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Even in the Odd Cases When Evolution Optimises, Unrelated Population Dynamical Details May Shine Through in the ESS

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Even in the Odd Cases When Evolution Optimises, Unrelated Population Dynamical Details May Shine Through in the ESS

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Even in the odd cases when evolution optimises, unrelated population dynamical details may shine through in the ESS

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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 assumptions: 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 ideas developed in the companion paper (Metz et al. 2008) to rig simply analysable, as they have an optimisation principle, eco-evolutionary scenarios to explore the potential of the environmental feedback to influence evolutionary predictions, and to see in what ways the predictions relate to the tools.

Results: Equipping the classical model for the evolution of maturation time with various possible feedback loops leads to different optimisation principles as well as qualitatively different predicted relations between the field values of adult mortality μ_A and maturation time T. When E influences only T, the ESS, T^*, decreases with μ_A. When E influences either only juvenile mortality or only both juvenile and adult mortality in equal measure, T^* increases with μ_A. When E influences only the reproduction rate, T^* is independent of μ_A. When E influences only adult mortality, the environmental feedback loop fixes adult mortality at a constant level so that there is no relationship between T^* and μ_A to speak of. These six cases are subject to three different optimisation principles. There turns out to be no relation between optimisation principle and predicted features.

Conclusions: Even in cases where there happens to exist an optimisation principle, the evolutionary outcomes can be largely determined by other aspects of the population dynamical embedding. The existence of an optimisation principle is technically helpful, biologically very restrictive and has in general no further biological relevance.

1. Introduction

This paper and its companion Metz et al. (2008) were originally conceived as a single manuscript. The reason for splitting that manuscript into two is that this way we hope to prevent it from suffering the same fate as its predecessor Mylius & Diekmann (1995), which is cited far more often for its description of tools for rigging eco-evolutionary models so as to give them an optimisation principle, rather than for the equally important message that models that have optimisation principles are exceptional, and that rigging a model to have such a principle potentially excludes a plethora of evolutionary phenomena, among which the persistence of any diversity (see appendix A).

Optimisation principles may be restrictive, but as long as we keep those restrictions in mind, it can help to rig a model to have one, as this makes for an easy evolutionary analysis. More specifically, when the goal is demonstrating particular phenomena as opposed to cataloguing potential ones, the rather severe restrictions entailed by imposing an optimisation principle may do little harm.

If a community resides at a coevolutionarily steady strategy coalition, each of its species also resides at an ESS for a community where only that species can evolve and the others have their traits fixed at the ESS values. Similarly, when we concentrate on but a few components of a vectorial trait that is sitting at an ESS, those components also reside at an ESS for a model where we only allow those component traits to evolve while all other component traits are kept fixed at the ESS values. Hence, as long as we only consider uninvadability, concentrating on a subproblem can give us correct insights, provided that the real system that we try to predict indeed has reached an evolutionary endpoint. Only the attractivity of a subproblem may differ from that of the problem as a whole. So, concentrating on a simpler subproblem that may allow an optimisation principle need not lead to wrong results. It only severely limits one's scope.

The above argument no longer applies when we, as we will do below, aim at comparing ESSes for different situations, for then additional traits that we implicitly assume to be fixed may actually also vary evolutionarily for the systems that we have in mind. Therefore additional justifications are needed. Below we consider the evolution of the age at maturation. The justification for restricting the attention to this trait on its own can only be that it may be supposed to respond rather quickly relative to other more deeply engrained life history characteristics, so that we may assume those other characteristics to stay constant on the time scale that is implicit in our considerations.

Below we will explore the extent to which the nature of the environmental feedback loop may influence life history predictions. We do not aim higher than proving that there can be large effects. This limited aim makes it methodologically sound to rig the model to have an optimisation principle. In all cases we assume that a community with residents having trait value X relaxes to a point attractor, with corresponding environment $E_{\mathrm{attr}}(X)$. In such environments the invasion fitness ρ reduces to the intrinsic rate of natural increase r. In addition to the general procedure for indirectly constructing an optimisation principle

(i) if there exists a quantity $\phi(E_{\mathrm{attr}}(X))$ minimized by evolution then evolution maximises

$$\psi(X) = -\phi(E_{\mathrm{attr}}(X)), \tag{1.1}$$

we use two direct optimisation principles that derive from special features of the life history:

(ii) whenever the environment makes itself felt only through an additional death rate $\mu(E)$, acting equally on all individuals, evolution maximises $r(X,E_0)$ for any fixed environment E_0,

and

(iii) when the life history can be subdivided into a number of subsequent stages, pre-reproductive ones, reproductive ones, and post-reproductive ones (where we call a stage reproductive when reproduction is possible in it or before as well as after it), then, if there is no overlap between the sets of pre-reproductive stages affected by X and E, and the reproductive stages are affected by at most one of those two variables, the average lifetime offspring number can be expressed as, with E_V the virgin environment,

$$R_0(X,E) = \phi(E)\, R_0(X, E_V), \tag{1.2}$$

and evolution maximises $R_0(X,E_0)$ for any fixed environment E_0.

The companion paper (Metz et al. 2008) discusses on a general level the conditions for the existence of evolutionary optimisation principles and their reduction to r- and R_0-maximisation, as well as the restrictions such an existence imposes on the ecological theatre.

2. Model description

As did Charnov (1993) and Mylius & Diekmann (1995), we consider the following simple family of life histories: Juveniles die at a rate μ_J and mature into adults at age T. Adults die at a rate μ_A and reproduce at a rate b. E may in principle affect all these parameters. Their values in the virgin environment E_V we shall indicate with an (additional) index V. The strategy parameter is the length of the juvenile period in the virgin environment, T_V. To keep the calculations as simple as possible we assume that the adult reproduction rate b increases linearly with T_V; in the virgin environment

$$b(T_V,E_V) = b_V(T_V) = \max\{0,T_V-1\}. \tag{2.1}$$

In addition we (i) brashly assume that population dynamical equilibrium obtains, and (ii) have the symbol E refer alternatively to a constant or to a constant function of time.

We combine this basic scenario with six alternative environmental feedback rules (parameters for which nothing is specified are assumed always to take the value for the virgin environment):

1. E only equally and additively affects the juvenile and adult mortality rates,

$$\mu_J(E) = \mu_{JV} + \gamma_1(E), \qquad \mu_A(E) = \mu_{AV} + \gamma_1(E) \tag{2.2}$$

2. E only additively affects the adult mortality rate,

$$\mu_A(E) = \mu_{AV} + \gamma_2(E), \tag{2.3}$$

3. E only multiplicatively affects the reproduction rate,

$$b(T_V,E) = \frac{b_V(T_V)}{\theta_3(E)}, \tag{2.4}$$

4. *E* only additively affects the age at maturation (without affecting the birth rate) in such a manner that for a constant environment

$$T(E) = T_V + \gamma_4(E), \tag{2.5}$$

5. *E* only multiplicatively affects the age at maturation (without affecting the birth rate), in such a manner that for a constant environment

$$T(E) = \theta_5(E)\, T_V, \tag{2.6}$$

6. E only additively affects the juvenile mortality rate,

$$\mu_J(E) = \mu_{JV} + \gamma_6(E). \tag{2.7}$$

For definiteness we assume that

$$\gamma_i(E) \geq \gamma_i(E_V) = 0 \text{ for } i = 1, 2, 4, 6,$$
and
$$\theta_j(E) \geq \theta_j(E_V) = 1 \text{ for } j = 3, 5. \tag{2.8}$$

3. Analysis

For fixed values of T_V and E we can, directly from our initial model description, derive the characteristic equation (for models of this ilk usually called Euler-Lotka equation)

$$\frac{b\, e^{-(r+\mu_J)T}}{r+\mu_A} = 1, \tag{3.1}$$

as well as an explicit expression for R_0,

$$R_0 = \frac{b\, e^{-\mu_J T}}{\mu_A}. \tag{3.2}$$

Below we shall use a * to mark the value of a quantity at the ESS.

Feedback rule 1 makes our model fall under Rule (ii) from the introduction. Therefore we can determine T_V^* by maximising $r(\cdot, E_V)$. In appendix C we describe a simple way to calculate the, unique, maximum.

Feedback rules 2 to 4 all lead to a formula for R_0 which, although the biological mechanism at first sight differs from that considered in rule (iii) from the introduction, can be brought into the form (1.2) with

$$R_0\left(T_V, E_V\right) = \frac{b_V(T_V)\, e^{-\mu_{JV} T_V}}{\mu_{AV}}, \tag{3.3}$$

and

$$\text{case 2:} \qquad \phi(E) = \frac{\mu_{AV}}{\mu_{AV} + \gamma_2(E)}, \tag{3.4}$$

$$\text{case 3:} \qquad \phi(E) = \frac{1}{\theta_3(E)}, \tag{3.5}$$

$$\text{case 4:} \qquad \phi(E) = e^{-\mu_{JV}\gamma_4(E)}. \tag{3.6}$$

In Appendix B we show how to reinterpret the model formulation of these cases so that they indeed fit Rule (iii) from the introduction. (Please note that our reinterpretations there are no more than conceptual tricks and need not bear any relation to the real mechanisms potentially underlying the chosen functional forms.)

Case 5 does not fall under the direct Rules (ii) or (iii) from the introduction. However, it is easily seen from the interpretation that $\theta_5(E)$ monotonically affects R_0, and that hence evolution minimises $\theta_5(E_{\text{attr}}(X))$. Therefore we fall back on the general procedure (i), with ϕ set equal to $1/\theta_5$, i.e., we set

$$R_0(T_V, E_{\text{attr}}) = \frac{b_V(T_V)\,\mathrm{e}^{-\mu_{JV}\theta_5(E_{\text{attr}})T_V}}{\mu_{AV}} = 1, \tag{3.7}$$

in order to calculate the optimisation principle $\psi(T_V) := -\theta_5(E_{\text{attr}}(T_V))$. It turns out that we are lucky, and we end up with the explicit expression (after multiplying out the constant factor μ_{JV})

$$\psi(T_V) = \frac{\ln\left(b_V(T_V)\right) - \ln(\mu_{AV})}{T_V}. \tag{3.8}$$

The story for case 6 is exactly the same as for case 5, with $-\gamma_6$ in the role of ϕ, even to the extent that we end up with the same optimisation principle.

Remark: In principle, case 1 can be analysed by exactly the same procedure as cases 5 and 6, except that it is not possible to find an explicit expression for $\gamma_1(E_{\text{attr}}(T_V))$. And rule (ii) from the introduction tells that anyway the resulting optimisation principle would be monotonically related to $r(\cdot, E_V)$.

Further details of the analysis may be found in appendix C.

4. Results

After the mathematics comes the interpretation problem. In the classic life history models this is less of a problem, as it is assumed that on the time scale of our measurements the life history parameters of individuals are constant, instead of being potentially under environmental control. In the case of the present model we have to distinguish two situations in which the measurements can be collected, called "laboratory" and "field". In the laboratory situation the environment is kept constant, whereas in the field situation the environment adjusts itself such that

$$R_0(T_V^*, E) = 1. \tag{4.1}$$

For the feedback rules 1 to 6 the values of the life history parameters in the laboratory situation differ from those in the virgin environment by at most either an additive or a multiplicative factor. The field values are obtained by adjusting the virgin parameter values, where appropriate, by $\gamma_i(E)$ or $\theta_j(E)$ determined from (4.1).

We focus on field observables. Figure 1 shows the correlations obtaining between T^* and μ_A, for a fixed value of μ_{JV}, for each of the six feedback rules as they operate in the field. Apparently different feedback rules can lead to radically different patterns. Figure 2 differs from panel 1 of Figure 1 by whether we plot cases with matching values of μ_{JV} (Figure 1) or matching values of μ_J (Figure 2). The second

picture corresponds to a protocol in which we select species, or populations, on the basis of their equality of the observed value of μ_J, the first picture to a protocol where we select them for their a priori expected similarity with respect to μ_{JV}. Although conceptually different, the two protocols induce similar predictions. In cases 2 to 6 the predictions for the two protocols are even exactly the same. In cases 2 to 5 this is due to the assumption that $\mu_J = \mu_{JV}$, in case 6 to what appears to be just an algebraic quirk.

As a contrast we may consider the relations between T_V^* and μ_{AV}, with μ_{JV} fixed, to give a feel for what may be expected for the relations between laboratory observables. The plots for cases 1, 3 and 6 look like the corresponding panels in Figure 1, those for cases 2 and 4 like panel 3, and the plot for case 5 is equal to that for case 6. Clearly there is a necessity to distinguish between field and laboratory observables as the same evolutionary outcomes can look very different when expressed in either type of observables.

Remark: Since the model is meant only as an illustration of principle, but probably does not match any specific real situation in quantitative detail, we refrained from including plots for all the different possible parameter combinations. Here is a description of the remaining possibilities. The plots of T^* against μ_J, with μ_{AV} fixed, all show a roughly hyperbolically decreasing relation, like in panel 4 of Figure 1. The plots of T_V^* against μ_{JV}, with μ_{AV} fixed, show either a decreasing relation, in cases 1 to 4, or a horizontal line in cases 5 and 6.

5. Concluding remarks

The model, and more in particular Figure 1, shows how the details of the environmental feedback loop can have a non-trivial influence on the predicted relationships between life-history parameters. The qualitative nature of the relation between the age at maturation in the field and the field adult mortality shows a clear relation with the nature of the environmental feedback loop. However, no such relation can be seen with the optimisation principles that the models happen to posses.

A secondary message is that any relations between field values of life history parameters may be rather different from the ones we would get if we were to cut the environmental feedback loop and measure the same parameters not in the field but in organisms grown in the lab.

The overall methodological conclusion is that although optimisation principles may come in handy for the analysis, they apparently have little biological meaning. In addition the restrictions that have to be imposed to produce an optimisation principle i.a. a priori exclude what may well be the most appealing feature of the evolutionary process, its power to adaptively generate diversity.

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Appendix A: Evolutionary optimisation excludes diversity

Only in the absence of an optimisation principle it is possible for a community to adaptively generate diversity at so-called branching points in the space of the trait vectors by which we distinguish our types (Metz et al., 1996a; Geritz et al., 1998). The results in Section 5 of the companion paper Metz et al. (2008) about the restricted nature of the PIPs of models with an optimisation principle imply that any singular points are necessarily either ESSes or both invadable and repelling, leaving no room for such exotics as repelling ESSes or branching points. The ecological explanation of the latter is that branching points require the possibility for the coexistence of two species in a so-called protected "polymorphism". In accordance with the general principle of competitive exclusion (e.g. Levin, 1970; Meszéna et al., 2006) such coexistence is impossible when locally the effective dimension of the environment is one, that is, if in the neighbourhood of the prospective branching point there exists a function ϕ of the environments E and a function β of the trait vectors X and the real numbers such that sign $\rho(X,E)$ = sign $\beta(X,\phi(E))$, $\rho(X,E)$ the invasion fitness of type X in the environment E. In the companion paper we prove that, if we restrict the considered environments to those environments $E_{\mathrm{attr}}(C)$ that can occur as community dynamical attractors for some coalition of phenotypes $C = \{X_1,\ldots,X_k\}$ such that $\rho(X,E_{\mathrm{attr}}(C)) = 0$ for all $X \in C$, the existence of such functions is implied by the existence of an optimisation principle. More strongly, the functions ϕ and β are global and in addition β is monotone in its second argument if and only if an optimisation principle exists. We refer to the full combination of requirements as the environment acting in a monotone one-dimensional manner.

To see that in the presence of an overarching optimisation principle generally no diversity can remain unless genetic constraints prevent the optimal type from being realized as a homozygote (assuming that we identify types that are equal in all their population dynamical properties, or, equivalently, that differ only in some population dynamically irrelevant markers), we can use an extension of the argument in Remark 3.1 from the companion paper. We first observe that the invasion fitness concept (Metz et al, 1992; Rand et al. 1995; Metz, 2008) that underlies our considerations is so general that it not only applies within but also among species as long as these are coupled within a single (possibly even spatially distributed) community. To explore the consequences of this generality we have to consider a trait space that is sufficiently encompassing that it allows differentiating between species as well as between types within a species. Now assume that an optimisation principle exists on that trait space. We have already seen that such is the case if and only if the environment acts effectively in a monotone one-dimensional manner. When on the way to an attractor no species in finite time runs out of reproductives (see Example 3.1 in Gyllenberg et al. (2003) for the reason for this proviso), necessarily out of a mixture of species and types within species only the type with the lowest ϕ remains. For if such were not the case, in the environment generated by the purported attractor, call it ***A,*** the type with the lowest ϕ would start growing in numbers, which contradicts that ***A*** is an attractor. Remains the rare possibility that more than one type globally minimises ϕ. Although this is possible in principle, in practice it will be so rare that we can ignore it for all practical purposes. In a more mathematical vein: almost any small perturbation of the modelling framework (such as in nature are brought about by changes in ecological circumstances) will remove the coincidence.

Appendix B: Bringing cases 2 to 4 in line with rule (iii) from the introduction.

We can, by slightly reinterpreting the model formulation, make each of the cases 2 to 4 into a special case subsumed under rule (iii) from the introduction. This is done by introducing a third stage which is either the only stage affected by E, and is not affected by T_V, or the only stage affected by T_V, and is not affected by E. We shall consider the cases in opposite order.

Case 4: We split the juvenile period into a basic juvenile period of length T_V, and a subadult period of length $\gamma_4(E)$.

Case 3: We introduce an infinitesimally short nursery stage before the juvenile stage. Adults reproduce according to $b_V(T_V)$. Nursery survival is $1/\theta_3(E)$.

Case 2: We again apply the nursery stage trick, except that we now assume that the adult reproduction rate and nursery survival are

$$b_M = \max_{T_V}\{b_V(T_V)\}, \quad \text{and} \quad \frac{b_V(T_V)}{b_M} \quad \text{respectively.} \tag{B.1}$$

Of course this trick only works for models with a maximum to the juvenile period, as else (B.1) makes no sense. The unconstrained case then is covered through the use of a limit argument.

Appendix C: Mathematical details of the analysis.

Case 1: We consider the maximisation of r defined by

$$g(r,T_V) = 1, \tag{C.1}$$

with

$$g(r,T_V) = \frac{b_V(T_V)\mathrm{e}^{-(r+\mu_{JV})T_V}}{r+\mu_{AV}}. \tag{C.2}$$

Implicit differentiation of (C.1) gives

$$\frac{\partial r}{\partial T_V}\frac{\partial g}{\partial r} = -\frac{\partial g}{\partial T_V}. \tag{C.3}$$

From (C.2) we see immediately that g decreases in r. Therefore $\partial g/\partial r < 0$. It is also easy to see (i) that $\partial g/\partial T_V < 0$ for T_V sufficiently large, and (ii) that the fact that $b_V(1) = 0$, and that b_V increases in T_V, imply that $\partial g/\partial T_V > 0$ for $T_V = 1$. Therefore r has at least one maximum in $(1,\infty)$.

To calculate that maximum we set $\partial r/\partial T_V = 0$ in (C.3). This tells us that at $T_V = T_V^*$

$$\frac{\partial g}{\partial T_V} = 0. \tag{C.4}$$

By differentiating (C.2) for T_V we find that

$$\frac{\partial g}{\partial T_V} = \frac{\partial b_V}{\partial T_V}\frac{g}{b_V} - \left(r+\mu_{JV}\right)g. \tag{C.5}$$

Substitution of the resulting relation

$$\left(r+\mu_{\mathrm{JV}}\right)=\frac{\mathrm{d}\ln\left[b_{\mathrm{V}}\right]}{\mathrm{d}T_{\mathrm{V}}} \tag{C.6}$$

in (C.1) with (C.2) gives

$$b_{\mathrm{V}}\left(T_{\mathrm{V}}\right)\exp\left[-\frac{\mathrm{d}\ln\left[b_{\mathrm{V}}\right]}{\mathrm{d}T_{\mathrm{V}}}T_{\mathrm{V}}\right]=\frac{\mathrm{d}\ln\left[b_{\mathrm{V}}\right]}{\mathrm{d}T_{\mathrm{V}}}+\left(\mu_{\mathrm{AV}}-\mu_{\mathrm{JV}}\right) \tag{C.7}$$

together with

$$\frac{\mathrm{d}\ln\left[b_{\mathrm{V}}\right]}{\mathrm{d}T_{\mathrm{V}}}>\mu_{\mathrm{JV}}-\mu_{\mathrm{AV}}\,. \tag{C.8}$$

The next step is to substitute (2.1). This reduces (C.7) to

$$\left(T_{\mathrm{V}}-1\right)\exp\left[-\frac{T_{\mathrm{V}}}{T_{\mathrm{V}}-1}\right]=\frac{1}{T_{\mathrm{V}}-1}+\left(\mu_{\mathrm{AV}}-\mu_{\mathrm{JV}}\right). \tag{C.9}$$

The introduction of

$$y\ :=\ \left(T_{\mathrm{V}}\text{-}1\right)^{-1} \tag{C.10}$$

lets us replace (C.9) by

$$y^{-1}\mathrm{e}^{-(1+y)}\text{ - }y\ =\ \mu_{\mathrm{AV}}\text{ - }\mu_{\mathrm{JV}}. \tag{C.11}$$

The left hand side of (C.11) decreases from ∞ at $y = 0$ to -∞ at $y = \infty$. We conclude that r has a unique optimum T_{V}^{*}, which can easily be determined from (C.11) with (C.10).

Formulas (C.10) and (C.11) moreover allow us immediately to plot the relation between T_{V}^{*} and μ_{A} at fixed μ_{JV} as a parametric curve, with y as a parameter.

Cases 2 to 4: From $\partial R_0/\partial T_{\mathrm{V}} = 0$ we find that

$$T_{\mathrm{V}}^{*}\ =\ 1+\left(\mu_{\mathrm{JV}}\right)^{-1}. \tag{C.12}$$

Apparently T_{V}^{*} is independent of μ_{AV}. This is clearly brought out in panel 3 of Figure 1, where the environmental feedback loop acts through the birth rate b. The decreasing relation in panel 4 derives entirely from the effect of the environmental feedback loop on $T^{*} = T_{\mathrm{V}}^{*}+\gamma_4(E)$. In panel 2 we see the effect of the environmental feedback loop keeping μ_{A} constant, independent of μ_{AV}.

Cases 5 and 6: Setting $\partial\psi/\partial T_{\mathrm{V}} = 0$ leads to

$$\left(T_{\mathrm{V}}-1\right)\exp\left[-\frac{T_{\mathrm{V}}}{T_{\mathrm{V}}-1}\right]=\mu_{\mathrm{AV}}\,. \tag{C.13}$$

When T_{V} increases from 1 to ∞ the left hand side of (C.13) increases from 0 to ∞. Therefore (C.13) has a unique solution.

In case 5 we plot the relation between $T^{*} = \theta_5(E)\,T_{\mathrm{V}}^{*}$ and μ_{A} as a parametric curve with T_{V}^{*} as parameter. Although in case 6 the feedback loop influences μ_{J}, it makes no difference whether we keep μ_{JV} or μ_{J} constant, as by (C.13) T^{*} is independent of μ_{JV}.

Legends to the figures

Figure 1: Correlations between the adult mortality rate μ_A and the duration of the evolutionarily stable juvenile period T^*, both "observed in the field", for the six models with alternative environmental feedback rules described in Section 2. The value of the "physiological parameter" juvenile mortality in the virgin environment, μ_{JV}, was kept fixed at $\mu_{JV} = 0.25$.

The numbering of the panels refers to the feedback rules. The plotted field observables are determined by a combination of the "physiological parameters" μ_{AV} (the adult death rate in the virgin environment) and T_V^* (the ESS value of T_V, the juvenile period in the virgin environment), and the corresponding feedback rule. This amounts to plotting T_V^* against $\mu_{AV}+\gamma_1(E_{attr}(T_V^*))$ for model 1, T_V^* against $\mu_{AV}+\gamma_2(E_{attr}(T_V^*))$ for model 2, T_V^* against μ_{AV} for model 3, $T_V^*+\gamma_4(E_{attr}(T_V^*))$ against μ_{AV} for model 4, $\theta_5(E_{attr}(T_V^*))T_V^*$ against μ_{AV} for model 5, and T_V^* against μ_{AV} for model 6. For the computational details we refer to the main text and Appendix C.

The, for all curves identical, upper limit of μ_A results from the fact that for higher values of μ_{AV} no strategy can invade into the virgin environment. Such values of μ_{AV} would lead in a, naive, calculation to $\gamma_i(E_{attr}(T_V^*)) < 0$ (in models 1, 2, 4, or 6) or $\theta_j(E_{attr}(T_V^*)) < 1$ (in models 3 or 5), i.e., values of γ_i or θ_j which were excluded a priori in our model specification. In panel 1 the lower limit of μ_A results from the additional mortality due to environmental feedback. In panel 2 we see that a feedback through the adult mortality by necessity exactly compensates for any difference in the adult mortality rate in the virgin environment.

The formulas indicate the optimisation principle satisfied by the set of models delimited by the grey lines, the shading which kind of life history traits were supposed to be affected by the environment. Note, that in order to use r or R_0 as an optimisation principle we have to decide on a reference environment. For definiteness we have chosen the virgin one. However, any other environment would have done equally well.

Figure 2: Correlation between the adult mortality rate μ_A and the evolutionarily stable duration of the juvenile period T^*, both "observed in the field", for feedback rule 1. The difference with panel 1 of Figure 1 is that now the value of the observed juvenile mortality μ_J, instead of the "physiological" parameter μ_{JV}, was kept fixed at $\mu_J = 0.5$.

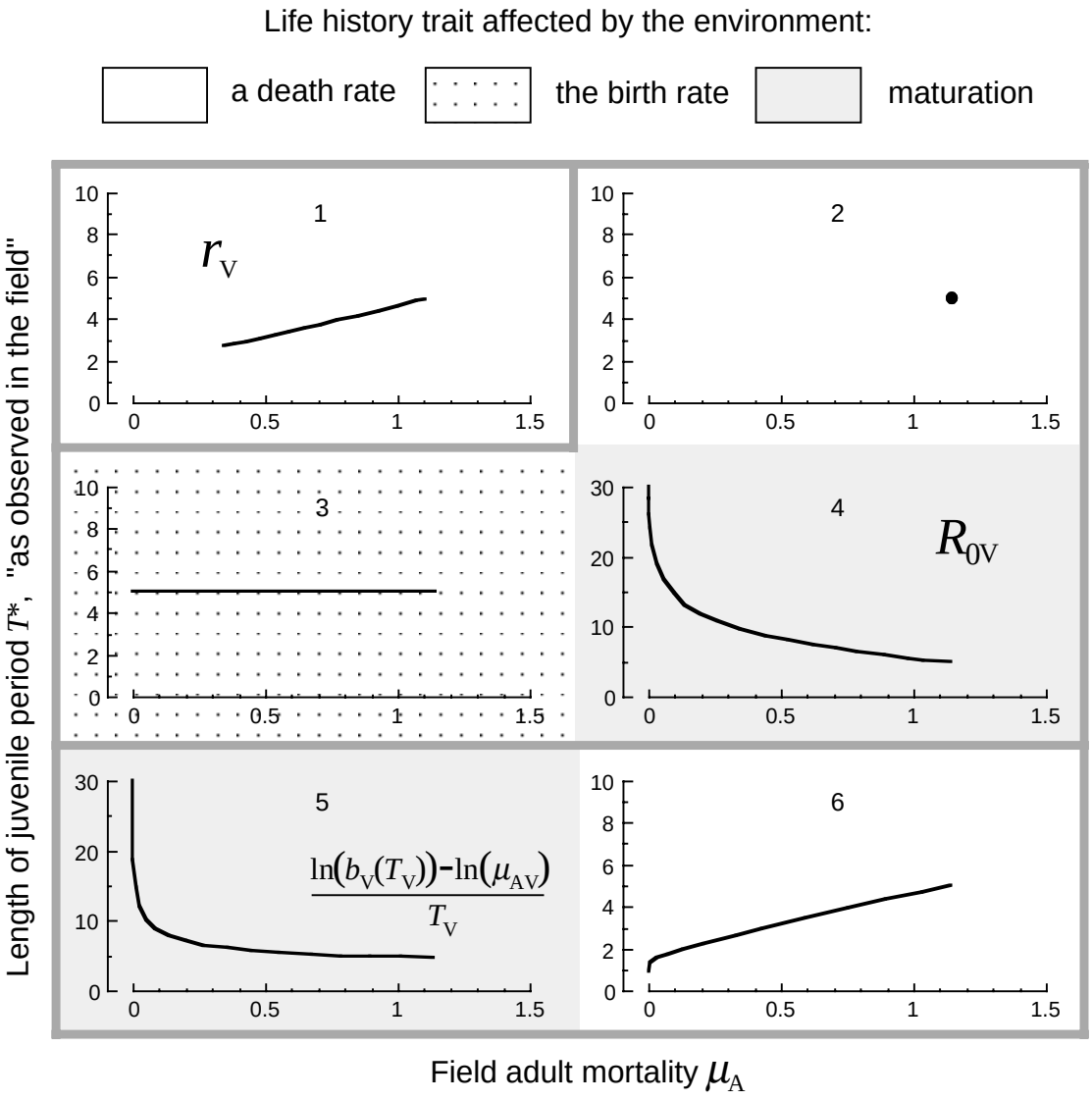
Life history trait affected by the environment:
a death rate
the birth rate
maturation
Length of juvenile period T*, "as observed in the field"
Field adult mortality μ_A
1
r_V
2
3
4
R_{0V}
5
$\frac{\ln(b_V(T_V))-\ln(\mu_{AV})}{T_V}$
6

Figure 1

model 1
Length of the juvenile period
T^*, as observed in the field
10
8
6
4
2
0
0
0.5
1
1.5
Field adult mortality μ_A

Figure 2