Evolutionary Ecology Research, 2008, **10**: 629–654

When does evolution optimize?

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ABSTRACT

Aim: To elucidate the role of the eco-evolutionary feedback loop in determining evolutionarily stable life histories, with particular reference to the methodological status of the optimization procedures of classical evolutionary ecology.

Key assumption: The fitness ρ of a type depends both on its strategy X and on the environment E, $\rho = \rho(X, E)$, where E comprises everything, biotic and abiotic, outside an individual that may influence its population dynamically relevant behaviour. Through the community dynamics, this environment is determined (up to non-evolving external drivers) by the resident strategy X_r: $E = E_{attr}(X_r)$.

Procedures: Use the indicated notation to derive necessary and sufficient conditions for the existence of an evolutionary optimization principle, and for the reduction of such a principle to straightforward r- or R_0-maximization. Develop quick tests to diagnose whether an eco-evolutionary model supports an optimization principle.

Results: It is necessary and sufficient for the existence of an optimization principle that the strategy affects fitness in an effectively monotone one-dimensional manner, or equivalently, that the environment affects fitness in an effectively monotone one-dimensional manner. In particular, there should exist functions ψ of the strategies and ϕ of the environments such that $\text{sign}[\rho(X, E)] = \text{sign}[\psi(X) + \phi(E)]$. Pairwise invasibility plots of an eco-evolutionary model that supports an optimization principle have a special, easily recognizable shape. Natural selection just maximizes r, or R_0, if and only if $r(X, E)$ can be written as $\alpha(r(X, E_0), E)$, or $R_0(X, E)$ can be written as $\exp[\alpha(\ln[R_0(X, E_0)], E)]$, with α increasing in its first argument, and E_0 fixed, but otherwise arbitrary.

Conclusion: A pure optimization approach holds water only when the eco-evolutionary feedbacks are of a particularly simple kind.

Keywords: eco-evolutionary feedback, environmental dimension, evolutionary optimization, invasion fitness, life-history theory, r-optimization, R_0-optimization.

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1. INTRODUCTION

The literature is replete with statements that evolutionary predictions about, for example, behavioural or life-history parameters should be based on the maximization of individual lifetime reproductive success, R_0 (for surveys, see Roff, 1992; Stearns, 1992; Charnov, 1993; Charlesworth, 1994), or else the intrinsic rate of natural increase, r (Roff, 1992; Stearns, 1992; Charlesworth, 1994; Caswell, 2000). In the former case it is often added, rather confusingly, that due to density dependence, necessarily $R_0 = 1$ (see, for example, Charnov, 1993; for a review, see Maynard Smith, 1993). No doubt most authors writing about life-history theory know how to interpret the last statement, and are aware of the implicit limitations of the traditional optimization considerations. However, it would appear that this awareness (a) is not widespread among experimentalists and (b) appears somewhat unclear even among most theorists. In a quick and dirty survey, we also found that the probable main cause of this limited awareness is that advertising positive predictions provides more kudos than spelling out limitations. Yet, we feel that delimiting the applicability of particular evolutionary arguments is a worthy effort, not only for philosophical but also for practical reasons: By extending the limits as far as one can, one usually also extends the effective toolbox.

In this paper we put forward three closely related messages:

(i) We argue that adhering to a simple explicit notation fosters the awareness of some implicit limitations of life-history arguments. Our notation differs from the traditional one only in that the roles of (a) the life-history traits and in particular (b) the environment, in determining the population dynamical behaviour of an individual, are made visible. This visibility also has the advantage of removing the minor confusion about R_0 simultaneously being maximized and kept equal to 1. We sincerely ask you to adopt this notation, or else to develop your own variant of it. The use of more simplified notations too often misleads!

(ii) We give necessary and sufficient conditions for the eventual outcome of the evolutionary process to be characterized by some optimization principle, and in particular by straight r- or R_0-maximization. These conditions are phrased in mathematical, structural, terms only. So far, we have not been able to delimit clear classes of corresponding physiological mechanisms. Dreaming up simple classes of mechanisms subsumed under our conditions is easy. We give some examples. But how wide exactly is the net cast?

(iii) We describe the special patterns visible in pairwise invasibility plots that are characteristic for the presence of an optimization principle.

In a companion paper (Metz *et al.*, 2008) in this issue, we demonstrate how the details of the population dynamical embedding may have considerable influence on evolutionary predictions. The models used in that paper were specifically rigged to allow various optimization principles, depending on the specific choice of the environmental feedback loop. For those models, the proposed explicit notation also alerted us to the fact that life-history parameters determined in the field often will show patterns that differ in a non-trivial way from those of parameters determined under laboratory conditions. The various feedback loops led to very different optimization principles and, without any clear relation to the optimization principles, very different relations between field adult mortality and maturation time. These results may act as an antidote to the apparently common belief that in most practical applications the proposed additional notation will only be a burden and not of much help. This is not the case. The added clarity not only prevents mistakes, it also opens new vistas.

The present paper may be seen as an extension of Mylius and Diekmann (1995). In this paper, various examples of sufficient conditions for the existence of an optimization principle are demonstrated. Here we characterize the collection of *all* possible scenarios allowing such principles.

2. SETTING THE STAGE: FITNESS, DENSITY DEPENDENCE, AND ESS CONSIDERATIONS

Our starting point is that there is one master fitness concept: the hypothetical average rate of exponential growth ρ, which results from the thought experiment in which we let a clone of the type under consideration grow in an ergodic environment (Tuljapurkar, 1989, 1990; Metz *et al.*, 1992; Charlesworth, 1994; Rand *et al.*, 1994; Ferrière and Gatto, 1995; Caswell, 2000; Metz, 2008). The term 'ergodic' is a key phrase used by mathematicians to indicate the most general conditions guaranteeing that temporal averaging operations yield definite results; in practice, the requirement boils down to the absence of any longer trends and the non-existence of different regimes occurring with non-zero probabilities that, once realized, exclude each other for all time. The term 'environment' is, in the tradition of the theory of structured populations, supposed to refer to everything, whether biotic or abiotic, outside an individual that has the potential to influence its population dynamically relevant behaviour.

The mental construction of hypothetical clonal individuals out of Mendelian ones still requires some elaboration: we have to discount offspring each generation by a factor of one-half to account for the fact that each individual only carries half of the alleles of one of its Mendelian parents. Hence, the fitness of a diploid phenotype is defined as the asymptotic time-averaged relative growth rate of the so discounted number of descendants, in a thought experiment where these descendants all have the same life-history parameters as their ancestor. These parameters include mating propensities, while mating opportunities are considered a component of the environment.

Remark 2.1. The reasons for our particular choice of a definition are: (i) It is consistent with the use of the word 'fitness' in the context of simple evolutionary scenarios on all points that are important in a long-term evolutionary context. (ii) For a large range of ecological scenarios, it is sufficiently precise to yield a definite number. (iii) The number so defined is almost the minimal information necessary to deduce predictions about both evolutionary final states and non-equilibrium evolutionary patterns. [For further elaboration, see the arguments below and Metz *et al.* (1996a) and Metz (2008).]

Our verbal definition immediately shows that ρ necessarily depends both on the type X of the clone and the environment E in which it supposedly lives. To keep our arguments clear, we should account explicitly for this dependency in the notation, by writing

$$\rho(X, E) \tag{2.1}$$

(cf. Diekmann and Metz, 1994; Mylius and Diekmann, 1995).

A potential source of confusion may be that as E refers to the environment as perceived by the individuals, for example, density and types of conspecifics may be part and parcel of E (Michod, 1979; Metz and Diekmann, 1986; Pásztor, 1988; Metz and de Roos, 1992; Kisdi and Meszéna, 1993; Diekmann and Metz, 1994; Pásztor *et al.*, 1996). Yet, in our thought experiment we consider those densities as given ergodic random functions of time, not influenced by the growth of our clone. The justification of this mental somersault is that we should think of fitness as the rate of invasion of a rare mutant multiplying amidst a large resident population. This presupposes that all evolutionarily relevant resident (sub)populations of the species are large, so that initially the influence of the mutant on the environment is properly diluted. The mutant heterozygote swarm reproduces faithfully by crossing with the residents. If dilution fails due to the interaction ranges of the individuals containing but a few more permanent sparring partners, we can sometimes take recourse to inclusive fitness considerations (see, for example, Taylor, 1988a, 1988b, 1989 for technicalities), but in general ultimately the concept of fitness resists further extension. Luckily, the range of conditions covered is sufficiently large that we need not be too bothered.

The corollary is that predictions about the trait values favoured by evolution should always derive from an ESS argument (e.g. Roughgarden, 1979; Lessard, 1990; Charlesworth, 1994; Eshel, 1996):

1. Maximize $\rho(X, E)$ for each given E over all potential trait values, resulting in a function $X_{\text{opt}}(E)$.
2. Determine for each trait value the environment that it generates as a resident, $E_{\text{attr}}(X)$. (The notional index 'attr' alludes to the assumption that the population dynamics converges to an attractor. If this were not the case, the resident phenotype would not have a well-defined environment attached to it.)
3. Vary X to find an evolutionarily unbeatable value X^*, i.e. an X^* such that
$$X_{\text{opt}}(E_{\text{attr}}(X^*)) = X^* . \tag{2.2}$$
4. Ascertain that the set of trait values X_0 from which X^* is approximated with non-zero probability through a sequence $X_0, X_1, X_2, \ldots$, such that $\rho(X_{i+1}, E_{\text{attr}}(X_i)) > 0$, possibly interspersed with polymorphisms, is sufficiently large to warrant consideration of X^* as a potential evolutionary trap.

Note that although the last condition is not part and parcel of the ESS concept as such (it should have been!), only the subset of attracting ESS's, customarily called CSS's, is relevant for making predictions (cf. Eshel, 1983, 1996; Taylor, 1989; Geritz *et al.*, 1998).

The above description is only meant as a definition, not as a practical algorithm. The general procedure from 1 to 4 has a habit of exceeding the available computer capacity, except in the simplest possible cases. Practical algorithms circumvent this by using special properties of particular cases.

Remark 2.2. In general, it cannot be excluded that the function E_{attr} is multi-valued. In theory, this does not invalidate our arguments, except that our present phrasing is definitely lacking in the details. But it may considerably complicate attempts at applying them in practice. The wording of the special arguments in Sections 3, 5, and 6 and the Appendix apply without change to the multi-valued case.

Monomorphic ESS's, as defined above, are not the only possible evolutionary endpoints, there also may exist polymorphic endpoints. To describe the corresponding intricacies, a little more notation is needed. Combinations of trait values that can co-exist will be denoted as $C = \{X_1, \ldots, X_k\}$, the corresponding environments as $E_{\text{attr}}(C)$. For monomorphic and for clonal populations,

$$\rho(X, E_{\text{attr}}(C)) = 0 \text{ whenever } X \in C. \tag{2.3}$$

In polymorphic Mendelian populations, (2.3) also holds true on the level of the (clonally reproducing!) alleles, where we have to interpret the elements of C as allelic traits, but in general not at the level of phenotypes (with ρ calculated as described in the introductory paragraphs of this section).

In clonal populations, the evolutionary endpoints – generically denoted here as C^* (or possibly X^* if we want to stress that we are dealing with the monomorphic case) – are always ESS's, characterized by (2.3) together with the fact that each trait in C^* maximizes fitness in $E_{\text{attr}}(C^*)$.

In the Mendelian case, there may exist other polymorphic endpoints where evolution gets stuck due to so-called genetic constraints. This can happen, for example, when the phenotypes can be ranked in a linear order from worst to best, independent of the environment, and the superior phenotypes can only be realized by genotypes with one or more heterozygote loci. Such constraints tend to be specific and there is little chance that a general theory can ever be built relating how and when they will occur. Hence we restrict the discussion to cases that are covered by

> **Assumption A**: *There are no long-term genetic constraints, or, more positively phrased, the only long-term constraints that are present are 'physiological', i.e. can be described in terms of a developmentally realizable subset of the trait space.*

Proposition 2.1 (e.g. Bulmer, 1994; see also Eshel and Feldman, 1984; Liberman, 1988; Metz, 2008). If the community dynamics goes to a point-attractor, and individuals have but a single birth state, then in the absence of genetic constraints, also in the Mendelian case any polymorphic evolutionary endpoints C^* are phenotypic ESS's, by which we mean that they satisfy (2.3) and each trait in C^* maximizes fitness in $E_{\text{attr}}(C^*)$.

Proof. Define R_0 of a phenotype as half the lifetime offspring production by that phenotype. Then, for phenotypes as well as for alleles, $R_0 \gtreqless 1 \Leftrightarrow \rho \gtreqless 0$. At a point attractor, the R_0 of the alleles involved in the polymorphism, which are all equal to 1, are averages of the R_0 of the phenotypes (see, for example, Diekmann *et al.*, 2003). Hence, if the R_0 of the phenotypes are not equal, some of them will be smaller and some of them larger than 1. Therefore, if (2.3) were not satisfied at the ESS, for the corresponding community attractor there exist trait values with positive fitness. However, in that case any mutant that would transform all phenotypes with negative fitness into one with positive fitness could invade. Hence, by contradiction, (2.3) applies. Similarly, if not all traits in C^* were to maximize fitness in $E_{\text{attr}}(C^*)$, there would exist a trait value having a positive fitness in $E_{\text{attr}}(C^*)$, and a mutant that transformed all phenotypes into that trait value could invade.

Remark 2.3. Whether or not convergence to the unbeatable strategy can occur will also depend on the (non-)presence of genetic constraints. The belief is that Assumption A, at least under the same conditions as in Proposition 2.1, guarantees that convergence for the Mendelian case parallels that for the clonal case, as it allows us to dream up any needed mutations, including mutations that break up heterotic polymorphisms (cf. Hammerstein and Selten, 1994; Hammerstein, 1996; see also Eshel, 1996; Weissing, 1996).

It is an open problem how far the consequent in Proposition 2.1 extends to fluctuating environments or life histories with multiple birth states (like populations distributed over patches with different local environmental conditions). Of course, the idea of the proof applies as soon as at a community attractor where the co-existing phenotypes have different fitnesses and not all of these fitnesses are negative (while the population persists indefinitely!). Therefore, the mathematical question is whether it is possible that although the allelic averages of the growth rate over birth states and time are zero, the corresponding averages for the phenotypes could be all negative. Although such a statement seems exceedingly counterintuitive, there exists so far no proof of its negation.

We would have preferred to make only the natural Assumption A. However, to reach any interesting conclusions, we need

Assumption B: *Relation* (2.3) *holds good at any ESS's.*

The previous considerations imply that Assumption A implies assumption B for (i) clonally reproducing populations, (ii) cases where there are no ESS's beyond the monomorphic ones, and (iii) when the community dynamics converges to a point-attractor and all individuals are born equal except possibly for differences in their genotype. Hence, unless otherwise specified, the results below hold good under only Assumption A at least in cases (i) to (iii).

Assumption B makes that in the definition of an ESS, we could just as well have restricted the attention to those E that can occur as $E_{\mathrm{attr}}(C)$ for which (2.3) holds good. As this restriction becomes essential in the arguments below, we introduce the following convention:

Convention: *Whenever we refer to E, we shall mean only those E that can occur as* $E_{\mathrm{attr}}(C)$ *for some C such that* (2.3) *holds true.*

3. WHEN DOES EVOLUTION OPTIMIZE?

This section deals largely with the abstract basics. Here we show that the outcome of the ESS calculation can be reached by the straightforward application of some extremization principle (like the maximization of R_0 or r or the minimization of a single limiting resource) only when the function $\rho(X, E)$ satisfies some rather stringent restrictions. Section 4 contains some representative examples. An additional set of examples, demonstrating some further intricacies, may be found in our companion paper (Metz *et al.*, 2008).

First we give some definitions:

Definitions. We shall say that *the trait vector acts in a monotone one-dimensional manner* whenever there exists a function ψ of X to the real numbers such that

$$\operatorname{sign} \rho(X, E) = \operatorname{sign} \alpha(\psi(X), E), \tag{3.1}$$

for some function α that increases in its first argument. Similarly, we shall say that *the environment acts in a monotone one-dimensional manner* whenever there exists a function ϕ of E to the real numbers such that

$$\operatorname{sign} \rho(X, E) = \operatorname{sign} \beta(X, \phi(E)), \tag{3.2}$$

for some function β that increases in its second argument. Note that 'acts' stands here as a shorthand for 'acts effectively', where the epithet 'effectively' refers to the fact that the action need only be one-dimensional monotone where it counts, i.e. around zero fitness.

Example 3.1. Assume that we need to deal only with constant environments. Whenever we can write the average lifetime offspring production as

$$R_0(X, E) = \phi(E) R_0(X, E_\mathrm{V}) \tag{3.3}$$

('V' for virgin, where the term 'virgin' refers to the absence of the focal organisms), we can arrive at (3.1) and (3.2) by defining

$$\psi := R_0(X, E_\mathrm{V}),\ \alpha(\psi(X), E) = \beta(X, \phi(E)) := \ln[\phi(E)] + \ln[\psi(X)] = \ln[R_0(X, E)] \tag{3.4}$$

(cf. Example 6.2).

Definitions. We shall call a function ψ of X to the real numbers with the property that evolution maximizes ψ under any constraint on X an *optimization principle*. Similarly, we call a function ϕ of E to the real numbers with the property that evolution minimizes $\phi(E_\mathrm{attr}(X))$ for any constraint on X a *pessimization principle* or *Verelendungs principle*.

The proviso 'for any constraint' in the previous definition mirrors the usual practice of combining an optimization principle, derived from the population dynamics, with a discussion of the dependence of the evolutionary outcome on the possible constraints.

Proposition 3.1. *Models in which the trait vector acts in a monotone one-dimensional manner have an optimization principle, and vice versa.*

The forward implication is immediate as any C satisfying (2.3) for which $\psi(X)$ is not maximal for the X in C is invadable. [Note that by (2.3) ψ is flat on C.] The argument underlying the somewhat unexpected reverse implication is spelled out in the Appendix.

Proposition 3.1 is, of course, a weakened form of the familiar justification for many of our commonly used optimization principles: 'Being more "efficient" increases your fitness in any relevant environment'. (The condition 'in any relevant environment' is crucial, but rarely is mentioned explicitly.)

Similarly, we have

Proposition 3.2. *Models in which the environment acts in a monotone one-dimensional manner have a pessimization principle, and vice versa.*

The forward implication is immediate as any E for which $\phi(E)$ is not minimal is invadable. The argument underlying the somewhat unexpected reverse implication is spelled out in the Appendix.

In the Appendix we construct a β such that (3.2) holds true for the pessimization principle ϕ. This construction also provided the heuristics for the term Verelendungs principle: any ϕ satisfying (3.2), with β increasing in its second argument, allows a natural interpretation as a *measure of environmental quality*, as perceived through the physiology of our individuals.

Proposition 3.2 is, of course, nothing but the ultimate generalization of two familiar evolutionary extremization principles pertaining to the case of population dynamical equilibrium: (i) 'Evolution minimizes the availability of a limiting resource' and (ii) 'Evolution maximizes total population density if the individual life-history parameters are negatively affected by the total population density (and are unaffected by any other environmental variable influenced by the population)'.

Remark 3.1. Principle (i) has a counterpart saying that also population dynamically (i.e. when we may neglect mutations altogether) if there is a single limiting resource for, say, all algae or bacteria in a chemostat, in the end the type that needs the minimum resource concentration to survive remains when the experiment is started with a mixture of types. (All rare mutations do is possibly extend the space of types from which the most thrifty type is chosen.) This extremization principle stands out for its long history and the resulting completeness of its analysis. The resource concentration on which a species just survives was dubbed R^* by Tilman (1982). Powell (1958) may have been the first to have given explicit expression to the general suite of ideas. Tilman (1976; written as Titman) and Hansen and Hubbell (1980) provide early experimental corroborations. For unstructured populations, Hsu *et al.* (1977), Armstrong and McGehee (1980), Wolkowics and Lu (1992), and Li (1999) gave increasingly more encompassing proofs for the purely population dynamical case.

All authors cited above assume that their populations do not have any internal structure. For physiologically structured populations, there exists the possibility of single species oscillations (see, for example, Gurney and Nisbet, 1985; De Roos *et al.*, 1990). Where the space of single resource densities is one-dimensional, the space of resource oscillations is infinite dimensional. Hence, except when the physiology handles the resource fluctuations in an excruciatingly special way, the environment will not act one-dimensionally. When the community dynamics goes to a point-attractor and no species in finite time irreversibly runs out of reproductives [see Example 3.1 in Gyllenberg *et al.* (2003) for the reason for the latter proviso], also in the structured case the species with the lowest R^* remains. For if such were not the case close to the purported equilibrium point the most thrifty species would start growing in numbers, and hence the point cannot be an attractor.

Principle (ii) has an almost equally long theoretical history. Some early papers are Charlesworth (1971; also 1994), Roughgarden (1976; also 1979), Kimura (1978), and Nagylaki (1979). This class of models has not led to any experiments, presumably due to the primarily phenomenological character of the model assumption.

Proposition 3.3. *Any pessimization principle carries an optimization principle in its wake and vice versa.*

This is easily proved by gauging the 'ability to cope' to the 'quality of the environment' through

$$\psi(X) = -\phi(E_{\mathrm{attr}}(X)). \tag{3.5}$$

The above recipe produces a ψ for any ϕ pried out of an expression for ρ, or vice versa. But beware, (3.5) usually does not hold true for a ψ and a ϕ arrived at separately. The strongest possible statement that can be made about two ψ's, or ϕ's, found by different means is that they are necessarily monotonically related.

The construction by which Proposition 3.3 is proved in the Appendix has as a corollary:

Proposition 3.4. *Whenever the trait vector acts in a monotone one-dimensional manner, it is possible to find a function ϕ of E to the real numbers, or alternatively, whenever the environment acts in a monotone one-dimensional manner, it is possible to find a function ψ of X to the real numbers, such that*

$$\operatorname{sign} \rho(X, E) = \operatorname{sign} [\psi(X) + \phi(E)]. \tag{3.6}$$

However, somewhat unexpectedly the aesthetically pleasing symmetry of (3.6) is not very helpful, as usually at most one of the functions ϕ and ψ occurring in it can be expressed as an explicit formula. In contrast, the seemingly less restrictive characterizations of one-dimensional action by means of either (3.1) or (3.2) often can be readily applied.

The arguments in the Appendix are only based on uninvadability considerations. For completeness we summarize some immediately associated evolutionary attractivity properties

Proposition 3.5. *When (i) evolution operates in a context that allows an optimization principle ψ that is at least piecewise continuous, (ii)* (2.3) *applies over all evolutionary trajectories under consideration (as will be the case when reproduction is clonal or when the trajectories do not pass through any polymorphisms), and (iii) the supports of any mutation distributions contain at least the intersection of an ε-neighbourhood of the trait value of the progenitor X with the developmentally realizable subset $\mathbb{X}$ of the trait space, with ε independent of X:*

1. *A unique global optimum of ψ that is not an isolated point of $\mathbb{X}$ has a non-negligible basin of evolutionary attraction. Better still, it will often be a global evolutionary attractor. This happens, for example, when (a) the supports of the mutation distributions equal $\mathbb{X}$, or (b) $\mathbb{X}$ is connected, ψ is continuous, and there are no local optima other than the global one.*
2. *When mutant trait values are restricted to a δ-neighbourhood of X, a particular local optimum of ψ that is not an isolated point of $\mathbb{X}$ will have a non-negligible basin of evolutionary attraction whenever δ is sufficiently small.*

The application of (3.5) immediately yields the corresponding proposition for pessimization principles.

As a final point we mention that (for a monotone one-dimensionally acting environment) $\phi(E_{\mathrm{attr}}(X))$ can be directly determined from

$$\beta(X, \phi(E_{\mathrm{attr}}(X))) = 0\,. \tag{3.7}$$

This allows the construction of a simple general algorithm for numerically analysing any model with a one-dimensionally acting environment: numerically maximize ψ defined by (3.5), where $\phi(E_{\mathrm{attr}}(X))$, at each iteration step, is numerically determined from (3.7). This way there is no need to calculate the potentially unpleasant object $E_{\mathrm{attr}}(X)$.

Remark 3.2. Whether a monomorphic ESS exists at all for an X that maximizes ψ still depends on whether X is in the domain of the map E_{attr}, or, less cryptically phrased, whether there exists an internal community dynamical attractor for X, or, in even more biological terms, whether the community dynamics will support an X-monomorphism. It can also happen that ψ is maximized by more than one value of X. Then the ESS's correspond to the subsets C of the set of optimizing values that are in the domain of E_{attr}. Such a situation will, for example, regularly occur when some high dimensional physiological trait space is mapped to a lower dimensional space of life-history traits. In that case, a manifold of physiological traits may underlie a unique optimal life history. For the clonal case, we may nevertheless expect the end result of an evolutionary transient to be monomorphic: in the presence of an optimization principle, generically two or more trait values brought together to determine whether they can co-exist will have different values of ψ and hence will fail to do so. The extension of this argument to a community constructed by evolution proceeds as follows. The presence of an optimization principle will keep a population monomorphic over the course of an evolutionary transient, as any discrepancy in their ψ values will destroy the co-existence of strains. Therefore, even when unbeatable polymorphisms exist, they do not as such attract, although once the community is at an ESS, in many (but not all) cases there will exist a set of trait values that are neutral relative to each other, which then allows diversification by random drift within this set. For Mendelian populations, the situation is less clear, due to the possibility of short-term attractors that do not satisfy (2.3). Our present guess is that even here a polymorphic ESS will at best attract only very rarely.

4. EXAMPLES

In this section, we consider three examples that may be considered representative for the results of the previous section. The first example serves to demonstrate the various concepts in rigorous detail, unencumbered by technical distractions. Its second purpose is to demonstrate how the formal definition of a one-dimensionally acting environment may possibly differ from one's uninformed mechanistic intuition. The second example demonstrates that, although we know that it exists, it may be difficult to find an explicit pessimization principle from a given optimization principle. The third example shows how it may be possible to find a pessimization principle for non-equilibrium attractors, leading to an otherwise non-obvious optimization principle.

Before starting on the examples, we introduce one more piece of notation as this considerably simplifies their presentation. In unstructured populations, fitness in a potentially fluctuating environment should in the discrete time case be calculated as the logarithm of the geometric mean of the per capita reproduction (starting from newly born individuals) in the different time steps. We shall denote the geometric mean operator as G,

$$G(z) := \lim_{T \to \infty} \sqrt[T]{\prod_{t=1}^{T} z(t)}, \tag{4.1}$$

and its logarithm as L, i.e.

$$L(z) := \lim_{T \to \infty} T^{-1} \sum_{t=1}^{T} \ln(z(t)). \tag{4.2}$$

So as not to unduly complicate the examples, we shall moreover proceed as if reproduction were clonal.

Example 4.1. Consider the following thought experiment. Birds are limited by the availability of nest sites. These sites have a density s. Only birds that have obtained a nest site in spring breed. The number of young M that they produce per capita is an increasing function of their ability to gather energy $\psi(X)$, where X is the trait that is assumed to be under evolutionary control. (X may take any well-defined values, be they discrete or continuous, finite dimensional vectors, or even whole functions.) We measure this ability by the number of offspring it produces:

$$M = \psi(X). \tag{4.3}$$

Old and young survive the winter with a probability p. Next spring, nest sites are allotted randomly among the survivors. Birds that fail to obtain a site are removed from the system.

An obvious choice for the condition of the environment in year t as perceived by a bird is the total density n of winter survivors, of all trait types together,

$$E(t) = n(t)\,. \tag{4.4}$$

We shall present side by side a classical population dynamical calculation, and a calculation along the route laid out above. In neither calculation we take the obvious shortcuts, as this would obstruct their comparison.

We shall distinguish the resident and mutant types by means of the indices 0 and 1. With this notation the population equations become, with $i = 0, 1$,

$$n_i(t+1) = \left(p(1 + M_i)\frac{s}{n(t)}\right) n_i(t) = \left(ps(1 + \psi(X_i))\frac{1}{E(t)}\right) n_i(t)\,, \tag{4.5}$$

with

$$E(t) = n(t) = n_0(t) + n_1(t).$$

(For notational simplicity, we confine ourselves to initial conditions such that consistently $n(t) > s$.)

Applying the definition of ρ from the introduction of Section 2 to (4.5) (without already confining attention to the $E_{\text{attr}}(X)$, which for this particular model necessarily are constant) results in

$$\begin{aligned}\rho(X, E) &= L\left(ps(1 + \psi(X))\frac{1}{E}\right)\\ &= \ln[ps] + \ln[1 + \psi(X)] - L(E).\end{aligned} \tag{4.6}$$

Given the functional form of (4.6) and the verbal model description with which we started, one natural choice for ϕ is

$$\phi(E) := \frac{1}{G(E)}, \tag{4.7}$$

i.e. we measure the quality of the environment of a bird as the inverse of (the geometric mean of) the density of competitors that it encounters when it is searching for a nest site. With this definition we can write

$$\rho(X, E) = \ln[ps] + \ln[1 + \psi(X)] + \ln[\phi(E)]\,. \tag{4.8}$$

From this formula we see that both the trait and the environment act one-dimensionally, with

$$\alpha(\psi(X), E) := \rho(X, E) =: \beta(X, \phi(E))\,. \tag{4.9}$$

The conclusions that ψ is an optimization principle, and ϕ a pessimization principle, come as no surprise. Combining (3.5) with (3.7) and (4.8) leads to the (equivalent) optimization principle:

$$\psi'(X) := -\phi(E_{\text{attr}}(X)) = \frac{-1}{ps(1 + \psi(X))} \tag{4.10}$$

Our first choice was to have our measure for the quality of the environment, ϕ, inversely proportional to the density of conspecifics. The matching ‘ability to cope’, ψ', given by

(4.10), is, of course, monotonically related to energy-gathering ability ψ. A measure of environmental quality that matches the optimization principle, ψ, is given by

$$\phi'(E) = 1 - \frac{1}{ps\phi(E)} = 1 - \frac{G(E)}{ps}. \tag{4.11}$$

For each of these pairs, (3.6) holds good:

$$\operatorname{sign} \rho(X, E) = \operatorname{sign}\,[\psi'(X) + \phi(E)] = \operatorname{sign}\,[\psi(X) + \phi'(E)]. \tag{4.12}$$

For the population dynamical invasion calculation, we set $E(t) = n_0(t)$, with $n_0(t)$ set equal to the mutant-unencumbered equilibrium $\bar{n}_0$, to get

$$n(t) = \bar{n}_0 = ps(1 + \psi(X_0))$$

and

$$\begin{aligned} n_1(t+1) &= ps(1 + \psi(X_1))\frac{n_1(t)}{\bar{n}_0} \\ &= \frac{1 + \psi(X_1)}{1 + \psi(X_0)} n_1(t). \end{aligned} \tag{4.13}$$

(4.13) tells that evolution leads to the optimization of $\psi''(X) := 1 + \psi(X)$.

This example also shows how our unguided intuition may clash with our formal characterizations. Mechanistically, bird density is regulated by the nest sites, but structurally (i.e. in terms of the mathematical relations connecting the various population dynamical variables) by the density of conspecifics competing for those sites. One should be aware of this type of discrepancy when applying Proposition 3.2 to 3.4 in mechanistically formulated examples.

Example 4.2. We make the following changes to the previous example. Losers of the lottery for nest sites are not removed, and winter survival is variable. In that case,

$$\rho(X, E) = L(p) + L\left(1 + \frac{\psi(X)s}{n}\right). \tag{4.14}$$

The fact that $\left(1 + \psi(X)\frac{s}{n(t)}\right)$ increases in ψ, independent of $n(t)$, implies that $L\left(1 + \psi(X)\frac{s}{n(t)}\right)$ and therefore $\rho(X, E)$ increases whenever $\psi(X)$ increases. Since ψ is an optimization principle, by Proposition 3.3 our model allows a pessimization principle ϕ. However, determining ϕ is a different matter. $L(p)$ can be determined by taking the average over time or equivalently over the stationary probability distribution of $p(t)$. Similarly, $L\left(1 + \psi(X)\frac{s}{n(t)}\right)$ can be calculated from the stationary probability distribution of $n(t)$. Hence the set of relevant evolutionary environments corresponds to a one-parameter family of probability distributions on the positive half-line of potential population densities, with scalar parameter ψ. Given such a distribution E, $\phi(E)$ has to be determined by solving (with the scalar dummy variable v in the position of $n(t)$)

$$\int_0^\infty \ln\left(1+\frac{-\phi s}{v}\right) E\{\mathrm{d}v\} + L(p) = 0\,. \tag{4.15}$$

When the $p(t)$, $t \in \mathbb{R}$, are independent, it is possible to write down an integral equation, parameterized with $\psi(X)$, that should be satisfied by the distributions $E_{\mathrm{attr}}(X)$. However, this equation does not appear to be analytically tractable. For general dependent $p(t)$ we cannot even write down an equation for E. E can only be determined by simulating the population development and recording the relative frequencies with which the various population densities are visited. This complicatedness of the recipe for calculating ϕ makes it rather unhelpful.

We primarily included Example 4.2 as a warning. Taken on face value, it might suggest that Propositions 3.1 to 3.4 are for all practical purposes useless. This is not the case. First of all, there are lots of examples where the recipes for going back and forth between a ψ and a ϕ are much nicer. Although such examples in principle are but a small minority among all possible cases, they actually crop up rather frequently among the models that we humans tend to devise. Even more important is that on an abstract level Propositions 3.1 to 3.4 establish a firm ground for further developments such as the ones in the following sections.

Example 4.3. Consider the population dynamical equations

$$n_i(t+1) = a_i(f(E(t)))^{b_i}\, n_i(t), \quad i = 0, \ldots, k,$$

with

$$E(t) = [c_0 n_0(t) + \ldots + c_k n_k(t)]\,, \tag{4.16}$$

all a_i, b_i, and $c_i > 0$, and f decreasing from 1 to 0 for E increasing from 0 to ∞.

With the choice

$$f(E(t)) = [1 + E(t)]^{-1}\,, \tag{4.17}$$

and $k = 0$, this model becomes the model launched into fashion by, among others, Hassell *et al.* (1976) as a touchstone for the appearance of chaotic fluctuations in single species population dynamics.

The trait vector appearing in (4.16) is

$$X = (a, b, c)\,. \tag{4.18}$$

The parameters a, $1/b$, and c can be interpreted in individual-based terms as the per capita reproduction in a boom environment, the ability to cope with a bust environment, and the per capita impingement on the common environment respectively.

From (4.16), we find

$$\rho(X, E) = L[a\,[f(E)]^b] = \ln[a] + b\,\phi(E)\,, \tag{4.19}$$

with

$$\phi(E) = L[f(E)]\,. \tag{4.20}$$

From $\rho(X, E_{\mathrm{attr}}(X)) = 0$, we deduce that

$$\phi(E_{\mathrm{attr}}(X)) = -b^{-1}\ln[a]\,. \tag{4.21}$$

We conclude that evolution maximizes

$$\psi(X) := \frac{\ln[a]}{b}. \tag{4.22}$$

In accordance with Propositions 3.3 and 3.4, we can define the functions α and β that occur in the definitions of monotone one-dimensional action as

$$\alpha(\psi(X), E) := \psi(X) + \phi(E) =: \beta(X, \phi(E)). \tag{4.23}$$

Observe that

$$\rho(X, E) = b(\psi(X) + \phi(E)), \tag{4.24}$$

which shows that α and β are indeed sign equivalent to ρ, but not equal to ρ as was the case in the previous example. It can even be proved that for ρ given by (4.19) it is impossible to find pairs α and ψ, or β and ϕ, for which such an equality holds good.

5. A QUICK AND NOT TOO DIRTY PRACTICAL TEST

In addition to being of general philosophical relevance in their own right (since they show what exceptional conditions have to be fulfilled for an extremization principle to exist), the criteria from Propositions 3.1 and 3.2 can be used as tools for deriving more practical criteria for special model families, or for answering general questions for more constrained scenarios such as when evolution will maximize r or R_0 (cf. Section 6). However, deriving more concrete criteria may still require considerable mathematical ingenuity. Hence, it is of interest in addition to have a quick practical test to determine whether a particular eco-evolutionary model might satisfy an optimization principle.

Whenever the types can be parameterized with a continuous one-dimensional trait x, the presence or absence of an optimization principle may be judged from the shape of the so-called pairwise invasibility plots (Metz *et al.*, 1996a; Geritz *et al.*, 1998) [the idea originated with Matsuda (1985) and independently with Van Tienderen and De Jong (1986)]. Pairwise invasibility plots (PIPs) are plots, with a one-dimensional x in the position of X and y in that of Y, of the sign structure of the invasion fitness function $s_X(Y) := \rho(Y, E_{\mathrm{attr}}(X))$ (see Fig. 1). The existence of an optimization principle is equivalent to

$$s_{X_1}(X_2) \gtreqless 0 \qquad \Leftrightarrow \qquad s_{X_2}(X_1) \lesseqgtr 0, \tag{5.1}$$

as counterpart of

$$\psi(X_2) \gtreqless \psi(X_1) \qquad \Leftrightarrow \qquad \psi(X_1) \lesseqgtr \psi(X_2),$$

together with

$$s_{X_1}(X_2) \gtreqless 0 \qquad \text{and} \qquad s_{X_2}(X_3) \gtreqless 0 \qquad \Rightarrow \qquad s_{X_1}(X_3) \gtreqless 0, \tag{5.2}$$

as counterpart of

$$\psi(X_2) \gtreqless \psi(X_1) \qquad \text{and} \qquad \psi(X_3) \gtreqless \psi(X_2) \qquad \Rightarrow \qquad \psi(X_3) \gtreqless \psi(X_1).$$

For one-dimensional X, the anti-symmetry condition (5.1) is equivalent to skew symmetry of the PIP, i.e. flipping the PIP over the main diagonal only exchanges the + and – signs (see Fig. 1). The transitivity condition (5.2) moreover has as a consequence that any

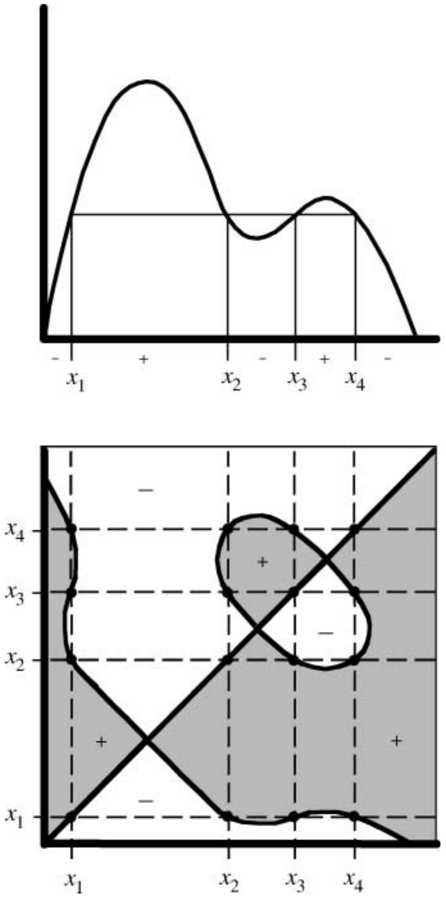

Fig. 1. The pictorial counterpart in a pairwise invasibility plot (PIP) of the skew symmetry and transitivity conditions (5.1) and (5.2). The PIP does not change when it is flipped over the diagonal and blank areas are shaded and vice versa. The trait values x_1 to x_4 are all equivalent, in the sense that $\psi(x_4) = \psi(x_3) = \psi(x_2) = \psi(x_1)$. The transitivity condition then implies that vertically above each of these trait values there should be the same alternation of plusses and minuses. Moreover, due to the skew symmetry of the PIP, the same pattern should show up, with plusses and minuses swapped, in the horizontal direction to the right of each of these trait values. The combined effect of all such equivalences is a characteristic relation between any isolas and wiggles of the remaining zero contours.

trait values x_i and x_j for which $\psi(x_i) = \psi(x_j)$ are equivalent. Hence, vertically above these trait values there should be the same alternation of plusses and minuses. Moreover, thanks to the skew symmetry of the PIP, the same pattern should show up, with plusses and minuses swapped, in the horizontal direction to the right of each of these trait values. The result is that any isolas of the non-diagonal zero-contour curve (corresponding to local maxima of the optimization principle that are exceeded by its global maximum) have counterparts in wiggles in any other non-diagonal zero-contour curves that span the same range of trait values, either horizontally or vertically (see Fig. 1). A representative sample of configurations is depicted in Fig. 2. Whenever the PIPs of a particular eco-evolutionary

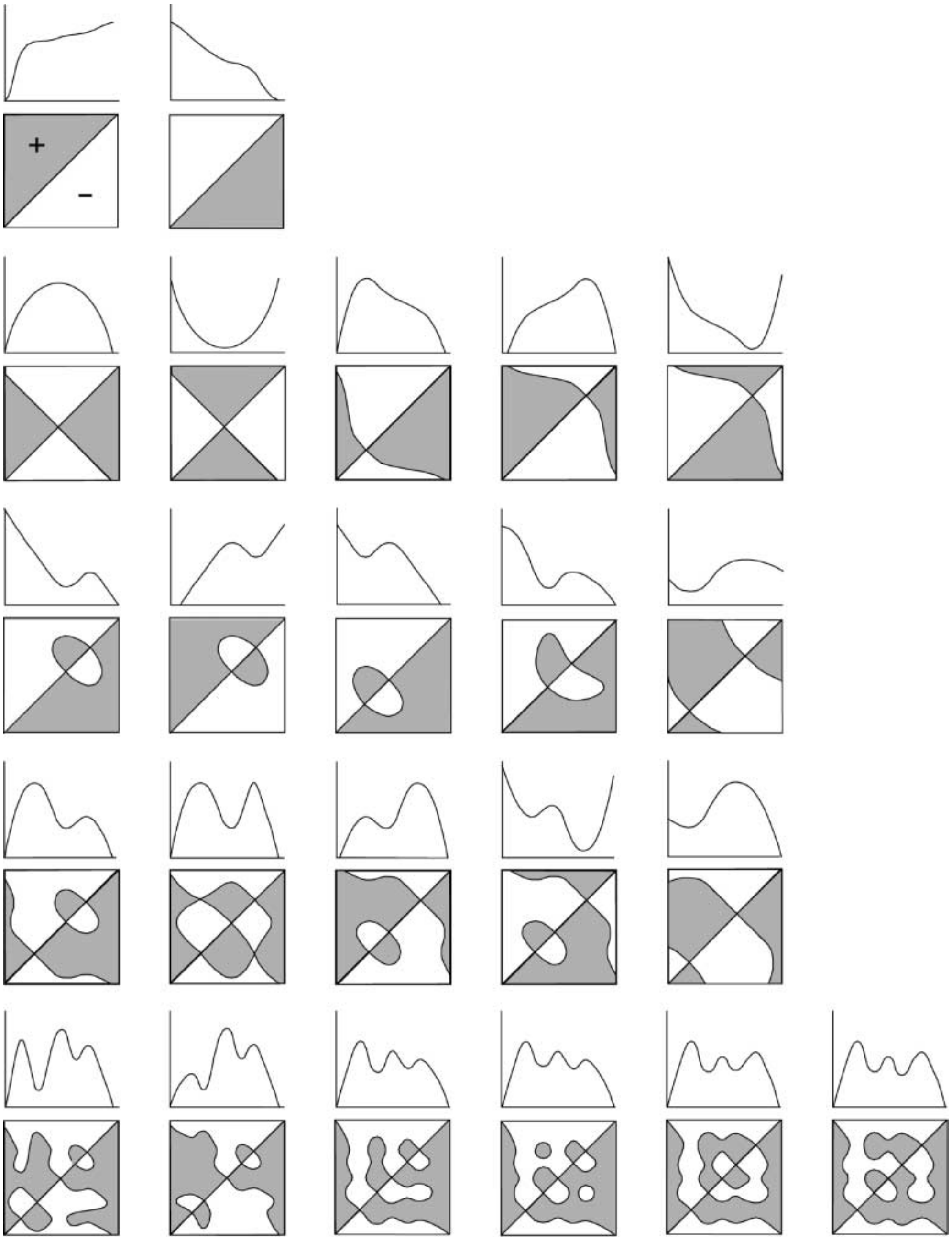

Fig. 2. Possible optimization principles (upper rows: horizontal axes = adaptive trait, vertical axes = quantity optimized by evolution), together with their corresponding pairwise invasibility plots (lower rows: horizontal axes = resident trait, vertical axes = mutant trait). [This figure appeared as Figure 5 in Dieckmann and Metz (2006).]

model look like the ones in Fig. 2, this can be considered as indicative for the existence of an optimization principle.

In the case of higher dimensional continuous traits, an eco-evolutionary model supports an optimization principle if and only if all possible one-dimensional sub-models with trait spaces defined by curves $\{X(x) \mid x \in \mathbb{R}\}$, support an optimization principle. Hence a good guess can be made whether a model with a higher dimensional trait space supports an optimization principle through the consideration of a representative sample of one-dimensional sub-models.

Some other criteria derived from Proposition 3.2 for the (non-)existence of an optimization principle applicable to higher dimensional trait spaces are discussed in Dieckmann and Metz (2006, Section 4 and Appendix A).

6. WHEN DOES EVOLUTION MAXIMIZE *r* OR R_0?

In this section, we consider the optimization principles of classical life-history theory, to wit r- and R_0- maximization, and thereby provide the larger context for the examples in Mylius and Diekmann (1995). Since r and R_0 are only defined for constant environments, we shall from now on (i) assume that population dynamical equilibrium obtains, and (ii) have the symbol E refer alternatively to a potential condition of the environment at a particular time, or to constant functions of time having that condition of the environment as their value.

For constant environments

$$\rho(X, E) = r(X, E). \tag{6.1}$$

Moreover,

$$r(X, E) \gtreqless 0 \qquad \text{if and only if} \qquad R_0(X, E) \gtreqless 1, \tag{6.2}$$

allowing the replacement of $\rho(X, E)$ in the recipes of Sections 2 and 3 by $\ln[R_0(X, E)]$ (see, for example, Roughgarden, 1979; Metz and Diekmann, 1986; Charlesworth, 1994).

Incidentally, although the usual definitions of r and R_0 are predicated upon all individuals being born equal, they can readily be extended to cater for variable birth states and spatial heterogeneity. The only proviso is that E should be constant in time (see, for example, Diekmann *et al.*, 1990; Jagers, 1991, 2001; Kawecki and Stearns, 1993; Kozlowski, 1993; Diekmann and Metz, 1994).

Below E_0 denotes some *a priori* chosen fixed value of E.

The following proposition is an immediate corollary of Proposition 3.1.

Proposition 6.1. $r(X, E_0)$, *or* $R_0(X, E_0)$, *is an optimization principle for, and only for, combinations of life histories and ecological embedding, such that there exists a function* α *increasing in its first argument such that*

$$\operatorname{sign} r(X, E) = \operatorname{sign} \alpha(r(X, E_0), E), \tag{6.3}$$

or

$$\operatorname{sign} \ln[R_0(X, E)] = \operatorname{sign} \alpha(\ln[R_0(X, E_0)], E) \tag{6.4}$$

respectively.

Remark 6.1. The result from Proposition 3.4 allows us to replace the characterizations from Proposition 6.1 by the characterization that there should exist a function ϕ of E to the real numbers such that

$$\text{sign}\, r(X, E) = \text{sign}\, [r(X, E_0) + \phi(E)] \tag{6.5}$$

or

$$\text{sign}\, \ln[R_0(X, E)] = \text{sign}\, [\ln[R_0(X, E_0)] + \phi(E)], \tag{6.6}$$

respectively. This characterization may in theory be equivalent to the characterization from Proposition 6.1, but in practice it is less useful as ϕ rarely pops up as an explicit formula, whereas it is usually fairly easy to spot the α occurring in the characterization from Proposition 6.1.

In the epidemiological literature, examples abound where $R_0(X, E_V)$ is an optimization principle, with E_V the virgin (i.e. disease-free) environment. When no E_0 is specified, as is often the case in the life-history literature, this entails the implicit assumption that every E_0 will do. Below we introduce the terminology to make this explicit and then show shat such situations are characterized by identities that do not involve the sign function.

Remark 6.2. A convention of logic is that when a statement is not explicitly indicated as pertaining to a specific individual case, or subset of cases, it should be interpreted as pertaining to all possible cases. This convention is itself but a formalization of the human habit of interpreting open statements such as 'ravens are black' as meaning that all ravens are black and not as some ravens are black, or as ravens are black only under certain circumstances.

Definitions. We shall say that *evolution just maximizes r, or* R_0, whenever $r(X, E_0)$ or $R_0(X, E_0)$ respectively is an optimization principle for every choice of E_0.

Proposition 6.2. *Evolution just maximizes r, or* R_0, *if and only if it deals with combinations of life histories and ecological embedding such that is possible to write*

$$r(X, E) = \alpha(r(X, E_0), E), \tag{6.7}$$

or

$$R_0(X, E) = \exp[\alpha(\ln[R_0(X, E_0)], E)] \tag{6.8}$$

respectively, with α *increasing in its first argument, and* E_0 *fixed.*

The particular choice of E_0 in (6.7) and (6.8) is arbitrary, as these formulas imply that formulas of a similar form result when we change to another value of E_0.

A proof of Proposition 6.2 is given in the Appendix.

Example 6.1. Whenever the environment makes itself felt only through an additional death rate $\mu(E)$, acting equally on all individuals, $r(X, E)$ can be expressed as

$$r(X, E) = r(X, E_V) - \mu(E), \tag{6.9}$$

where E_V is the virgin environment. Therefore, evolution within those confines just maximizes r.

Example 6.2. In this example, we generalize the classic finding (e.g. De Jong *et al.*, 1987; Charnov, 1993) that if all density dependence is due to nursery competition, we may use R_0 optimization to determine the ESS's for any post-nursery traits.

Let the life history consist of a number of subsequent stages. Call a stage reproductive if reproduction is possible during, or before as well as after that stage, and all preceding stages 'pre-reproductive'. If there is no overlap between the sets of pre-reproductive stages affected by, respectively, X and E and the reproductive stages are affected by at most one of those two variables, the average lifetime offspring production can be expressed as

$$R_0(X, E) = \phi(E)\, R_0(X, E_\text{V}), \tag{6.10}$$

where E_V is the virgin environment. Therefore, evolution within those confines just maximizes R_0.

We refer the reader to the companion paper (Metz *et al.*, 2008) in this issue for some contrived examples that show that scenarios where the trait and the environment act in well-separated groups of life stages are not the only ones where the ESS can be calculated by just maximizing R_0. Although we expect the former scenarios to be the only ones leading to R_0 optimization that come with a clear direct mechanistic basis, we have not yet been able to formalize the necessary concepts sufficiently for this statement to become (dis)provable. Hence we only showcase the above ideas as an example instead of a proposition.

7. CONCLUDING REMARKS

The main relevance of our propositions is that they rigorously show that on an abstract level the suite of simple Examples 4.1 to 4.3 are representative of all population dynamical scenarios allowing an evolutionary extremization principle. Such scenarios only differ in the – unfortunately sometimes quite horrible – technical details of the calculations.

Our propositions also show that having an extremization principle really is a rather special property.

In the intuitively obvious case, we can point to an intermediate scalar quantity, which, when increased, increases fitness *in all relevant environments*. As it turns out, the environments that matter are those stationary environments that can potentially be generated by the family of communities under consideration as reactions to particular values of the trait vector. A technical elaboration moreover shows that the initial requirement can be weakened by replacing the word 'fitness' by the phrase 'some quantity that is sign-equivalent with fitness'. This technical variant we have dubbed 'monotone one-dimensional action' of the trait vector (or strategy parameters, if your leaning is ecological instead of taxonomical).

The other, slightly less obvious, scenario is that the environment acts in a monotone one-dimensional manner (in the aforementioned technical sense). We have proved that these two cases are effectively only one case and, what is more, the *only* case allowing an evolutionary extremization principle. Proposition 3.4 tells moreover that in that case the trait vector and the environment by necessity act not only in a monotone one-dimensional manner but also, in a certain technical sense, independently.

It is our conviction that it is only our own, unwitting or deliberate, moulding of evolutionary scenarios that leads to the frequent occurrence of extremization principles in the life-history models studied in the literature. For more complicated feedback rules, shortcuts in the form of an optimization principle do not exist!

There is an abundance of papers in the literature dealing with models in which the environment acts higher dimensionally. One interesting aspect of such models is that they may allow for evolutionary diversification, which cannot occur with effectively one-dimensional environments. A good assortment of references may be found on the website http://mathstat.helsinki.fi/~kisdi/ad.htm kept up by Éva Kisdi. These models are generally not so much geared to analysing the effect of the effective dimensionality *per se*, as to showcasing particular biological phenomena. On the foundational side, the next step should be to develop concepts and tools for systematically cataloguing the possible scenarios when there are not one but two essential scalar components of environmental action. Some of the first contributions to such an analysis can be found in Meszéna and Metz (1999) and Heino *et al.* (1997).

The cases where evolution just maximizes r or R_0 are still considerably more rare. First, the community should generate only constant environments. Second, the dependencies of r or R_0 on the trait vector in these different environments should be monotonically related.

In conclusion, the choice of a single optimization criterion, be it R_0 or r or still something else, entails very special assumptions about the nature of the environmental feedback loop. The current literature consistently under-emphasizes this aspect.

ACKNOWLEDGEMENTS

The work of S.D. Mylius was supported by the Life Sciences Foundation (SLW) subsidized by the Netherlands Organization for Scientific Research (NWO). Peter Klinkhamer, James McAllister, and Jan Sevenster provided useful comments on a previous version of the manuscript. This paper is an extended version of the first part of IIASA Working Paper #WP-96-04 (Metz *et al.*, 1996b). After having had this paper in the drawer after initial rejections for more than 10 years, we are grateful to *Evolutionary Ecology Research* for allowing its comeback, to Éva Kisdi for soliciting us to submit and exposing us to two rounds of extensive and very useful comments, and to Michael Rozenzweig for whipping the abstract into the required shape.

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APPENDIX: THEOREMS UNDERLYING THE STATEMENTS IN SECTIONS 3 AND 6

In the main text, we presented our propositions in an order that seemed natural in view of their interpretation and/or application. The order in which these results are naturally deducible is rather different. Therefore, we make a fresh start. The propositions of the main text should be seen primarily as a convenient summary of the results from the arguments below.

Convention. Whenever we refer to r or R_0 we implicitly restrict ourselves to community dynamical scenarios for which $E_{\mathrm{attr}}(C)$ is time-constant for all relevant C. Otherwise, we only require E to be ergodic (and realizable as $E_{\mathrm{attr}}(C)$ for some C). The virgin environment will be denoted as E_{V}.

The following four theorems and corollaries are trivial. The crux is in the questions that follow them.

Theorem A1. If there exist functions ψ of X, and α of ψ and E, to the real numbers, with α increasing in ψ, such that

$$\operatorname{sign} \rho(X, E) = \operatorname{sign} \alpha(\psi(X), E), \tag{A1}$$

then evolution maximizes $\psi(X)$ (or equivalently $\alpha(\psi(X), E)$ for any fixed E).

Theorem A2 (universal Verelendungs principle). If there exist functions ϕ of E, and β of X and ϕ, to the real numbers, with β increasing in ϕ, such that

$$\operatorname{sign} \rho(X, E) = \operatorname{sign} \beta(X, \phi(E)), \tag{A2}$$

then evolution minimizes $\phi(E_{\mathrm{attr}}(C))$ (or equivalently $\beta(Y, \phi(E_{\mathrm{attr}}(C)))$ for any Y).

Corollary A3. If we can write $r(X, E)$ in the form

$$r(X, E) = \alpha(\psi(X), E), \tag{A3}$$

with α increasing in ψ, then evolution maximizes $r(X, E_{\mathrm{V}})$ (and, more generally, $r(X, E_0)$ for any fixed E_0).

Corollary A4. If we can write $R_0(X, E)$ in the form

$$R_0(X, E) = \exp[\alpha(\psi(X), E)], \tag{A4}$$

with α increasing in ψ, then evolution maximizes $R_0(X, E_V)$ (and, more generally, $R_0(X, E_0)$ for any fixed E_0).

Questions:

1. Is there any relation between Theorems A1 and A2?
2. Can Theorems A1 and A2 be made into 'if and only if' statements, for example by requiring that the extremization principle should hold independent of whatever choice we may still make for a constraint on X?
3. Is this also possible for Corollaries A3 and A4?

Theorem A5 (answer to Question 1). The assumptions of both Theorems A1 and A2 are equivalent to: There exist functions ϕ of E and ψ of X to the real numbers, such that

$$\operatorname{sign} \rho(X, E) = \operatorname{sign} [\psi(X) + \phi(E)]. \tag{A5}$$

Proof. Assumption 1: Define the function ϕ of E to the real numbers by $\alpha(-\phi(E), E) = 0$. Then,

$$\operatorname{sign} \rho(X, E) = \operatorname{sign} \alpha(\psi(X), E) = \operatorname{sign} [\psi(X) + \phi(E)]. \tag{A6}$$

Therefore, the assumption of Theorem A1 implies the assumption made above. The converse implication follows by taking $\alpha(\psi, E) = \psi + \phi(E)$.

Assumption 2: Let $\psi(X) := -\phi(E_{\mathrm{attr}}(X))$. As $\beta(X, \phi(E_{\mathrm{attr}}(X))) = 0$,

$$\operatorname{sign} \rho(X, E) = \operatorname{sign} \beta(X, \phi(E)) = \operatorname{sign} [\phi(E) - \phi(E_{\mathrm{attr}}(X))] = \operatorname{sign} [\phi(E) + \psi(X)]. \tag{A7}$$

Therefore, the assumption of Theorem A2 implies the assumption made above. The converse implication is obvious.

Apparently we may without loss of essential information replace $\alpha(\psi, E)$ by $\psi + \phi(E)$ and $\beta(X, \phi)$ by $\psi(X) + \phi$, with ϕ and ψ defined above.

Remark A1. The use of the sign function in (A5) is essential and the reasoning underlying Theorem A5 does not extend to Corollaries A3 and A4. From $r(X, E) = \alpha(\psi(X), E)$, we cannot even conclude that there exist functions ϕ' of E and ψ' of X such that $r(X, E) = \psi'(X) + \phi'(E)$. Neither can we conclude from $R_0(X, E) = \exp[\alpha(\psi(X), E)]$ that there exists functions ϕ' of E and ψ' of X such that $R_0(X, E) = \exp[\psi'(X) + \phi'(E)]$.

The next lemma is again trivial. However, it forms a natural introduction to the somewhat unexpected, though on second thoughts equally trivial, Theorem A7.

Lemma A6. If we require that we can determine the ESS under any possible constraint by maximizing a function ψ of X, then

$$\operatorname{sign} [\psi(X_1) - \psi(X_2)] = \operatorname{sign} \rho(X_1, E_{\mathrm{attr}}(X_2)) \tag{A8}$$

Proof. Put as a constraint that X is restricted to $\{X_1, X_2\}$ and just check the identity for all values that the left-hand side might have.

Theorem A7 (first part of the answer to Question 2):

(1) If there exists a function ψ of X to the real numbers such that we can determine the ESS value(s) of X (whenever such values exist) by maximizing ψ, independent of any choice that we may still make for a constraint on X, then there exists a function ϕ of E such that (A5) applies.

(2) If there exists a function ϕ of E to the real numbers such that we can determine the ESS value of X by minimizing $\phi(E_{\text{attr}}(X))$, independent of any choice that we may still make for a constraint on X, then there exists a function ψ of X such that (A5) applies.

Proof. In case (1) we define ϕ by $\phi(E_{\text{attr}}(X)) := -\psi(X)$. In case (2) we define $\psi(X) := -\phi(E_{\text{attr}}(X))$. To derive (A5), consider all possible constraints of the type $X \in \{X_1, X_2\}$ and use Lemma A6. This gives (A5) for all E that can be written as $E_{\text{attr}}(X)$. To extend the result to the remaining E, using (2.3) implies that

– if the trait acts monotonically as well as one-dimensionally,

$$\psi(X_1) = \psi(X_2) \text{ whenever there exists a } C \text{ such that } X_1, X_2 \in C; \tag{A9}$$

– if the environment acts monotonically as well as one-dimensionally,

$$\phi(E_{\text{attr}}(X_i)) = \phi(E_{\text{attr}}(C)) \qquad \text{for all } X_i \in C. \tag{A10}$$

Just for completeness, we give a result about the degree of uniqueness of the functions ϕ and ψ.

Theorem A8:

(1) If we require that we can determine the ESS under any possible constraint by maximizing a function ψ of X, then this function is uniquely determined up to an increasing transformation.

(2) If we require that that we can determine the ESS under any possible constraint by minimizing a function ϕ of $E \in E_{\text{attr}}(X)$, then this function is uniquely determined up to an increasing transformation.

(3) The functions ϕ and ψ are uniquely determined by their counterparts.

Proof. (1) Consider two different functions ψ_1 and ψ_2 that both allow determination of the ESS under any constraint, then by Lemma 6

$$\operatorname{sign}[\psi_1(X_1) - \psi_1(X_2)] = \operatorname{sign} \rho(X_1, E_{\text{attr}}(X_2)) = \operatorname{sign}[\psi_2(X_1) - \psi_2(X_2)]. \tag{A11}$$

Hence

$$\psi_1(X_1) \gtrless \psi_1(X_2) \qquad \text{iff} \qquad \psi_2(X_1) \gtrless \psi_2(X_2) \tag{A12}$$

(3) Consider again all constraints where X is restricted to $\{X_1, X_2\}$. Maximizing $\psi(X)$ or minimizing $\phi(E_{\text{attr}}(X))$ will only predict the right ESS for these constraints if $\operatorname{sign}[\psi(X_i) + \phi(E_{\text{attr}}(X_j))] = \operatorname{sign} \rho(X_i, E_{\text{attr}}(X_j))$ for all values of i and j. Uniqueness of ϕ given ψ and of ψ given ϕ follows from the fact that $\operatorname{sign}[\psi(X) + \phi(E_{\text{attr}}(X))]$ should be 0.

(2) follows from (1) and (3).

Apparently, any optimization principle ψ automatically carries a pessimization principle ϕ in its wake, and vice versa.

Corollary A9 (last part of the answer to Question 2). We may replace the opening 'if's of Theorems A1 and A2 by 'iff's.

Proof. Choose $\alpha(\psi(X), E) := \psi(X) + \phi(E) =: \beta(X, \phi(E))$.

Corollary A10 (first part of the answer to Question 3):

(1) If we can determine the ESS value of X by maximizing $r(X, E_0)$ for some special value E_0 of E, independent of any choice that we may still make for a constraint on X, then there exists a function ϕ of E such that

$$\operatorname{sign}\,[r(X, E_0) + \phi(E)] = \operatorname{sign}\, r(X, E)\,. \tag{A13}$$

(2) If we can determine the ESS value of X by maximizing $R_0(X, E_0)$ for some special value E_0 of E, independent of any choice that we may still make for a constraint on X, then there exists a function ϕ of E such that

$$\operatorname{sign}\,[\ln[R_0(X, E_0)] + \phi(E)] = \operatorname{sign}\,\ln[R_0(X, E)]\,. \tag{A14}$$

To get any representation of $r(X, E)$ or $R_0(X, E)$ itself, we need to make a stronger assumption about the sense in which evolution maximizes r and R_0.

Theorem A11 (last part of the answer to Question 3):

(1) If the maximization principle from Corollary A10 (1) holds good for all possible choices of E_0, then it is possible to write

$$r(X, E) = \alpha(\psi(X), E)\,, \tag{A15}$$

with α increasing in its first argument and $\psi(X) = r(X, E_0)$ for some arbitrary, but fixed, E_0.

(2) If the maximization principle from Corollary A10 (2) holds good for all possible choices of E_0, then it is possible to write

$$R_0(X, E) = \exp[\beta(\psi(X), E)]\,, \tag{A16}$$

with β increasing in its first argument and $\psi(X) = \ln[R_0(X, E_0)]$ for some arbitrary, but fixed, E_0.

Proof. The maximization of, say, $\gamma(X, E)$, with E fixed, can only lead to the same solution as the maximization of $\gamma(X, E_0)$ for all possible constraints if $\gamma(X, E_0)$ and $\gamma(X, E)$, considered as functions of X, are related by an increasing function: $\gamma(X, E) = f(\gamma(X, E_0), E, \gamma)$, where the last argument is at this stage only notational. For any given E (and γ), this function f is necessarily unique. (To prove this, copy the idea of the proof of Lemma A6.) In cases (1) and (2) respectively, we define $\alpha(\psi, E) := f(\psi, E, r)$ and $\beta(\psi, E) := \ln[f(\psi, E, R_0)]$.