

Function-valued adaptive dynamics and optimal control theory

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Abstract In this article we further develop the theory of adaptive dynamics of function-valued traits. Previous work has concentrated on models for which invasion fitness can be written as an integral in which the integrand for each argument value is a function of the strategy value at that argument value only. For this type of models of direct effect, singular strategies can be found using the calculus of variations, with singular strategies needing to satisfy Euler's equation with environmental feedback. In a broader, more mechanistically oriented class of models, the function-valued strategy affects a process described by differential equations, and fitness can be expressed as an integral in which the integrand for each argument value depends both on the strategy and on process variables at that argument value. In general, the calculus of variations cannot help analyzing this much broader class of models. Here we explain how to find singular strategies in this class of process-mediated models using optimal control theory. In particular, we show that singular strategies need to satisfy Pontryagin's maximum principle with environmental feedback. We demonstrate the

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utility of this approach by studying the evolution of strategies determining seasonal flowering schedules.

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1 Introduction

Adaptive dynamics (Metz et al. 1992, 1996; Dieckmann and Law 1996; Geritz et al. 1997, 1998) was originally formulated for scalar strategies $s \in \mathbb{R}$. Dieckmann et al. (2006) and Parvinen et al. (2006) presented theory for the adaptive dynamics of function-valued traits, i.e., strategies of the form $s(a) \in \mathbb{R}$ for $a \in \mathbb{R}$. In addition to developing this theory, Dieckmann et al. (2006) studied the evolution of metabolic investment strategies and the evolution of seasonal flowering schedules. Parvinen et al. (2006) further investigated models of metabolic investment strategies. The adaptive dynamics of function-valued strategies has been examined in various other applications, including maturation reaction norms (Ernande et al. 2004), foraging strategies on resource gradients (Heino et al. 2008), condition-dependent dispersal (Gyllenberg et al. 2008), timing of reproduction (Eskola 2009; Eskola et al. 2011), size-dependent flowering (Rees and Ellner 2009), and age-dependent sex-reversal (Calsina and Ripoll 2010). This illustrates the wide applicability of function-valued traits to questions in evolutionary ecology.

Dieckmann et al. (2006) introduced the canonical equation of function-valued adaptive dynamics, which describes the expected rate of evolutionary change in a function-valued strategy. This canonical equation can be used to study the transient dynamics and convergence towards evolutionarily singular strategies (see, e.g., Heino et al. 2008). Already for vector-valued strategies, conditions for such convergence are more complicated than for scalar strategies (Christiansen 1991; Marrow et al. 1996; Matessi and Di Pasquale 1996; Geritz et al. 1998; Leimar 2001; Meszéna et al. 2001), usually requiring dynamical analysis of the kind the canonical equation allows. In some simple cases, the equilibria of the canonical equation can be solved analytically, and singular strategies thus can be obtained. For using the canonical equation, the selection gradient needs to be calculated. The complexity of a model determines how difficult that calculation is.

Alternatively, for single-species evolution, singular strategies can be found by using the fact that they are local maxima or minima of a fitness function. Therefore, it is natural that the optimization method provided by the calculus of variations is a useful tool for finding singular strategies of function-valued traits and, under some circumstances, for determining their evolutionary stability (Parvinen et al. 2006). In particular, the calculus of variations is applicable when the invasion fitness (Metz et al. 1992) of a mutant with strategy s_{mut} in the environment E_{res} created by the resident population can be written as an integral of the form

$$r(s_{\text{mut}}, E_{\text{res}}) = \int_{a_{\text{min}}}^{a_{\text{max}}} F(a, s_{\text{mut}}(a), s'_{\text{mut}}(a), E_{\text{res}}) da, \quad (1)$$

where $s_{\text{mut}}(a)$ is defined for $a_{\text{min}} \leq a \leq a_{\text{max}}$. Analogous methods, as described in Section 7 of Parvinen et al. (2006), can be used in more complex cases, in which the invasion fitness $r(s_{\text{mut}}, E_{\text{res}}) = Z(I_1, I_2, \dots, I_n)$ is a function of several integrals $I_j = \int_{a_{\text{min}}}^{a_{\text{max}}} F_j(a, s_{\text{mut}}(a), s'_{\text{mut}}(a), E_{\text{res}}) da$ with $j = 1, \dots, n$. The main result of Parvinen et al. (2006) is that singular strategies in models of type (1) need to satisfy Euler's equation with environmental feedback. See, e.g., Heino et al. (2008) and Gyllenberg et al. (2008) for applications. In some special cases, the integrand $F(a, s_{\text{mut}}(a), s'_{\text{mut}}(a), E_{\text{res}})$ does not depend on $s'_{\text{mut}}(a)$ and is a linear function of the strategy value $s_{\text{mut}}(a)$ of the mutant, so the resultant Euler's equation does not depend on s_{mut} . Finding singular strategies may then appear problematic, because s_{mut} cannot be solved from an equation in which it does not appear. Instead, one obviously needs to find a resident environment E_{res} such that Euler's equation is satisfied for any s_{mut} , for which model-specific methods may be needed (Eskola 2009; Calsina and Ripoll 2010). From an ecological point of view, the presence in Eq. (1) of the derivative $s'_{\text{mut}}(a) = \frac{d}{da} s_{\text{mut}}(a)$ may seem puzzling at first sight. Many problems of such type arise in physics, for example when $s(a)$ describes the position and $s'(a)$ the velocity of an object. Also in evolutionary ecology, fitness functions of this form may naturally arise, albeit much more rarely, such as in the metabolic investment model of Parvinen et al. (2006).

The main purpose of this article is to present methods for analysing the evolution of function-valued traits in a broader class of models than those in which fitness is of form (1). We call this broader class of models *process-mediated models*. In this more mechanistically oriented class of models, the function-valued strategy affects a process described by ordinary differential equations

$$\frac{d}{da} y_i(a) = f_i(a, y_1(a), \dots, y_n(a), s_{\text{mut}}(a), E_{\text{res}}), \quad (2a)$$

with state variables $y_i(a)$ for $i = 1, \dots, n$. The invasion fitness of a mutant in the environment E_{res} created by the resident population is then assumed to be of the form

$$r(s_{\text{mut}}, E_{\text{res}}) = \int_{a_{\text{min}}}^{a_{\text{max}}} F(a, y_1(a), \dots, y_n(a), s_{\text{mut}}(a), E_{\text{res}}) da. \quad (2b)$$

In contrast, we refer to the simpler models of form (1) as *direct-effect models*.

For process-mediated models, the task of finding singular strategies becomes a problem of optimal control theory. The theory of optimal control has been used in the context of function-valued traits in game theory (Hamelin and Lewis 2010), in quantitative genetics (Gomulkiewicz and Kirkpatrick 1992; Gomulkiewicz and Beder 1996; Beder and Gomulkiewicz 1998; Jaffrézic and Pletcher 2000; Kingsolver et al. 2001), and in life-history theory (Perrin and Sibly 1993; Gilchrist et al. 2006).

The novel feature considered in this article is the extension of the methods of optimal control theory to problems with environmental feedback, which is essential for tackling biologically realistic models.

Below we show that singular strategies in process-mediated models (2) need to satisfy Pontryagin's maximum principle (Pontryagin et al. 1962) with environmental feedback (Sect. 2.2). To facilitate future applications, we present two worked-out examples by extending the seasonal flowering model of Dieckmann et al. (2006). In the first process-mediated extension (Sect. 5), plants have a limited amount of resources that they can allocate to flower production at different times of the season. We illustrate that also in process-mediated models, a monomorphic singular function-valued strategy can be invadable by mutants, which can result in its evolutionary branching (Dieckmann et al. 2006). In the second process-mediated extension (Sect. 6), plants split their allocation of the incoming energy flow between the growth of leaves and flowers. Both examples have been chosen such that the singular strategies can alternatively be found also based on the canonical equation: in this way, we can show how much more straightforward the analysis becomes by using the theory of optimal control.

2 Theory for direct-effect and process-mediated models

Following Metz et al. (1992), let $r(s_{\text{mut}}, E_{\text{res}})$ denote the invasion fitness of a mutant, i.e., the exponential growth rate of a rare mutant with strategy s_{mut} in the environment E_{res} created by the resident. Let S denote the set of possible strategies, often called the strategy space. According to Dieckmann et al. (2006), the following equation, referred to as the canonical equation of function-valued adaptive dynamics, describes the rate $\frac{d}{dt}s$ of expected evolutionary change in a function-valued strategy $s \in S$,

$$\frac{d}{dt}s(a) = \frac{1}{2}\mu(s)\bar{n}(s) \int_{a_{\min}}^{a_{\max}} \sigma^2(a', a)G(a') da', \quad (3)$$

where a is the argument of the function s , $\mu(s)$ is the mutation probability of trait s , $\bar{n}(s)$ is the trait-dependent equilibrium population size of the evolving population, σ^2 is the variance-covariance function of the mutation distribution, and G is the selection gradient

$$G(a) = \frac{d}{d\epsilon}r(s + \epsilon\delta_a)|_{\epsilon=0} = \lim_{\Delta s \rightarrow \delta_a} \left[\frac{d}{d\epsilon}r(s + \epsilon\Delta s)|_{\epsilon=0} \right]. \quad (4)$$

The second equality specifies that the differentiation with respect to ϵ is to be done before the disturbance function Δs is let to approach the Dirac delta function δ_a , where $\delta_a(a') = \delta(a' - a)$.

Obviously, strategies for which the selection gradient vanishes, $G(a) = 0$ for all a , are equilibria of the canonical equation (3), and are called evolutionarily singular strategies. More in general, evolutionarily singular strategies are defined as strategies satisfying

$$\frac{d}{d\epsilon} r(s + \epsilon \Delta s) \Big|_{\epsilon=0} = 0 \tag{5}$$

for all Δs for which $s + \epsilon \Delta s \in S$ when $|\epsilon|$ is sufficiently small.

As mentioned above, model complexity determines how easy (or difficult) calculating the selection gradient is. Next we discuss applicable methods for the evolutionary analysis of function-valued traits in two classes of models. First, we review the methods for direct-effect models, for which the calculation of the selection gradient is relatively easy, and singular strategies can be found using the calculus of variations; this summarizes the theory presented in Parvinen et al. (2006). Second, we extend the methods to process-mediated models, for which there is no general simplifying rule for calculating the selection gradient. We show how, instead, the theory of optimal control can be used to find singular strategies in such models.

2.1 Direct-effect models and the calculus of variations

Let us first consider models of function-valued traits $s(a)$, with $a_{\min} \leq a \leq a_{\max}$, for which a mutant’s fitness can be written as an integral of form (1). As shown by Parvinen et al. (2006, their equation 63), the selection gradient $G(a)$ for $a_{\min} < a < a_{\max}$ in this case becomes

$$G(a) = F_s(a, s(a), s'(a), E_{\text{res}}) - \frac{d}{da} F_{s'}(a, s(a), s'(a), E_{\text{res}}), \tag{6}$$

where the subscripts denote partial derivatives,

$$\begin{aligned} F_s(a, s(a), s'(a), E_{\text{res}}) &= \frac{\partial}{\partial s(a)} F(a, s(a), s'(a), E_{\text{res}}), \\ F_{s'}(a, s(a), s'(a), E_{\text{res}}) &= \frac{\partial}{\partial s'(a)} F(a, s(a), s'(a), E_{\text{res}}). \end{aligned} \tag{7}$$

When there are no constraints on the strategy, and the strategy space S is thus the set of all piecewise continuous functions $s : [a_{\min}, a_{\max}] \rightarrow \mathbb{R}$, evolutionarily singular strategies are strategies s for which the selection gradient vanishes, $G(a) = 0$. According to (6), this condition is given by complementing the Euler’s equation of the calculus of variations with the condition for ecological equilibrium under environmental feedback (Parvinen et al. 2006),

$$\begin{cases} \frac{d}{da} F_{s'}(a, s(a), s'(a), E) = F_s(a, s(a), s'(a), E), \\ r(s, E) = 0. \end{cases} \tag{8}$$

See Parvinen et al. (2006) for a more detailed description of the use of the calculus of variations for finding singular strategies. Here we just discuss the selection gradient and conditions for singular strategies at boundaries a_{\min} and a_{\max} , because these require special attention when F depends on the derivative $s'(a)$.

When F does not depend on the derivative $s'(a)$, the selection gradient (6) reduces to $G(a) = F_s(a, s(a))$ (Dieckmann et al. 2006, Eq. 3c). This equality is valid for all relevant arguments a , $a_{\min} \leq a \leq a_{\max}$, including the boundaries, which thus require no special treatment. However, as we show in Appendix A, for a dependence of F on $s'(a)$, the selection gradient at the boundaries is infinite, unless $F_{s'} = 0$ at a_{\min} and a_{\max} . Therefore, the selection pressure at the boundaries is infinitely stronger than elsewhere, keeping $F_{s'} = 0$ at the boundaries at all times.

Considering the other components of the canonical equation derived by selection gradient derived by Dieckmann et al. (2006), the mutation probability $\mu(s)$ and the equilibrium population size $\bar{n}(s)$ require no special treatment compared with the case without the s' dependence. It is also reasonable to assume that the derivative s' has no effect on the variance-covariance function σ^2 of the mutation distribution. We thus obtain the following result:

Proposition 1 *If the fitness function is of form (1), the selection gradient (4) for $a_{\min} < a < a_{\max}$ can be written as (6). For the canonical equation (3), we obtain the boundary condition $F_{s'} = 0$ at a_{\min} and a_{\max} .*

Proof The derivation of equation (6) was already given by Parvinen et al. (2006). In Appendix A we repeat this proof of the first part of Proposition 1 and then complement it by proving the second part of Proposition 1.

While earlier work had already shown that $F_{s'} = 0$ at the boundaries has to be satisfied for singular strategies, i.e., for potential evolutionary outcomes, Proposition 1 makes it clear that it has to hold for evolutionary transients.

We study an example of this type of model in Sect. 4, by extending the seasonal flowering model of Dieckmann et al. (2006). In that model, flowers opening at different times of the season experience different conditions, such as different probabilities of setting seed. It is therefore natural to study the flowering intensity as a function-valued trait, in which case fitness can be expressed as an integral of form (1).

A more mechanistic approach results from assuming that a plant's flowering intensity is determined by various processes, such as the use of energy reserves for flower production at different times of the season, the time-dependent resource allocation between leaf growth and flower production, and the loss of flowers due to dropping or pests. This requires studying a more general class of models, which we consider next.

2.2 Process-mediated models and the theory of optimal control

Let us now consider the class of models (2) described by state variables $y_i(a)$ for $i = 1, \dots, n$ and by a function-valued strategy $s(a)$ with $a_{\min} \leq a \leq a_{\max}$. We assume that the functions $y_i(a)$ satisfy the following system of ordinary differential equations,

$$\frac{d}{da} y_i(a) = f_i(a, y_1(a), \dots, y_n(a), s(a), E_{\text{res}}), \quad (9)$$

and that the invasion fitness of a mutant with strategy s_{mut} in the environment E_{res} created by the resident can be expressed as

$$r(s_{\text{mut}}, E_{\text{res}}) = \int_{a_{\text{min}}}^{a_{\text{max}}} F(a, y_1(a), \dots, y_n(a), s_{\text{mut}}(a), E_{\text{res}}) da. \tag{10}$$

In order to determine the selection gradient, we need to calculate the derivative of $r(s + \epsilon \Delta s, E_{\text{res}})$ with respect to ϵ . Since the state variables $y_i(a)$ depend on the strategy, and thus on ϵ , this derivative does not yield as simple an expression as for the previous class of models. Sections 5.1 and 6.1 nevertheless show examples of the model-specific calculation of such selection gradients. For determining selection gradients in process-mediated models, no general method exists.

For process-mediated models, the task of finding evolutionarily stable strategies (Maynard Smith 1976, 1982), or more in general, evolutionarily singular strategies, is closely related to problems of optimal control. As in models of form (1), singular strategies cannot be found through the straightforward application of a standard optimization method because of the environmental feedback. More specifically, the task is to find a strategy s which creates the environment E_{res} such that s solves the problem of optimal control given by (9) and (10). In other words, such singular strategies need to satisfy Pontryagin’s maximum principle (Theorem 1) with environmental feedback, $r(s, E) = 0$.

For the sake of completeness, we repeat the corresponding theorem below. While the original theorem was presented for a minimization problem, here we have formulated it for a maximization problem, because evolutionarily stable strategies are local maxima of invasion fitness. The proof in its full form is rather lengthy; details can be found in Pontryagin et al. (1962) or in textbooks on optimal control theory.

Theorem 1 (Pontryagin’s maximum principle) *If $s(a)$ is a piecewise smooth optimal control function maximizing*

$$r(s, E) = \Psi(\mathbf{y}(a_{\text{max}}), E) + \int_{a_{\text{min}}}^{a_{\text{max}}} F(a, \mathbf{y}(a), s(a), E) da \tag{11a}$$

with $\mathbf{y}(a) = (y_1(a), \dots, y_n(a))$ and

$$\begin{aligned} \frac{d}{da} y_i(a) &= f_i(a, \mathbf{y}(a), s(a), E) \quad \text{for } i = 1, \dots, n, \\ y_i(a_{\text{min}}) &= y_{0,i} \quad \text{for } i = 1, \dots, n, \\ y_i(a_{\text{max}}) &= \hat{y}_i \quad \text{for } i \in N \subset \{1, \dots, n\}, \end{aligned} \tag{11b}$$

then there exists a nonzero vector $\lambda(a)$, that satisfies the conditions

$$\begin{aligned} \frac{d}{da} \lambda_i(a) &= -H_{y_i} \quad \text{for } i = 1, \dots, n, \\ \lambda_i(a_{\text{max}}) &= \Psi_{y_i}(\mathbf{y}(a_{\text{max}}), E) \quad \text{for } i \notin N, \end{aligned} \tag{12}$$

where

$$\begin{aligned} H(a, \mathbf{y}(a), s(a), \lambda(a), E) \\ = F(a, \mathbf{y}(a), s(a), E) + \sum_{i=1}^n \lambda_i(a) f_i(a, \mathbf{y}(a), s(a), E) \end{aligned} \quad (13)$$

is called the Hamiltonian function, which is maximized by $s(a)$ for each a ,

$$\begin{aligned} H(a, \mathbf{y}(a), s(a), \lambda(a), E) \\ = \min_{\hat{s}(a)} H(a, \mathbf{y}(a), \hat{s}(a), \lambda(a), E) \quad \text{for all } a \in [a_{\min}, a_{\max}]. \end{aligned} \quad (14)$$

Corollary A necessary condition for a strategy s to be evolutionarily stable is that it satisfies the conditions for a piecewise smooth optimal control function maximizing (11) together with $r(s, E) = 0$.

For the special case $n = 1$ with $y_1'(a) = f_1(a, y_1(a), s(a)) = s(a)$ the optimal control problem (11) can be solved by the calculus of variations. If there are no constraints on the optimal control function s , the maximization of the Hamiltonian means that

$$0 = H_s(a, y_1(a), s(a), \lambda_1(a)) = F_s(a) + \lambda_1(a), \quad (15)$$

and thus $\lambda_1(a) = -F_s(a)$. Substituting that into the differential equation for λ_1 yields

$$\frac{d}{da} F_s(a) = F_{y_1}(a), \quad (16)$$

which recovers Euler's equation. Therefore, for direct-effect models (1) with unconstrained strategies, approaches alternatively based on the calculus of variations or on the theory of optimal control (Theorem 1) are equivalent.

To explain and demonstrate the utility of optimal control theory for analyzing the adaptive dynamics of function-valued traits is the main purpose of this article. For illustration, we apply the resultant methods to extensions of the seasonal-flowering model by Dieckmann et al. (2006). The conclusion of this section on theory is the following table of available methods (Table 1).

3 The seasonal flowering model by Dieckmann et al. (2006)

Before presenting examples of applying the methods outlined above, we summarize the model upon which the examples are built. Following Dieckmann et al. (2006), we study the evolution of seasonal flowering schedules in plants that inhabit a temporally varying environment. Flowers opening at different times of the season experience different ecological conditions. Let $s(a)$ describe the flowering intensity of a plant at time a , with a scaled so that $0 \leq a \leq 1$. The flowering intensity could be measured as a plant's biomass comprised by flowers, and is naturally represented as a function-valued

Table 1 Description of methods applicable to different model classes

	Direct-effect models	Process-mediated models
Fitness $r(s, E)$	$\int_{a_{\min}}^{a_{\max}} F(a, s(a), s'(a), E) da$	$\int_{a_{\min}}^{a_{\max}} F(a, \mathbf{y}(a), s(a), E) da$ with state variables y_i satisfying $\frac{d}{da} y_i(a) = f_i(a, \mathbf{y}(a), s(a), E)$
Method for finding singular strategies	Calculus of variations	Theory of optimal control
Selection gradient $G(a)$	$F_s(a, s(a), s'(a)) - \frac{d}{da} F_{s'}(a, s(a), s'(a))$ for $a_{\min} < a < a_{\max}$	Model-specific, using Eq. (4)

trait (Dieckmann et al. 2006; Parvinen et al. 2006). Evidently, all flowering intensities are non-negative, $s(a) \geq 0$. Flowers produced at any time during the flowering season compete for pollinators and herbivore-free space. The effect of such competition is to decrease a plant’s probability

$$p \left(\frac{Ns(a)}{K(a)} \right) \tag{17}$$

of setting seed, where N is the plant’s population size, and $Ns(a)$ is thus the total number of flowers open at time a . The time-dependent carrying capacity $K(a)$ describes seasonal factors affecting pollination success. The function p is assumed to be decreasing from a maximum of 1: $p(0) = 1$ and $p'(x) \leq 0$ for all $x \geq 0$. In the specific examples below, we use the functions

$$p(x) = e^{-x} \tag{18}$$

and

$$K(a) = 100 \left(2 + \sin \left(2\pi((a - 1)^2 - 1/4) \right) \right). \tag{19}$$

Plants having a larger flowering intensity than other plants attract more pollinators. We assume that this asymmetric competition affects the probability of setting seed according to a factor $g(\delta)$, where $\delta = (s_{\text{mut}}(a) - s_{\text{res}}(a))/s_{\text{res}}^\beta(a)$ describes the difference of flowering intensities, measured in a way that ranges from absolute ($\beta = 0$) to relative ($\beta = 1$). The function g is assumed to have the properties $g(0) = 1$ and $g'(0) = \alpha/2 > 0$. In the specific examples below, we use the function

$$g(\delta) = \frac{2}{1 + e^{-\alpha\delta}}. \tag{20}$$

The total production of seeds can now be calculated by integrating reproductive success over the flowering season. Therefore, fitness is given by an integral of form (1), where the environment E_{res} is determined by s_{res} and N_{res} ,

$$\begin{aligned}
 & r(s_{\text{mut}}, s_{\text{res}}, N_{\text{res}}) \\
 &= \int_0^1 s_{\text{mut}}(a) p \left(\frac{s_{\text{res}}(a) N_{\text{res}}}{K(a)} \right) g \left(\frac{s_{\text{mut}}(a) - s_{\text{res}}(a)}{s_{\text{res}}(a)^\beta} \right) da - d, \quad (21)
 \end{aligned}$$

where d is the death rate of plants. The resident population size N_{res} can be solved from the condition for ecological equilibrium,

$$r(s_{\text{res}}, s_{\text{res}}, N_{\text{res}}) = 0. \quad (22)$$

The production of flowers according to a schedule $s(a)$ requires resources. [Dieckmann et al. \(2006\)](#) assumed that flowering schedules are for this reason constrained by the inequality constraint

$$\int_0^1 s(a) da \leq 1. \quad (23)$$

[Dieckmann et al. \(2006\)](#) used this model as an illustration of the use of the canonical equation of function-valued traits, and in this manner were the first to demonstrate that evolutionary branching can occur also in function-valued traits. As they already noted, the model summarized above is rather simplistic: this fact was reflected by the observation of evolutionary branching resulting in two coexisting strategies with completely separate flowering seasons, which implies abrupt changes in their flowering schedules ([Dieckmann et al. 2006](#), Fig. 3). Actually, such unrealistically complete temporal separation could become even more extreme, since the model allows evolutionary branching to occur over and over again, until infinitely many strategies coexist whose flowering periods are infinitesimally short and non-overlapping. In nature, such abrupt changes are unrealistic. For this reason, we study in this article three extensions of the seasonal flowering model of [Dieckmann et al. \(2006\)](#); these extensions are intended to add more ecological realism to the model, and to serve as examples of the use of theory presented in this article.

In the first extension (Sect. 4), we add a cost of plasticity directly to the fitness function (21). Fitness is thus expressed as an integral that depends on the strategy $s(a)$ and its derivative $s'(a)$, which means that it remains a direct-effect model of form (1). [Parvinen et al. \(2006\)](#) already showed how to use the calculus of variations to find singular strategies in models of this type. Here we illustrate how to use the canonical equation with derivative dependence (Sect. 2.1) to study transient adaptive dynamics and evolutionary convergence to the previously identified singular strategy.

The second (Sect. 5) and third (Sect. 6) extensions result in process-mediated models of form (2), for which the calculus of variations is no longer applicable. In the resultant more mechanistic setups, the strategy $s(t)$ describes how resources are used, and the actual flowering schedule $y(t)$ is obtained from a (system of) ordinary differential equation(s) affected by $s(t)$. These extensions are used to show how the theory of optimal control (Sect. 2.2) can help to find singular strategies. For better

comparison of methodologies, we also calculate the selection gradient for both examples, even though this is rather tedious. While it is not feasible to solve the equilibria of the canonical equation (3) analytically, the canonical-equation dynamics can be calculated numerically.

4 First extension: adding a direct cost of plasticity using the derivative

In general, mechanisms that accurately separate the flowering intensities between two nearby moments in time can be expected to be costly. Therefore, in the first model extension, we assume that deviations of the derivative $s'_{\text{mut}}(a) = \frac{d}{da} s_{\text{mut}}(a)$ from zero have a direct negative effect on fitness,

$$r(s_{\text{mut}}, s_{\text{res}}, N_{\text{res}}) = \int_0^1 \left[s_{\text{mut}}(a) p \left(\frac{s_{\text{res}}(a) N_{\text{res}}}{K(a)} \right) g \left(\frac{s_{\text{mut}}(a) - s_{\text{res}}(a)}{s_{\text{res}}(a)^\beta} \right) - \kappa (s'_{\text{mut}}(a))^2 \right] da - d, \tag{24}$$

where κ measures the strength of these plasticity costs.

4.1 Selection gradient

By differentiating the integrand in Eq. (24), we obtain the derivatives

$$F_{s_{\text{mut}}}(a, s_{\text{mut}}(a), s_{\text{res}}(a)) = p \left(\frac{N s_{\text{res}}(a)}{K(a)} \right) \times \left[g \left(\frac{s_{\text{mut}}(a) - s_{\text{res}}(a)}{s_{\text{res}}(a)^\beta} \right) + s_{\text{mut}}(a) g' \left(\frac{s_{\text{mut}}(a) - s_{\text{res}}(a)}{s_{\text{res}}(a)^\beta} \right) \frac{1}{s_{\text{res}}(a)^\beta} \right] \tag{25}$$

and $F_{s'_{\text{mut}}}(s'_{\text{mut}}(a)) = -2\kappa s'_{\text{mut}}(a)$, and thus the selection gradient (6),

$$G(a) = F_{s_{\text{mut}}}(a, s_{\text{mut}}(a), s_{\text{res}}(a)) - \frac{d}{da} F_{s'_{\text{mut}}}(s'_{\text{mut}}(a)) \Big|_{s_{\text{mut}}=s_{\text{res}}=s} = \left(1 + \frac{\alpha}{2} s(a)^{1-\beta} \right) p \left(\frac{Ns(a)}{K(a)} \right) + 2\kappa s''(a). \tag{26}$$

4.2 Singular strategies with calculus of variations

Because of the inequality constraints (23) and $s(a) \geq 0$, the Euler–Lagrange equation for singular strategies obtained with the calculus of variations is $G(a) = C > 0$ for $s(a) > 0$ and $G(a) < C$ for $s(a) = 0$.

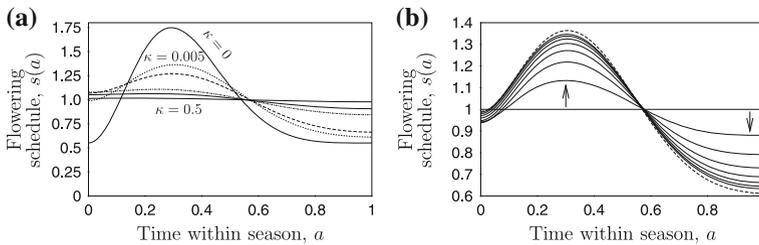


Fig. 1 **a** Evolutionarily singular flowering schedules for different costs of plasticity, $\kappa = 0, 0.005, 0.01, 0.05, 0.1, 0.5$. **b** Evolution of the flowering schedule according to the canonical equation, starting from the initial flowering schedule $s(a) = 1$ towards the evolutionarily singular strategy, for $\kappa = 0.005$. Other parameters: $\alpha = 1$, $\beta = 0.9$, and $d = 0.5$

Note that the population size N in (26) depends on the strategy s . Therefore, N and $s(a)$ must be solved together from (22) and (26). For $\kappa = 0$, this solution is found algebraically, but for $\kappa > 0$, it requires solving a second-order differential equation. The necessary boundary conditions, resulting from Eq. (21) of Parvinen et al. (2006) (see also Proposition 1), are $F_{s'} = -2\kappa s' = 0$ at either boundary, yielding $s'(0) = 0$ and $s'(1) = 0$.

Figure 1a illustrates singular strategies for different values of the plasticity cost κ . Other parameters are chosen as in Dieckmann et al. (2006); therefore, the singular strategy for $\kappa = 0$ in Fig. 1a matches that in Fig. 3 of Dieckmann et al. (2006). For $\kappa = 0$, it is easy to show that any singular strategy can be invaded by some mutants with extremely concentrated flowering schedules, so such a singular strategy is not evolutionarily stable. For $\kappa > 0$, the corresponding analysis is not straightforward, but our numerical results suggest that when κ is large enough, the singular strategy turns into a fitness maximum, and thus becomes evolutionarily stable.

4.3 Canonical-equation dynamics

We have already calculated the selection gradient (26) for the model (24). It is needed for applying the canonical equation (3), which describes the rate of expected evolutionary change in a function-valued strategy (Dieckmann et al. 2006). The equilibrium population size N for strategy s is obtained from (24) by requiring $r(s, s, N) = 0$. In addition, we need to specify the mutation probability $\mu(s)$ and the variance-covariance function σ^2 of the mutation distribution. Here we have assumed that $\sigma^2(a', a) = \sigma^2[\delta(a - a') - 1]$, which means that an increase or decrease of s at a particular argument value a is compensated uniformly across all other argument values, thus ensuring that the trait normalization (23) stays intact. Note, however, that the choice of the variance-covariance function can substantially affect the dynamics and evolutionary equilibrium of the canonical equation (Heino et al. 2008, Fig. 5).

Figure 1b illustrates the dynamics of the canonical equation starting from a uniform initial strategy $s(a) = 1$. As expected, the monomorphic strategy approaches the singular strategy predicted by the calculus of variations (Fig. 1a).

5 Second extension: process-mediated flower production through gradual resource allocation

In the previous section, we have assumed that the flowering schedule at time a within the season is the evolving strategy. However, it is more reasonable to assume that the flowering schedule is actually a result of the time-dependent intensity $s(t) \geq 0$ according to which resources are allocated to flower production, and that it is this resource-allocation schedule that is the function-valued trait under natural selection. The flowering schedule thus becomes a state variable, denoted by $y(t)$, which is assumed to satisfy the differential equation

$$\frac{d}{dt}y(t) = h(s(t)) - \xi y(t), \quad y(0) = 0, \tag{27}$$

where the function $h(s)$ is the functional response of flower production, and ξ is the rate at which flowers die. Since available resources are necessarily limited, we have the constraint

$$\int_0^1 s(t) dt \leq S_{\max}, \tag{28}$$

but since plants should not leave available resources unused, this inequality constraint will be satisfied as an equality constraint instead. Flower and seed dynamics are otherwise as in Sect. 3, except that in this second example the cost of plasticity is included in the function h , so it is not necessary to include it in the fitness function as a dependence on $y'(t)$. Furthermore, an inequality constraint on the total amount of flowers, as in (23), is not needed, because such a constraint follows from (28). We thus assume that fitness is given by

$$r(s_{\text{mut}}, E_{\text{res}}) = \int_0^1 \underbrace{y_{\text{mut}}(t) p \left(\frac{y_{\text{res}}(t) N_{\text{res}}}{K(t)} \right) g \left(\frac{y_{\text{mut}}(t) - y_{\text{res}}(t)}{y_{\text{res}}(t)^\beta} \right)}_{F(t, y_{\text{mut}}(t), y_{\text{res}}(t))} dt - d, \tag{29}$$

where the environment E_{res} created by the resident is characterized by the resident population size N_{res} and the flowering schedule y_{res} that solves the differential equation (27) for the resident resource-allocation strategy s_{res} . Analogously, the flowering schedule y_{mut} of the mutant solves the differential equation (27) for the mutant resource-allocation strategy s_{mut} .

5.1 Selection gradient

Since the fitness function (29) is not of form (1), Eq. (6) for the selection gradient cannot be used. We thus need to employ equation (4) directly. Let us first note that the

solution of the differential equation (27) with $s^*(t) = s(t) + \epsilon \Delta s(t)$ can be written as

$$y^*(t) = e^{-\xi t} \int_0^t e^{\xi \tau} h(s^*(\tau)) d\tau = e^{-\xi t} \int_0^t e^{\xi \tau} h(s(\tau) + \epsilon \Delta s(\tau)) d\tau. \quad (30)$$

Thus we obtain

$$\begin{aligned} \frac{d}{d\epsilon} y^*(t) \Big|_{\epsilon=0} &= e^{-\xi t} \int_0^t e^{\xi \tau} h'(s(\tau)) \Delta s(\tau) d\tau \\ &\rightarrow \begin{cases} 0, & \text{if } t < \hat{t}, \\ e^{\xi(\hat{t}-t)} h'(s(\hat{t})), & \text{if } t > \hat{t}, \end{cases} \end{aligned} \quad (31)$$

when Δs tends to the Dirac delta function $\delta_{\hat{t}}$. This result can be used in the calculation of the selection gradient,

$$\begin{aligned} G(t) &= \lim_{\Delta s \rightarrow \delta_{\hat{t}}} \left[\frac{d}{d\epsilon} r(s + \epsilon \Delta s, E_{\text{res}}) \Big|_{\epsilon=0} \right] \\ &= \lim_{\Delta s \rightarrow \delta_{\hat{t}}} \int_0^1 F_{y_{\text{mut}}}(\hat{t}, y_{\text{mut}}(\hat{t}), y_{\text{res}}(\hat{t})) \frac{d}{d\epsilon} y^*(\hat{t}) \Big|_{\epsilon=0} d\hat{t} \\ &= h'(s(t)) \int_t^1 F_{y_{\text{mut}}}(\hat{t}, y_{\text{mut}}(\hat{t}), y_{\text{res}}(\hat{t})) e^{\xi(t-\hat{t})} d\hat{t}. \end{aligned} \quad (32)$$

Without constraints set on the evolving strategy s , evolutionarily singular strategies are strategies for which the selection gradient vanishes, $G(t) = 0$. In the present model, increased allocation intensity will always increase flowering intensity, and thus fitness. Therefore, $G(t) > 0$ for all $t < 1$. Since allocatable resources are necessarily limited, we have the global inequality constraint (28), which for singular strategies is fulfilled with equality. In addition, we have the constraint $s(t) \geq 0$, because allocation intensity is necessarily non-negative. For a singular strategy, a fitness increase due to increased resource allocation at one time must be exactly compensated by a fitness decrease due to decreased resource allocation at other times. More precisely, for singular strategies s , a mutant strategy $s + \epsilon \Delta s$ belongs to the strategy space S for small $|\epsilon|$ only if $\int_{t_{\min}}^{t_{\max}} \Delta s(t) dt = 0$, and if $\Delta s(t) = 0$ for such t for which $s(t) = 0$. The definition (5) of singular strategies can only be fulfilled if the first-order fitness increase for increased resource allocation at time t , which is measured by the selection gradient $G(t)$, is the same ($= C$) for such t for which $s(t) > 0$. For such t for which $s(t) = 0$, the fitness increase must be less than C . Altogether, we obtain

$$G(t) - C \begin{cases} = 0, & \text{if } s(t) > 0, \\ < 0, & \text{if } s(t) = 0, \end{cases} \quad (33)$$

where the constant $C > 0$ is determined such that the constraint (28) holds with equality. See also Sect. 2.3.2 of Parvinen et al. (2006).

5.2 Singular strategies with theory of optimal control

The model (27–29) can be written in the standard form used in the theory of optimal control (11),

$$\begin{aligned} \frac{d}{dt}y_1(t) &= h(s(t)) - \xi y_1(t), & y_1(0) &= 0, \\ \frac{d}{dt}y_2(t) &= s(t), & y_2(0) &= 0, \end{aligned} \tag{34}$$

with the condition $y_2(1) \leq S_{\max}$, so that (28) is satisfied. As explained before, this condition will actually be satisfied with equality, $y_2(1) = S_{\max}$. Now the Hamiltonian (13) is given by

$$H = F(t, y_1(t)) + \lambda_1(t) (h(s(t)) - \xi y_1(t)) + \lambda_2(t)s(t). \tag{35}$$

Because the Hamiltonian does not depend on y_2 , the condition (12) for λ_2 is

$$\frac{d}{dt}\lambda_2(t) = -H_{y_2} = 0, \tag{36}$$

so $\lambda_2(t)$ does not depend on t , $\lambda_2(t) = \lambda_2$. Note that since the value of $y_2(1)$ is fixed, the value of $\lambda_2(1)$ is free, and is set to satisfy $y_2(1) = S_{\max}$. For λ_1 , we obtain from (12) the differential equation

$$\frac{d}{dt}\lambda_1(t) = -H_{y_1} = -F_{y_1} + \lambda_1(t)\xi \quad \text{with } \lambda_1(1) = 0. \tag{37}$$

Because $F_{y_1} > 0$, the solution of (37) satisfies $\lambda_1(t) \geq 0$ for $0 \leq t \leq 1$. In each moment, $s(t)$ is chosen such that the Hamiltonian is maximized. The only terms in the Hamiltonian (35) that depend on s are $\lambda_1 h(s(t))$ and $\lambda_2 s(t)$. If $\lambda_2 \geq 0$, the Hamiltonian is maximized by $s(t) \rightarrow \infty$, but that solution cannot satisfy the constraint $y_2(1) \leq S_{\max}$. Therefore, $\lambda_2 < 0$, and possible values for $s(t)$ are

$$s(t) = 0, \quad \text{if } \lambda_1(t)h'(0) + \lambda_2 < 0, \tag{38a}$$

$$s(t) > 0, \quad \text{such that } \lambda_1(t)h'(s(t)) + \lambda_2 = 0. \tag{38b}$$

Especially, if the functional response h is strictly concave, $h''(s) < 0$, Eq. (38b) has no solution if (38a) holds, and a unique solution if (38a) does not hold.

We thus obtain the evolutionarily singular strategy $s(t)$ by solving the differential equations (34) and (37) together with (38) from $t = 0$ with two unknowns: $\lambda_1(0)$ and λ_2 , which are used to satisfy the conditions $y_2(1) = S_{\max}$ and $\lambda_1(1) = 0$. In addition, we have the condition $r(s, N) = 0$ for a population at ecological equilibrium, and thus

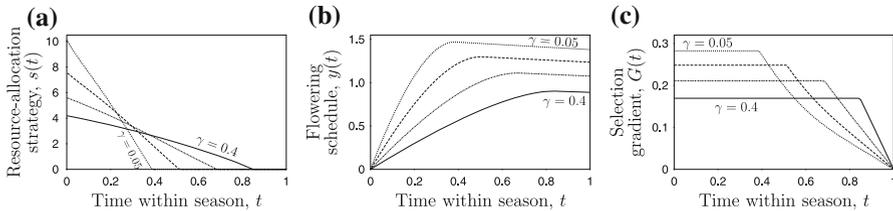


Fig. 2 Evolutionarily singular strategies in the model (27–29) obtained with the theory of optimal control for different functional-response parameters, $\gamma = 0.05, 0.1, 0.2,$ and 0.4 . **a** Resource-allocation strategy $s(t)$. **b** Resultant flowering schedule $y(t)$. **c** Resultant selection gradient according to Eq. (32). Other parameters: $\alpha = 1, \beta = 0.9, \xi = 0.1, S_{\max} = 2,$ and $d = 0.5$

this is a problem of optimal control with environmental feedback. Another option is to start solving the differential equations from $t = 1$ with initial conditions $\lambda_1(1) = 0$ and $y_2(1) = S_{\max}$, and then to use the unknowns λ_2 and $y_1(1)$ to satisfy the conditions $y_1(0) = y_2(0) = 0$.

In our numerical explorations we obtained better accuracy using the second alternative. For the numerical examples below, we use the same parameters as Dieckmann et al. (2006) and assume that the functional response of flower production is of Holling type II,

$$h(s(t)) = \frac{s(t)}{1 + \gamma s(t)}. \tag{39}$$

Therefore, the possible values for $s(t)$ from condition (38) are

$$s(t) = \begin{cases} 0, & \text{if } 0 \leq \lambda_1(t) \leq -\lambda_2, \\ \frac{1}{\gamma} \left(\sqrt{-\frac{\lambda_1(t)}{\lambda_2}} - 1 \right), & \text{if } \lambda_1(t) > -\lambda_2 > 0. \end{cases} \tag{40}$$

Figure 2a illustrates evolutionarily singular resource-allocation schedules $s(t)$ obtained with the optimal-control method described above, for different values of γ . Figure 2b illustrates the resulting flowering schedules. For comparison, Fig. 2c illustrates the selection gradient calculated from (32) for the singular strategy obtained with optimal control theory; this shows that the condition (33) is satisfied. Note, however, that the theory of optimal control only gives necessary conditions for a strategy to be a fitness maximum, and thus uninvadable. Unlike in the calculus of variations, there is no general theory that would provide sufficient conditions for fitness maxima. Furthermore, the theory of optimal control cannot be used to study whether a singular strategy is convergence stable or not. For this purpose, we need to investigate the corresponding canonical-equation dynamics, which we therefore do next.

5.3 Canonical-equation dynamics

Figure 3 illustrates the canonical-equation dynamics (3) of the model (27–29) starting from a uniform resource-allocation schedule, $s(t) = 2$. As in our first example, we

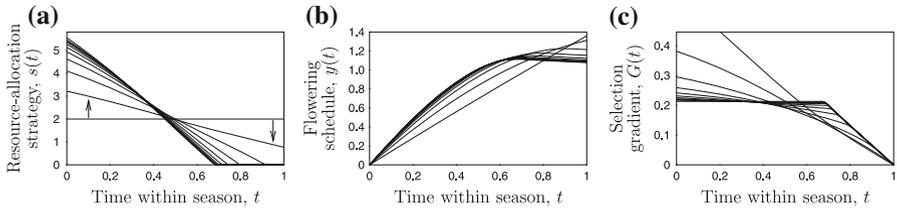


Fig. 3 Canonical-equation dynamics of the model (27–29), starting from a uniform resource-allocation strategy, $s(t) = 2$. **a** Resource-allocation strategy $s(t)$. **b** Resultant flowering schedule $y(t)$. **c** Resultant selection gradient according to Eq. (32). The strategy converges towards the same evolutionarily singular strategy as shown in Fig. 2. Other parameters: $\alpha = 1$, $\beta = 0.9$, $\gamma = 0.2$, $\xi = 0.1$, $S_{\max} = 2$, and $d = 0.5$

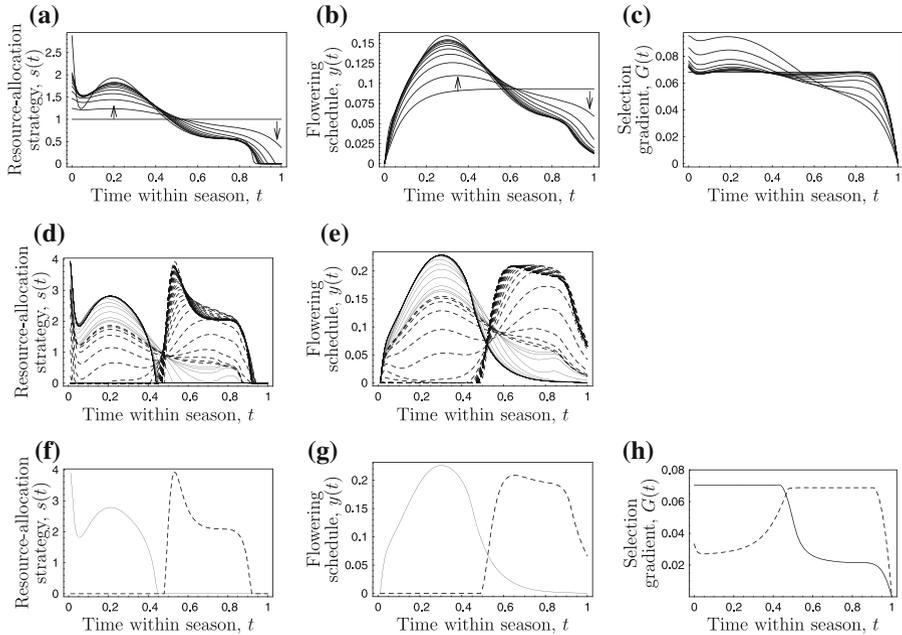


Fig. 4 Monomorphic and dimorphic canonical-equation dynamics of the model (27–29), starting from a uniform resource-allocation strategy, $s(t) = 1$. **a–c** Convergence towards a monomorphic evolutionarily singular strategy that is not evolutionarily stable. **d, e** Dimorphic convergence, after evolutionary branching, towards an evolutionarily singular coalition. **f, g** Members of this coalition. **h** Corresponding selection gradients. Parameters: $\alpha = 1$, $\beta = 0.9$, $\gamma = 0.02$, $\xi = 10.5$, $S_{\max} = 1$, and $d = 0.05$

again assume that $\sigma^2(t', t) = \sigma^2[\delta(t - t') - 1]$. We observe that the resource-allocation schedule converges to the same singular strategy that was obtained with the theory of optimal control, as illustrated in Fig. 2. Our numerical investigations suggest that this singular strategy is uninaversable, and thus an evolutionary endpoint.

Figure 4a–c illustrates monomorphic canonical-equation dynamics for another set of parameter values. In this case, however, the monomorphic singular strategy is not uninaversable. In such a case, evolutionary branching can occur. Figure 4d, e illustrates dimorphic canonical-equation dynamics towards an evolutionarily singular coalition

of two strategies, shown for greater clarity in Fig. 4f, g, with the corresponding two selection gradients illustrated in Fig. 4h. While the two resource-allocation schedules are strictly segregated in time, the resulting flowering schedules show considerable overlap. Furthermore, the dimorphic flowering schedules we obtain for this extended model are much smoother than those in the original model of Dieckmann et al. (2006).

6 Third extension: process-mediated flower production through gradual and differential resource allocation

As another example of a process-mediated model, we study a third extension of the flowering model by Dieckmann et al. (2006). As in the second extension, the function-valued trait affects a process of flower growth, but now the trait determines the resource allocation between leaf growth and flower production.

We denote by $x(t)$ the biomass of leaves in a plant and by $y(t)$ the biomass of flowers or flowering intensity. The leaf biomass at the beginning of a season is x_0 . We assume that there is incoming energy from sunlight with intensity $E(t)$, and that the plant uses its leaves to collect that energy. The plant allocates the proportion $s(t) \geq 0$ of $E(t)$ to flower production and the proportion $1 - s(t) \geq 0$ to leaf growth. There is a functional response in both allocation processes, described by the functions f and h , respectively: the nonlinearity described by the function h occurs at the (global) plant level, while the nonlinearity described by the function f occurs at the (local) level of leave tissue. Furthermore, leaves decay with rate ω and flowers decay with rate ξ . As a result, we obtain the following system of differential equations,

$$\begin{aligned} \frac{d}{dt}x(t) &= x(t)f(E(t)(1 - s(t))) - \omega x(t), & x(0) &= x_0, \\ \frac{d}{dt}y(t) &= h(E(t)s(t)x(t)) - \xi y(t), & y(0) &= 0. \end{aligned} \quad (41)$$

Otherwise, the model is as described before, so fitness is given by Eq. (29), which is of the process-mediated form (10).

6.1 Selection gradient

As in the second extension, the fitness function is not of form (1). Therefore, Eq. (6) for the selection gradient cannot be used, and Eq. (4) needs to be used directly. For this purpose, note that the differential equation for the leaf biomass $x(t, s)$ in (41) is linear with respect to $x(t, s)$ and does not depend on $y(t, s)$. Therefore, the solution is

$$x(t, s) = x_0 \exp \left(\int_0^t [f(E(\tau)(1 - s(\tau))) - \omega] d\tau \right). \quad (42)$$

Using the notation $Q(t, s) = h(E(t)s(t)x(t))$, we can write the solution for the flowering intensity $y(t, s)$ as

$$y(t, s) = e^{-\xi t} \int_0^t Q(\tau, s) e^{\xi \tau} d\tau. \tag{43}$$

From Eq. (42) we obtain the derivative

$$\begin{aligned} x^*(t, s, \Delta s) &= \left. \frac{d}{d\epsilon} x(t, s + \epsilon \Delta s) \right|_{\epsilon=0} \\ &= x(t, s) \int_0^t f'(E(\tau)(1 - s(\tau))) (-E(\tau) \Delta s(\tau)) d\tau, \end{aligned} \tag{44}$$

and the limit for $\Delta s(\tau)$ tending to the Dirac delta function $\delta_{\hat{t}}$ is

$$\hat{x}(t, s, \hat{t}) = \lim_{\Delta s \rightarrow \delta_{\hat{t}}} x^*(t, s, \Delta s) = \begin{cases} 0, & \text{if } t < \hat{t}, \\ -x(t, s) E(\hat{t}) f'(E(\hat{t})(1 - s(\hat{t}))), & \text{if } t > \hat{t}. \end{cases} \tag{45}$$

From (43) we obtain the derivative

$$\begin{aligned} y^*(t, s, \Delta s) &= \left. \frac{d}{d\epsilon} y(t, s + \epsilon \Delta s) \right|_{\epsilon=0} \\ &= e^{-\xi t} \int_0^t h'(E(\tau)s(\tau)x(\tau, s)) E(\tau) (\Delta s(\tau)x(\tau, s) \\ &\quad + s(\tau)x^*(\tau, s, \Delta s)) e^{\xi \tau} d\tau. \end{aligned} \tag{46}$$

We also need the limit of $y^*(t, s, \Delta s)$ for $\Delta s(\tau)$ tending to the Dirac delta function $\delta_{\hat{t}}$. Since changing the resource allocation by $\epsilon \delta_{\hat{t}}$ can only affect flowering intensities at time \hat{t} and later, we have $\lim_{\Delta s \rightarrow \delta_{\hat{t}}} y^*(t, s, \Delta s) = 0$ for $t < \hat{t}$. For $t \geq \hat{t}$, we have

$$\begin{aligned} \hat{y}(t, s, \hat{t}) &= \lim_{\Delta s \rightarrow \delta_{\hat{t}}} y^*(t, s, \Delta s) = e^{-\xi t} E(\hat{t}) \left[h'(E(\hat{t})s(\hat{t})x(\hat{t}, s)) x(\hat{t}, s) e^{\xi \hat{t}} \right. \\ &\quad \left. - f'(E(\hat{t})(1 - s(\hat{t}))) \int_{\hat{t}}^t h'(E(\tau)s(\tau)x(\tau, s)) E(\tau)s(\tau)x(\tau, s) e^{\xi \tau} d\tau \right]. \end{aligned} \tag{47}$$

Finally, the selection gradient is

$$G(t) = \lim_{\Delta s \rightarrow \delta_t} \left[\left. \frac{d}{d\epsilon} r(s + \epsilon \Delta s) \right|_{\epsilon=0} \right] = \int_t^1 F_{y_{\text{mut}}}(\tau) \hat{y}(\tau, s, t) d\tau. \tag{48}$$

The selection gradient is thus obtained through double integration, which is tedious, but can be done numerically for any known strategy. Therefore, calculating the canonical-equation dynamics and waiting until it converges allows finding the evolutionarily singular strategies numerically. Numerically solving for these strategies directly from Eq. (48) is difficult. Instead, it is relatively easy to use the theory of optimal control for that purpose.

6.2 Singular strategies with theory of optimal control

Like the second extension, the model (41) can be written in the standard form (11b) used in the theory of optimal control,

$$\begin{aligned} \frac{d}{dt}y_1(t) &= y_1(t)f(E(t)(1-s(t))) - \omega y_1(t), & y_1(0) &= x_0, \\ \frac{d}{dt}y_2(t) &= h(E(t)s(t)y_1(t)) - \xi y_2(t), & y_2(0) &= 0. \end{aligned} \tag{49}$$

Now the Hamiltonian (13) is

$$\begin{aligned} H &= F(t, y_2) + \lambda_1(t)\frac{dy_1(t)}{dt} + \lambda_2(t)\frac{dy_2(t)}{dt} \\ &= y_2(t)p^*(t)g^*(y_2(t), t) + \lambda_1(t)[y_1(t)f(E(t)(1-s(t))) - \omega y_1(t)] \\ &\quad + \lambda_2(t)[h(E(t)s(t)y_1(t)) - \xi y_2(t)], \end{aligned} \tag{50}$$

where $p^*(t) = p(\frac{y_{res}(t)N_{res}}{K(t)})$ and $g^*(y_2(t), t) = g(\frac{y_2(t)-y_{res}(t)}{y_{res}(t)^\beta})$. The conditions (12) for λ_1 and λ_2 are

$$\begin{aligned} \frac{d}{dt}\lambda_1(t) &= -H_{y_1} = -\lambda_1(t)[f(E(t)(1-s(t))) - \omega] \\ &\quad - \lambda_2(t)h'(E(t)s(t)y_1(t))E(t)s(t) \end{aligned} \tag{51}$$

and

$$\frac{d}{dt}\lambda_2(t) = -H_{y_2} = -p^*(t)\left[g^*(y_2(t), t) + y_2(t)\frac{\partial}{\partial y_2(t)}g^*(y_2(t), t)\right] + \lambda_2(t)\xi \tag{52}$$

with $\lambda_1(1) = \lambda_2(1) = 0$.

We thus obtain the evolutionary singular strategy $s(t)$ by solving the differential equations (49), (51), and (52), and choosing $s(t)$ such that it maximizes the Hamiltonian (50) for each t . In addition, we have the equilibrium condition $r(s, N) = 0$, and thus this is a problem of optimal control with environmental feedback. We can either start from $t = 0$ with two unknowns, $\lambda_1(0)$ and $\lambda_2(0)$, which are used to get

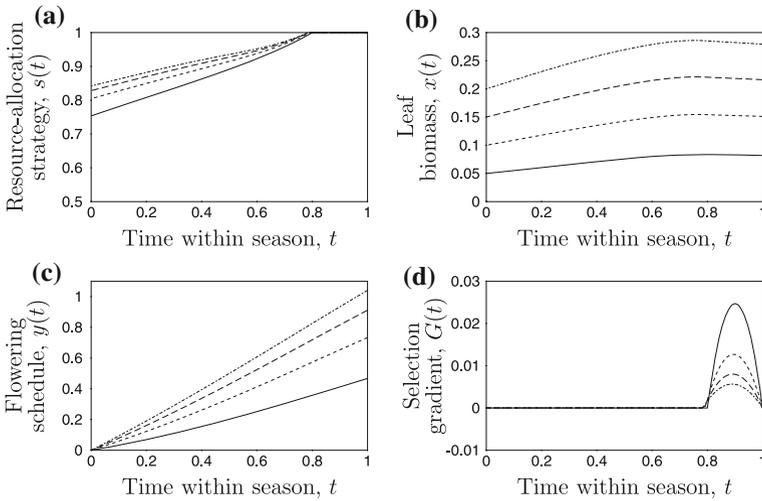


Fig. 5 Evolutionarily singular strategies in the model (41) obtained with the theory of optimal control for different values of initial leaf biomass, $x_0 = 0.05, 0.1, 0.15,$ and 0.2 . **a** Resource-allocation strategy $s(t)$. **b** Resultant leaf biomass $x(t)$. **c** Resultant flowering schedule $y(t)$. **d** Resultant selection gradient according to Eq. (48). As expected, the selection gradient is 0 for $0 < s(t) < 1$ and positive for $s(t) = 1$. Parameters: $\alpha = 1, \beta = 1, \omega = 0.1, \xi = 0.1, d = 0.2, f(z) = h(z) = z/(1 + 0.5z),$ and $E(t) = 10$

conditions $\lambda_1(1) = \lambda_2(1) = 0$ satisfied. Another option is to start solving the differential equations from $t = 1$ with initial conditions $\lambda_1(1) = \lambda_2(1) = 0,$ and use the unknowns $y_1(1)$ and $y_2(1)$ to get the conditions $y_1(0) = x_0$ and $y_2(0) = 0$ satisfied.

Figure 5a illustrates evolutionary singular resource-allocation strategies $s(t)$ obtained with the optimal-control method described above, for different values of x_0 . Figure 5b illustrates the resulting leaf biomass and Fig. 5c the resulting flowering schedules. For comparison, Fig. 5d shows the resulting selection gradients calculated from (48) for the evolutionarily singular strategy, obtained using the theory of optimal control.

6.3 Canonical-equation dynamics

Figure 6 illustrates the canonical-equation dynamics (3) of the model (41) starting from a uniform resource-allocation strategy $s(t) = 0.75$. This time we have assumed that $\sigma^2(t', t) = \sigma^2\delta(t - t')$, which means that an increase or decrease of s at a particular argument value has no effect on other argument values. We observe that the strategy of the evolving population approaches the same evolutionarily singular strategy that was obtained with the theory of optimal control and shown in Fig. 5.

7 Conclusions

In this article we have further developed the theory of adaptive dynamics of function-valued traits. Previously, we had shown how the calculus of variations can be used to find evolutionarily singular strategies in direct-effect models, in which the invasion

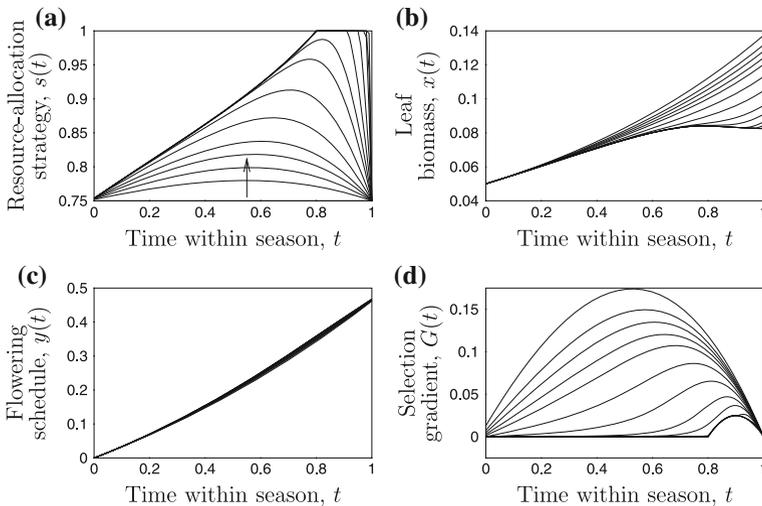


Fig. 6 Canonical-equation dynamics of the model (41) starting from the uniform strategy $s(t) = 0.75$. **a** Resource-allocation strategy $s(t)$. **b** Resultant leaf biomass $x(t)$ **c** Resultant flowering schedule $y(t)$. **d** Selection gradient according to Eq. (48). The strategy converges towards the same evolutionarily singular strategy as shown in Fig. 5. Parameters as in Fig. 5 with $x_0 = 0.05$

fitness can be written as an integral in which the integrand for each argument value is a function of the strategy value at that point only (Parvinen et al. 2006). Here we have broadened our methods of analysis to tackle process-mediated models, a rather general class of models that includes direct-effect models as a subset. In particular, we have described how to use optimal control theory to find singular strategies in process-mediated models, in which the function-valued strategy affects a process described by differential equations, and fitness can be expressed as an integral in which the integrand depends both on the strategy and the process variables. Our results show that singular strategies of such models need to satisfy Pontryagin's maximum principle with environmental feedback.

Although the class of process-mediated models is wide, not all models of interest are of such form. For example, the metapopulation model in Section 7 of Parvinen et al. (2006) is an example of a direct-effect model in which invasion fitness is a function of several integrals. Although Euler's equation of the calculus of variations cannot be used directly to analyze that model, Parvinen et al. (2006) have shown how to adapt the derivation of Euler's equation to find evolutionarily singular strategies in that model. This approach is applicable also for solving other direct-effect models in which invasion fitness is a function of several integrals. Analogously, it is straightforward to construct process-mediated models in which invasion fitness is a function of several integrals. For such models, Pontryagin's maximum principle cannot be used directly, but one may be able to adapt its derivation.

The expansion of the theory of adaptive dynamics of function-valued traits developed here is not only mathematically interesting, but also allows investigating biologically more realistic models. We hope this work will further stimulate the application of function-valued traits in theoretical evolutionary ecology. As an example, here we

have shown how function-valued traits can be used to study the evolution of flowering schedules. In particular, our model in Sect. 5 shows that in the presence of asymmetric competition temporal segregation in flowering schedules can evolve. Known as staggered flowering, this phenomenon is known in tropical plant communities and could be a mechanism for reproductive isolation between closely related species (Snow 1965; Stiles 1977). We hope to further explore staggered flowering in a forthcoming study.

Appendix A: Proof of Proposition 1

Proof When the fitness function is of form (1), differentiation results in (see also Equation 10 of Parvinen et al. 2006)

$$\begin{aligned} \frac{d}{d\epsilon} r(s + \epsilon \Delta s) \Big|_{\epsilon=0} &= \int_{a_{\min}}^{a_{\max}} \frac{d}{d\epsilon} F(a, s(a) + \epsilon \Delta s, s'(a) + \epsilon \Delta s') da \Big|_{\epsilon=0} \\ &= \int_{a_{\min}}^{a_{\max}} F_s(a, s(a), s'(a)) \Delta s + F_{s'}(a, s(a), s'(a)) \Delta s' da. \end{aligned} \tag{53}$$

Integration by parts yields

$$\begin{aligned} \frac{d}{d\epsilon} r(s + \epsilon \Delta s) \Big|_{\epsilon=0} &= \int_{a_{\min}}^{a_{\max}} \left[F_s(a, s(a), s'(a)) - \frac{d}{da} F_{s'}(a, s(a), s'(a)) \right] \Delta s da \\ &\quad + F_{s'}(a_{\max}, s(a_{\max}), s'(a_{\max})) \Delta s(a_{\max}) \\ &\quad - F_{s'}(a_{\min}, s(a_{\min}), s'(a_{\min})) \Delta s(a_{\min}). \end{aligned} \tag{54}$$

For $\Delta s \rightarrow \delta_a$ with $a_{\min} < a < a_{\max}$, both $\Delta s(a_{\min}) \rightarrow 0$ and $\Delta s(a_{\max}) \rightarrow 0$, and the integral tends to the value of the integrand at a , which gives

$$G(a) = F_s(a, s(a), s'(a)) - \frac{d}{da} F_{s'}(a, s(a), s'(a)) \quad \text{for } a_{\min} < a < a_{\max}. \tag{55}$$

However, for $\Delta s \rightarrow \delta_a$ with $a = a_{\min}$, $\Delta s(a_{\min}) \rightarrow \infty$; the corresponding limit for $a = a_{\max}$ is also infinite. Therefore, unless $F_{s'} = 0$ at a boundary, the selection pressure at that boundary is an order of magnitude stronger than elsewhere, forcing $F_{s'}$ to become zero practically immediately compared to the speed of evolution elsewhere, from which the result follows.

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