),E)\,\Big]\;. \tag{12}$$

Analogously, we say that the *environment acts one-dimensionally* whenever there exists a function $\eta : \mathbb{E} \to \mathbb{R}$ and a function $\mathcal{E} : \mathbb{X} \times \mathbb{R} \to \mathbb{R}$ which increases in its second argument, such that

$$\operatorname{sign}\Big[\,\rho(X,E)\,\Big] \;=\; \operatorname{sign}\Big[\,\mathcal{E}(X,\eta(E))\,\Big]\;. \tag{13}$$

Because the definitions of one-dimensional action may sound rather abstract, we first represent the maps in a diagram and then illustrate them with two examples.

$$\begin{tikzcd}
 & \mathbb{R}\times\mathbb{E} \arrow[r, dotted, "\mathcal{X}"] & \mathbb{R} \arrow[ddr, dotted, "\mathrm{sign}"] & \\
\text{if the \textit{trait} acts one-dimensionally:} & & & \\
 & \mathbb{X}\times\mathbb{E} \arrow[uu, dotted, "{(\xi,I)}"] \arrow[dd, dotted, "{(I,\eta)}"'] \arrow[r, "\rho"] & \mathbb{R} \arrow[r, "\mathrm{sign}"] & \{-,0,+\} \\
\text{if the \textit{environment} acts one-dimensionally:} & & & \\
 & \mathbb{X}\times\mathbb{R} \arrow[r, dotted, "\mathcal{E}"] & \mathbb{R} \arrow[uur, dotted, "\mathrm{sign}"'] &
\end{tikzcd} \tag{14}$$

where I is the identity map.

Box 2 Example 1

Imagine an eco-evolutionary model in which population dynamics converges to a steady state. Then the expected life-time production of offspring, $R(X,E)$, is defined (see, *e.g.*, Roughgarden, 1979; Yodzis, 1989; Diekmann *et al.*, 1990).

Suppose that environmental deterioration reduces life-time reproductive success by an E-dependent multiplication factor θ. (See also example 5.) Then we can write

$$R(X,E) \;=\; R_{\mathrm{V}}(X)\cdot\theta(E)\;, \tag{15}$$

where $R_{\mathrm{V}}(X) := R(X,E_{\mathrm{V}})$ is the life-time reproductive success of type X in the virgin environment and $\theta(E)$ is a measure of the environmental quality with $0 \le \theta(E) \le \theta(E_{\rm V}) = 1$.

Because

$$\rho \overset{>}{\underset{<}{=}} 0 \qquad \text{if, and only if,} \qquad R \overset{>}{\underset{<}{=}} 1 \tag{16}$$

(see also section 4 below), ρ and $\ln[R]$ have equal sign structures. If we now choose

$$\begin{array}{rll} X \mapsto R_{\rm V}(X) & \text{for} & \xi : \mathbb{X} \to \mathbb{R} \\ (\xi, E) \mapsto \ln\left[\xi \cdot \theta(E)\right] & \text{for} & \mathcal{X} : \mathbb{R} \times \mathbb{E} \to \mathbb{R} \end{array} \tag{17}$$

we see that (12) is satisfied: the trait acts one-dimensionally.

Analogously, if we choose

$$\begin{array}{rll} E \mapsto \theta(E) & \text{for} & \eta : \mathbb{E} \to \mathbb{R} \\ (X, \eta) \mapsto \ln\left[R_{\rm V}(X) \cdot \eta\right] & \text{for} & \mathcal{E} : \mathbb{X} \times \mathbb{R} \to \mathbb{R} \end{array} \tag{18}$$

we see that (13) is satisfied: the environment acts one-dimensionally.

Box 3 Example 2

In this example, we allow the environment to be fluctuating, for example due to a periodic or stochastic external driver. Imagine an eco-evolutionary model with an ecological embedding, such that density dependence makes itself felt by means of an E-dependent, but otherwise constant, additional term δ to the individual death rate. Then we can write

$$\rho(X, E) \quad = \quad \rho_{\rm V}(X) - \overline{\delta(E(t))}\,, \tag{19}$$

where $\rho_{\rm V}(X) := \rho(X, E_{\rm V})$ is the long-term average growth rate of type X in the virgin (*i.e.*, the best possible) environment. $\overline{\delta(E(t))}$ Is the average of $\delta(E(t))$ over time, which can be interpreted as a measure of the environmental deterioration at time t, with $0 = \delta(E_{\rm V}(t)) \le \delta(E(t))$. (In a constant environment, one can take $\rho(X, E) = r(X, E)$ and $\overline{\delta(E(t))} = \delta(E_{\rm attr})$.)

If we now choose

$$\begin{array}{rll} X \mapsto \rho_{\rm V}(X) & \text{for} & \xi : \mathbb{X} \to \mathbb{R} \\ (\xi, E) \mapsto \xi - \overline{\delta(E(t))} & \text{for} & \mathcal{X} : \mathbb{R} \times \mathbb{E} \to \mathbb{R} \end{array} \tag{20}$$

we see [by (12)] that the trait acts one-dimensionally.

Moreover, if we choose

$$\begin{array}{rll} E(t) \mapsto \overline{\delta(E(t))} & \text{for} & \eta : \mathbb{E} \to \mathbb{R} \\ (X, \eta) \mapsto \rho_{\rm V}(X) - \eta & \text{for} & \mathcal{E} : \mathbb{X} \times \mathbb{R} \to \mathbb{R} \end{array} \tag{21}$$

we see [by (13)] that the environment acts one-dimensionally.

One can think of the 'one-dimensional action' property as the weakest link of a chain: If the environmental feedback loop extends over several components, then the component with the lowest dimensionality sets the property for the total loop. The problem, however, is that E generally is a (measure on a set of) function(s) of time. This often makes the chain difficult to fathom.

Mylius & Diekmann (1995) have described some special ecological scenarios in which finding the ESS is equivalent to solving an optimization problem. Metz *et al.* (1996^b) have generalized and proved these special cases by providing necessary and sufficient conditions for evolution to be optimizing. We will sketch their results in the next sections.

Results

A familiar, special case of an optimization principle is: "Being more 'efficient' increases fitness in any relevant environment". Most importantly, a particular change in (a particular trait value that affects) efficiency should *always* either increase or decrease fitness: the crucial restriction in the argument, "in any relevant environment", is rarely mentioned explicitly. As a generalization of this special case we state the following results:

Result 1 (Fitness measure) *Eco-evolutionary models have a fitness measure if, and only if, the trait acts strictly one-dimensionally.*

The 'if' direction is trivially true. To prove the 'only if' we start by assuming that there exists a fitness measure ξ. First we observe that $\rho(X_2, E) = \rho(X_1, E)$ for all E whenever $\xi(X_2) = \xi(X_1)$. Therefore we can just define $\mathcal{X}(\xi, E) = \rho(X_1, E)$.

Optimization principles are a natural generalization of fitness measures. The corresponding characterization is given by:

Result 2 (Optimization principle) *Eco-evolutionary models have an optimization principle if, and only if, the trait acts one-dimensionally.*

Examples of pessimization principles are also common. If the ecological embedding is such that there is a single limiting resource (which is a clear example of a one-dimensionally acting environment) an obvious example is: "Evolution minimizes the availability of a limiting resource". Another possibility is that individual life-history parameters are negatively affected by the total population density. The interpretation is then: "Evolution maximizes population density". Generalizing from these examples we arrive at the next result:

Result 3 (Pessimization principle) *Eco-evolutionary models have a pessimization principle if, and only if, the environment acts one-dimensionally.*

Finally, notice that through the assignment

$$\xi(X) = -\eta(E_{\text{attr}}(X)) \tag{22}$$

we can create an optimization principle out of a pessimization principle and *vice versa* (see also examples 2 and 3). So the two never come alone. The proofs of results 2 and 3 are analogous to (but considerably more complicated than) the proof of result 1. They can be found in Metz *et al.* (1996^b).

4 The special case of maximization of r_0 or R_0

The two fitness measures that are used most often are the population growth rate r_0 and the expected life-time production of offspring R_0. (See Roff 1992; Stearns 1992; Charnov 1993; Kozłowski 1993, and Pásztor *et al.* 1996 for an overview.) r_0 Is also called the intrinsic rate of natural increase, and is defined as the exponential growth rate of a clone on a continuous time basis (see, *e.g.*, Roughgarden, 1979; Yodzis, 1989). R_0 is also known as the basic reproduction number, and is defined as the multiplicative growth rate of a clone on a discrete, generation basis (Roughgarden, 1979; Yodzis, 1989; Diekmann *et al.*, 1990).

Because r_0 and R_0 are only defined for constant environments, we shall suppose in this section that the population dynamical feedback is such that E_{attr} is constant in time. [Notice that r_0 is usually called r. We try to be consistent in our notation, by writing r (and equally R) when the growth rate (life-time offspring production) is a function of two variables, X and E, and writing r_0 (and R_0) when E has a fixed value, to be called E_0.]

For a population in an ecological point equilibrium, we have both $r = 0$ and $R = 1$. That R is 1 can easily be verified from the observation that the population number stays constant from generation to generation, so on average each individual produces one offspring. Moreover,

$$r \;\substack{>\\=\\<}\; 0 \qquad \text{if, and only if,} \qquad R \;\substack{>\\=\\<}\; 1\,. \tag{23}$$

This allows, with preservation of sign structure, the replacement of $\rho(X,E)$ in the definitions of one-dimensional action (12) and (13) by $r(X,E)$ as well as $\ln[R(X,E)]$ (see also Roughgarden 1979; Charlesworth 1994; Diekmann & Metz 1994, and examples 2 and 3).

The understanding that we gained from section 3 guides us to rephrase the question "When does evolution optimize r_0 or R_0?" in:

When is $X \mapsto r(X,E)$ or $X \mapsto R(X,E)$ maximal at $\hat{X}$ for all E?

Using (2) and (12) we see, as a direct application of result 2, that $r_0(X)$ [$= r(X,E_0)$] is an optimization principle for fixed $E_0 \in \mathbb{E}$, provided that the eco-evolutionary model allows the existence of a function $\mathcal{X}_r : \mathbb{R} \times \mathbb{E} \to \mathbb{R}$ which increases in its first argument, such that

$$\operatorname{sign}\Big[\, r(X,E) \,\Big] \;=\; \operatorname{sign}\Big[\, \mathcal{X}_r(r_0(X),E) \,\Big]\,. \tag{24}$$

Analogously, with the help of (2), (12) and (23) we see that $R_0(X)$ [$= R(X,E_0)$] is an optimization principle for fixed E_0 provided that there exists a function $\mathcal{X}_R : \mathbb{R} \times \mathbb{E} \to \mathbb{R}$ which increases in its first argument, such that

$$\operatorname{sign}\Big[\, \ln\left[R(X,E)\right] \,\Big] \;=\; \operatorname{sign}\Big[\, \mathcal{X}_R(\ln\left[R_0(X)\right],E) \,\Big]\,. \tag{25}$$

We shall say that *evolution just maximizes r_0, or R_0,* whenever $r(X,E_0)$, or $R(X,E_0)$, is an optimization principle for every choice of $E_0 \in \mathbb{E}$. In this definition, the clause 'just maximizes' reflects the lack of any constraint on the environment E. This is analogous to the condition 'for all possible constraints on $\mathbb{X}$' in the definition of an optimization principle.

As a direct corollary of result 2 we obtain the following result:

Result 4 (Maximization of r_0 or R_0) *Evolution just maximizes r_0, or R_0, if and only if the eco-evolutionary model makes it possible to write*

$$r(X,E) \quad = \quad \mathcal{X}(r(X,E_0),E) \tag{26}$$

or

$$\ln[R(X,E)] \quad = \quad \mathcal{X}(\ln[R(X,E_0)],E) \tag{27}$$

respectively, for some function $\mathcal{X}: \mathbb{R}\times\mathbb{E}\rightarrow\mathbb{R}$ which increases in its first argument, and arbitrary but fixed $E_0 \in \mathbb{E}$.

Box 4 Example 3

Suppose that density dependence makes itself felt only by an additional death rate $\mu(E)$, acting equally for all individuals. Then we can write

$$r(X,E) \quad = \quad r(X,E_{\mathrm{V}}) - \mu(E)\ , \tag{28}$$

where E_{V} is the virgin environment. Therefore evolution within those confines just maximizes r_0 (see also Mylius & Diekmann, 1995).

In example 2 we saw, for steady-state population dynamics, one-dimensional action of trait and environment when life-time reproductive success was reduced by an E-dependent multiplication factor θ. A biologically meaningful scenario in which this might occur is when θ is the probability of dying, due to density dependence, in a life stage before the trait starts acting. This leads us to the following example:

Box 5 Example 4

Suppose that the life history and ecological embedding are such that the model has non-overlapping life stages. Then we can write

$$R(X,E) \quad = \quad R(X,E_{\mathrm{V}})\cdot\theta(E) \tag{29}$$

and consequently $\ln[R(X,E)] \ = \ \ln[R(X,E_{\mathrm{V}})] + \ln[\theta(E)]$. Therefore, in these eco-evolutionary model families evolution just maximizes R_0 (see also Mylius & Diekmann, 1995).

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5 Case study: different ecological embeddings

In this section, we will explore the consequences of different scenarios for the population dynamical feedback, for the evolution of the age at maturity of a hypothetical example organism. Note that we assume that all feedback loops are one-dimensional. For an example with a higher-dimensional feedback loop, we refer to Heino *et al.* (1997).

Model description

First of all, we simplify by assuming that the virgin environment is constant in time and that population dynamics converges to a unique equilibrium.

We consider the following simple life history: Juveniles mature into adults at age T, after which they produce offspring at a constant rate b. Juveniles and adults die at rates μ_J and μ_A, respectively. All these parameters may be affected by the environment E, as a consequence of the population-dynamical feedback loop. We shall indicate their values in the virgin environment E_V with an index $_V$. The evolutionary strategy parameter of our organism is the length of its juvenile period in the virgin environment, T_V. Postponing maturation leads to an increased adult reproduction rate. Specifically, we suppose that b increases linearly with T_V in the virgin environment

$$b_V(T_V) \ := \ b(T_V, E_V) \ := \ \max(0, T_V - 1)\ . \tag{30}$$

To this basic model, we add six alternative scenarios for the environmental feedback loop:

I. E only affects the juvenile as well as the adult mortality rate by an equal additional term for both:

$$\mu_J(E) \ = \ \mu_{JV} + \phi(E) \quad \text{and} \quad \mu_A(E) \ = \ \mu_{AV} + \phi(E) \tag{31}$$

II. E only affects the juvenile mortality rate additively:

$$\mu_J(E) \ = \ \mu_{JV} + \phi(E) \tag{32}$$

III. E only affects the adult mortality rate additively:

$$\mu_A(E) \ = \ \mu_{AV} + \phi(E) \tag{33}$$

IV. E only affects the reproduction rate by a multiplicative factor:

$$b(T_V, E) \ = \ b_V(T_V) \cdot \psi(E) \tag{34}$$

V. E only affects the age at maturation additively, without affecting the birth rate:

$$T(E) \ = \ T_V + \phi(E) \tag{35}$$

VI. E only affects the age at maturation multiplicatively, without affecting the birth rate:

$$T(E) \ = \ \frac{T_V}{\psi(E)} \tag{36}$$

In all these cases

$$\phi(E) \ \geq \ \phi(E_V) \ = \ 0 \qquad \text{and} \qquad 0 \ < \ \psi(E) \ \leq \ \psi(E_V) \ = \ 1\ . \tag{37}$$

For each scenario, we assume that parameters for which nothing is specified always take the value for the virgin environment. That is, for scenario I we have $T(E) = T_V$ and $b(T_V, E) = b_V(T_V)$, for scenario II we have $\mu_A(E) = \mu_{AV}$, $T(E) = T_V$ and $b(T_V, E) = b_V(T_V)$, etcetera.

For fixed values of T_V and E we can, directly from the basic model description, calculate the probability of surviving the juvenile period as $e^{-\mu_J(E)\,T(E)}$. The expected total offspring production during the adult life span, conditional on survival until adulthood, is $b/\mu_A(E)$. Multiplying these two expressions gives us an explicit formula for R:

$$R(T,E) \quad = \quad \frac{b(T,E)}{\mu_A(E)}\, e^{-\mu_J(E)\,T(E)} \,. \tag{38}$$

In the following we will use a shorthand notation, by writing R as a function of T_V and either ϕ or ψ, where we use ϕ and ψ as parameterizations of the environment.

The clonal growth rate r is the unique real root of the characteristic equation

$$\frac{b(T,E)\, e^{-[r(T,E)+\mu_J(E)]\,T(E)}}{r(T,E)+\mu_A(E)} \quad = \quad 1 \tag{39}$$

(see, *e.g.*, Roughgarden, 1979; Yodzis, 1989).

Optimization principles for the different feedback scenarios

Feedback scenario I (*i.e.*, density dependence uniformly tunes the mortality rate) makes our model a special case of the model family considered in example 4. In this case, evolution just maximizes the clonal growth rate r and consequently we can determine the evolutionary stop $\hat{T}_V$ by maximizing $T_V \mapsto r(T_V, E)$ for $E = E_V$, or any other fixed E.

The case of scenario II (density dependence tunes the juvenile mortality rate) is different from examples 4 and 5. However, it is easily seen from the interpretation [and (38)] that in this case R is a decreasing function of the environmentally induced mortality $\phi(E)$. Therefore, we can still use result 2 for one-dimensionally acting environments. After a little manipulation of the equations (see Box 6) it turns out that we can use $-\phi$ for the pessimization principle η and $\ln[R(T_V, -\phi)]/T_V$ for $\mathcal{E}$. Subsequently, we can use (22) to calculate the optimization principle from the pessimization principle: $\xi(T_V) = -\eta(E_{\text{attr}}(T_V)) = \phi(E_{\text{attr}}(T_V))$. So we end up with an optimization principle $\ln[R(T_V, E_V)]/T_V$ which (after leaving out the constant terms) simplifies to:

$$\xi(T_V) \quad = \quad \frac{\ln[b_V(T_V)]}{T_V} \,. \tag{40}$$

Feedback scenarios III to V all lead to a formula for $R(T,E)$ which, although the biological mechanism differs from that of the models considered in example 5, can be brought into the form (29):

$$R(T_V,E) \quad = \quad R(T_V,E_V)\cdot\theta(E) \,, \tag{41}$$

with

$$R(T_V,E_V) \quad = \quad \frac{b_V(T_V)}{\mu_{AV}}\, e^{-\mu_{JV} T_V} \tag{42}$$

and (see Box 6 for the derivations)

$$\theta(E) \quad = \quad \begin{cases} \dfrac{\mu_{\mathrm{AV}}}{\mu_{\mathrm{AV}} + \phi(E)} & \text{(scenario III)} \\ \psi(E) & \text{(scenario IV)} \\ e^{-\mu_{\mathrm{JV}}\,\phi(E)} & \text{(scenario V)}\,. \end{cases} \tag{43}$$

The case of scenario VI is analogous to that of scenario II (also see Box 6). Substituting ψ for η and $\ln[R(T_{\mathrm{V}}, \psi)]/T_{\mathrm{V}}$ for $\mathcal{E}$, we even end up with the same optimization principle (40).

Box 6 The equations behind the case study

Scenario II In this case, we can rewrite (38) as

$$R(T_{\mathrm{V}}, E) \quad = \quad \frac{b_{\mathrm{V}}(T_{\mathrm{V}})}{\mu_{\mathrm{AV}}}\, e^{-[\mu_{\mathrm{JV}}+\phi(E)]\,T_{\mathrm{V}}} \quad = \quad R(T_{\mathrm{V}}, E_{\mathrm{V}})\, e^{-\phi(E)\,T_{\mathrm{V}}}\,. \tag{44}$$

By substituting $E = E_{\mathrm{attr}}(T_{\mathrm{V}})$ in this equation and using the steady-state condition $R(T_{\mathrm{V}}, E_{\mathrm{attr}}(T_{\mathrm{V}})) = 1$, we see that

$$R(T_{\mathrm{V}}, E_{\mathrm{V}}) \quad = \quad e^{\phi(E_{\mathrm{attr}}(T_{\mathrm{V}}))\,T_{\mathrm{V}}} \tag{45}$$

which yields, by solving for ϕ:

$$\begin{aligned} \phi(E_{\mathrm{attr}}(T_{\mathrm{V}})) \quad &= \quad \frac{\ln\,[R(T_{\mathrm{V}}, E_{\mathrm{V}})]}{T_{\mathrm{V}}} \quad = \quad \frac{1}{T_{\mathrm{V}}}\,\ln\left(\frac{b_{\mathrm{V}}(T_{\mathrm{V}})}{\mu_{\mathrm{AV}}}\,e^{-\mu_{\mathrm{JV}}\,T_{\mathrm{V}}}\right) \\ &= \quad \frac{1}{T_{\mathrm{V}}}\,\ln\left(\frac{b_{\mathrm{V}}(T_{\mathrm{V}})}{\mu_{\mathrm{AV}}}\right) - \mu_{\mathrm{JV}}\,. \end{aligned} \tag{46}$$

□

Scenarios III, IV and V In these cases, we can rewrite (38) as

$$R(T_{\mathrm{V}}, E) \quad = \quad \begin{cases} \dfrac{b_{\mathrm{V}}(T_{\mathrm{V}})}{\mu_{\mathrm{AV}} + \phi(E)}\, e^{-\mu_{\mathrm{JV}}\,T_{\mathrm{V}}} & \text{(scenario III)} \\ \dfrac{b_{\mathrm{V}}(T_{\mathrm{V}})\,\psi(E)}{\mu_{\mathrm{AV}}}\, e^{-\mu_{\mathrm{JV}}\,T_{\mathrm{V}}} & \text{(scenario IV)} \\ \dfrac{b_{\mathrm{V}}(T_{\mathrm{V}})}{\mu_{\mathrm{AV}}}\, e^{-\mu_{\mathrm{JV}}\,(T_{\mathrm{V}}+\phi(E))} & \text{(scenario V)}\,, \end{cases} \tag{47}$$

which yields

$$R(T_{\mathrm{V}}, E) \quad = \quad R(T_{\mathrm{V}}, E_{\mathrm{V}}) \cdot \begin{cases} \dfrac{\mu_{\mathrm{AV}}}{\mu_{\mathrm{AV}} + \phi(E)} & \text{(III)} \\ \psi(E) & \text{(IV)} \\ e^{-\mu_{\mathrm{JV}}\,\phi(E)} & \text{(V)}\,. \end{cases} \tag{48}$$

□

Scenario VI In this case, we can rewrite (38) as

$$R(T_{\mathrm{V}}, E) = \frac{b_{\mathrm{V}}(T_{\mathrm{V}})}{\mu_{\mathrm{AV}}} e^{-[\mu_{\mathrm{JV}}+\phi(E)]\,T_{\mathrm{V}}} = R(T_{\mathrm{V}}, E_{\mathrm{V}})\, e^{-\phi(E)\,T_{\mathrm{V}}} . \tag{49}$$

By substituting $E = E_{\mathrm{attr}}(T_{\mathrm{V}})$ in this equation and using the steady-state condition $R(T_{\mathrm{V}}, E_{\mathrm{attr}}(T_{\mathrm{V}})) = 1$, we see that

$$R(T_{\mathrm{V}}, E_{\mathrm{V}}) = e^{\phi(E_{\mathrm{attr}}(T_{\mathrm{V}}))\,T_{\mathrm{V}}} \tag{50}$$

which yields, by solving for ϕ:

$$\begin{aligned}\phi(E_{\mathrm{attr}}(T_{\mathrm{V}})) &= \frac{\ln[R(T_{\mathrm{V}}, E_{\mathrm{V}})]}{T_{\mathrm{V}}} = \frac{1}{T_{\mathrm{V}}} \ln\left(\frac{b_{\mathrm{V}}(T_{\mathrm{V}})}{\mu_{\mathrm{AV}}} e^{-\mu_{\mathrm{JV}}\,T_{\mathrm{V}}}\right) \\ &= \frac{1}{T_{\mathrm{V}}} \ln\left(\frac{b_{\mathrm{V}}(T_{\mathrm{V}})}{\mu_{\mathrm{AV}}}\right) - \mu_{\mathrm{JV}} . \end{aligned} \tag{51}$$

□

In principle, scenario I can be analysed by exactly the same procedure as scenarios II and VI, except that it is not possible to find an explicit expression for $\phi(E_{\mathrm{attr}}(T_{\mathrm{V}}))$. And our general results tell that anyway the resulting optimization principle would be monotonically related to $T_{\mathrm{V}} \mapsto r(T_{\mathrm{V}}, E_{\mathrm{V}})$.

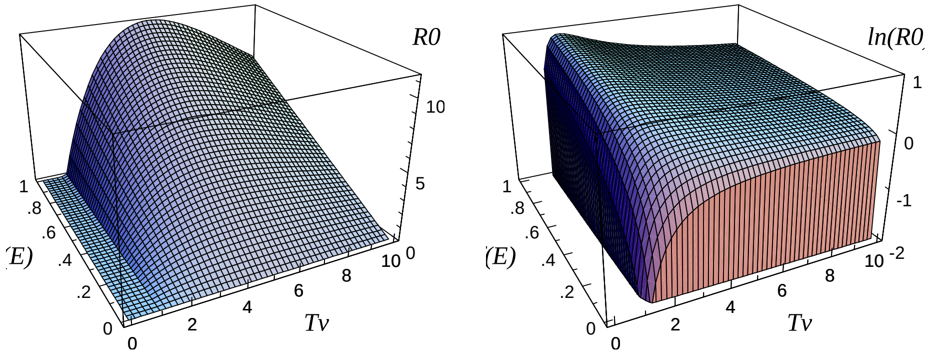
Comparison of two scenarios and their principles

To illustrate the effect of two of the abovementioned feedback scenarios, in this case IV and VI, on their own corresponding optimization principles, $T_{\mathrm{V}} \mapsto R(T_{\mathrm{V}}, E)$ and $T_{\mathrm{V}} \mapsto \ln[R(T_{\mathrm{V}}, E)]/T_{\mathrm{V}}$, respectively, and on each other's optimization principles, we have added two figures. Figure 1 shows, for both feedback scenarios, three-dimensional surface plots of both optimization principles, as functions of the trait value and the environmental condition. The environment is parameterized by the multiplication factor $\psi(E)$, as given by equations (34) and (36). Contour plots of the surfaces are given in Figure 2. We indicated the steady-state environmental condition $\psi(E_{\mathrm{attr}}(T_{\mathrm{V}}))$ with bold curves. They correspond to the contour lines $R(T_{\mathrm{V}}, \psi(E)) = 1$ and $\ln[R(T_{\mathrm{V}}, \psi(E))]/T_{\mathrm{V}} = 0$, respectively. The maxima of R and $\ln[R]$ are indicated with dashed curves.

In these pictures, one can find a non-invasible strategy by intersecting two curves: the contour line defining the steady-state environment (bold) and a curve where fitness as a function of the trait value is maximal (dashed). Notice that this description is completely analogous to our characterization of non-invasible strategies by (4) in section 2.

We clearly see that in case of scenario IV, the maximum of $T_{\mathrm{V}} \mapsto R(T_{\mathrm{V}}, \psi(E))$, which is the optimization principle for this scenario, is independent of the environmental condition, whereas the optimal value of T_{V} for $T_{\mathrm{V}} \mapsto \ln[R(T_{\mathrm{V}}, E)]/T_{\mathrm{V}}$, which is the optimization principle for the other scenario, is only equal to the non-invasible trait value $\hat{T}_{\mathrm{V}}$ at the steady-state environmental condition $\psi(E_{\mathrm{attr}}(\hat{T}_{\mathrm{V}}))$. For scenario VI it is exactly the other way around. The key point is that for the proper optimization principles we do not need to com-

(**a1**) scenario IV (**a2**) scenario IV



(**b1**) scenario VI (**b2**) scenario VI

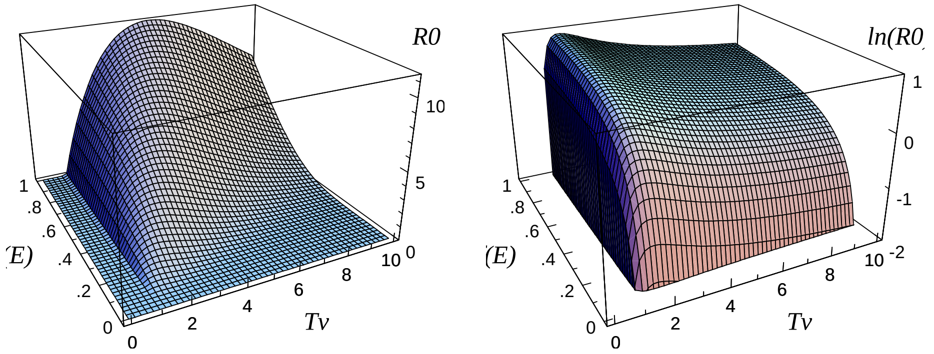


Figure 1: Surface plots of the functions $R(T_\mathrm{V}, \psi(E))$ and $\ln[R(T_\mathrm{V}, \psi(E))]/T_\mathrm{V}$ for feedback scenarios IV and VI of the case study model described in section 5. Upper panels: feedback scenario IV, R (**a1**) and $\ln[R]/T_\mathrm{V}$ (**a2**) as functions of T_V and $\psi(E)$. Lower panels: feedback scenario VI, R (**b1**) and $\ln[R]/T_\mathrm{V}$ (**b2**). See also Figure 2.

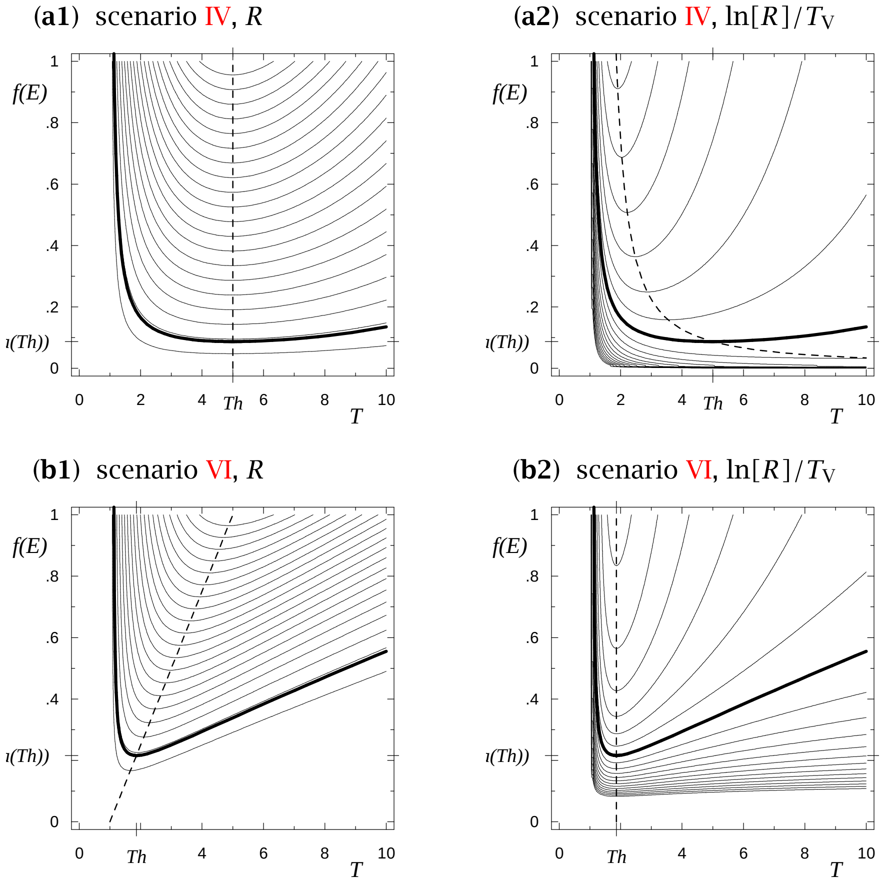


Figure 2: Contour plots of the functions $R(T_\mathrm{V}, \psi(E))$ and $\ln[R(T_\mathrm{V}, \psi(E))]/T_\mathrm{V}$ for feedback scenarios IV and VI of the case study model in section 5. The numbering of the panels corresponds with Figure 1. Contour curves of $\psi(E_\mathrm{attr}(T_\mathrm{V}))$ are bold, and the maxima of $T_\mathrm{V} \mapsto R(T_\mathrm{V}, \psi(E))$ and $T_\mathrm{V} \mapsto \ln[R(T_\mathrm{V}, \psi(E))]/T_\mathrm{V}$ are indicated with dashed curves.

pute $\psi(E_{\text{attr}}(T_{\text{V}}))$, since the dashed curve is a vertical line. This is the graphical representation of result 2.

Notice that for each scenario, the bold curves $\psi(E_{\text{attr}}(T_{\text{V}}))$ are equal for both optimization principles (compare the left and the right panels). This expresses the sign equivalence between R and $\ln[R] - 1$. We can also clearly see that $\psi(E)$ is pessimized by evolution in both cases. Finally, we stress that it is only possible to make the plots in Figures 1 and 2 at all because trait and environment act one-dimensionally.

Laboratory versus field

How should we interpret the difference between heriditary parameters (as showing up in the virgin environment) and parameters under environmental control? In classic life history models this problem is defined away, by assuming that the life history parameters of an individual are constants, instead of being potentially under environmental control. In the case of the present model we distinguish two situations, called *laboratory* and *field*. In the laboratory situation the environment is kept constant artificially, whereas in the field situation the environment E is adjusted such that

$$R(\hat{T}_{\text{V}}, E) \quad = \quad 1\,. \tag{52}$$

The picture that we have in mind is that by experimental manipulation in the laboratory situation, the values of the life-history parameters differ from those in the virgin environment by at most either an additive or a multiplicative constant. In the field situation, the values of the parameters that are not under environmental control are equal to the virgin values whereas the remaining, controlled parameter is obtained by either adding $\phi(E_{\text{attr}}(\hat{T}_{\text{V}}))$ or multiplying (dividing) by $\psi(E_{\text{attr}}(\hat{T}_{\text{V}}))$, defined by (52).

From an evolutionary viewpoint, the 'field' situation is the most interesting one. Figure 3 shows the correlations obtaining between the field observables $\hat{T}$ and μ_{A}, for a fixed value of μ_{JV}, for each of the six feedback scenarios.

The numbering of the panels in Figure 3 refers to the feedback scenarios. The plotted field observables are determined by a combination of the 'physiological parameters' μ_{AV} (the adult death rate in the virgin environment) and $\hat{T}_{\text{V}}$ (the non-invasible value of T_{V}, the juvenile period in the virgin environment), and the corresponding feedback scenario.

Quite a few things about these plots are worth mentioning. First of all: different feedback scenarios can lead to radically different patterns, and even to reversed correlations between life-history variables! Looking more to the details, we see that the upper limit of μ_{A} is identical for all curves. This results from the fact that for higher values of μ_{AV} no strategy can invade into the virgin environment. [Such values of μ_{AV} would lead in a, naive, calculation to $\phi(E_{\text{attr}}(\hat{T}_{\text{V}})) < 0$ or $\psi(E_{\text{attr}}(\hat{T}_{\text{V}})) < 1$, *i.e.*, values of ϕ or ψ which were excluded *a priori* in our model specification.] In panel I, the lower limit of μ_{A} results from the additional mortality due to environmental feedback. In panel III, we see that a feedback through the adult mortality by necessity exactly compensates for any difference in the adult mortality rate in the virgin environment. For other possible parameter combinations we refer to Metz *et al.* (1996^{b}).

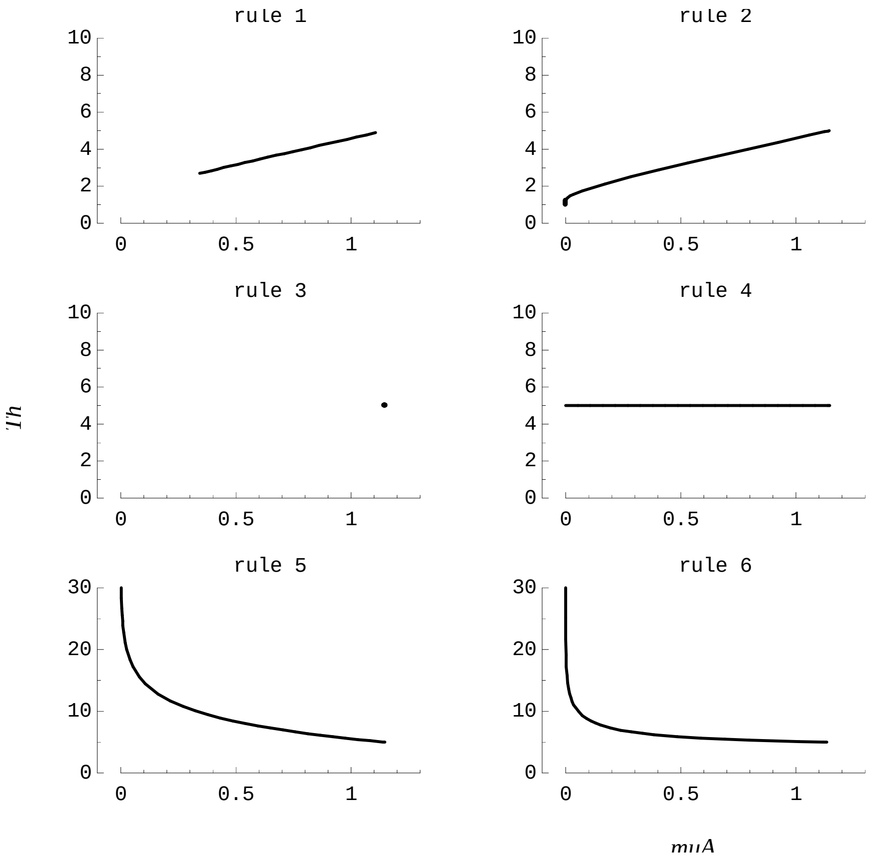


Figure 3: Correlations between the adult mortality rate μ_A and the duration of the evolutionarily stable juvenile period $\hat{T}$, both as "observed in the field", for the six alternative environmental feedback scenarios described in section 5. For scenarios I and III, we plotted $\hat{T}_V$ versus $\mu_{AV} + \phi(E_{attr}(\hat{T}_V))$; for scenarios II and IV, $\hat{T}_V$ versus μ_{AV}; for scenario V, $\hat{T}_V + \phi(E_{attr}(\hat{T}_V))$ versus μ_{AV}; and for scenario VI, $\hat{T}_V\,\psi(E_{attr}(\hat{T}_V))$ versus μ_{AV}. The value of the "physiological parameter" juvenile mortality in the virgin environment was kept fixed at $\mu_{JV} = 0.25$.

6 Optimization principles and PIPs

From a pairwise invasibility plot (PIP; see van Tienderen & de Jong, 1986; Geritz & Kisdi, to appear) it is rather straightforward to see whether an eco-evolutionary model supports an optimization principle or not.

The zero-contour lines in a PIP indicate which trait values are equivalent to each other with respect to invasion. Sets of precisely those trait values that are equivalent to each other are called equivalence classes. If the model supports an optimization principle then we can order all equivalence classes, and the zero-lines connect trait values that have identical values of the optimization principle: Trait values with a higher (or lower) value of the optimization principle can (or cannot) invade. Because equivalence relations are symmetric (*i.e.*, if A is equivalent to B, then B is equivalent to A), all zero-lines in the PIP are mirror-symmetric with respect to the 45° line (where $X_{\text{inv}} = X_{\text{res}}$, with *inv* referring to *invader* and *res* to *resident*). Additionally, the PIPs have to be anti-symmetric: if A is invasible by B then B is not invasible by A and *vice versa*. The transitivity of equivalence relations (*i.e.*, if A is equivalent to B and B is equivalent to C then A is also equivalent to C) results in another characteristic property: All points in the plot where a zero curve has a horizontal or vertical tangent line correspond to a crossing of a zero curve with the 45° line at a point exactly perpendicular to the tangent line. This property shapes the 'islands' around the 45° line. Last but not least, there is generally one point X_{res} which is non-invasible by any X_{inv}, and which can invade all X_{inv}. Only in the degenerate case that the global maximum of the optimization principle is not unique there are more such points.

In Figure 4 we plotted some sign structures of $\rho(X_{\text{inv}}, E_{\text{attr}}(X_{\text{res}}))$ which support an optimization principle, to illustrate the abovementioned characteristics.

The advantage of judging by means of PIPs, whether an eco-evolutionary model supports an optimization principle, is that they provide an operational method. Even for very complicated models, a PIP can be constructed by numerical simulation.

7 Conclusions and discussion

We have argued that the analysis of certain special models can be done by optimization- or pessimization arguments, instead of by evolutionary invasibility arguments. Because extremization methods are much easier to use than game theoretical methods, they provide a useful tool. However, the conditions under which extremization methods apply are very special, and if these conditions are not met then the results of optimization- or pessimization methods do not make sense. Conceptually, an evolutionary invasibility analysis is the primary way to go.

The 'fittest', *i.e.* the type favoured by evolution, need not be the best strategy in other environments than the one it generates if it is the resident type in the population. We have seen that if, and only if, there exists such a fixed optimization principle, the fittest is optimal in *any* environment.

The existence of an optimization principle or, equivalently, a pessimization principle, is a property of the complete eco-evolutionary model, which is a combination of an evolving trait, a life history and an ecological embedding. Hence,

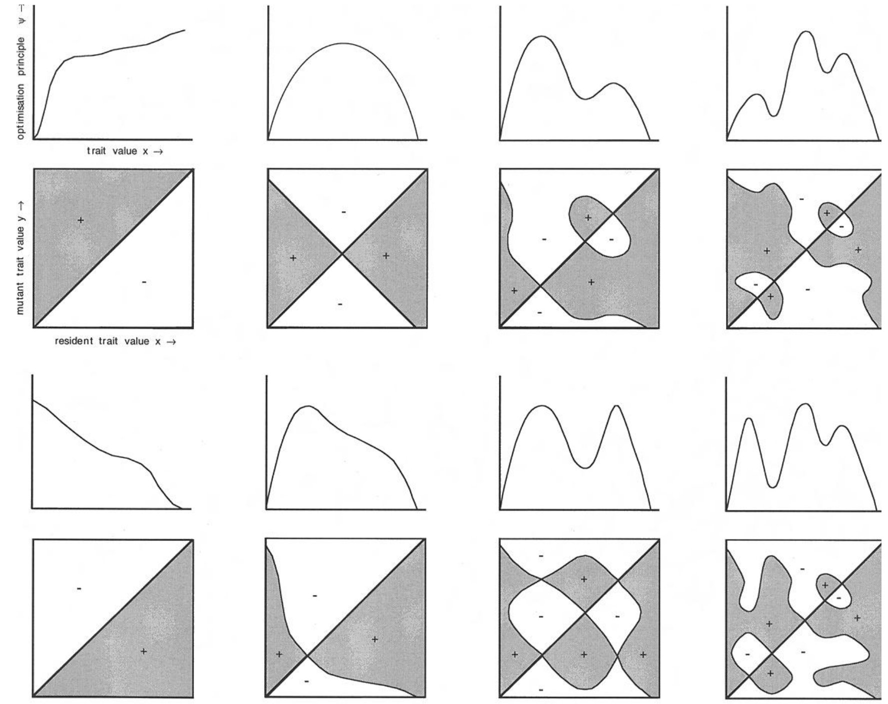


Figure 4: Some PIPs which support an optimization principle. For each pair of panels, the upper one is the optimization principle as a function of the trait value, and the lower one is the corresponding PIP. In the shaded areas, mutants have positive fitness, in the white areas mutants have negative fitness.

the use of an extremization principle can only be justified by taking all these elements of the model into account.

Especially the effect of the ecological embedding, shaped by the way in which density dependence is felt by the individuals, is generally underestimated. Given the crucial role of density dependence, this seems an undervalued field of research.

For more complicated ecological embeddings, shortcuts in the form of extremization criteria cease to exist. This is in particular the case if the dimension of the environmental feedback loop is higher than one (see Heino *et al.*, 1997; Heino, to appear). Mathematically, the existence of an optimization criterion is degenerate. The question is, of course, whether it is beyond biological reality. We conjecture that it is our own limited imagination in dreaming up alternative feedback scenarios for evolutionary models that makes the occurrence of certain optimization principles in the literature relatively widespread.

Admittedly, it is somewhat disappointing that we can only give necessary and sufficient conditions for the existence of optimization- and pessimization principles. We are not able to provide a recipe for the construction of an extremization principle, for eco-evolutionary models that show a one-dimensionally acting trait or environment. Actually, there is no general recipe. This is reminiscent of the problem with Lyapunov functions in dynamical systems theory: once a Lyapunov function has been found it is an extremely powerful tool, but they are difficult to find. For the clonal case, optimization principles act as Lyapunov functions. But an evolutionary ecologist, using a fixed extremization principle to determine ESS's without any further foundation, is like a mathematician using a Lyapunov function to determine limiting behaviour of a dynamical system without a proof that it actually *is* a Lyapunov function.

This brings us to the problem that we have not taken into account the mode of inheritance. Hammerstein & Selten (1994; Hammerstein 1996) have postulated that genetic constraints may be negligible in long-term evolution, in favour of game theoretical approaches (see also Matessi & Di Pasquale, 1996). In case of simple Mendelian genetics, optimization principles act as Lyapunov functions, provided the heterozygote phenotype are intermediate of the homozygote phenotypes. For more complicated modes of inheritance, it will generally not be possible to find an optimization principle, because they do not exist. Especially convergence will be problematic.

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