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Function-valued adaptive dynamics and the calculus of variations

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Abstract

Adaptive dynamics has been widely used to study the evolution of scalar-valued, and occasionally vector-valued, strategies in ecologically realistic models. In many ecological situations, however, evolving strategies are best described as function-valued, and thus infinite-dimensional, traits. So far, such evolution has only been studied sporadically, mostly based on quantitative genetics models with limited ecological realism. In this article we show how to apply the calculus of variations to find evolutionarily singular strategies of function-valued adaptive dynamics: such a strategy has to satisfy Euler's equation with environmental feedback. We also demonstrate how second-order derivatives can be used to investigate whether or not a function-valued singular strategy is evolutionarily stable. We illustrate our approach by presenting several worked examples.

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1 Introduction

To date, research in theoretical evolutionary ecology has mainly focused on adaptations in traits that can be represented by a single number, or by a small collection of numbers. For example, the rate at which a consumer harvests a resource is a one-dimensional trait. While too low a harvesting rate will not provide the consumer population with enough resources to maintain itself, too high a harvesting rate may cause the resource population to go extinct. Models have thus been devised to predict the intermediate harvesting rates that are expected as evolutionary outcomes in such a system. In nature, however, consumers may have opportunities for using many different types of resource, and harvesting them all at an equal rate will usually not be efficient. When the number of resource types is large, it will often be realistic to describe the harvesting rates of a consumer by a function defined on a continuum of resource types. Such a harvesting strategy, traditionally referred to as a resource utilization spectrum, will thus be infinite-dimensional. It is easy to think of many other ecological settings in which considering function-valued strategies is advantageous.

The evolution of function-valued strategies has already been studied in quantitative genetics (Beder and Gomulkiewicz, 1998; Gomulkiewicz and Beder, 1996; Gomulkiewicz and Kirkpatrick, 1992; Jaffrézic and Pletcher, 2000; Kingsolver et al., 2001). While these models are relatively realistic in terms of genetic detail, they give little emphasis to ecological detail. In particular, environmental feedback, which is generally essential for understanding all but the most simple effects of natural selection, is not yet addressed by these earlier models. By contrast, adaptive dynamics theory (Metz et al., 1992, 1996; Dieckmann and Law, 1996; Geritz et al., 1997, 1998) has been devised as a general framework to analyze the phenotypic evolutionary dynamics of populations under environmental feedback. It is only very recently that adaptive dynamics theory has been extended to function-valued strategies (Dieckmann et al., 2004), and applied to maturation reaction norms (Ernande et al., 2004) and resource utilization strategies (Heino et al., 2004).

According to Dieckmann et al. (2004), the following equation, referred to as the canonical equation of function-valued adaptive dynamics, describes the rate of expected evolutionary change, $\frac{d}{dt}s$, in a function-valued strategy s,

$$\frac{d}{dt}s(a) = \frac{1}{2}\mu_s \bar{n}_s \int \sigma_s^2(a', a)G_s(a')da', \tag{1}$$

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where a is the argument of the function s, μ_s is the mutation probability of trait s, $\bar{n}_s$ is the trait-dependent equilibrium population size of the evolving population, σ_s^2 is the variance-covariance function of the mutation distribution, and G_s is the selection gradient (see equation 62). Equilibria of the dynamics defined by equation (1) are called evolutionarily singular strategies. These can be of different types, one of which is an evolutionarily stable strategy (ESS; Maynard Smith, 1976): a resident population expressing such a strategy is evolutionarily unbeatable, in the sense that no mutants can invade, such that evolution comes to a halt.

In this article we complement the analysis of equation (1) by applying the calculus of variations. To explain the idea underlying this approach, let us assume that a resident population has reached an evolutionarily stable strategy. While a mutant with a strategy equal to that of the resident has zero fitness, any small variation in the mutant strategy around the resident strategy will decrease fitness below zero. In other words, the evolutionarily stable function-valued trait maximizes fitness, which is given as a function of the trait. Such situations are commonly addressed in the field of mathematical optimization known as the calculus of variations. Here we investigate how the calculus of variations can be used to find evolutionarily singular strategies, when strategies are real-valued functions defined on an interval $[a_{\min}, a_{\max}]$. We demonstrate that a singular strategy has to satisfy Euler's equation with environmental feedback.

The methods introduced in this article have important advantages and disadvantages relative to the direct integration of equation (1):

- *Evolutionary stability.* A one-dimensional singular strategy is generally either a local fitness minimum or a maximum. If a one-dimensional strategy is an evolutionarily attracting fitness minimum, evolutionary branching (Geritz et al., 1998) is expected, resulting in a population dimorphism. A vector-valued singular strategy, as well as a function-valued singular strategy, is not either a fitness minimum or a maximum, but can be a saddle instead. The calculus of variations often allows us to determine whether a singular strategy is a fitness maximum, and thus an evolutionarily stable strategy.

- *Convergence stability.* In case of one-dimensional strategies, conditions for whether a singular strategy is an evolutionary attractor are relatively easy to analyze (Geritz et al., 1998). Already with two-dimensional strategies this analysis becomes more complicated (Marrow et al., 1996; Leimar, 2001; Meszéna et al., 2001). In the case of function-valued strategies, convergence stability is best addressed by analyzing equation (1) and consequently is not covered here.

- *Evolutionary constraints.* A key advantage of using the calculus of variations is that incorporation of some evolutionary constraints is particularly easy. The appendix provides a detailed comparison of how one especially important type of such constraints is handled by the two approaches.

The purpose of this paper is to illustrate in general how the calculus of variations can be used to find and analyze evolutionarily singular function-valued strategies of adaptive dynamics. After introducing our modeling framework in Section 2, we continue with presenting a sequence of five worked examples in Sections 3 to 7. These examples serve to highlight the approach's utility and to explain in detail how to cope with various typical complications modelers are bound to encounter in applications. The article concludes with a summary and outlook in Section 8.

2 Modeling framework

Throughout this study we focus on function-valued strategies, or infinite-dimensional traits of the form

$$s(a) \in \mathbb{R}, a \in \mathbb{R}, a_{\min} \leqslant a \leqslant a_{\max}. \tag{2}$$

The variable a is referred to as the strategy's determinant; $[a_{\min}, a_{\max}]$ is thus called the determinant space of the function-valued trait s.

2.1 Resident equilibrium

Depending on the considered population dynamics, a population comprising individuals with one or more strategies s will reach a population-dynamical attractor. We consider the environmental interaction variable E that contains all essential information about the environment individuals experience on such an attractor. A necessary condition for the attractor having been reached is that the population's basic reproduction ratio, given by the expected number of offspring produced by an individual, is equal to one (Diekmann et al., 1998, 2001),

$$R(s_{\mathrm{res}}, E_{\mathrm{res}}) = 1. \tag{3}$$

2.2 Invasion fitness of a mutant

We now consider a resident population at its population dynamical attractor, with corresponding environmental interaction variable E_{res}. If a small mutant population with a different strategy from that of the resident appears, this mutant population will not initially affect the population dynamics of the resident, and the environmental interaction variable will remain at E_{res}. The mutant population size will thus initially increase or decrease exponentially. Specifically, the mutant population will grow, if its basic reproduction ratio

$$R(s_{\mathrm{mut}}, E_{\mathrm{res}}) > 1. \tag{4}$$

Equivalently, the mutant population will grow, if its long-term exponential growth rate

$$r(s_{\mathrm{mut}}, E_{\mathrm{res}}) > 0. \tag{5}$$

Either one of these quantities can be used as a measure of invasion fitness of a mutant in an environment set by the resident.

Evolutionarily stable strategies (ESSs; Maynard Smith, 1976) have been widely studied in evolutionary ecology. A resident expressing such a strategy s^* is evolutionarily unbeatable, since no mutants can invade the resident. By contrast, a strategy s^* is convergence stable, and thus serves as an evolutionary attractor, if the repeated invasion and replacement of resident strategies by nearby mutant strategies lets the resultant sequence of resident strategies converge to s^* (Christiansen, 1991). If an evolutionary attractor is also evolutionarily stable, it is called a continuously stable strategy (CSS; Eshel, 1983) and may be regarded as a possible final outcome of the considered evolutionary process. If an evolutionary attractor is not evolutionarily stable, disruptive selection may result in evolutionary branching (Geritz et al., 1998): an initially monomorphic population will first converge to the attractor and then divide into two phenotypic groups that subsequently will evolve further away from each other.

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When a resident population has reached an evolutionarily stable strategy, we may consider the fitness of mutants in the environment set by such a resident. As no mutant can invade, all mutants necessarily have lower fitness than the resident, such that the resident strategy is a (local) fitness maximum. For finite-dimensional strategies $\vec{s} = (s_1, \ldots, s_n)$, the selection gradient, i.e., the derivative of invasion fitness with respect to the components of the mutant's strategy vector, vanishes at such points,

$$\left. \frac{\partial}{\partial s_{i,\text{mut}}} r(\vec{s}_{\text{mut}}, E_{\text{res}}) \right|_{\vec{s}_{\text{mut}} = \vec{s}_{\text{res}}} = 0 \tag{6}$$

for all i. More generally, strategies for which the selection gradient is zero, are called evolutionarily singular strategies (Geritz et al., 1998). We are aiming at an analogous criterion for infinite-dimensional strategies.

In simple models featuring an infinite-dimensional strategy, invasion fitness can be written as an integral of the following type,

$$r(s_{\text{mut}}, E_{\text{res}}) = \int_{a_{\text{min}}}^{a_{\text{max}}} F(a, s_{\text{mut}}(a), E_{\text{res}}) da, \tag{7}$$

where E_{res} describes the environment set by the resident. We now consider a mutant with strategy $s_{\text{res}}(a) + \epsilon \Delta s(a)$, where $\Delta s(a)$ is an arbitrary function, and $|\epsilon|$ is small. When s_{res} is evolutionarily singular, the mutant's invasion fitness $r(s_{\text{res}} + \epsilon \Delta s, E_{\text{res}})$ possesses either a local minimum or a local maximum at $\epsilon = 0$. This connects the notion of evolutionarily singular function-valued traits to a standard procedure in the calculus of variations: identifying the evolutionarily singular strategies determined by a specific fitness function is equivalent to minimizing or maximizing that function by variation of the underlying function-valued strategy. As a next step we will therefore present some salient results from the general theory of calculus of variations, including an explanation of how this method's central result, the so-called Euler's equation, is derived. While the section below provides a general introduction to the calculus of variations, we use the same notation as elsewhere in this article. An example of a textbook in which these results are presented in greater detail is Wan (1993).

2.3 Calculus of variations and Euler's equation

The general problem in the calculus of variations is to minimize a function J,

$$J(s) = \int_{a_{\text{min}}}^{a_{\text{max}}} F(a, s(a), s'(a)) da, \tag{8}$$

through the variation of s, while respecting the boundary conditions $s(a_{\text{min}}) = A_{\text{min}}$ and $s(a_{\text{max}}) = A_{\text{max}}$. The function s is assumed to be continuous and piecewise differentiable. Compared to equation (7), the integrand function F is allowed to depend also on $s'(a) = \frac{d}{da} s(a)$. We now retain this potential dependence in the equations, but we will also explicitly show conditions for singular strategies in the absence of this dependence. Notice that in equation (7) there are no boundary conditions of the form described above. How free values at boundaries are handled in the calculus of variations is explained in Section 2.3.3.

A solution of the minimization problem (8) is called an extremal. Let us assume that the function s minimizes (8). We can then study the value of the function J for $s + \epsilon \Delta s$, assuming that the perturbation Δs is an arbitrary continuous and piecewise

differentiable function. We also assume that $\Delta s(a_{\min}) = \Delta s(a_{\max}) = 0$ to satisfy the boundary conditions. For sufficiently small values of $|\epsilon|$, we have

$$J(s) \leqslant J(s + \epsilon \Delta s). \tag{9}$$

The right-hand side thus has a local minimum at $\epsilon = 0$. We therefore obtain, through integration by parts,

$$
\begin{aligned}
\frac{d}{d\epsilon} J(s + \epsilon \Delta s)\Big|_{\epsilon=0} &= \int_{a_{\min}}^{a_{\max}} \frac{d}{d\epsilon} F(a, s(a) + \epsilon \Delta s, s'(a) + \epsilon \Delta s') da\Big|_{\epsilon=0} \\
&= \int_{a_{\min}}^{a_{\max}} F_s(a, s(a), s'(a)) \Delta s + F_{s'}(a, s(a), s'(a)) \Delta s' da \\
&= \int_{a_{\min}}^{a_{\max}} \left[F_s(a, s(a), s'(a)) - \frac{d}{da} F_{s'}(a, s(a), s'(a)) \right] \Delta s \, da \\
&\quad + F_{s'}(a_{\max}, s(a_{\max}), s'(a_{\max})) \Delta s(a_{\max}) \\
&\quad - F_{s'}(a_{\min}, s(a_{\min}), s'(a_{\min})) \Delta s(a_{\min}) \\
&= \int_{a_{\min}}^{a_{\max}} \left[F_s(a, s(a), s'(a)) - \frac{d}{da} F_{s'}(a, s(a), s'(a)) \right] \Delta s \, da = 0
\end{aligned}
\tag{10}
$$

for all possible perturbations Δs. This results in the so-called Euler's equation, which is a necessary condition for a function s to be a local minimum of (8),

$$\frac{d}{da} F_{s'}(a, s(a), s'(a)) = F_s(a, s(a), s'(a)), \tag{11}$$

where

$$F_s(a, s(a), s'(a)) = \frac{\partial}{\partial s(a)} F(a, s(a), s'(a)) \tag{12}$$

and

$$F_{s'}(a, s(a), s'(a)) = \frac{\partial}{\partial s'(a)} F(a, s(a), s'(a)). \tag{13}$$

Euler's equation usually yields a differential equation for s, unless the quantity $F(a, s(a), s'(a))$ does not depend on $s'(a)$.

Not all continuous functions are necessarily allowed as possible strategies. Natural constraints arise from the interpretations underlying the model in question. For example, in the case of $s(a)$ describing the harvesting time invested on different resources a, $s(a)$ cannot be negative at any time a, and the total time spent on harvesting, $\int_{a_{\min}}^{a_{\max}} s(a) da$, cannot exceed the maximal time available for harvesting. Below we explain how such constraints are incorporated into the analysis of function-valued traits using the calculus of variations.

2.3.1 Local inequality constraints

Many ecological variables are necessarily non-negative. Population sizes, rates, and probabilities are examples. Consequently, when such variables are considered in connection with function-valued traits, certain inequality constraints have to be satisfied.

Problems with inequality constraints for $s(a)$ that are local in determinant space, such as $s(a) \leqslant g_1(a)$ and $s(a) \geqslant g_2(a)$, have been widely studied in the general theory of the calculus of variations. If an extremal satisfies these inequality constraints with strict

inequality, such as $s(a) < g_1(a)$ and $s(a) > g_2(a)$, the extremal is said to be an interior solution. By contrast, if an extremal satisfies one or more inequality constraints with equality, we say that the extremal is on the border. Euler's equation (11) need not be satisfied on the border. The extremal can be a combination of an interior solution and borders.

At points a where the extremal changes from a border to the interior, the derivative $s'(a)$ often is discontinuous. Such points $(a, s(a))$ are called corners. At corners, the so-called corner conditions of Erdmann have to be satisfied,

$$F_{s'}(a, s, s'_-) = F_{s'}(a, s, s'_+),$$ (14)

$$F - s' F_{s'} \text{ is continuous at corners.}$$ (15)

2.3.2 Global equality and inequality constraints

In some models, functions s need to satisfy equality constraints of the type

$$C_i(s) = \int_{a_{\min}}^{a_{\max}} \Psi_i(a, s(a), s'(a)) da = \gamma_i$$ (16)

with $i = 1, \ldots, n$, which involve integrals and thus apply globally in determinant space. As in the method of Lagrange multipliers in ordinary constrained optimization, conditions (16) result in a Lagrange function

$$L = F - (\lambda_1, \ldots, \lambda_n)^T (\Psi_1, \ldots, \Psi_n),$$ (17)

and Euler's equation takes the form

$$\frac{d}{da} L_{s'}(a, s(a), s'(a)) = L_s(a, s(a), s'(a)),$$ (18)

known as the Euler-Lagrange equation. The extremal then has to satisfy equation (18), and the unknown Lagrange multipliers λ_i are solved from (16).

Inequality constraints of the form $C_i(s) \leqslant \gamma_i$ require equations (17) and (18) to be satisfied together with the so-called Karush-Kuhn-Tucker conditions,

$$\{\lambda_i = 0 \text{ and } C_i(s) < \gamma_i\} \text{ or } \{\lambda_i \geqslant 0 \text{ and } C_i(s) = \gamma_i\}.$$ (19)

2.3.3 Local equality constraints and free boundary values

In the general problem of the calculus of variations, the boundary conditions $s(a_{\min}) = A_{\min}$ and $s(a_{\max}) = A_{\max}$ have to be satisfied. Such conditions may be referred to as local equality constraints and often occur in problems related to physics, e.g., when determining the shape of a chain hanging from its two endpoints.

In other problems, however, the values $s(a_{\min})$ or $s(a_{\max})$ are free. This is typically the case in ecological models. When boundary values are free, Euler's boundary condition has to be satisfied, which is obtained from equation (10),

$$F_{s'}(a_{\min}, s(a_{\min}), s'(a_{\min})) = 0,$$ (20)

with an analogous condition for $a_{\max}$.

2.3.4 Conditions for minimality

Euler's equation does not guarantee the minimality or maximality of an extremal. A necessary condition for a minimum is

$$F_{s's'}(a, s(a), s'(a)) \geqslant 0 \text{ for all } a \in [a_{\min}, a_{\max}]. \tag{21}$$

The condition $F_{s's'}(a, s(a), s'(a)) > 0$ is called the strong Legendre condition. It is not a sufficient condition for minimality. By contrast, a sufficient condition for a global minimum is provided by the following theorem.

Theorem 1. *If $F(a, s, s')$ is differentiable and convex with respect to s and s', then an extremal is a global minimum of* (8).

2.3.5 No dependence on derivative

In many problems related to physics, the integrand of (8) depends on both $s(a)$ and $s'(a)$, especially when $s(a)$ describes the position and $s'(a)$ the velocity of an object. In many ecological models, however, the integrand does not depend on s', but instead is of the simpler form $F(a, s(a))$. In such cases, Euler's equation (11) takes the form

$$F_s(a, s(a)) = 0, \tag{22}$$

from which s can be solved implicitly.

Euler's equation (22) has to be satisfied also at the boundaries $a_{\min}$ and $a_{\max}$. As a result, no fixed boundary conditions of the form $s(a_{\min}) = A_{\min}$, $s(\max) = A_{\max}$ can be satisfied in general. This is not a problem, because in ecological models the boundary values are typically free, and Euler's boundary conditions (20) $F_{s'}(a_{\min}, s(a_{\min}), s'(a_{\min})) = 0$ and the analogous condition for $a_{\max}$ are automatically satisfied, because $F_{s'} = 0$.

When there are local inequality constraints for the function $s(a)$, the extremal consists of the corresponding borders together with an interior solution satisfying (22). The first corner condition (14) of Erdmann is automatically satisfied, and the second corner condition (15) is satisfied if s is continuous at the corners. The extremal is then a continuous curve, consisting of the interior solution together with the borders.

2.4 Applying the calculus of variations to ecological models

Based on the above considerations, we now assume that the invasion fitness of a mutant in an environment set by the resident can be written as

$$r(s_{\mathrm{mut}}, E_{\mathrm{res}}) = \int_{a_{\min}}^{a_{\max}} F(a, s_{\mathrm{mut}}(a), s'_{\mathrm{mut}}(a), E_{\mathrm{res}}) da. \tag{23}$$

In most ecological models, finding a function-valued evolutionarily singular strategy requires more than merely applying the calculus of variations. The reason is that the integrand F usually depends also on the environment set by the resident. We therefore have to analyze the following fixed-point problem: find a resident strategy s with resulting environment E such that s solves the problem of calculus of variations given by (23) for E. In short, a singular strategy satisfies Euler's equation with environmental feedback,

$$\begin{cases} r(s, E) = 0 \\ \frac{d}{da} F_{s'}(a, s(a), s'(a), E) = F_s(a, s(a), s'(a), E). \end{cases} \tag{24}$$

In contrast to the infinite-dimensional strategy s, the dimension of the environmental variable E is usually finite, and frequently small. It is therefore often easier to find evolutionarily singular strategies in the following way: find the environmental variable E, for which the resulting extremal strategy s begets the same environmental variable E.

Only in very simple ecological models with frequency-independent selection, environmental feedback is absent, such that finding evolutionarily singular strategies is a direct optimization problem. Such a simple situation is addressed in the example considered in the following section. After that we will present four other examples of increasing ecological complexity, to illustrate the use of various tools derived from the calculus of variations.

3 First example: Frequency-independent selection

As a first example, we will study a model in which finding the evolutionarily singular strategy reduces to a direct optimization problem. This simplification applies whenever the strategy giving a mutant maximum fitness is the same in all environments potentially set by the resident.

For coherence's sake, all examples in this article address the evolution of metabolic investment strategies, by extending a model introduced by Dieckmann et al. (2004).

3.1 Model description

We consider consumers that can feed on a variety of resources. In general, the utilization of different resources requires prior physiological or morphological investments into handling and processing. Such investments are expected to be costly. How should a consumer allocate these metabolic investments across the range of different resources?

Let $0 \leqslant a \leqslant 1$ characterize the digestibility of the different types of resource, with the value $a = 0$ corresponding to highest digestibility. Values $s(a)$ of the function-valued trait s now describe the metabolic effort invested on different resource types a. This investment is necessarily non-negative: $s(a) \geqslant 0$ for all a. With metabolic effort $s(a)$, the gain obtained from consuming one resource unit of type a is assumed to equal

$$e(a, s(a)) = \frac{s(a)}{s(a) + a}. \tag{25}$$

This quantity is called the metabolic efficiency, and ensures that there is diminishing return of metabolic investment. If the density of resource type a is $n(a)$, the consumer's total gain is

$$G(s, n) = \int_0^1 n(a)e(a, s(a))da. \tag{26}$$

Without constraints, evolution of the function-valued strategy s would cause metabolic effort $s(a)$ to approach infinity for all types of resources a. However, as investment is costly, the total investment

$$S(s) = \int_0^1 s(a)da \tag{27}$$

must necessarily be limited. To reflect this, we assume that increasing total investment is costly, decreasing the consumer's growth rate. Specifically, we assume that consumers

with trait s, experiencing resource densities n and a total consumer population size of N, have a per capita growth rate of

$$r(s, N) = G(s, n) - cS(s) - \frac{N}{K}$$
$$= \int_0^1 n(a)\frac{s(a)}{s(a) + a} - cs(a) - \frac{N}{K}da, \tag{28}$$

where K is the consumer's carrying capacity, and c is a constant measuring the cost of metabolic investment. To keep this first example simple, we assume that the availability of resource types, described by n, remains unaffected by the consumer, even though this is not always realistic in nature.

3.2 Invasion fitness

For a given resident strategy s_res, the equilibrium condition $r(s_\mathrm{res}, N_\mathrm{res}) = 0$ results in $N_\mathrm{res} = K(G(s_\mathrm{res}, n) - cS(s_\mathrm{res}))$, if $G(s_\mathrm{res}, n) - cS(s_\mathrm{res}) \geqslant 0$, and in $N_\mathrm{res} = 0$ otherwise. We can then consider a small mutant population with strategy s_mut. The mutant's invasion fitness is given by

$$r(s_\mathrm{mut}, N_\mathrm{res}) = \int_0^1 F(a, s_\mathrm{mut}(a), N_\mathrm{res})da$$
$$= \int_0^1 \left[n(a)\frac{s_\mathrm{mut}(a)}{s_\mathrm{mut}(a) + a} - cs_\mathrm{mut}(a) - \frac{N_\mathrm{res}}{K} \right] da, \tag{29}$$

where the environment set by the resident is characterized by the resident's population size, $E_\mathrm{res} = N_\mathrm{res}$.

3.3 Analysis based on the calculus of variations

We can use the calculus of variations to identify the models' evolutionarily singular strategies. According to (29), Euler's equation (22) becomes

$$F_s(a, s(a), N) = \frac{n(a)a}{(s(a) + a)^2} - c = 0. \tag{30}$$

In general, we would now have to find a strategy s, whose equilibrium population size is N, and which satisfies Euler's equation for N, $F_s(a, s(a), N) = 0$. In this first example, however, we notice that equation (30) does not depend on population size N. The problem of finding evolutionarily singular strategies is thus a direct optimization problem. This does not come as a surprise, because the environment that the mutant experiences depends only on the one-dimensional variable N, the resident's population size. In such a case, evolution proceeds according to an optimization principle (Metz et al., 1996; Heino et al., 1998), and selection is said to be frequency-independent.

We can thus obtain the evolutionarily singular strategy directly from solving equation (30). Any solution must, however, be non-negative. Wherever the strategy satisfying (30) is negative, the correct solution follows the border $s(a) = 0$. The sought evolutionarily singular strategy is therefore given by

$$s(a) = \begin{cases} \sqrt{\frac{n(a)a}{c}} - a & \text{if } n(a) \geqslant ac \\ 0 & \text{otherwise,} \end{cases} \tag{31}$$

recovering an earlier result obtained by Dieckmann et al. (2004).

The calculus of variations allows us to prove that the singular strategy (31) is evolutionarily stable. The second derivative

$$F_{ss}(a, s(a), N) = -\frac{2n(a)a}{(s(a) + a)^3} \leqslant 0, \tag{32}$$

is non-positive, which means that the function $F(a, s(a), N)$ is concave with respect to $s(a)$. According to Theorem 1, the evolutionarily singular strategy thus is a global maximum of $r(s, N)$, and is therefore evolutionarily stable.

3.4 Illustrations

Figure 1b shows an example of an evolutionarily stable investment strategy s^*. For the purpose of this illustration, we have assumed that the resource densities are given by

$$n(a) = 4a(1 - a), \tag{33}$$

shown in figure 1a. Figure 1b shows that, above the threshold value $a = 1 - c/4 = 0.875$, resources are too indigestible (large a) and rare (low $n(a)$) for any metabolic effort to be invested.
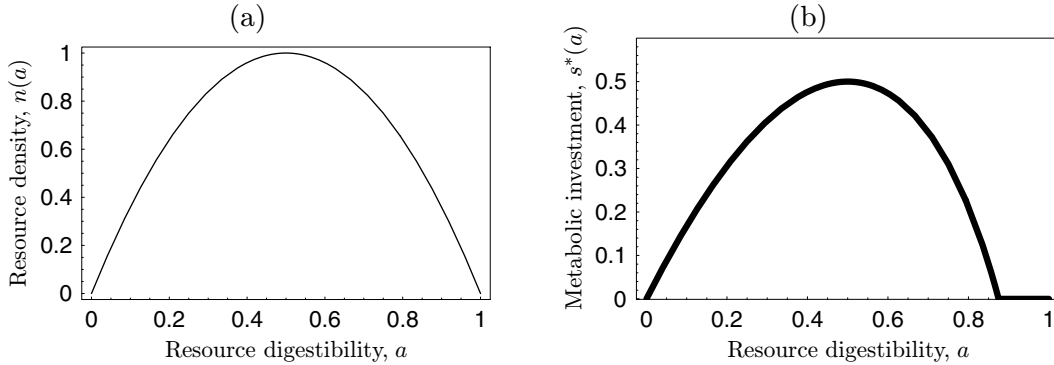
Figure 1: (a) Resource densities $n(a)$ according to equation (33). (b) Evolutionarily stable metabolic investment strategy s^* in the first example, according to equation (31). Parameters: $c = 0.5$.

4 Second example: Global inequality constraints

The second example illustrates how global inequality constraints on function-valued traits are handled through the calculus of variations.

4.1 Model description and invasion fitness

As mentioned earlier, total investment $S(s)$ in the metabolic investment model is necessarily limited. In the first example above, this limitation was incorporated by assuming a cost of total metabolic investment in terms of reduced population growth rate. In our second example we proceed differently, by removing this cost from the model's invasion fitness,

$$r(s_{\mathrm{mut}}, N_{\mathrm{res}}) = \int_0^1 \left[n(a) \frac{s_{\mathrm{mut}}(a)}{s_{\mathrm{mut}}(a) + a} - \frac{N_{\mathrm{res}}}{K} \right] da, \tag{34}$$

10

while considering the global inequality constraint $S(s) \leqslant C$. The environment set by the resident is again characterized by the resident's population size, $E_{\text{res}} = N_{\text{res}}$.

4.2 Analysis based on the calculus of variations

As explained in Section 2.3.2, an inequality constraint can be reflected by considering a Lagrange function, $L = n(a)\frac{s_{\text{mut}}(a)}{s_{\text{mut}}(a)+a} - \frac{N_{\text{res}}}{K} - \lambda s_{\text{mut}}(a)$, in Euler's equation (18),

$$L_s(a, s(a), N) = \frac{n(a)a}{(s(a) + a)^2} - \lambda = 0. \tag{35}$$

In addition, the Karush-Kuhn-Tucker conditions (19) have to be satisfied. Again, the equation (35) does not depend on the resident population size, and finding the singular strategies is a direct optimization problem.

For $\lambda = 0$, equation (35) cannot be satisfied, unless there are no resources at all, $n(a) = 0$ for all a. Since we are not interested in this trivial case, the inequality constraint $S(s) \leqslant C$ is always satisfied with equality $S(s) = C$. This condition results in (31), where the model parameter c is replaced by the Lagrange multiplier λ. The value of λ can be found numerically from $S(s) = C$.

4.3 Illustrations

Some illustrations are shown in Figure 2a.
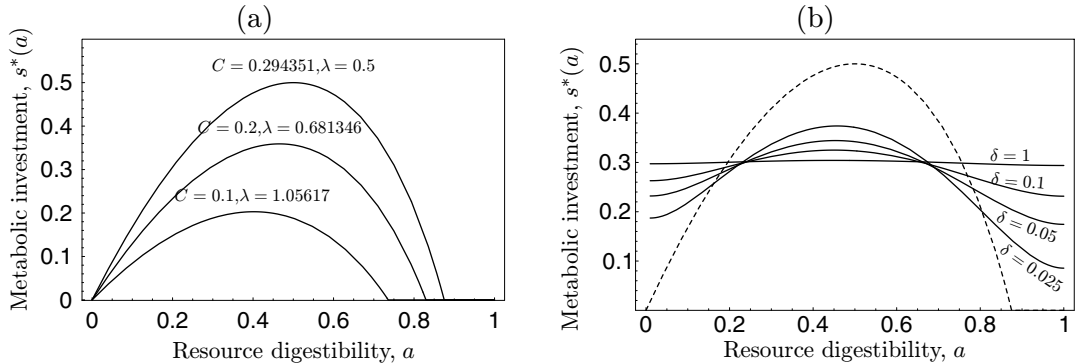
Figure 2: (a) Evolutionarily stable metabolic investment strategies s^* in the second example, with global inequality constraint $S(s) \leqslant C$, for different values of C. The value $C = 0.1$ corresponds to $\lambda = 1.05617$, $C = 0.2$ to $\lambda = 0.681346$, and $C = 0.294351$ to $\lambda = 0.5$. The result for the latter case is thus identical to that in Figure 1b. (b) Evolutionarily stable metabolic investment strategies s^* in the third example, for different plasticity costs δ. The dashed curve corresponds to the case without plasticity costs, $\delta = 0$. Parameters: $c = 0.5$.

5 Third example: Dependence of fitness on a trait's derivative

The third example shows how to address evolutionary problems in which invasion fitness depends on a function-valued trait's derivative $s'(a) = \frac{d}{da}s(a)$, in addition to the dependence on the trait $s(a)$ itself.

5.1 Model description and invasion fitness

In conjunction with assuming that metabolic investment itself is costly, it is interesting to explore situations in which physiological mechanisms that accurately separate the investment between two similar resource types are also costly. In other words, in addition to the direct costs of metabolic investment, there may be a cost of plasticity. The derivative s' describes how plastic a strategy s is. We assume that the cost of plasticity increases with the absolute value of $s'(a)$, and choose the function $(s'(a))^2$ to describe this dependence. Assuming that the cost of plasticity reduces the growth rate r, we obtain the following invasion fitness,

$$
\begin{aligned}
r(s_{\mathrm{mut}}, N_{\mathrm{res}}) &= \int_0^1 F(a, s_{\mathrm{mut}}(a), s'_{\mathrm{mut}}(a), N_{\mathrm{res}}) da \\
&= \int_0^1 \left[n(a) \frac{s_{\mathrm{mut}}(a)}{s_{\mathrm{mut}}(a) + a} - c s_{\mathrm{mut}}(a) - \delta(s'_{\mathrm{mut}}(a))^2 - \frac{N_{\mathrm{res}}}{K} \right] da,
\end{aligned}
\tag{36}
$$

with $\delta \geqslant 0$ scaling the cost of plasticity. For simplicity, we again use the assumption that n remains constant. For $\delta = 0$, the model above is identical to that in the first example.

5.2 Analysis based on the calculus of variations

Since $F_{s'} = -2\delta s'(a)$, Euler's equation (11) becomes

$$
\frac{d}{da} F_{s'} = -2\delta s''(a) = \frac{n(a)a}{(s(a) + a)^2} - c = F_s.
\tag{37}
$$

Again, finding the singular strategies is a direct optimization problem. As the resource density n can be an arbitrary function, we are not able, in general, to solve this differential equation analytically. Numerical solution is, however, possible.

Since the strategy's boundary values $s(0)$ and $s(1)$ are not prescribed, we obtain the two necessary conditions for determining the constants of the solution of (37) from Euler's boundary condition (20): $F_{s'}(0, s(0), s'(0)) = -2\delta s'(0) = 0$, resulting in $s'(0) = 0$ and, analogously, in $s'(1) = 0$. If the extremal consisted of an interior solution satisfying (37) together with a border solution $s(a) = 0$, abutting at a^*, Erdmann's corner conditions (14) and (15) would reduce to $s'(a^*) = 0$. From equation (32) we obtain $F_{ss} \leqslant 0$, and since $F_{s's'} = -2\delta < 0$, the conditions of Theorem 1 are satisfied: any singular strategy is therefore evolutionarily stable.

5.3 Illustrations

We have solved equation (37) for different values of δ, using numerical methods for the solution of ordinary differential equations. The resulting evolutionarily stable investment strategies s^* are shown in figure 2b. These results demonstrate how, starting from the cost-free case indicated by the dashed curve, increasing the cost parameter δ causes the evolutionarily stable strategy s^* to become more and more uniform.

6 Fourth example: Frequency-dependent selection

The previous examples were deliberately kept rather simplistic in that selection remained frequency-independent. Our fourth example now shows how to analyze function-valued traits exposed to frequency-dependent selection.

6.1 Model description

To enhance the ecological realism of our metabolic investment model, we assume that the resource densities n respond to consumption according to the following differential equation,

$$\frac{d}{dt}n(a) = \left(1 - \frac{n(a)}{k(a)}\right)n(a) - \gamma n(a)Ne(a, s(a)), \tag{38}$$

where $k(a)$ is the density the resource of type a would attain in the absence of consumers, and the parameter $\gamma \geqslant 0$ is the consumer's per capita harvesting rate. The intensity with which a consumer with strategy s harvests resources of type a is assumed to be proportional to its metabolic efficiency $e(a, s(a))$. For simplicity, we assume that the resource population grows much faster than the consumer population, and is thus always at an equilibrium that can be determined from $\frac{d}{dt}n(a) = 0$,

$$n^*(a, N, s(a)) = \begin{cases} k(a)(1 - \gamma Ne(a, s(a))) & \text{if } 1 - \gamma Ne(a, s(a)) > 0 \\ 0 & \text{otherwise.} \end{cases} \tag{39}$$

For $\gamma \to 0$, corresponding to consumers that affect their resources only very weakly, this results in $n^*(a) = k(a)$, such that we recover the simpler model considered in the first example as a special case.

6.2 Invasion fitness

In this example, the environment mutants experience is characterized by both the resident's population size N_{res} and the resource density $n^*(a, N_{\text{res}}, s_{\text{res}}(a))$. This means that this environment is no longer one-dimensional, and selection therefore is frequency-dependent. Analogously to equation (29), the mutant's invasion fitness is given by

$$r(s_{\text{mut}}, N_{\text{res}}, s_{\text{res}}) = \int_0^1 \left[n^*(a, N_{\text{res}}, s_{\text{res}}(a))\frac{s_{\text{mut}}(a)}{s_{\text{mut}}(a) + a} - cs_{\text{mut}}(a) - \frac{N_{\text{res}}}{K}\right] da. \tag{40}$$

6.3 Analysis based on the calculus of variations

Euler's equation for this example has the same form as in the frequency-independent case, equation (30), with the difference that the resource densities are not fixed, but are now obtained from equation (39). In order to find the evolutionarily singular strategy for this example, we must find a strategy s, for which the consumer's equilibrium population size is N, and resource densities are $n^*(a, N, s(a))$. This strategy s must satisfy Euler's equation (30) in the environment N, $n^*(a, N, s(a))$.

In practice, however, it is much easier to (i) choose a particular population size N, (ii) obtain the corresponding resource densities and extremal strategy from solving the implicit equations (31) and (39), and (iii) vary N until $r(s, N, s) = 0$ is satisfied. We used numerical methods to accomplish this task.

As in the frequency-independent case in the first example, we obtain for the second derivative $F_{ss} \leqslant 0$. The conditions of Theorem 1 are thus satisfied, and once an evolutionarily singular strategy is identified, it is necessarily evolutionarily stable.

6.4 Illustrations

Figure 3 shows the different evolutionarily stable strategies resulting for different values of the harvesting rate γ. We have again chosen $k(a) = 4a(1 - a)$, so that in the absence

of consumers, or for $\gamma \to 0$, the resource densities are identical to those in the frequency-independent case. Our numerical results illustrate how increasing γ causes metabolic investment to become less beneficial.
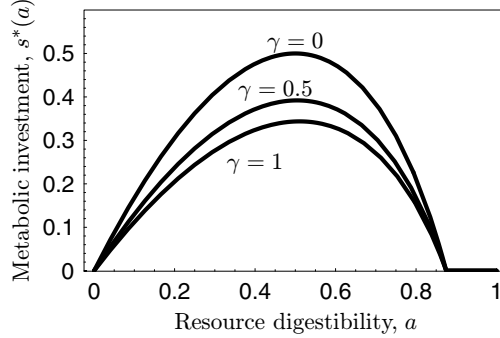

Figure 3: Evolutionarily stable metabolic investment strategies s^* in the fourth example, for $\gamma = 0$, $\gamma = 0.5$, and $\gamma = 1$. For $\gamma = 0$, selection becomes frequency-independent, and the evolutionarily singular strategy coincides with that in figure 1b. Parameters: $c = 0.5$, $K = 10$.

7 Fifth example: Complex fitness functions

In all previous examples, the fitness of a mutant could be written as a single integral of the form shown in equation (7). This is not always the case. To illustrate how to use the calculus of variations for analyzing models with more complex fitness functions, our fifth example extends the metabolic investment model to a metapopulation setting. As in the fourth example, resultant selection again is frequency-dependent.

7.1 Model description

A metapopulation consists of local populations living in different habitat patches (Levins, 1969, 1970). Here we consider M such patches. In patch $i = 1, \dots, M$, the density of resources of type a is $n_i(a)$. For simplicity, we again assume that the resource densities $n_i(a)$ are unaffected by the consumer.

In each patch, consumer populations grow according to the same birth and death processes considered in the first example. In addition, dispersal between patches occurs with per capita emigration rate m, so that population dynamics in the different patches are coupled. Emigrants survive dispersal with probability p, and immigrate randomly into other patches. As a result, the population size N_i in patch i change according to the following differential equation,

$$\frac{dN_i}{dt} = g_i(s, N_i)N_i - mN_i + p\overline{N}m, \tag{41}$$

where $\overline{N} = \frac{1}{M}\sum_{i=1}^{M} N_i$ is the average population size across patches. The local population growth rate in patch i is given by

$$\begin{aligned}
g_i(s, N_i) &= \int_0^1 F^i(a, s(a), N_i)da \\
&= \int_0^1 \left[n_i(a)\frac{s(a)}{s(a) + a} - cs(a) - \frac{N_i}{K_i} \right] da.
\end{aligned} \tag{42}$$

7.2 Invasion fitness

The differential equation (41) can be written in matrix form,

$$\frac{d}{dt}\vec{N} = \vec{A}(s,\vec{N})\vec{N},$$
$$A_{ii} = g_i(s,N_i) - m + p\frac{m}{M},$$
$$A_{ij} = p\frac{m}{M}, \text{ if } i \neq j.$$

(43)

We now assume that a resident population with strategy s_{res} has reached its population-dynamical equilibrium $\vec{N}_{\text{res}} = (N_{1,\text{res}}, N_{2,\text{res}}, \dots, N_{M,\text{res}})$. Therefore, a small mutant population with strategy s_{mut} will initially grow or decrease according to the linear differential equation $\frac{d}{dt}\vec{N}_{\text{mut}} = \vec{A}(s_{\text{mut}}, \vec{N}_{\text{res}})\vec{N}_{\text{mut}}$. The mutant's invasion fitness is given by the dominant eigenvalue of the matrix $\vec{A}(s_{\text{mut}}, \vec{N}_{\text{res}})$, which is the long-term exponential growth rate of the mutant in the environment set by the resident.

However, in this example it is more practical to use, instead, the basic reproduction ratio R as a measure of invasion fitness. This quantity describes the expected number of offspring produced by an individual during its entire life. In a metapopulation setting, the basic reproduction ratio can be determined as the expected number of immigrants produced by an immigrating mutant during its entire life (Gyllenberg and Metz, 2001; Metz and Gyllenberg, 2001).

When a mutant arrives in patch i, it encounters a resident population of size $N_{i,\text{res}}$. Initially, the mutant population is rare, and therefore does not affect the population dynamics of the resident. Consequently, the mutant population will grow according to the differential equation

$$\frac{d}{dt}N_{i,\text{mut}} = N_{i,\text{mut}}\left[g_i(s_{\text{mut}}, N_{i,\text{res}}) - m\right].$$

(44)

This means that the mutants population size at time τ after arrival of the initial mutant population of size $N_{i,\text{mut}}(0)$ will equal

$$N_{i,\text{mut}}(\tau) = N_{i,\text{mut}}(0)e^{[g_i(s_{\text{mut}}, N_{i,\text{res}}) - m]\tau}.$$

(45)

This mutant population will produce mutant emigrants at rate $mN_{i,\text{mut}}(\tau)$. Therefore, the expected number of immigrants produced by a mutant with strategy s_{mut} that has immigrated into habitat patch i is

$$R_{i,\text{mut}}(s_{\text{mut}}, N_{i,\text{res}}) = p\int_0^\infty m\frac{N_{i,\text{mut}}(\tau)}{N_{i,\text{mut}}(0)}d\tau = p\int_0^\infty me^{[g_i(s_{\text{mut}}, N_{i,\text{res}}) - m]\tau}d\tau$$
$$= \begin{cases} \frac{pm}{m - g_i(s_{\text{mut}}, N_{i,\text{res}})} & \text{if } m - g_i(s_{\text{mut}}, N_{i,\text{res}}) > 0 \\ \infty & \text{otherwise.} \end{cases}$$

(46)

An immigrating mutant has a probability of $1/M$ to immigrate into patch i. Analogously to Parvinen (2002), we obtain the expected number of immigrants produced by an immigrating mutant as

$$R_{\text{mut}}(s_{\text{mut}}, \vec{N}_{\text{res}}) = \frac{1}{M}\sum_{i=1}^M R_{i,\text{mut}}(s_{\text{mut}}, N_{i,\text{res}}).$$

(47)

Notice that the environment set by the resident is now M-dimensional, $E_{\text{res}} = \vec{N}_{\text{res}}$, and selection is therefore frequency-dependent for $M > 1$.

At population-dynamical equilibrium, the resident populations are stationary in all patches, $\frac{dN_i}{dt} = 0$ for all $i = 1, \ldots, M$. From equation (41) we obtain

$$m - g_i(s_{\text{res}}, N_{i,\text{res}}) = \frac{pm\overline{N}_{\text{res}}}{N_{i,\text{res}}} > 0, \tag{48}$$

and therefore

$$R_{\text{mut}}(s_{\text{res}}, \vec{N}_{\text{res}}) = \frac{1}{M} \sum_{i=1}^{M} \frac{pm}{m - g_i(s_{\text{res}}, N_{i,\text{res}})} = \frac{1}{M} \sum_{i=1}^{M} \frac{N_{i,\text{res}}}{\overline{N}_{\text{res}}} = 1. \tag{49}$$

This confirms that, at population-dynamical equilibrium, each resident individual exactly replaces itself, as consistency requires.

7.3 Analysis based on the calculus of variations

In the previous examples, we could use the calculus of variations directly to find evolutionarily singular strategies. In the metapopulation model the situation is more complex. In equation (42), the local growth rates g_i in patches i are expressed as integrals of the form shown in equation (7). Yet, the fitness measure in equation (47) is a function of these growth rates g_i, and cannot be expressed as one integral of the form shown in equation (7). This means that we cannot apply the calculus of variations in its usual form. However, we can find candidate singular strategies by a method that is similar to that for deriving Euler's equation (11).

We assume that a given resident strategy s_{res} is an evolutionarily singular strategy, which means that it is a local minimum or maximum of the fitness measure $R_{\text{mut}}(s_{\text{mut}}, \vec{N}_{\text{res}})$. Therefore, the fitness of a mutant with function-valued strategy $s_{\text{mut}} = s_{\text{res}} + \epsilon \Delta s$, $R_{\text{mut}}(s_{\text{res}} + \epsilon \Delta s, \vec{N}_{\text{res}})$, will be at a local maximum or a minimum for $\epsilon = 0$. This implies

$$\left. \frac{d}{d\epsilon} R_{\text{mut}}(s_{\text{res}} + \epsilon \Delta s, \vec{N}_{\text{res}}) \right|_{\epsilon=0} = 0 \tag{50}$$

for all possible perturbation functions Δs. We can calculate this derivative by first obtaining the corresponding derivative of $\frac{d}{d\epsilon} R_{i,\text{mut}}$,

$$\frac{d}{d\epsilon} R_{i,\text{mut}}(s_{\text{res}} + \epsilon \Delta s, N_{i,\text{res}}) = \frac{pm \frac{d}{d\epsilon} g_i(s_{\text{res}} + \epsilon \Delta s, N_{i,\text{res}})}{[m - g_i(s_{\text{res}} + \epsilon \Delta s, N_{i,\text{res}})]^2}, \tag{51}$$

for which we need the derivative $\frac{d}{d\epsilon} g_i$ according to equation (42),

$$\frac{d}{d\epsilon} g_i(s_{\text{res}} + \epsilon \Delta s, N_{i,\text{res}}) = \int_0^1 F_s^i(a, s_{\text{res}}(a) + \epsilon \Delta s(a), N_{i,\text{res}}) \Delta s(a) da, \tag{52}$$

so that we obtain, by combining equations (48), (51), and (52),

$$\left. \frac{d}{d\epsilon} R_{i,\text{mut}}(s_{\text{res}} + \epsilon \Delta s, N_{i,\text{res}}) \right|_{\epsilon=0} = \frac{1}{pm} \left(\frac{N_{i,\text{res}}}{\overline{N}_{\text{res}}} \right)^2 \int_0^1 F_s^i(a, s_{\text{res}}(a)) \Delta s(a) da. \tag{53}$$

Using equation (47), we thus obtain

$$\left. \frac{d}{d\epsilon} R_{\text{mut}}(s_{\text{res}} + \epsilon \Delta s, \vec{N}_{\text{res}}) \right|_{\epsilon=0} = \frac{1}{Mpm} \int_0^1 \left(\sum_{i=1}^{M} \left(\frac{N_{i,\text{res}}}{\overline{N}_{\text{res}}} \right)^2 F_s^i(a, s_{\text{res}}(a)) \right) \Delta s(a) da. \tag{54}$$

According to (50), this derivative has to be zero for all possible perturbation functions Δs, which implies

$$\sum_{i=1}^{M} \left(\frac{N_{i,\mathrm{res}}}{\overline{N}_{\mathrm{res}}} \right)^2 F_s^i(a, s_{\mathrm{res}}(a), N_{i,\mathrm{res}}) = 0. \tag{55}$$

This means that an evolutionarily singular strategy s_{res} in the metapopulation model has to satisfy

$$\sum_{i=1}^{M} \left(\frac{N_{i,\mathrm{res}}}{\overline{N}_{\mathrm{res}}} \right)^2 \left(\frac{n_i(a)a}{(s_{\mathrm{res}}(a) + a)^2} - c \right) = 0, \tag{56}$$

from which we obtain the solutions s^*,

$$s^*(a) = \begin{cases} \sqrt{\tilde{n}(a, \vec{N}_{\mathrm{res}})\frac{a}{c}} - a, & \text{if } \tilde{n}(a) \geqslant ac \\ 0 & \text{otherwise,} \end{cases} \tag{57}$$

with

$$\tilde{n}(a, \vec{N}_{\mathrm{res}}) = \frac{\sum_{i=1}^{M} \left(N_{i,\mathrm{res}}/\overline{N}_{\mathrm{res}} \right)^2 n_i(a)}{\sum_{i=1}^{M} \left(N_{i,\mathrm{res}}/\overline{N}_{\mathrm{res}} \right)^2}. \tag{58}$$

The remaining unknowns $\vec{N}_{\mathrm{res}} = (N_{1,\mathrm{res}}, N_{2,\mathrm{res}}, \dots, N_{M,\mathrm{res}})$ in (57) are determined from setting $\frac{d}{dt} N_{i,\mathrm{res}} = 0$ in equation (41). As a result, we have $R_{\mathrm{mut}}(s^*, \vec{N}_{\mathrm{res}}) = 1$.

If the second derivative of invasion fitness with respect to the mutant's strategy is negative for all perturbation functions Δs,

$$\frac{d^2}{d\epsilon^2} R_{\mathrm{mut}}(s_{\mathrm{res}} + \epsilon\Delta s, \vec{N}_{\mathrm{res}})\big|_{\epsilon=0} < 0, \tag{59}$$

the evolutionarily singular strategy s_{res} is a local fitness maximum, and thus evolutionarily stable. Using the same technique as above, we obtain

$$\begin{aligned} \frac{d^2}{d\epsilon^2} R_{\mathrm{mut}}(s_{\mathrm{res}} + \epsilon\Delta s, \vec{N}_{\mathrm{res}})\big|_{\epsilon=0} = & \frac{1}{Mp^2m^2} \sum_{i=1}^{M} \left(\frac{N_{i,\mathrm{res}}}{\overline{N}_{\mathrm{res}}} \right)^3 \\ & \left[\int_0^1 \frac{pm\overline{N}_{\mathrm{res}}}{N_{i,\mathrm{res}}} F_{ss}^i(a, s_{\mathrm{res}}(a))(\Delta s(a))^2 da \right. \\ & \left. + 2 \left(\int_0^1 F_s^i(a, s_{\mathrm{res}}(a))\Delta s(a) da \right)^2 \right]. \end{aligned} \tag{60}$$

The first term in the square brackets is negative because, according to equation (32), we have $F_{ss}^i(a, s_{\mathrm{res}}(a)) \leqslant 0$. Since the second term is positive, it is difficult to determine the second derivative's sign in general. Yet we can conclude that for small dispersal rates m the second term dominates relative to the first, which means that the second derivative is positive. By contrast, for large values of m the first term dominates. Therefore, for small dispersal rates, evolutionary branching may be possible, whereas for large dispersal rates, the singular strategy is expected to be evolutionarily stable.

7.4 Illustrations

To illustrate evolutionarily singular strategies in the fifth example, we use the following functions for describing the resource densities in patch i,

$$n_i(a) = \frac{4a(1-a)}{1 + 2(a - \hat{a}_i)^2}, \ \ i = 1, 2, \ \text{with } \hat{a}_1 = 0.1 \text{ and } \hat{a}_2 = 0.9, \tag{61}$$

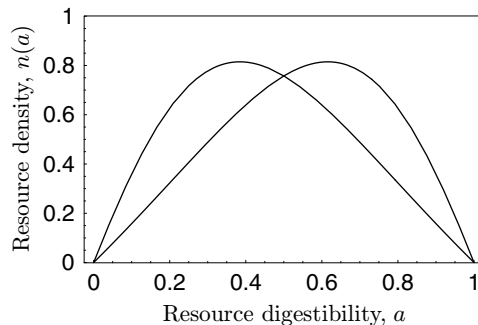which result in skewed resource density distributions as illustrated in figure 4.

Figure 4: Resource densities $n_i(a)$ according to equation (61).

Numerical solutions for the resulting evolutionarily singular strategies s^* are shown in figure 5, which depicts different evolutionarily stable monomorphic and dimorphic solutions for a two-patch metapopulation, $M = 2$. For comparison, we also display the locally optimal metabolic investment strategies in the two patches as dashed curves. For sufficiently small values of the dispersal rate m, the monomorphic singular strategy is not evolutionarily stable, and a protected dimorphism of two strategies is possible (Figure 5a-c). For very small values of m, the two coexisting strategies essentially are specialists, each adapted to one of the two patches (Figure 5a). When the dispersal rate m is increased, these strategies converge (Figure 5bc). When the dispersal rate is increased further, coexistence of the two strategies is no longer possible: instead a monomorphic generalist strategy becomes evolutionarily stable (Figure 5d). Notice that the stable coexistence of three or more strategies is excluded, since the number of patches serves as an upper limit to the number of stably coexisting strategies (Parvinen, in prep.).

Figure 6 illustrates how parameters in the metapopulation model affect the potential for the emergence of an evolutionarily stable dimorphism of metabolic investment strategies. The figure demonstrates that the evolutionary effect of increased dispersal rate m shown in figure 5 applies more generally. For small values of m, the two specialist strategies can always coexist. When m is increased, dimorphic coexistence becomes impossible, and instead a monomorphically singular strategy becomes evolutionarily stable. The critical value of m at which this change from dimorphism to monomorphism occurs, varies with the carrying capacity K_2. For intermediate values of K_2, the two patches are more balanced, and coexistence remains possible for higher dispersal rates m. For smaller or larger values of K_2, either one of the two patches dominates, and coexistence is possible only for lower dispersal rates. Balanced patches have been shown to support the coexistence of scalar-valued strategies in metapopulation models (Parvinen, 2002).
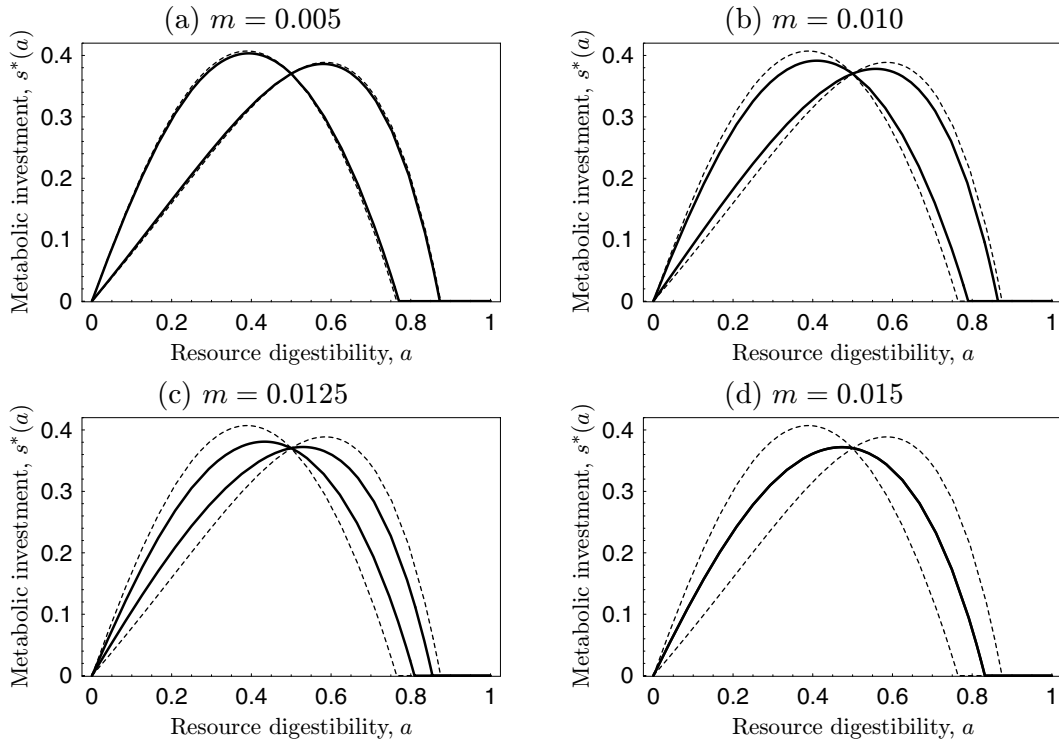
Figure 5: Evolutionary outcomes for the metapopulation model considered in the fifth example. (a-c) For low dispersal rates, the monomorphicially evolutionarily singular strategy is not evolutionarily stable, enabling coexistence of two dimorphically singular strategies. (d) For high dispersal rates, the monomorphically singular strategy is evolutionarily stable, and a dimorphism does not evolve. Optimal investment strategies in the two patches are shown as dashed curves. Parameters: $p = 0.95$, $c = 0.5$, $K_1 = 10$, $K_2 = 16$.
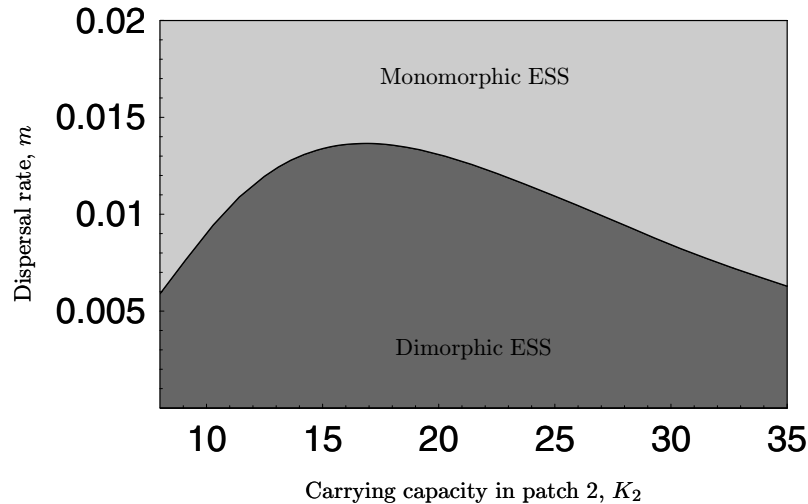

Figure 6: Dependence of evolutionary outcomes in the fifth example on carrying capacity K_2 and dispersal rate m. Parameter combinations enabling the evolutionarily stable coexistence of two strategies are shown in dark grey, while combinations resulting in a monomorphic evolutionarily stable strategy are shown in light grey. Parameters: $p = 0.95$, $c = 0.5$, $K_1 = 10$.

8   Discussion

In this article we have introduced a general approach to using the calculus of variations for finding and analyzing evolutionarily singular function-valued strategies of adaptive dynamics. While previous work focused on the canonical equation of function-valued adaptive dynamics (Dieckmann et al., 2004; Ernande et al., 2004; Heino et al., 2004), the general result derived here shows that an evolutionarily singular strategy has to satisfy Euler's equation with environmental feedback. The resultant two alternative approaches to function-valued adaptive dynamics constructively complement each other:

- As demonstrated by equations (10) and (62), Euler's equation is satisfied if and only if a function-valued strategy causes the corresponding selection gradient to vanish. Therefore, analyses based, alternatively, on the calculus of variations or the canonical equation of adaptive dynamics result in the same predictions for evolutionarily singular strategies, provided there are no constraints on which strategies can be realized.

- In the canonical equation, evolutionary constraints are expressed via the variance-covariance function of a strategy's mutation distribution. Although this perspective is essential for correctly describing the expected transient dynamics of a function-valued trait, it makes it relatively difficult to derive evolutionary outcomes. By contrast, as we have showed above and in the appendix, incorporating several standard types of evolutionary constraints into the calculus of variations is easy.

- The calculus of variations also helps in evaluating the second-order conditions that determine the evolutionary stability of singular strategies.

- The canonical equation, on the other hand, can be used in situations in which the calculus of variations is not applicable, since the canonical equation allows considering variance-covariance constraints of arbitrary form.

- The calculus of variations cannot be used to evaluate the convergence stability of an evolutionarily singular strategy, which determines whether or not such a strategy serves as an evolutionary attractor. Also for describing transient evolutionary dynamics, the canonical equation is needed.

We have presented several worked examples to illustrate the various methods presented in this article. All examples addressed the evolution of a metabolic investment strategy, in a variety of different ecological settings. In the first example (Section 3), ecological conditions were so simple that no environmental variables appeared in Euler's equation. This is characteristic of models without frequency-dependent selection: finding evolutionarily singular strategies in such models thus is a direct optimization problem, without the need to consider environmental feedback. The second example (Section 4) served to illustrate the treatment of global inequality constraints, which may be used to reflect costs involved in the expression of function-valued traits. The third example (Section 5) explained how to address problems in which fitness depends not only on strategy values $s(a)$ but also on a strategy's derivative $s'(a) = \frac{d}{da}s(a)$. Whereas in the first three examples selection was frequency-independent, the fourth example (Section 6) illustrated the treatment of frequency-dependent selection, which naturally occurs in virtually all ecological models with realistic environmental feedback. Also in the fifth example (Section 7) selection was frequency-dependent: the analysis of a metapopulation model showed how to deal with

models in which fitness cannot be expressed as a single integral. This example also featured an evolutionarily stable dimorphism in a function-valued strategy.

Together with Dieckmann et al. (2004), this article provides a systematic framework for studying the adaptive dynamics of function-valued traits. Concrete applications of this framework are presented by Ernande et al. (2004) and Heino et al. (2004). We hope that the new tools introduced here will help to raise the profile of function-valued traits in theoretical evolutionary ecology, and result in interesting applications in the future.

Appendix: Calculus of variations and the canonical equation

According to Dieckmann et al. (2004), the expected dynamics of a function-valued trait can be described by the so-called canonical equation of function-valued adaptive dynamics, equation (1). For evolutionarily singular strategies, the selection gradient $G_s(a) = \frac{d}{d\epsilon}J(s + \epsilon\delta_a)\big|_{\epsilon=0}$ is zero for all a.

When we compare the selection gradient with equation (10), we see that the latter gives the selection gradient at a if we choose the considered perturbation function to equal a Dirac delta function peaked at a, $\Delta s = \delta_a$. Equation (10) then reduces to

$$G_s(a) = \frac{d}{d\epsilon}J(s + \epsilon\delta_a)\big|_{\epsilon=0} = F_s(a, s(a), s'(a)) - \frac{d}{da}F_{s'}(a, s(a), s'(a)). \tag{62}$$

This implies that the selection gradient vanishes if and only if Euler's equation (11) is satisfied. In this sense, the alternative methods for identifying evolutionarily singular strategies, by using the calculus of variations or the canonical equation, are equivalent.

However, some differences between these two methods arise for constrained evolution. Sections 2.3.1 to 2.3.3 described how to reflect several standard evolutionary constraints in the calculus of variations. Yet, the mutation structure of a function-valued strategy might impose constraints that cannot be represented in terms of local or global constraints of the form considered in these sections. In the approach of Dieckmann et al. (2004), such restrictions are incorporated into the canonical equation via a function-valued trait's mutational variance-covariance function.

A global equality constraint of the form

$$C(s) = \int_{a_{\min}}^{a_{\max}} \Psi(a, s(a))da = \gamma. \tag{63}$$

is readily transformed into a mutational variance-covariance function that, when applied in the canonical equation of function-valued adaptive dynamics (1), ensures that the constraint remains respected. From equation (63) it follows that

$$\frac{d}{dt}\int_{a_{\min}}^{a_{\max}} \Psi(a, s(a))da = \int_{a_{\min}}^{a_{\max}} \Psi_s(a, s(a))\frac{d}{dt}s(a)da = 0, \tag{64}$$

where $\Psi_s(a, s(a)) = \frac{\partial}{\partial s}\Psi(a, s(a))$. Using equation (1) and swapping the order of integration, we obtain

$$\frac{1}{2}\mu_s\bar{n}_s \int_{a_{\min}}^{a_{\max}} \left[G_s(a') \int_{a_{\min}}^{a_{\max}} \Psi_s(a, s(a))\sigma_s^2(a', a)da \right] da' = 0. \tag{65}$$

This condition is satisfied, if for all a' we have

$$\int_{a_{\min}}^{a_{\max}} \Psi_s(a, s(a))\sigma_s^2(a', a)da = 0. \tag{66}$$

There are infinitely many variance-covariance functions that satisfy this condition. One of them is

$$\sigma_s^2(a', a) = A(a)\delta(a - a') - 1, \tag{67}$$

with $A(a) = (\Psi_s(a, s(a)))^{-1} \int_{a_{\min}}^{a_{\max}} \Psi_s(a'', s(a''))da''$.

We have thus shown that all global equality constraints of type (63) can be expressed through a variance-covariance function according to equation (67). Many variance-covariance functions, however, do not correspond to a constraint of the simple form indicated in equation (63). When analyzing evolutionary outcomes under such non-standard constraints, the canonical equation (1) has to be used.

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