When Does Evolution Optimise?

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Contents

When does evolution optimise?

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ABSTRACT

Goal: Elucidating the role of the eco-evolutionary feedback loop in determining evolutionarily stable life histories, with particular reference to the methodological status of the optimisation 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 stategy X_r: $E = E_{attr}(X_r)$.

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

Results: It is necessary and sufficient for the existence of an optimisation 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 optimisation principle, have a special easily recognisable shape. Natural selection just maximises r, or R_0, if and only if $r(X,E)$ can be written as $\alpha(r(X,E_0),E)$, respectively $R_0(X,E)$ 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 optimisation approach holds water only when the eco-evolutionary feedbacks are of a particularly simple kind.

1. Introduction

The literature is replete with statements that evolutionary predictions about e.g. behavioural or life history parameters should be based on the maximisation of individual lifetime reproductive success, R_0 (Stearns, 1992, Roff, 1992, Charnov, 1993, Charlesworth, 1994, provide surveys), or else the intrinsic rate of natural increase, r (Stearns, 1992, Roff, 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 e.g. Charnov, 1993, and its review by Maynard Smith, 1993). No doubt most authors dealing with life history theory know how to interpret the last statement, and are aware of the implicit limitations of the traditional optimisation considerations. However, some asking around indicated that this awareness (i) has little diffusion among experimentalists, and (ii) appears rather dim even among most theorists. Our quick and dirty survey also revealed that probably the main cause of this small awareness is that advertising positive predictions gives 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 maximised 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 characterisable by some optimisation principle, and more in particular by straight r- or R_0-maximisation. 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?
(iii) We describe the special patterns visible in Pairwise Invasibility Plots that are characteristic for the presence of an optimisation principle.

In a companion paper (Metz et al., 2008) 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 optimisation 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 the patterns in the parameters determined under laboratory conditions. The various feedback loops led to very different optimisation principles and, without any clear relation to the optimisation 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 without being 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 & Diekmann (1995). There various examples of sufficient conditions for the existence of an optimisation

principle are demonstrated. Here we characterise 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 (Charlesworth, 1994; Tuljapurkar, 1989, 1990; Caswell, 2000; Metz et al., 1992; Rand et al., 1994; Ferrière & Gatto, 1995; Metz, 2008). The term "ergodic" in the preceding statement 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 nonexistence of different regimes occurring with nonzero 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 needs some elaboration: We have to discount offspring each generation by a factor 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 count 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. See the arguments below, and Metz et al. (1996a) and Metz (2008) for a further elaboration.

Our verbal definition immediately brings out 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

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

(c.f. Diekmann & Metz, 1994, and Mylius & Diekmann, 1995).

A potential source of confusion may be that as E refers to the environment as perceived by the individuals, for instance density and types of conspecifics may come as part and parcel of E (Michod, 1979; Metz & Diekmann, 1986; Pásztor, 1988; Metz & de Roos, 1992; Diekmann & 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 e.g. Taylor, 1988a, 1988b, 1989 for technicalities), but in ultimate generality the concept of fitness resists further extension. Luckily, the range of conditions covered is sufficiently large that we need not be overly bothered.

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

1. Maximise $\rho(X,E)$ for each given E over all potential trait values, resulting in a function $X_{opt}(E)$.
2. Determine for each trait value the environment that it generates as a resident, $E_{attr}(X)$. (The notional index "attr" alludes to the assumption that the population dynamics converges to an attractor. If such 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

$$X_{opt}(E_{attr}(X^*)) \ = \ X^*. \tag{2.2}$$

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 $\rho(X_{i+1},E_{attr}(X_i)) > 0$, 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 ESSes, customarily called CSSes, is relevant for making predictions (c.f. Eshel, 1983; Taylor, 1989; Eshel, 1996; Geritz et al. 1998).

The above description is only meant as a definition, not as a practical algorithm. The general procedure 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 ESSes, 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 coexist will be denoted as $C = \{X_1,\ldots, X_k\}$, the corresponding environments as $E_{attr}(C)$. For monomorphic and for clonal populations

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

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 ESSes, characterised by (2.3) together with the fact that each trait in C^* maximises fitness in $E_{attr}(C^*)$.

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 realised by genotypes with one or more heterozygote loci. Such constraints tend to be specific and there is little chance that ever a general theory can be built telling 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 realisable subset of the trait space.*

Proposition 2.1 (e.g. Bulmer, 1994; see also Eshel & 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 ESSes, by which we mean that they satisfy (2.3) and each trait in C^* maximises fitness in $E_{attr}(C^*)$.

Proof: Define R_0 of a phenotype as half the lifetime offspring production by that phenotype. Then for phenotypes as well as for alleles $R_0 \gtrless 1 \Leftrightarrow \rho \gtrless 0$. 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 e.g. 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 each trait in C^* were to maximise fitness in $E_{attr}(C^*)$, there would exist a trait value having a positive fitness in $E_{attr}(C^*)$, 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 (c.f. Hammerstein & Selten, 1994, and 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 coexisting phenotypes have different fitnesses not all of these fitnesses are negative (while yet the population persists indefinitely!). Therefore, the mathematical question is whether it is possible that while the allelic averages of the growth rate over birth states and time are zero, yet the corresponding averages for the phenotypes could be all negative. Although such a statement feels 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 ESSes.*

The previous considerations imply that Assumption A implies assumption B for (i) clonally reproducing populations, (ii) cases where there are no ESSes 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 $E_{attr}(C)$ for which (2.3) holds good. As this restriction becomes essential in the arguments below we introduce the

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

3. When does evolution optimise?

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 extremisation principle (like the maximisation of R_0 or r or the minimisation 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 the companion paper Metz et al (2008).

First we give some

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

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

for some function α which 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

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

for some function β which 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 needs 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

$$R_0(X,E) = \phi(E)R_0(X,E_V) \tag{3.3}$$

('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

$$\psi := R_0(X, E_v), \quad \alpha(\psi(X), E) = \beta(X, \phi(E)) := \ln[\phi(E)] + \ln[\psi(X)] = \ln[R_0(X, E)] \quad (3.4)$$

(c.f. Example 6.2).

Definitions: We shall call a function ψ of X to the real numbers with the property that evolution maximises ψ under any constraint on X an *optimisation principle*. Similarly, we call a function ϕ of E to the real numbers with the property that evolution minimises $\phi(E_{\text{attr}}(X))$ for any constraint on X, a *pessimisation 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 optimisation 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 optimisation principles: "Being more "efficient" increases your fitness in any relevant environment." (The condition "in any relevant environment" is crucial, but rarely is mentioned explicitly.)

Likewise we have

Proposition 3.2: *Models in which the environment acts in a monotone one-dimensional manner have a pessimisation 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 pessimisation 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 generalisation of two familiar evolutionary extremisation principles pertaining to the case of population dynamical equilibrium: (i) "Evolution minimises the availability of a limiting resource", and (ii) "Evolution maximises 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 which 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 extremisation 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 be the first to have given explicit expression to the general suite of ideas. Tilman (1976;

written as Titman) and Hansen & Hubbell (1980) provide early experimental corroborations. For unstructured populations Hsu et al. (1977), Armstrong & McGehee (1980), Wolkowics & 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 e.g. Gurney & Nisbet (1985) and 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 about equally long theoretical history. Some early papers are Charlesworth (1971; also 1994), Roughgarden (1976; also 1979), Kimura (1978) and Nagylaki (1979; also 1992). 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 pessimisation principle carries an optimisation principle in its wake and vice versa.*

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

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

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*

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

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 characterisations 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 summarise some immediately associated evolutionary attractivity properties

Proposition 3.5: *When (i) evolution operates in a context that allows an optimisation 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 realisable 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 pessimisation principles.

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

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

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

Remark 3.2: Whether a monomorphic ESS exists at all for an X that maximises 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 maximised by more than one value of X. Then the ESSes correspond to the subsets C of the set of optimising 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 optimisation principle generically two or more trait values brought together to see whether they can coexist will have different values of ψ and hence will fail to do so. The extension of this argument to a community constructed by evolution goes as follows. The presence of an optimisation principle will keep a population monomorphic over the course of an evolutionary transient, as any discrepancy in their ψ values will destroy the coexistence 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 demonstrating 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 pessimisation principle from a given optimisation principle. The third example shows how it may be possible to find a pessimisation principle for non-equilibrium attractors, leading to an otherwise non-obvious optimisation 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.

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

In order 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 $i = 0, 1$,

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

with $\quad\quad\quad\quad\quad\quad\quad\quad\quad\quad\quad\quad\quad\quad\quad\quad\quad\quad\quad\quad\quad\quad\quad\quad\quad\quad$ (4.5)

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

(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 the attention to the $E_{attr}(X)$ which for this particular model necessarily are constant) results in

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

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

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

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

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

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

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

The conclusions that ψ is an optimisation, and ϕ a pessimisation principle, will not come as a surprise. Combining (3.5) with (3.7) and (4.8) leads to the, equivalent, optimisation principle

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

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 which matches the optimisation principle ψ, is given by

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

For each of these pairs (3.6) holds good:

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

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

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

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

This example also shows how our unguided intuition may clash with our formal characterisations. Mechanistically the 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 watch out for this type of discrepancy when applying proposition 3.2 to 3.4 in mechanistically formulated examples.

Example 4.2: We make the following changes in 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 $L\left(1+\psi(X)\frac{s}{n}\right)$ and therefore $\rho(X,E)$ increases whenever $\psi(X)$ increases. Since ψ is an optimisation principle, by Proposition 3.3 our model allows a pessimisation 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, parametrised 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 put example 4.2 in 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 forth and back 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

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

with $\qquad$ (4.16)

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

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

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

and $k = 0$, this model becomes the model launched into fashion by i.a. Hassell, Lawton & May (1976) as a touchstone for the appearance of chaotic fluctuations in single species population dynamics.

The trait vector appearing in (4.16) is

$$X = (a,b,c). \qquad (4.18)$$

The parameters a, $1/b$, and c can be interpreted in individual-based terms as respectively 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.

From (4.16) we find

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

with

$$\phi(E) = L[f(E)]. \qquad (4.20)$$

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

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

We conclude that evolution maximises

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

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

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

Please observe that

$$\rho(X,E) = b(\psi(X) + \phi(E)) \qquad (4.24)$$

showing 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 extremisation 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 like when evolution will maximise r or R_0 (c.f. Section 6). However, deriving more concrete criteria may still ask for considerable mathematical ingenuity. Hence, it is of interest in addition to have a quick practical test to see whether a particular eco-evolutionary model might satisfy an optimisation principle.

Whenever the types can be parameterised with a continuous one-dimensional trait x, the presence or absence of an optimisation 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,1995, and independently with Van Tienderen & De Jong, 1996). 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 $s_X(Y) := \rho(Y, E_{attr}(X))$; see Figure 1. The existence of an optimisation principle is equivalent to

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

as counterpart of

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

together with

$$s_{X_1}(X_2) \gtreqless 0 \quad \& \quad s_{X_2}(X_3) \gtreqless 0 \quad \Rightarrow \quad s_{X_1}(X_3) \gtreqless 0, \qquad\qquad (5.2)$$

as counterpart of

$$\psi(X_2) \gtreqless \psi(X_1) \quad \& \quad \psi(X_3) \gtreqless \psi(X_2) \Rightarrow \quad \psi(X_3) \gtreqless \psi(X_1).$$

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 Figure 1. The transitivity condition (5.2) moreover has as consequence that any 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 optimisation 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 Figure 1). A representative sample of configurations is depicted in Figure 2. Whenever the PIPs of a particular eco-evolutionary model look like the ones in that figure, this can be considered as indicative for the existence of an optimisation principle.

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

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

6. When does evolution maximise r or R_0?

In this section we consider the optimisation principles of classical life history theory, to wit r- and R_0- maximisation, and thereby provide the larger context for the examples in Mylius & 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 value.

For constant environments

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

Moreover,

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

allowing the replacement of $\rho(X,E)$ in the recipes of Sections 2 and 3 by $\ln[R_0(X,E)]$. (See e.g. Roughgarden, 1979, Charlesworth, 1994, Metz & Diekmann, 1986.)

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 e.g. Diekmann et al., 1990, Jagers, 1991, 2001, Kawecki & Stearns, 1993, Kozlowski, 1993, Diekmann & 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 optimisation 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*

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

or

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

respectively.

Remark 6.1: The result from Proposition 3.4 allows us to replace the characterisations from Proposition 6.1 by the characterisation 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 characterisation may in theory be equivalent to the characterisation 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 characterisation from Proposition 6.1.

In the epidemiological literature examples abound where $R_0(X,E_V)$ is an optimisation 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 characterised 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 formalisation of the human habit of interpreting open statements like "raven are black" as meaning that all raven are black and not as some raven being black, or raven being black only under certain circumstances.

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

Proposition 6.2: *Evolution just maximises* 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 can be found 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

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

E_V the virgin environment. Therefore evolution within those confines just maximises r.

Example 6.2: In this example we generalise 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 optimisation for determining the ESSes 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

$$R_0(X,E) \,=\, \phi(E)\, R_0(X, E_V), \tag{6.10}$$

E_V the virgin environment. Therefore evolution within those confines just maximises R_0.
We refer to the companion paper Metz et al. (2008) 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 maximising R_0. Although we expect the former scenarios to be the only ones leading to

R_0 optimisation that come with a clear direct mechanistic basis, we have not yet been able to formalise the necessary concepts sufficiently for this statement to become (dis)provable. Hence we only showcase the above ideas as 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 extremisation principle. Such scenarios only differ in the, unfortunately sometimes quite horrible, technical details of the calculations.

Our propositions also show that having an extremisation 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 extremisation 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 extremisation principles in the life history models studied in the literature. For more complicated feedback rules shortcuts in the form of an optimisation 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 well as to showcasing particular biological phenomena. At the foundational side the next step should be to develop concepts and tools for systematically cataloguing the possible scenarios when there is not one but two essential scalar components of environmental action. Some first contributions to such an analysis can be found in Meszéna (1999) and Heino et al. (1997).

The cases where evolution just maximises r or R_0 are still considerably more rare. First of all the community should generate only constant environments. Secondly 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 optimisation 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 underemphasises this aspect.

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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 which 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 $E_{attr}(X)$ is time-constant for all relevant X. Otherwise we only require E to be ergodic (and realisable as $E_{attr}(X)$ for some X). 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 A.1: If there exist functions ψ of X, and α of ψ and E, to the real numbers, with α increasing in ψ, such that

$$\text{sign } \rho(X,E) \quad = \text{ sign } \alpha(\psi(X),E) \tag{A.1}$$

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

Theorem A.2 (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

$$\text{sign } \rho(X,E) \quad = \text{ sign } \beta(X,\phi(E)) \tag{A.2}$$

then evolution minimises $\phi(E_{attr}(X))$ (or equivalently $\beta(Y,\phi(E_{attr}(X)))$ for any Y).

Corollary A.3: If we can write $r(X,E)$ in the form

$$r(X,E) = \alpha(\psi(X),E), \tag{A.3}$$

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

Corollary A.4: If we can write $R_0(X,E)$ in the form

$$R_0(X,E) = \exp[\alpha(\psi(X),E)], \tag{A.4}$$

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

Questions:
1. Is there any relation between Theorems A.1 and A.2?
2. Can Theorems A.1 and A.2 be made into "if and only if" statements, e.g. by requiring that the extremisation principle should hold independent of whatever choice we may still make for a constraint on X?
3. Is this also possible for Corollaries A.3 and A.4?

Theorem A.5 (answer to question 1)**:** The assumptions of both Theorems A.1 and A.2 are equivalent to: There exist functions ϕ of E, and ψ of X to the real numbers, such that

$$\text{sign } \rho(X,E) \ = \ \text{sign } [\psi(X)+\phi(E)]. \tag{A.5}$$

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

$$\text{sign } \rho(X,E) \ = \text{sign } \alpha(\psi(X),E) \ = \ \text{sign } [\psi(X)+\phi(E)]. \tag{A.6}$$

Therefore the assumption of Theorem A.1 implies the assumption made above. The converse implication follows by taking $\alpha(\psi,E) = \psi + \phi(E)$.

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

$$\text{sign } \rho(X,E) \ = \text{sign } \beta(X,\phi(E)) = \text{sign}[\phi(E)-\phi(E_{\text{attr}}(X))] = \ \text{sign}[\phi(E)+\psi(X)]. \tag{A.7}$$

Therefore the assumption of Theorem A.2 implies the assumption made above. The converse implication is obvious.

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

Remark A.1: The use of the sign function in (A.5) is essential and the reasoning underlying Theorem A.5 does not extend to Corollaries A.3 and A.4: 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 thought equally trivial, Theorem A.7.

Lemma A.6: If we require that we can determine the ESS under any possible constraint by maximising a function ψ of X, then

$$\text{sign}[\psi(X_1)-\psi(X_2)] \ = \ \text{sign } \rho(X_1, E_{\text{attr}}(X_2)) \tag{A.8}$$

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 sign might have.

Theorem A.7 (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 maximising 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 (A.5) 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 minimising $\phi(E_{\text{attr}}(X))$, independent of any choice that we may still make for a constraint on X, then there exists a function ψ of X such that (A.5) 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 (A.5) consider all possible constraints of the type $X \in \{X_1,X_2\}$ and use Lemma A.6. This gives (A.5) for all E that can be written as $E_{\text{attr}}(X)$. To extend the result to the remaining E use that (2.3) implies that

- if the trait acts monotonically as well as one dimensionally

$$\psi(X_1) = \psi(X_2) \ \text{ whenever there exists a } C \text{ such that } X_1, X_2 \in C, \tag{A.9}$$

as well as

- if the environment acts monotonically as well as one dimensionally

$$\text{for all } X_i \in C \qquad \phi(E_{attr}(X_i)) = \phi(E_{attr}(C)).$$
(A.10)

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

Theorem A.8:
(1) If we require that we can determine the ESS under any possible constraint by maximising 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 minimising a function ϕ of $E \in E_{attr}(X)$ then this function is uniquely determined up to an increasing transformation.
(3) The functions ϕ respectively ψ are uniquely determined by their counterparts.

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

$$\text{sign}[\psi_1(X_1)\text{-}\psi_1(X_2)] = \text{sign }\rho(X_1, E_{attr}(X_2)) = \text{sign}[\psi_2(X_1)\text{-}\psi_2(X_2)].$$
(A.11)

Hence

$$\psi_1(X_1) \gtreqless \psi_1(X_2) \qquad \text{iff} \qquad \psi_2(X_1) \gtreqless \psi_2(X_2)$$
(A.12)

(3) Consider again all constraints where X is restricted to $\{X_1, X_2\}$. Maximising $\psi(X)$ or minimising $\phi(E_{attr}(X))$ will only predict the right ESS for these constraints if $\text{sign}[\psi(X_i)+\phi(E_{attr}(X_j))] = \text{sign }\rho(X_i, E_{attr}(X_j))$ for all values of i and j. Uniqueness of ϕ given ψ respectively ψ given ϕ follows from the fact that $\text{sign}[\psi(X)+\phi(E_{attr}(X))]$ should be 0.
(2) follows from (1) and (3).

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

Corollary A.9 (last part of the answer to question 2)**:** We may replace the opening "if"s of Theorems A.1 and A.2 by "iff"s.

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

Corollary A.10 (first part of the answer to question 3)**:**
(1) If we can determine the ESS value of X by maximising $r(X,E_0)$ 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

$$\text{sign}[r(X,E_0)+\phi(E)] = \text{sign }r(X,E).$$
(A.13)

(2) If we can determine the ESS value of X by maximising $R_0(X,E_0)$ 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

$$\text{sign}[\ln[R_0(X,E_0)]+\phi(E)] = \text{sign }\ln[R_0(X,E)].$$
(A.14)

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 maximises r respectively R_0:

Theorem A.11 (last part of the answer to question 3)**:**
(1) If the maximisation principle from Corollary A.10 (1) holds good for all possible choices of E_0, then it is possible to write

$$r(X,E) = \alpha(\psi(X),E), \quad\quad\quad (A.15)$$

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

(2) If the maximisation principle from Corollary A.10 (2) holds good for all possible choices of E_0, then it is possible to write

$$R_0(X,E) = \exp[\beta(\psi(X),E)], \qu\quad\quad (A.16)$$

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 maximisation of, say, $\gamma(X,E)$, E fixed, can only lead to the same solution as the maximisation 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 A.6.) In cases (1) and (2) we define $\alpha(\psi,E) := f(\psi,E,r)$ respectively $\beta(\psi,E) := \ln[f(\psi,E,R_0)]$.

Legends to the figures

Figure 1: The pictorial counterpart in a 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 all such equivalences is a characteristic relation between any isolas and wiggles of the remaining zero contours.

Figure 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 Fig. 5 in Dieckmann & Metz (2006).
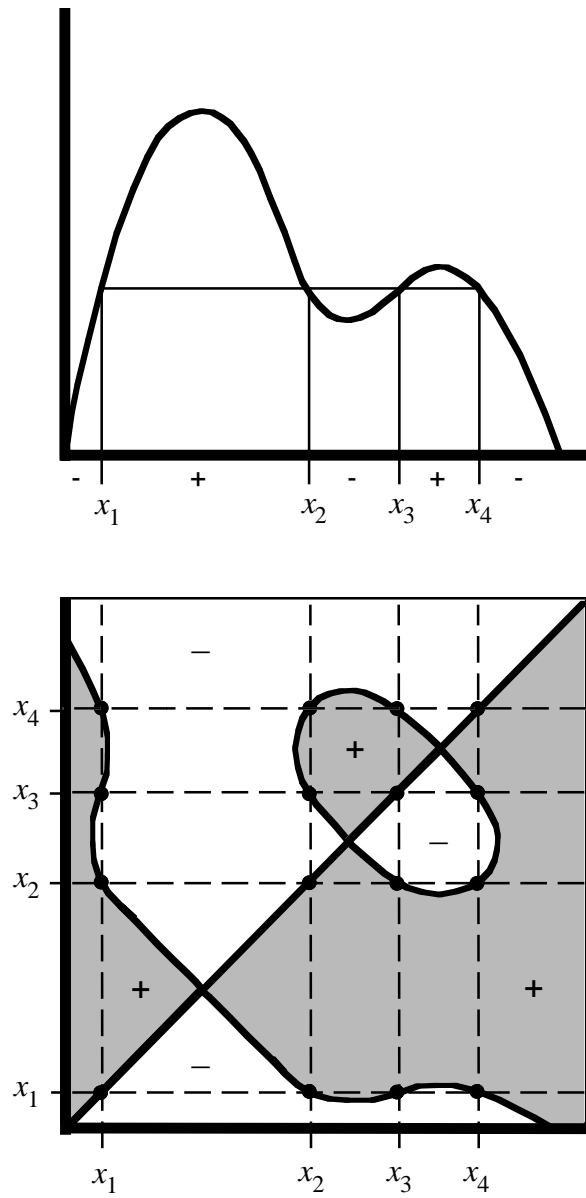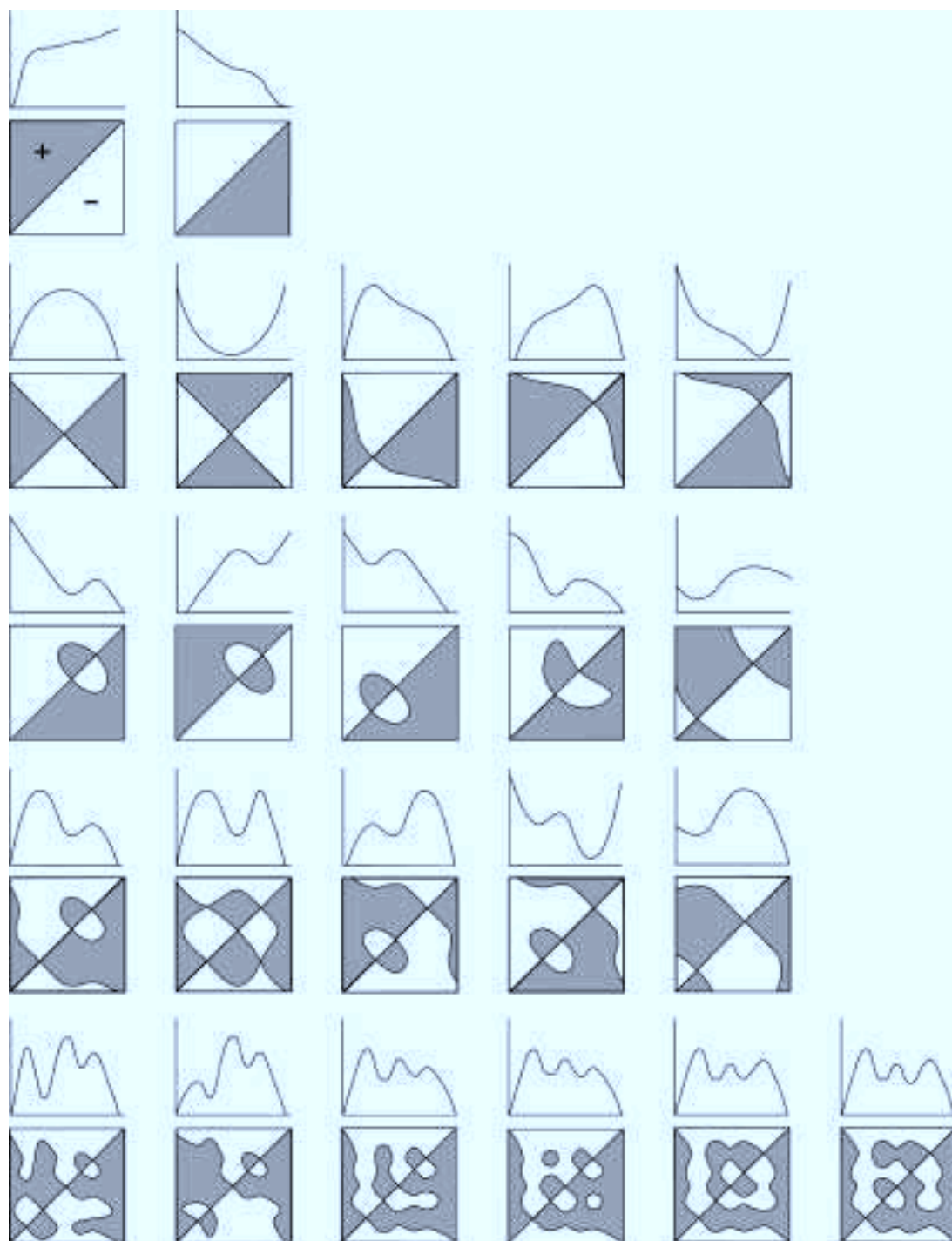
Figure 1

Figure 2