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Interim Report **IR-06-083**

The Evolution of Simple Life-Histories: Step Towards a Classification

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Contents

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The Evolution of Simple Life-Histories: Steps Towards a Classification

Abstract We present a classification of the evolutionary dynamics for a class of simple life-history models. The model class considered is characterised by

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discrete time population dynamics, density-dependent population growth, by the assumption that individuals can occur in two states, and that two evolving traits are coupled by a trade-off. Individual models differ in the choice of traits that are presumed to evolve and in the way population regulation is incorporated. The classification is based on a fitness measure that is sign equivalent to invasion fitness but algebraically simpler. We classify models according to curvature properties of the fitness landscape and whether the evolutionary dynamics can be analysed by means of an optimisation criterion. The first classification allows us to infer whether trait combinations that are characterised by a zero fitness gradient are susceptible to invasion by similar trait combinations. The second classification distinguishes models where evolutionary change is frequency-independent from models that give rise to frequency dependence. Given certain symmetry assumptions we can extend the classification in the latter case by splitting selection into a density-dependent and a frequency-dependent component. We apply our approach to several simple life-history models and demonstrate how our classification facilitates an analytical analysis. We conclude by discussing some general patterns that emerge from our analysis and by hinting at several possible extensions.

Keywords adaptive dynamics · density dependence · fitness · frequency dependence · life-history theory · matrix model · optimisation · trade-off

1 Introduction

Evolutionary change is guided by two factors. First, constraints delimit the range of possible mutant phenotypes. Such constraints to evolutionary change emerge for various reasons. For example, pleiotropy can couple a change in one trait to a change in another trait and can thereby render certain parts of the trait-space unattainable (Stearns, 1992; Roff, 2002). Specific trait combinations might be physically impossible or they can result in non-viable organisms, hence individuals with these trait combinations cannot establish populations and evolve. Either mechanism can have as a consequence that the evolutionary dynamics are constrained to a subset of the trait space. This result is called a trade-off when we observe that an improvement in one function is bought at the expense of deterioration in another function. Second, whether a given mutant is favoured by selection depends on the topography of the fitness landscape (Wright, 1931). In case of two-dimensional trait spaces a fitness landscape can be visualised as a three-dimensional graph or as a two-dimensional contour plot (Levins, 1962). Evolutionary change driven by selection can only occur in an upward direction on such a fitness landscape.

The evolutionary dynamics of two quantitative traits that are coupled by a trade-off can lead to several qualitatively different endpoints. The long term evolutionary dynamics could lead to an intermediate phenotype in the sense that the two evolving traits constitute a compromise between conflicting demands. Such phenotypes have been named “generalists” when the trade-off determines the ability of an organism to exploit different food resources or habitats (Futuyma and Moreno, 1988). In the context of life-history theory such an intermediate phenotype would be an iteroparous organism if it balances energy allocation between current reproduction and self-maintenance (Stearns, 1992; Takada, 1995). Alternatively, selection could favour an extreme phenotype that sacrifices one function to achieve maximal performance in another function. In the context of resource acquisition such a phenotype corresponds to a resource or habitat specialist while in the context of life-history evolution such a phenotype corresponds to an semelparous organism when it allocates all resources to current reproduction and none to self-maintenance or to an organism that delays maturation for the opposite allocation pattern (Heino et al., 1997). In yet another scenario selection can drive a population towards a point in trait-space where the population experiences disruptive selection. Such points are known as evolutionary branching points (Metz et al., 1996*a*; Geritz et al., 1998) where populations experience selection for increased phenotypic variation (Rueffler et al., 2006*a*). When analysing an eco-evolutionary model one usually aims at necessary and sufficient conditions that determine which of the different evolutionary scenarios is favoured. It is an even stronger result when we can show that such conditions are not only valid for one specific model but for a large class of models. In this paper we attempt to find such general conditions in terms of properties of constraints and the fitness landscape for one well defined class of models.

The class of models analysed in this paper is characterised by a life-cycle that can be described with two states and where any set of two traits are allowed to change mutationally while all other parameters are assumed to be fixed. We introduce a constraint by assuming that the two evolving traits are coupled by a trade-off. Density dependence can act on any set of demographic parameters and different parameters can be affected by different subgroups of the population. The specific choice of the ecological scenario affects properties of the fitness landscape. Some specific members of this model family have been analysed with different techniques (Takada, 1995; Heino et al., 1997; Diekmann, 2004; Heino, in press). Other authors analysed models closely related to those investigated here, these are either formulated in continuous time (Meszéna et al., 1997; Day et al., 2002), allow for evolutionary change of more than two traits (Kisdi, 2002), incorporate sexual reproduction (Kisdi and Geritz, 1999), assume a type of density dependence that leads to Levene's (1953) 'soft selection' model (Geritz et al., 1998; Kisdi and Geritz, 1999) or involve three instead of two states (Takada and Nakajima, 1992, 1996), indicating the potential value of such a classification and several directions for extensions.

2 The Modelling Framework

This section starts with a description of the envisaged life-cycles and the population dynamics of monomorphic and polymorphic populations. We then describe the ecology of a population by introducing how population density feeds back to population growth. In a next step we introduce mutant types that deviate in two evolving parameters from the resident types. Invasion fitness will be introduced as a means to determine the long term fate of mutants. After deriving a sign equivalent fitness proxy, that is algebraically simpler than invasion fitness proper, we briefly describe how evolutionary dynamics can be inferred. Finally, we establish a link between the population dynamics and the evolutionary dynamics by explaining the concept of the evolutionary feedback environment and its implications for optimisation.

2.1 The Life Cycle

We restrict ourselves to life-histories that can be described with two discrete i-states (i for individual, see Metz and Diekmann (1986)) in a discrete time framework (fig. 1). Population census takes place just before reproduction and after a potential transition from one i-state to another. Individuals in i-state l produce f_{kl} offspring in i-state k surviving until the next census point. After a potential reproductive event individuals make a transition from i-state l at time t to state k at time $t+1$ with probability t_{kl}. The population projection matrix A is then a two-by-two matrix with components

$$a_{kl} = t_{kl} + f_{kl}. \tag{1}$$

These matrix components give the total amount of individuals in i-state k at time $t+1$ that descend from individuals in i-state l at time t. The population dynamics of a population is then given by

$$\boldsymbol{N}_{t+1} = \mathsf{A}\boldsymbol{N}_t, \tag{2}$$

where $\boldsymbol{N}_t$ is the p-state at time t (p for population), that is, the vector of densities in the two i-states. This setting includes i-states such as age, size or location in a two-patch model but also sex. Individuals can either occur in one i-state at birth (e.g. immature, or small) or in two i-states (e.g. birth in either of two different locations, or as different sexes).

This paper is concerned with the evolution of different matrix components. We restrict ourselves to the case where different phenotypes deviate from each other in only two traits $x_1, x_2 \in \{t_{11}, f_{11}, t_{12}, f_{12}, t_{21}, f_{21}, t_{22}, f_{22}\}$ while all other traits are assumed to stay constant. Hence, any possible phenotype is uniquely determined by a two-dimensional trait vector. However, we will assume that within the two-dimensional trait space phenotypes are confined to a one-dimensional manifold to which we will refer as trade-off curve $x_2(x_1)$ (fig. 2). The rationale behind this assumption is as follows. The dominant eigenvalue of a non-negative matrix, hence long term population growth, is an increasing function of all matrix components and therefore selection acts to increase each of the evolving traits. We assume that a constraint exists that sets upper limits to the value of each trait and that once this limit is reached, an increase in one trait can only be bought at the expense of a decrease in another trait. We then make the simplifying assumption that the evolutionary dynamics are confined to the set of trait combinations (x_1, x_2) that constitute the trade-off relationship. We parameterise the trade-off curve $x_2(x_1)$ with a coefficient θ that lies between zero and one (fig. 2). Hence, any phenotype is uniquely determined by the trade-off coefficient θ corresponding to the trait values $\boldsymbol{x}(\theta) = (x_1(\theta), x_2(\theta))$. A community consisting of n types is characterised by $\boldsymbol{\Theta} = (\theta^1, \ldots, \theta^n)$. To denote the population dynamics of the jth type from a community $\boldsymbol{\Theta}$ we rewrite equation (2) as $N^j_{t+1} = \mathsf{A}(\theta^j)N^j_t$.

For numerical calculations we use the following trade-off parameterisation:

$$\boldsymbol{x}(\theta) = (x_1(\theta), x_2(\theta)) = (x_{1\max}(1-\theta)^{1/z}, x_{2\max}\theta^{1/z}), \tag{3}$$

where $x_{1\max}$ and $x_{2\max}$ are positive constants. The parameter z determines the curvature of the trade-off such that $z < 1$ correspond to a convex (or strong) trade-off ($\mathrm{d}^2x_2/\mathrm{d}x_1^2 > 0$) while $z > 1$ corresponds to a concave (or weak) trade-off ($\mathrm{d}^2x_2/\mathrm{d}x_1^2 < 0$). For $z = 1$ the trade-off is linear.

2.2 Density Dependence

Since no population shows unbounded growth, population regulation has to be incorporated in a population dynamical model. Any growing population affects its environment negatively, for example, the availability of resources and nesting sites might decrease while the abundance of predators and parasites might increase. Here we will not model the changing environment explicitly but only implicitly via negative density dependence by assuming that the growth rate of any specific type j depends both on its own phenotype and on all other phenotypes present in the population and their densities. Hence, the population projection matrix becomes time dependent: $N_{t+1}^j = \mathsf{A}_t(\theta^j)N_t^j$ (Caswell, 2001). All demographic parameters t_{kl} or f_{kl} can be affected by population density and throughout this paper such parameters will be marked with a tilde, e.g. $\tilde{f}_{12}$. Hence, $\tilde{f}_{12}$ corresponds to the demographic parameter as we could measure it in the field while f_{12} corresponds to the hereditary trait-value that could only be measured under standardised laboratory conditions. In the context of age-structured populations Charlesworth (1994) coined the term “critical age-group” for the subgroup of a population that affects density-dependent demographic parameters. Here we assume that different parameters can be affected by different subgroups or "critical state-groups". We restrict ourselves to functions of population regulation such that the population dynamics settle on a unique nontrivial stable equilibrium $\hat{\boldsymbol{N}}^{\boldsymbol{j}} = (\hat{N}_1^j, \hat{N}_2^j)$ for all $j \in \{1, \ldots, n\}$. Note that at least all $f_{kl} > 1$ have to be density regulated for a stable population dynamical equilibrium to exist. At equilibrium the time index t of the population projection matrix A can be dropped.

How does population density influence the demography? In this paper we restrict ourselves to functional forms of density dependence such that we can write the demographic parameter $\tilde{x}_t^j$ as a product of the heritable trait x^j and a function of density D_x.

$$\tilde{x}_t^j = x^j D_x(\theta^1, \boldsymbol{N}_t^1, \ldots, \theta^n, \boldsymbol{N}_t^n). \tag{4}$$

The functions of density D_x are scalar-valued functions of the traits and densities of all types present in the population with co-domain $[0, 1]$. We assume that D_x is monotonic decreasing in the N_t's. Furthermore, we assume that D_x has a property that we call "separability". Separability is given whenever D_x is independent of x^j for $\boldsymbol{N}_t^j = 0$. In particular, this means that for a rare mutant characterised by $\theta' \notin \boldsymbol{\Theta}$ we can write $\tilde{x}(\theta') = x(\theta') D_x(\theta^1, \hat{\boldsymbol{N}}^{\boldsymbol{1}}, \ldots, \theta^n, \hat{\boldsymbol{N}}^{\boldsymbol{n}})$. This allows us to separate the traits that are affected by a mutation from the effect of the resident population on such a mutant phenotype. This can be done by factoring out the functions of density from a sum of several demographic parameters, provided the functions of density are the same for the different demographic parameters. An example for a function of density D_x that allows for separability and that we will use throughout this paper is a Beverton-Holt type function with the densities of different states as arguments:

$$\tilde{x}_t^j = x^j D_x = x(\theta^j)/(1 + c_1 \sum_{j=1}^{n} N_{1t}^j + c_2 \sum_{j=1}^{n} N_{2t}^j). \tag{5}$$

The weighting factors $c_1, c_2 \in \mathbb{R} \geq 0$ are assumed to be constant and identical for all types j, however, they are allowed to differ for different demographic rates $\tilde{x}$, indicating that specific traits can be affected by different critical state-groups.

2.3 Invasion Fitness

The fate of a rare mutant θ' occurring in a specific resident community is given by its invasion fitness, that is, its long term average growth rate in an environment that is determined by the resident community (Metz et al., 1992; Rand et al., 1994). We assume that mutations are rare and of small effect. The first assumption is made to assure that the resident community has settled on its attractor before a new mutant arises. This means that a resident population is completely described by the vector $\boldsymbol{\Theta} = (\theta^1, \ldots, \theta^n)$ because these traits determine the unique non-trivial population dynamical equilibria $\hat{\boldsymbol{N}}^{\boldsymbol{j}}$. Hence, at population dynamical equilibrium equation (4) becomes, with some abuse of notation, $\tilde{x} = xD_x(\boldsymbol{\Theta})$. The second assumption assures that mutants with the ability to invade a resident type, and which cannot be invaded by the resident when common themselves, go to fixation (Metz et al., 1996a; Geritz et al., 1998, 2002; Dercole, 2002; Geritz, 2005).

The dynamics of an initially rare mutant population is described by the projection matrix $\mathsf{A}(\theta', \boldsymbol{\Theta})$ where the entries for the evolving traits are given by $\tilde{x}(\theta') = x(\theta')D_x(\boldsymbol{\Theta})$. We will mark all matrix components $\tilde{a}_{kl}$ with a tilde as long as we have not specified which traits are density regulated. Invasion fitness is then given by the dominant eigenvalue $\lambda_{\mathrm{d}}(\theta', \boldsymbol{\Theta})$ of the mutant's projection matrix $\mathsf{A}(\theta', \boldsymbol{\Theta})$. In the following paragraph we introduce a sign equivalent fitness proxy w for invasion fitness. This fitness proxy is algebraically simpler than the dominant eigenvalue λ_{d} and it will be a fundamental tool in this paper.

The characteristic polynomial of a mutant's population projection matrix equals

$$P(\lambda, \theta', \boldsymbol{\Theta}) = \lambda^2 - \mathrm{trace}\mathsf{A}(\theta', \boldsymbol{\Theta})\lambda + \det\mathsf{A}(\theta', \boldsymbol{\Theta}).$$

As $\mathsf{A}(\theta', \boldsymbol{\Theta})$ is a non-negative matrix, it has two real eigenvalues with the dominant one positive. The dominant eigenvalue λ_{d} is given by the rightmost root of $P(\lambda, \theta', \boldsymbol{\Theta})$. Since $\lambda^2 > 0$, $P(\lambda, \theta', \boldsymbol{\Theta})$ is a parabola in λ opening upward. Therefore, if $P(1, \theta', \boldsymbol{\Theta}) < 0$, then $\lambda_{\mathrm{d}} > 1$. If, however, $P(1, \theta', \boldsymbol{\Theta}) > 0$, we need $\mathrm{d}P(1, \theta', \boldsymbol{\Theta})/\mathrm{d}\lambda = 2 - \mathrm{trace}\mathsf{A}(\theta', \boldsymbol{\Theta}) < 0$ for $\lambda_{\mathrm{d}} > 1$. In this case both eigenvalues are larger than one. Hence, $\lambda_{\mathrm{d}} > 1$ if

$$\mathrm{trace}\mathsf{A}(\theta', \boldsymbol{\Theta}) - \det\mathsf{A}(\theta', \boldsymbol{\Theta}) = \tilde{a}_{11} + \tilde{a}_{22} - \tilde{a}_{11}\tilde{a}_{22} + \tilde{a}_{12}\tilde{a}_{21} > 1$$

or

$$\mathrm{trace}\mathsf{A}(\theta', \boldsymbol{\Theta}) = \tilde{a}_{11} + \tilde{a}_{22} > 2,$$

and $\lambda_{\mathrm{d}} < 1$ if and only if

$$\mathrm{trace}\mathsf{A}(\theta', \boldsymbol{\Theta}) - \det\mathsf{A}(\theta', \boldsymbol{\Theta}) < 1 \quad \text{and} \quad \mathrm{trace}\mathsf{A}(\theta', \boldsymbol{\Theta}) < 2.$$

Note, that for $\theta' \in \boldsymbol{\Theta}$ we have $\lambda_{\mathrm{d}}(\theta', \boldsymbol{\Theta}) = 1$ while the subordinate eigenvalue is less than one. Hence, for any resident type at population dynamical equilibrium we find $\mathrm{trace}\mathsf{A}(\theta, \boldsymbol{\Theta}) < 2$ and therefore for any mutant type θ' that differs but slightly from the resident type such that $\mathrm{trace}\mathsf{A}(\theta', \boldsymbol{\Theta}) < 2$ is still fulfilled, we have

$$\mathrm{sign}[\lambda_{\mathrm{d}}(\theta', \boldsymbol{\Theta}) - 1] = \mathrm{sign}[\mathrm{trace}\mathsf{A}(\theta', \boldsymbol{\Theta}) - \mathrm{det}\mathsf{A}(\theta', \boldsymbol{\Theta}) - 1] = \mathrm{sign}[-P(1, \theta', \boldsymbol{\Theta})].$$

Therefore $1 - P(1, \theta', \boldsymbol{\Theta}) = \tilde{a}_{11} + \tilde{a}_{22} - \tilde{a}_{11}\tilde{a}_{22} + \tilde{a}_{12}\tilde{a}_{21}$ can be used as a fitness proxy. We denote this fitness proxy as $w(\theta', \boldsymbol{\Theta})$ and, to simplify matters, we will refer to it as invasion fitness in the remainder of this paper though it is only sign equivalent to invasion fitness proper. Metz (unpublished) proved that, given that the trait space is connected, global uninvadability of a singular trait θ^* is given when $w(\theta', \theta^*) \leq 1$ for all possible θ', that is, the condition $\mathrm{trace}\mathsf{A}(\theta', \theta^*) < 2$ becomes superfluous. Note that this fitness proxy describes the direction of evolutionary change but not its speed (Dieckmann and Law, 1996; Durinx and Metz, 2005). The idea to exploit the characteristic polynomial evaluated at $\lambda = 1$ for invasion considerations can be found in Taylor and Bulmer (1980) and Courteau and Lessard (2000).

Let us briefly note some useful properties of w. First, it equals R_0 in age-structured models with $t_{22} = 0$. Second, in models where f_{12} is the only fecundity term, for instance, in age-structured models with reproduction only in the second year, the condition $\mathrm{trace}\mathsf{A}(\theta', \boldsymbol{\Theta}) < 2$ is fulfilled automatically. Third, under the assumption of small mutational steps $\tilde{a}_{11}, \tilde{a}_{22} < 1$. To see this, we note that at population dynamical equilibrium for all $\theta \in \boldsymbol{\Theta}$ we have $\mathrm{trace}\mathsf{A}(\theta, \boldsymbol{\Theta}) - \det(\theta, \boldsymbol{\Theta}) = 1$, which can be rewritten as $0 = (1 - \tilde{a}_{11})(1 -$

$\tilde{a_{22}}) - \tilde{a}_{12}\tilde{a}_{21}$. For this equality to hold either $\tilde{a}_{11}, \tilde{a}_{22} > 1$ or $\tilde{a}_{11}, \tilde{a}_{22} < 1$. The first case violates $\mathrm{trace}\mathsf{A}(\theta, \boldsymbol{\Theta}) < 2$ and therefore the second case is proven.

The direction of evolutionary change is given by the fitness gradient, the first derivative of invasion fitness with respect to the mutant trait. For the time being we limit ourselves to resident communities that consist of single type θ. Points θ^* in trait space where the fitness gradient equals zero, that is

$$0 = \left.\frac{\partial w(\theta', \theta^*)}{\partial \theta'}\right|_{\theta' = \theta^*}, \tag{6}$$

are of special interest and were named "evolutionarily singular points" by Metz and co-workers (Metz et al., 1996*a*; Geritz et al., 1998). Singular points can be classified according to two properties: convergence stability and invadability (Metz et al., 1996*a*; Geritz et al., 1998). Singular points that are both convergence stable and uninvadable are final stops of evolution and we refer to them as "continuously stable strategies" or CSSs (Eshel, 1983). Singular points that are convergence stable but invadable by nearby mutants are particularly interesting. Directional selection drives the mean trait value of a population towards such points and once the mean population trait value has reached the singular point, selection turns disruptive and favours an increase in phenotypic variance (Rueffler et al., 2006*a*). It case of clonal organisms this increase can be realised by the emergence of two independent lineages and it is this scenario that earned such points the name "evolutionary branching points" (Metz et al., 1996*a*; Geritz et al., 1998). Singular points that lack convergence stability are evolutionarily repelling. When such singular points are invadable we refer to them as evolutionary repellers and when they are immune to invasion by nearby mutants we refer to them as

”Garden of Eden-points” (Nowak, 1990). In the latter case any perturbation results in directional selection away from the singular point and no natural population is ever expected to occupy a Garden of Eden-point.

2.4 Feedback Environment

A considerable part of this paper will be concerned with finding conditions that allow to derive the evolutionary dynamics from an optimisation criterion (Mylius and Diekmann, 1995; Metz et al., 1996*b*; Dieckmann and Metz, 2006). By this we mean a function from the trait values to the real numbers such that a CSS corresponds to a maximum of this function while a minimum corresponds to an evolutionary repeller. In order to get to grips with this problem we start from a slightly different perspective. We consider invasion fitness as a function of the mutant's trait and of an input $\boldsymbol{I}$ from the environment. With a slight abuse of notation we therefore denote invasion fitness as $w(\theta', \boldsymbol{I})$ (Heino et al., 1997, 1998; Diekmann et al., 2003; Meszéna et al., 2006; Rueffler et al., 2006*b*). The m-dimensional vector $\boldsymbol{I}$ characterises the condition of the feedback environment, that is, those aspects of the environment that are determined by the resident population and simultaneously feed back to affect the fitness of individuals in the population. Each $I_j \in \boldsymbol{I}$ channels specific effects of population density and composition to demographic parameters. On an ecological time scale, the defining property of the feedback environment is that individuals become independent of each other when the feedback is given as a function of time (Diekmann et al., 2003; Meszéna et al., 2006). The ecological feedback environment of a focal population at time t is usually given by the p-state of the population as a whole. On an evolutionary time scale the trait values of the interacting types can change. In order to achieve independence between individuals on this time scale, the feedback environment not only has to account for the equilibrium densities of the con-specifics but also for their traits, since these can re-scale density effects.

The dimension of $\boldsymbol{I}$ is of great interest because it imposes an upper limit to the number of species that can possibly coexist (Diekmann et al., 2003; Meszéna et al., 2006). To see this consider two coexisting types θ^1 and θ^2. At population dynamical equilibrium both $w(\theta^1, \boldsymbol{I}(\theta_1, \theta_2)) = 1$ and $w(\theta^2, \boldsymbol{I}(\theta_1, \theta_2)) = 1$. When $\dim(\boldsymbol{I}) = 2$ these two equalities constitute a system of two equations in two unknowns which can have a robust solution. If, however, $\dim(\boldsymbol{I}) = 1$, then we have a system of two equations in one unknown and no generic solution exists. This proves that in one-dimensional feedback environments robust coexistence is impossible (Metz et al., 1996*b*; Meszéna et al., 2006). If, additionally, invasion fitness w is a monotonic decreasing (increasing) function of the interaction variable I for all θ, then I is an optimisation (pessimisation) criterion and the evolutionary dynamics can be predicted by maximising (minimising) I (Metz et al., 1996*b*).

Under the assumption of separability (cf. eq. 4) the interaction variables $I_j \in \boldsymbol{I}$ can be equated with the different functions of density $D_{x_{kl}}$ with $x_{kl} \in \{t_{11}, f_{11}, t_{12}, f_{12}, t_{21}, f_{21}, t_{22}, f_{22}\}$. In case all transition rates are density dependent and all functions of density are different, $\dim(\boldsymbol{I})$ can become as high as eight. However, for some special cases $\dim(\boldsymbol{I})$ will be lower. For instance, if we assume that the functions of density $D_{x_{kl}}$ only depend on the population at time t via the summed densities of the different types but not explicitly via their trait values θ^j, then the maximum dimension of $\boldsymbol{I}$ decreases to two. This assumption is realised in the Beverton-Holt type function (eq. 5) where $D_{x_{kl}}$ is a decreasing function of the weighted sum of the densities in the two states. Then $\sum_{j=1}^{n} \hat{N}_1^j$ and $\sum_{j=1}^{n} \hat{N}_2^j$ are the arguments of the functions of density $D_{x_{kl}}$ and it is sufficient to consider $\boldsymbol{I} = (\sum_{j=1}^{n} \hat{N}_1^j, \sum_{j=1}^{n} \hat{N}_2^j)$ as input from the environment in order to achieve independence between individuals. This holds true independent of the number of types present in the community and of the number of traits that are affected by density dependence.

3 Results

Here we classify the members of the introduced model family with respect to properties of the fitness landscape and whether or not the evolutionary analysis can be conducted by analysing an optimisation criterion.

3.1 Invasion Boundaries

Invasion boundaries (IBs) are manifolds in trait space consisting of all trait combinations that are selectively neutral with respect to a given resident community $\boldsymbol{\Theta}$. A more complete account of how IBs can be used to infer the direction of evolutionary change can be found in Rueffler et al. (2004). For our model class the IBs are implicitly defined by

$$w((x, y), \boldsymbol{\Theta}) = 1. \tag{7}$$

Hence, IBs are curves given by all trait combinations (x, y) that have an invasion fitness equal to one. IBs divide the trait space into two regions. Trait combinations (x, y) that lie above such a curve are able to invade since for them $w((x, y), \boldsymbol{\Theta}) > 1$ holds true. Trait combinations that lie below an IB are characterised by $w((x, y), \boldsymbol{\Theta}) < 1$ and are therefore not able to invade. An IB necessarily intersects with the trade-off curve at all resident trait values $\theta^j \in \boldsymbol{\Theta}$. At a singular trait value θ^* (cf. eq. 6) an IB is tangent to the trade-off curve (Rueffler et al., 2004). When, except for the point of tangency θ^*, the IB lies below the trade-off curve, then all trait values θ' in the neighbourhood of θ^* have $w(\theta', \theta^*) > 1$ and are therefore able to invade; θ^* corresponds to a minimum of the fitness landscape, hence, to either a repeller or branching point. If the opposite patterns holds true, that is, if the IB, except for the point of tangency, lies above the trade-off curve, then θ^* is uninvadable by all nearby mutants. In this case the singular point has to be either a CSS or a Garden of Eden-point. From this brief treatment follows that the relative curvature of the IBs and trade-off curves are an important determinant of the of the evolutionary dynamics (de Mazancourt and Dieckmann, 2004; Rueffler et al., 2004; Bowers et al., 2005).

The curvature of the trade-off depends on the morphological, physiological and genetic constraints of the organism under study. In this paper we show that the qualitative curvature properties of the IBs, that is, whether the IBs are convex, linear or concave, depends on the combination of traits that is considered evolvable. Interestingly, under the assumption of separability, the qualitative curvature of the IBs is independent of the ecology, that is, on the details of the population regulation. However, it is the ecology that determines whether a singular point is convergence stable (CSS or branching point) or evolutionary repelling (evolutionary repeller or Garden of Eden-point). Convergence stability of a singular point can be deduced from the pattern of intersection of the IBs and the trade-off in the neighbourhood of a singular point (Rueffler et al., 2004).

To derive the shape of invasion boundaries we have to solve equation (7) for y. Since the matrix component a_{kl} is a linear function of the contributing parameters t_{kl} and f_{kl}, it is sufficient to solve for the matrix component a_{kl} that depends on y. We can classify trade-offs into four qualitatively different types:

1. *Trade-Off Within One Matrix Component*: When evolution occurs in the two traits t_{kl} and f_{kl} of the same matrix component a_{kl}, then the IBs are linear. This follows from the fact that a_{kl} is the sum of the two traits and that w is linear in a_{kl}. As an example we give the equation for the invasion boundary in case $\tilde{t}_{11}$ and $\tilde{f}_{11}$ are evolving:

$$\tilde{f}_{11} = 1 + \frac{\tilde{a}_{12}\tilde{a}_{21}}{1 - \tilde{a}_{22}} - \tilde{t}_{11}. \tag{8}$$

2. *Trade-Off Between Diagonal and Off-Diagonal Components*: When evolution affects both a diagonal component a_{kk} and an off-diagonal component a_{kl} the IBs are linear again. To see this we rearrange equation (7) to

$$\tilde{a}_{12}\tilde{a}_{21} = (1 - \tilde{a}_{11})(1 - \tilde{a}_{22}). \tag{9}$$

From this equation, linearity follows whenever mutations affect components on both the right- and the left-hand side. For instance, if f_{12} and

t_{22} are evolving, then

$$\tilde{f}_{12} = \frac{(1-\tilde{t}_{11}-\tilde{f}_{11})(1-\tilde{t}_{22}-\tilde{f}_{22})}{\tilde{t}_{21}+\tilde{f}_{21}} - \tilde{t}_{12}.$$

3. *Trade-Off Between Diagonal Components*: If evolution occurs in components that affect the diagonal components $\tilde{a}_{11}$ and $\tilde{a}_{22}$, then invasion boundaries are concave. To see this, we rearrange equation (7) such that

   $$\tilde{a}_{22} = 1 - \frac{\tilde{a}_{12}\tilde{a}_{21}}{1-\tilde{a}_{11}}. \qquad (10)$$

   The second derivative of equation (10) with respect to $\tilde{a}_{11}$ is

   $$\frac{\mathrm{d}^2\tilde{a}_{22}}{\mathrm{d}\tilde{a}_{11}^2} = -\frac{2\tilde{a}_{12}\tilde{a}_{21}}{(1-\tilde{a}_{11})^3}. \qquad (11)$$

   In the previous section we proved that at population dynamical equilibrium $\tilde{a}_{11} < 1$ holds. The same argument can be applied to traits that lie on the IBs. Hence, the left hand side of equation (11) is negative, and therefore the invasion boundaries are concave.

   In case neither a_{11} nor a_{22} are density dependent, traits can be re-scaled such that the invasion boundaries become linear:

   $$\ln\tilde{a}_{12} + \ln\tilde{a}_{21} = \ln(1-a_{11}) + \ln(1-a_{22}). \qquad (12)$$

   From this we see that $\ln(1-a_{22})$ is a linear function of $\ln(1-a_{11})$.

4. *Trade-Off Between Off-Diagonal Components*: If evolution occurs in traits that affect the off-diagonal components of the projection matrix A, then the IBs are convex. This can be seen from equation (9). Since the two off-diagonal components occur in a the product on the left-hand side they are inversely related to each other and the IBs have to be convex. From equation (12) we see that if neither a_{12} nor a_{21} are density dependent, then invasion boundaries are linear on a logarithmic scale.

From this list we can draw three general conclusions. First, if the two evolving traits affect either the two traits in a single component of the transition matrix or a diagonal and an off-diagonal component, then all concave trade-offs give rise to singular points that are uninvadable by nearby mutants while all convex trade-offs will result in singular points that are invadable. In these cases invasion boundaries are linear and therefore a singular point on a convex trade-off has to be a fitness minimum while a singular point on a concave trade-off has to be a fitness maximum (Rueffler et al., 2004; de Mazancourt and Dieckmann, 2004; Bowers et al., 2005). Second, if the two evolving traits affect the two diagonal components of the transition matrix, then only strongly concave trade-offs give rise to singular points that are uninvadable. Third, if the two evolving traits affect the two off-diagonal components, then not only all concave trade-offs but also weakly convex trade-offs give rise to singular points that are uninvadable. Hence, the last scenario is most conducive to produce evolutionary endpoints that strike a balance between two negatively correlated life-history parameters.

3.2 Optimisation

Only under some rather restrictive conditions can the course of evolution be predicted by seeking the extrema of an optimisation criterion (Mylius and Diekmann, 1995; Metz et al., 1996*b*; Dieckmann and Metz, 2006). In the section on the feedback environment we gave necessary and sufficient conditions for one specific criterion: if (i) $\dim(\boldsymbol{I}) = 1$ and if (ii) w is a monotonic decreasing (increasing) function of I, then I is maximised (minimised). Here we assume that all functions of density $D_{x_{kl}}$ are monotonic functions of I that change in the same direction with increasing I. This is for example the case when all fecundity terms f_{kl} and survival terms t_{kl} decrease with total population density. Then we can prove that for the considered class of models condition (ii) follows from condition (i). Since $\dim(\boldsymbol{I}) = 1$ implies that no two types can coexist, we only need to consider monomorphic resident populations. Invasion fitness becomes

$$\begin{aligned} w(\theta', \theta) = {} & (f_{12}D_{f_{12}} + t_{12}D_{t_{12}})(f_{21}D_{f_{21}} + t_{21}D_{t_{21}}) + f_{11}D_{f_{11}} + t_{11}D_{t_{11}} \\ & + f_{22}D_{f_{22}} + t_{22}D_{t_{22}} - (f_{11}D_{f_{11}} + t_{11}D_{t_{11}})(f_{22}D_{f_{22}} + t_{22}D_{t_{22}}), \end{aligned}$$

where two traits depend on θ' and all functions $D_{x_{kl}}$ depend on θ. To check for the monotonicity condition (ii) we have to differentiate w with respect to I. After some simplification we get

$$\frac{\mathrm{d}w}{\mathrm{d}I} = (1-\tilde{a}_{11})(f_{22}\frac{\mathrm{d}D_{f_{22}}}{\mathrm{d}I} + t_{22}\frac{\mathrm{d}D_{t_{22}}}{\mathrm{d}I}) + (1-\tilde{a}_{22})(f_{11}\frac{\mathrm{d}D_{f_{11}}}{\mathrm{d}I} + t_{11}\frac{\mathrm{d}D_{t_{11}}}{\mathrm{d}I}) + Q,$$

with $Q = \mathrm{d}(f_{12}D_{f_{12}} + t_{12}D_{t_{12}})(f_{21}D_{f_{21}} + t_{21}D_{t_{21}})/\mathrm{d}I$. In this equation all derivatives have the same sign and $\tilde{a}_{11} < 1, \tilde{a}_{22} < 1$. Therefore the whole expression is negative for $\mathrm{d}D_{x_{kl}}/\mathrm{d}I < 0$ and positive for $\mathrm{d}D_{x_{kl}}/\mathrm{d}I > 0$. Therefore w is monotonic in I, the necessary and sufficient condition for it to be an optimisation criterion. Note, that this proof holds also if only a subset of the parameters is density dependent. For the special case that only a single demographic parameter is density dependent or that all functions of density $D_{x_{kl}}(I)$ are identical such that they can be factored out from the fitness function, $D_{x_{kl}}$ is a pessimisation criterion. Whenever population growth depends on a single resource, consumers will evolve so as to minimise the resource abundance (e.g. Mylius and Diekmann, 1995).

In most cases optimisation in terms of I can only be done numerically because analytical expressions for $\hat{\boldsymbol{N}}$ will only exist for the simplest scenarios of population regulation. Metz et al. (1996*b*) proved that optimisation is also possible when a function ψ from the traits to the real numbers and a function α increasing in its first argument exist such that $\text{sign}[w(\boldsymbol{x}, \boldsymbol{I}) - 1] = \text{sign}[\alpha(\psi(\boldsymbol{x}), \boldsymbol{I}) - 1]$. Then ψ is an optimisation criterion. It can often be analysed analytically because it does not involve any aspects of the population dynamics. Metz et al. (1996*b*) also show that once I is established as an optimisation criterion a corresponding criterion ψ exists that is related to I through $\psi(\theta) = I(\theta)$ and $\text{sign}[w(\theta', I(\theta))] = \text{sign}[\psi(\theta') - I(\theta)]$. Therefore, whenever I is one-dimensional it is possible to find an optimisation criterion ψ by solving $w(\theta, I(\theta)) = 1$ for $I(\theta)$ (see also Dieckmann and Metz (2006)). For many members of our model family it is possible to find a criterion ψ in a simpler way than just described. Table 1 gives an overview over all members of our model family with a reference to the conditions that allow for optimisation according to the following list.

1. Whenever population regulation affects only a single trait x_{kl} we are able to find a simple optimisation criterion ψ by solving $w(\theta, D_{x_{kl}}(\theta)) = 1$ for $D_{x_{kl}}(\theta)$. Since $D_{x_{kl}}(\theta)$ acts as a pessimisation criterion the function ψ acts as an optimisation criterion.
2. Population regulation is such that the functions of density can be factored out from the sum of terms that contain the two evolving parameters. This

means that all $D_{x_{kl}}$ that are factors of an evolving trait are identical and have the same argument and that $D_{x_{kl}}$ does not appear squared as a factor of an evolving trait. Then the sum of the terms that contain the evolving traits is the optimisation criterion ψ. Two different scenarios can lead to this case: (i) Both t_{kl} and f_{kl} of the same matrix component a_{kl} are evolving. (ii) The two evolving traits affect both a diagonal and an off-diagonal components of the projection matrix A.

3. The two evolving traits occur in a single product in the fitness function w. This is can only be the case when the evolving traits affect the off-diagonal components of the projection matrix A and when additionally each off-diagonal component consists only of a single term, that is, when $a'_{12}a'_{21} \in \{f'_{12}t'_{21}, f'_{12}f'_{21}, t'_{12}f'_{21}, t'_{12}t'_{21}\}$. Then $\psi = a'_{12}a'_{21}$.
4. In the fitness function w none of the evolving characters occurs in a product with a function $D_{x_{kl}}$. This is the case when both diagonal components a_{11} and a_{22} are evolving while density dependence only acts on the off-diagonal components a_{12} and a_{21}, or vice versa. Then $\psi = a'_{11} + a'_{22} - a'_{11}a'_{22}$ or $\psi = a'_{12}a'_{21}$, respectively. Note that this case can only apply if the evolving a_{kl}'s do not include a fecundity term f_{kl}.
5. When the evolving traits affect both an diagonal and an off-diagonal component of the fitness function w, an optimisation criterion ψ can exist, given density regulation affects only one of the two diagonal components. To see this we note that

$$\operatorname{sign}[w-1] = \operatorname{sign}\left[\frac{\tilde{a}_{12}\tilde{a}_{21}}{1-a_{kk}} + \tilde{a}_{ll} - 1\right] \quad \text{for} \quad k,l \in \{1,2\} \quad \text{and} \quad k \neq l. \tag{13}$$

If the numerator of the above fraction can be decomposed into the evolving trait and a factor containing the functions of density, then $\psi = a'_{12}/(1-a'_{kk})$ or $\psi = a'_{21}/(1-a'_{kk})$.

6. All matrix elements x are density dependent in the same way, that is, $D_{x_{kl}} = D_x = D_{x_{mn}}$ for $k, l, m, n \in \{1, 2\}$. Then it is straightforward to verify that the dominant Eigenvalue $\lambda_d(\theta', \boldsymbol{\Theta})$ of $\mathsf{A}(\theta', \boldsymbol{\Theta})$ can be decomposed such that $\lambda_d(\theta', \boldsymbol{\Theta}) = D_x(\boldsymbol{\Theta})\lambda_d(\theta')$, where $\lambda_d(\theta')$ is the dominant eigenvalue of the density independent projection matrix. From this follows immediately that $\lambda_d(\theta')$, or, equivalently, the density independent intrinsic growth rate $r(\theta')$ serve as optimisation criteria for all possible trade-off relationships. A similar argument has been given earlier (Metz et al., 1992; Mylius and Diekmann, 1995; Metz et al., 1996*b*).

Based on this list we can draw two general and important conclusions. First, in life-cycles where evolutionary change only affects transitions that are necessary in order to pass through both *i*-states optimisation is always possible. Conversely, in these life-cycles phenotypic diversification through evolutionary branching is impossible because selection is frequency-independent. In these cases the two evolving traits occur in a single product in the fitness function (see 3) in the preceding list). Second, only in life-cycles where at least one of the evolving traits is not necessary in order to pass through both *i*-states can selection be frequency-dependent. This is a prerequisite for phenotypic diversification through evolutionary branching. In these cases the two evolving traits affect different summands of the fitness function. The items 1,2, 4, and 5 in the preceding list give conditions where even in such cases optimisation can be possible.

4 Higher-Dimensional Feedback Environments

Whenever $\dim(\boldsymbol{I}) = 1$ the direction of evolutionary change can be derived from an optimisation criterion. In these cases, convergence stability is tightly linked to uninvadability: singular points that are uninvadable are also convergence stable and vice versa. In feedback environments with $\dim(\boldsymbol{I}) > 1$ in general an optimisation criterion does not exist and convergence stability and uninvadability can occur in any combination: in addition to CSSs and evolutionary repellers, evolutionary branching points and Garden of Eden-points become possible. We refer to selection in feedback environments with $\dim(\boldsymbol{I}) > 1$ as frequency-dependent. If the interaction of the evolving population with the feedback environment allows for a rare type advantage, coexistence of different types becomes possible.

The wider array of possible dynamics makes it more difficult to achieve a general classification. The difficulty is to infer the direction of evolutionary change in the neighbourhood of singular points, that is, their convergence stability, without calculating fitness gradients for each model. Here we present a classification for models that are characterised by a high degree of symmetry, for example as when the two i-states correspond to two habitats of equal size and quality and a trade-off exists between the same measure of performance in each habitat. In this case we can understand the selective forces that determine the direction of evolutionary change by splitting invasion fitness into a density-dependent and a frequency-dependent component.

- **Density-Dependent Component** (DDC) Invasion fitness in a two-dimensional feedback environment is given by $w(\theta', (I_1, I_2))$. We can calculate invasion fitness as it would result from a homogenous feedback environment where $I_1 = I_2$. Without loss of generality we choose $\bar{I} = (I_1 + I_2)/2$ as reference environment, hence, we consider the function $w(\theta', (\bar{I}, \bar{I}))$. This function can account for density dependence but not for frequency dependence and we therefore refer to it as the density-dependent component of fitness. In the previous section we have proven that when population regulation is mediated via a single variable while all functions of density are monotonic functions of I that change in the same direction with increasing I, then this variable is maximised in the course of evolution. Hence, evolution in the reference environment $\boldsymbol{I} = (\bar{I}, \bar{I})$ would maximise $(I_1 + I_2)/2$. As mentioned in the previous section, under this condition a function ψ from the evolving traits to the real numbers exists such that evolution in the reference environment would maximise ψ. We denote the density-dependent component of $w(\theta', \theta)$ by $DDC(\theta', \theta)$.
- **Frequency-Dependent Component** (FDC) We define the frequency-dependent component of fitness as the difference between invasion fitness proper and its density-dependent component: $FDC(\theta', \theta) = w(\theta', \theta) - DDC(\theta', \theta)$. The frequency-dependent component can be visualised by its effect on invasion boundaries. An invasion boundary in the reference environment is defined implicitly by $w((x, y), (\bar{I}, \bar{I})) = 1$ (cf. eq. 7). Any

deviation of such an invasion boundary from the real invasion boundary, implicitly defined by $w((x,y),(I_1,I_2)) = 1$, is the result of frequency-dependent selection.

We are interested in the difference of each of these components between a mutant and a resident: $\Delta DDC(\theta',\theta) := DDC(\theta',\theta) - DDC(\theta,\theta)$ and $\Delta FDC(\theta',\theta) := FDC(\theta',\theta) - FDC(\theta,\theta)$. A mutant benefits from the DDC when $\Delta DDC(\theta',\theta) > 0$ and it benefits from the FDC when $\Delta FDC(\theta',\theta) > 0$. These two effects determine the direction of evolutionary change and the properties of evolutionarily singular points. Whether a mutant benefits from the DDC depends on whether the mutation corresponds to an increase in the optimisation criterion ψ. In this case the mutant phenotype is less susceptible to the detrimental effects of competition than the resident phenotype. Whether a mutant benefits from the FDC depends on the relative difference between the two interaction variable I_1 and I_2. Whenever a mutation directs effort away from demographic parameters that suffer strongly from density dependence towards demographic parameters that suffer relatively less from density dependence, the mutant benefits from the differential impact of the resident population on the different environmental components and $\Delta FDC(\theta',\theta) > 0$.

In the following we describe a set of rather restrictive conditions that allows us to derive conditions for both convergence stability and uninvadability in terms of $\Delta DDC(\theta',\theta)$ and $\Delta FDC(\theta',\theta)$. We assume that (i) a θ^* exists such that $I_1(\theta^*) = I_2(\theta^*)$, (ii) $\mathrm{d}I_i(\theta)/\mathrm{d}\theta$, evaluated at θ^*, has opposite signs for $i = 1$ and $i = 2$, and (iii) the optimisation criterion $\bar{I}$ has a local extremum at θ^*. The first condition means that a resident population with trait value θ^* affects both interaction variables equally. The second condition means that any deviation from θ^* alters the two interaction variables in opposite directions. The third condition in combination with the first one means that θ^* is a singular point. The example in section 5.3 fulfils above symmetry conditions.

Under these conditions, which amount to a model with highly symmetric structure, we have a good understanding of the selective forces driving the evolutionary dynamics in the neighbourhood of θ^* (table 2). Under the above assumptions $\Delta FDC(\theta', \theta^*)$ equals zero and invadability of θ^* purely depends on $\Delta DDC(\theta', \theta^*)$. If $\Delta DDC(\theta', \theta^*)$ has a local minimum for $\theta' = \theta^*$, then θ^* is invadable by nearby mutants. Since selection in the reference environment is frequency-independent this condition is fulfilled if and only if we can choose an $r \in \mathbb{R} > 0$ such that $\Delta DDC(\theta', \theta) < 0$ for all $\theta', \theta \in B = (\theta^* - r, \theta^* + r)$ with $\theta < \theta' < \theta^*$ or $\theta > \theta' > \theta^*$ (left and right column in table 2). Likewise, if $\Delta DDC(\theta', \theta^*)$ has a local maximum for $\theta' = \theta^*$ then θ^* is uninvadable by nearby mutants. This condition is equivalent to $\Delta DDC(\theta', \theta) > 0$ with $\theta < \theta' < \theta^*$ or $\theta > \theta' > \theta^*$. Whether $\Delta DDC(\theta', \theta^*)$ has a local minimum or maximum at θ^* is determined by the curvature of the trade-off relative to that of the invasion boundary at θ^* (cf. section 3.1).

The singular point θ^* is convergence stable from within an interval $B = (\theta^* - r, \theta^* + r)$, where $r \in \mathbb{R} > 0$, when for all $\theta \in B \backslash \theta^*$ a mutational change in the direction of θ^* results in an invasion fitness larger than one, or, equivalently, when $\Delta DDC(\theta', \theta) + \Delta FDC(\theta', \theta) > 0$. This condition is fulfilled either when both summands are positive, that is, when DDC and FDC act in the same direction, or when the two summands have opposite signs but with the positive summand overruling the negative one (table 2). From the preceding paragraph follows that a convergence stable singular point is a CSS when $\Delta DDC(\theta', \theta) > 0$ and an evolutionary branching point when $\Delta DDC(\theta', \theta) < 0$ where $\theta', \theta \in B = (\theta^* - r, \theta^* + r)$ with $\theta < \theta' < \theta^*$ or $\theta > \theta' > \theta^*$. An analogue distinction can be made for evolutionarily singular points that lack convergence stability, that is, when either both summands are negative or when the negative summand is larger in absolute value than the positive one. When $\Delta DDC(\theta', \theta) > 0$ such an evolutionarily repelling singular point is a Garden of Eden-point. The singular point corresponds to an evolutionary repeller when $\Delta DDC(\theta', \theta^*) < 0$ (table 2).

5 Examples

Here we analyse three examples of evolution in structured populations. For each case we consider several different types of population regulation. The purpose of these examples is to show how the results of this paper can be applied.

5.1 Age-Structured Life-Cycle

Consider an age-structured population where fecundity of yearlings is given by f_{11}. Yearlings survive with probability t_{21} to the second year. Once this age is reached, individuals produce f_{12} offspring each year and survive with probability t_{22} to the next breeding season. First we consider the case where mutational change occurs in f_{11} and t_{21} which are traded off: individuals that invest a lot in reproduction when they are young suffer from a decreased survival to adulthood. For a non-trivial population dynamical equilibrium to exist reproduction has to be density dependent. In the first scenario we assume that individuals in both age-groups rely on a common resource for the production of offspring and therefore the functions of density $D_{f_{11}}$ and $D_{f_{12}}$ have $(c_1N_1 + c_2N_2)$ as argument $(c_1, c_2 \in \mathbb{R} \geq 0)$. In a second scenario we assume that each age-group makes use of a different resource and that therefore reproduction decreases with the density in the corresponding age-group such that $D_{f_{11}}(N_1)$ and $D_{f_{12}}(N_2)$. In both cases invasion fitness is given by

$$w(\theta', \theta) = f_{11}(\theta')D_{f_{11}}(\theta) + t_{22} - f_{11}(\theta')D_{f_{11}}(\theta)t_{22} + t_{21}(\theta')f_{12}D_{f_{12}}(\theta) \quad (14)$$

For the first scenario it follows from section 3.2 that $I = c_1N_1 + c_2N_2$ is an optimisation criterion. When both age-groups are equally susceptible to competition, that is, when $D_{f_{11}} = D_{f_{12}}$ the simpler function $\psi = f_{11}(\theta') - f_{11}(\theta')t_{22} + t_{21}(\theta')f_{12}$ is an optimisation criterion (see the cell given by the 4th row and 2nd column in table 1). Since evolution affects a diagonal and an off-diagonal component, the IBs are linear and we can conclude that a singular point on a concave trade-off curve corresponds to a CSS while a singular point on convex trade-off curves corresponds to an evolutionary repeller. Figure 3a shows a numerically calculated bifurcation diagram confirming our qualitative predictions.

Heino et al. (1997) analysed a similar model (see also Diekmann, 2004) resulting in an equivalent fitness function. In their model yearlings either reproduce and die or postpone reproduction to the second year and die then. The probability to adopt one life-cycle or the other is assumed to be evolutionary labile, resulting in a linear trade-off. Hence, the optimisation criterion ψ is a monotonic decreasing or increasing function of θ. Depending on parameters, selection favours either an annual or a biennial organism (compare fig. 3a for $z = 1$).

If $\tilde{f}_{11}$ and $\tilde{f}_{12}$ are decreasing functions of N_1 and N_2, respectively, then $\dim(\boldsymbol{I}) = 2$ and selection is frequency-dependent. Since the IBs are linear we can predict that all singular points will be invadable for convex trade-offs (characterised by $z < 1$, see eq. [3]) and uninvadable for concave trade-offs (characterised by $z > 1$). However, we cannot predict whether a singular point is convergence stable because we cannot sensibly assume the symmetry conditions that are necessary to apply the results of section 4. In figure 3 we show numerical results. Figure 3b shows the bifurcation of singular points based on the same parameter-values as in the previous case. This figure shows that the change in population regulation affects the results only quantitatively. For figure 3c we assumed that two-year old individuals die after reproduction ($t_{22} = 0$) and that fecundity in the second year is lower than in the first year. For this set of parameters we find a bifurcation pattern that shows evolutionary branching for moderately strong trade-offs. The special case where the trade-off is constrained to be linear is dealt with in Heino et al. (1997) and Diekmann (2004).

In our last example of an age-structured model we assume a different trade-off. Individuals that increase their chance to survive to adulthood t_{21}

suffer from decreased future fecundity f_{12}. As mentioned in section 3.1 such cases give rise to convex IBs. Since each off-diagonal component of the transition matrix consists of only a single trait this is a case where evolutionary change affects two traits that are both necessary to complete the life-cycle. The conditions for $t_{21} * f_{12}$ to be an optimisation criterion are met for all possible scenarios of density regulation (cf. table 1, 4th column). For the trade-off parameterisation given by equation (3) it is easy to prove that $\theta^* = 0.5$ is a unique maximum of the optimisation criterion for all values of z.

5.2 Size-Structured Life-Cycle

Assume that individuals can be categorised as either small or large with only the latter capable of reproduction. In this model we assume a trade-off between survival of mature individuals t_{22} and their reproductive output f_{12}. The model therefore addresses the question whether selection favours a single large reproductive event (semelparity, $t_{22} = 0$) or a compromise between reproduction and survival that results in several reproductive events (iteroparity, $t_{22} > 0$). Invasion fitness is given by

$$w(\theta', \theta) = t_{11} + t_{22}(\theta') - t_{11}t_{22}(\theta') + t_{21}f_{12}(\theta'). \tag{15}$$

We investigate three alternative scenarios with respect to population regulation. In the first case only fecundity is a decreasing function of total population density; the function of density $D_{f_{12}}$ has $c_1N_1 + c_2N_2$ as argument. This model was analysed by Takada (1995). From section 3.2 follows that selection maximises $c_1\hat{N}_1 + c_2\hat{N}_2$. From the first row in table 1 we can see that an optimisation criterion ψ can be derived. By applying the first recipe given in the list in section 3.2 we find that $\psi = f_{12}(\theta')/(1 - t_{22}(\theta'))$ is maximised. Since evolution occurs in a diagonal and an off-diagonal element of the transition matrix, invasion boundaries are linear (see section 3.1). Hence, singular points correspond to evolutionary repellers in the case of strong trade-offs and to CSSs in the case of weak trade-offs (see fig. 4a).

For the second ecological scenario we assume that fecundity of mature individuals and survival of small individuals are density-regulated according to $\tilde{f}_{12} = f_{12}D_{f_{12}}(N_2)$ and $\tilde{t}_{11} = t_{11}D_{t_{11}}(N_1)$. From table 1 we can see that the case at hand is described by the cell given by the 5th row and 2nd column. Applying equation (13) we find the same optimisation criterion as in the first ecological scenario: $\psi = f_{12}(\theta')/(1-t_{22}(\theta'))$; the properties of singular points as a function of z are again given by figure 4a.

In the last ecological scenario we assume that the two evolving traits are density dependent according to $\tilde{f}_{12} = f_{12}D_{f_{12}}(N_1)$ and $\tilde{t}_{22} = t_{22}D_{t_{22}}(N_2)$. This case corresponds to the cell given by 2nd column and the 4th row in table 1. However, the conditions for optimisation are not met and selection is frequency-dependent. Because of the inherent asymmetry in this model we cannot make use of the results of section 4. Based on the linearity of the invasion boundaries we know that singular points are invadable in combination with strong trade-offs ($z < 1$) and uninvadable in combination with weak trade-offs ($z > 1$). Figure 4b shows that the change in ecology has merely a quantitative effect on the evolutionary dynamics.

5.3 Spatially Structured Population with Juvenile Dispersal

Assume an iteroparous population which occupies two different habitats. New-borns disperse and settle in one of the two habitats where they stay for the rest of their life. Mutational change occurs in the habitat specific adult survival probabilities t_{11} and t_{22}, which are assumed to be traded off. We distinguish two scenarios of population regulation. (i) Adult fertility depends on one common resource (e.g., freely floating plankton) and therefore the offspring number decreases with increasing total population size $N_1 + N_2$. (ii) Adult fertility depends on a local resource (e.g., space within each habitat) and therefore habitat specific fecundities decrease with local population densities. Invasion fitness is given by

$$\begin{aligned} w(\theta', \theta) = {} & f_{11} D_{f_{11}}(\theta) + t_{11}(\theta') + f_{22} D_{f_{22}}(\theta) + t_{22}(\theta') - \\ & (f_{11} D_{f_{11}}(\theta) + t_{11}(\theta'))(f_{22} D_{f_{22}}(\theta) + t_{22}(\theta')) + f_{12} D_{f_{12}}(\theta) f_{21} D_{f_{21}}(\theta). \end{aligned} \tag{16}$$

First we consider the case with global competition. From section 3.2 we know that $I = \hat{N}_1 + \hat{N}_2$ is an optimisation criterion. An optimisation criterion ψ can be found by solving $w(\theta, I(\theta)) = 1$ for $I(\theta)$. However, both $\hat{N}_1 + \hat{N}_2$ and ψ are lengthy expressions that do not allow for an analytical treatment. Nevertheless, we can make the following general statements. Since evolution affects the diagonal components a_{11} and a_{22} the IBs are concave. Therefore, any singular point on a convex trade-off is necessarily a repeller. Conversely, for a singular point to be a CSS the trade-off curve has to be more strongly concave than the IB. With symmetric parameter-values the habitat generalist, characterised by $\theta = 0.5$, is a singular point. For this generalist the bifurcation from a repeller to a CSS has to occur for some $z > 1$. Figure 5a shows a numerically calculated bifurcation diagram confirming our qualitative predictions.

Next we analyse the case where fecundities are decreasing functions of local densities: $D_{f_{11}}(N_1), D_{f_{21}}(N_1), D_{f_{22}}(N_2), D_{f_{12}}(N_2)$. In this case the feedback environment is given by $\boldsymbol{I} = (\hat{N}_1, \hat{N}_2)$ and selection is frequency-dependent. Given symmetric parameter-values we can apply the results of section 4. Assume that adults have equal fecundity in both patches ($f_{11} + f_{21} = f_{22} + f_{12}$) and that juveniles are equally likely to settle in either patch, hence: $f_{11} = f_{12} = f_{21} = f_{22}$. Furthermore, we assume that the trade-off is symmetric, that is, $t_{11\max} = t_{22\max}$ (cf. eq. 3) and that all juveniles are equally susceptible to crowding: $D_{f_{11}} = D_{f_{12}} = D_{f_{21}} = D_{f_{22}}$. From these symmetries follows that the habitat generalist with $\theta^* = 0.5$ is a singular point. From section 4 we can conclude that a threshold $z_t > 1$ exists such that for all $z > z_t$ we can find an $r \in \mathbb{R} > 0$ such that for all $\theta', \theta \in B = (0.5 - r, 0.5 + r)$ with $\theta \lesseqgtr \theta' \lesseqgtr 0.5$ we find $\varDelta DDC(\theta', \theta) > 0$. This means that the singular point at $\theta^* = 0.5$ is locally uninvadable for $z > z_t$ (table 2). Conversely, for $z < z_t$ the singular point $\theta^* = 0.5$ is locally invadable because we can find a neighbourhood of θ^* where $\varDelta DDC(\theta', \theta) < 0$ for $\theta \lesseqgtr \theta' \lesseqgtr 0.5$. In order to understand the convergence properties of θ^* we have to investigate $\varDelta FDC(\theta', \theta)$. Under the given symmetry assumptions we can prove that a neighbourhood B of θ^* exists such that for $\theta', \theta \in B$ we find $\theta \lesseqgtr \theta' \lesseqgtr 0.5 \Rightarrow \varDelta FDC(\theta', \theta) > 0$ for all values of z (Appendix A). From table 2 we conclude that for $z > z_t$ the generalist θ^* is a CSS. If

z is slightly smaller than z_t, then $\Delta DDC(\theta', \theta)$ becomes negative, however, $\Delta DDC(\theta', \theta) + \Delta FDC(\theta', \theta)$ stays positive and θ^* turns into an evolutionary branching point. When z becomes small enough such that the negative $\Delta DDC(\theta', \theta)$ overrules the positive $\Delta FDC(\theta', \theta)$ the singular trait-value θ^* turns into an evolutionary repeller. Figure 5b shows a numerically calculated bifurcation diagram of singular points that confirms our qualitative predictions concerning the habitat generalist.

6 Discussion

In this article we classify a family of simple life-history models with respect to criteria driving the evolution in two traits that are connected by a trade-off. Our main tools are a sign-equivalent and algebraically simpler expression for invasion fitness, curvature properties of invasion boundaries, the dimension of the feedback environment and the decomposition of invasion fitness into a density-dependent and a frequency-dependent component.

The results we present are not primarily motivated by questions about the evolution of specific life-cycles but rather by a desire to understand the mechanisms that govern the evolutionary dynamics in a larger class of models. Our aim is to formulate principles of a more general nature that are independent of a specific model and it is these principles that we consider the most valuable result of our work. For the presented class of models the following conclusions can be drawn: (i) Trade-offs between an off-diagonal and a diagonal matrix component as well as between the two traits within a single matrix components correspond to linear invasion boundaries. In these cases all singular points on trade-offs parameterised by $z < 1$ are susceptible to invasion by nearby mutants while the opposite holds true for singular points on trade-offs parameterised by $z > 1$. (ii) Trade-offs between two diagonal components of the projection matrix A correspond to concave IBs. As a result, trade-off curves parameterised by $z \in (0, z_t)$ with $z_t > 1$ give rise to singular points where populations experience disruptive selection. Populations with mean trait-values equal to the singular trait-value are susceptible to invasion by mutants with both smaller and larger trait-values. In models with frequency dependence this can lead to disruptive selection and phenotypic diversification. (iii) Trade-offs between two off-diagonal components correspond to convex IBs. As a result, trade-off curves parameterised by $z \in (0, z_t)$ with $z_t < 1$ give rise to singular points where populations experience disruptive selection. Trade-off curves parameterised by $z > z_t$ give rise to singular points where populations are not invadable by nearby mutants and experience stabilising selection. Hence, for a wide range of z-values such trade-offs favour the evolution of intermediate phenotypes. (iv) Trade-offs between traits that are both necessary to pass through both i-states result in frequency-independent selection. This scenario applies when both off-diagonal components of the population projection matrix consist of only a single term, that is, a transition from one i-state to the other is either only possible in terms of t_{kl} or in terms of f_{kl}. Under this condition the two evolving traits occur in a single product in the fitness function and it is this product that is maximised by selection. From (iii) we see that the majority of trade-off curvatures leads to intermediate phenotypes that strike a balance between the conflicting traits. (v) Trade-offs between traits that are not both necessary to pass through both i-states are a prerequisite for frequency-dependent selection. Such traits affect different summands of the fitness function. Selection becomes frequency-dependent when each evolving trait occurs in a product with a function of density such that the traits are affected by differently weighted sums of the total population size $c_1N_1+c_2N_2$. In the extreme case one evolving trait decreases with an increasing number of individual in i-state one while the other decreases with increasing N_2. Such trade-offs give rise to either linear IBs (in case of a diagonal and an off-diagonal component or in case of two traits that affect a single matrix component) or concave IBs (in case of two diagonal components). From (i) and (ii) we see that in this case either all convex trade-off or all convex plus weakly concave trade-offs give rise to disruptive selection, facilitating the occurrence of evolutionary branching points.

6.1 Open Questions and Extensions

The analysed family of model represents only a fraction of eco-evolutionary scenarios. In the following we describe some extensions to our model family and point out some remaining unresolved questions within the model family.

Our approach allows us to identify models that show frequency-dependent selection. However, once one has decided that frequency dependence does act in a specific model, further analysis is only possible when several symmetry assumptions are met. Though moderate deviations from symmetric conditions will only lead to small quantitative changes in the bifurcation pattern of singular points, we have to admit that we lack strong analytical tools for the general case. Developing such tools seems to be a most challenging and rewarding extension. Further steps in this direction might be possible using techniques presented in the work by de Mazancourt and Dieckmann (2004) and Bowers et al. (2005). These authors give conditions for convergence stability that do not rely on the pattern of intersection of invasion boundaries and the trade-off curve in the neighbourhood of a singular point. However, since their method involves differentiating the fitness function with respect to the trait of the resident, analytical results can only be obtained when the population dynamical equilibria can be solved explicitly. This will only be possible for the simplest cases of population regulation.

In our model class we allow only for the simultaneous evolution of two traits. However, it is possible that one trade-off affects more than two matrix components. This is the case in a model analysed by Kisdi (2002) who studies the evolution of habitat specific fecundity in a two-patch model. Relaxing this assumption makes the derivation of invasion boundaries more complicated and the existence of optimisation criteria will be more restricted.

Another possible route to extend our results is to allow for non-equilibrium attractors. Especially for simple attractors like 2-cycles it might be possible to extend the logic of our approach. The population dynamics for a large class of two-state models has been described by Neubert and Caswell (2000).

The described model structure becomes considerably more complex when we drop the "separability"-assumption. Separability is not given when the effect of a resident type with trait-value θ on a focal individual with trait-value

θ' depends on the trait-values of both types as it is for example the case when competition is mediated by coefficients such as $\alpha(\theta' - \theta) = \exp[-(\theta - \theta')^2/2\sigma]$ with σ being the width of the competition kernel (e.g. Roughgarden, 1979; Doebeli and Dieckmann, 2000). The interpretation is that inter-specific interactions are mediated by quantitative traits like body size that determine the outcome of competition. In this particular case the dimension of the feedback environment becomes potentially infinite. When the feedback is mediated through competition coefficients of the above form the tools developed here do not work. Firstly, the equation for invasion boundaries lose their simple form and in some cases it will even be impossible to find explicit expressions. Secondly, optimisation becomes impossible.

Finally, the presented classification for the evolution of organisms with two i-states can be extended to models with more states. The fitness proxy w can be derived for models with more i-states in an analogous manner. We expect that the general results given in list at the beginning of the discussion are not restricted to two-state models but apply for any number of states.

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A Appendix:

Spatially-Structured Population with Local Density Dependence

Given $f := f_{11} = f_{12} = f_{21} = f_{22}$, $D_f := D_{f_{11}} = D_{f_{12}} = D_{f_{21}} = D_{f_{22}}$ and $t_{11\max} = t_{22\max}$ we prove in this appendix that for all combinations of mutant θ' and resident θ with $\theta \lesseqgtr \theta' \lesseqgtr 0.5$ we find $\Delta FDC(\theta', \theta) > 0$. First we note that at population dynamical equilibrium

$$\begin{aligned}\hat{N}_1 &= (t_{11}(\theta) + \tilde{f}_{11})\hat{N}_1 + \tilde{f}_{12}\hat{N}_2 \Leftrightarrow 1 = t_{11}(\theta) + \tilde{f}_{11} + \tilde{f}_{12}\hat{N}_2/\hat{N}_1\\ \hat{N}_2 &= (t_{22}(\theta) + \tilde{f}_{22})\hat{N}_2 + \tilde{f}_{21}\hat{N}_1 \Leftrightarrow 1 = t_{22}(\theta) + \tilde{f}_{22} + \tilde{f}_{21}\hat{N}_1/\hat{N}_2.\end{aligned}$$

For a resident specialised for habitat type 1 ($\theta < 0.5 \Longleftrightarrow t_{11} > t_{22}$) it follows

$$\tilde{f}_{22} + \tilde{f}_{21}\hat{N}_1/\hat{N}_2 > \tilde{f}_{11} + \tilde{f}_{12}\hat{N}_2/\hat{N}_1.$$

Given the above symmetries we can rewrite the last inequality as

$$fD_f(\hat{N}_2)\left(1 - \frac{\hat{N}_2}{\hat{N}_1}\right) > fD_f(\hat{N}_1)\left(1 - \frac{\hat{N}_1}{\hat{N}_2}\right),$$

which can only hold when $\hat{N}_1 > \hat{N}_2$. An analogous reasoning holds for $\theta > 0.5$.

Next we calculate the frequency-dependent component of invasion fitness (eq. 16) for both a mutant θ' and a resident θ with respect to the reference environment $\bar{I} = (\hat{N}_1 + \hat{N}_2)/2$ as determined by the resident θ:

$$\begin{aligned}FDC(\theta', \theta) &= w(\theta', [I_1(\theta), I_2(\theta)]) - w(\theta', [\bar{I}(\theta), \bar{I}(\theta)])\\ &= f(D_f(\bar{I})t_{22}(\theta') - D_f(\hat{N}_1)t_{22}(\theta') + D_f(\bar{I})t_{11}(\theta') - D_f(\hat{N}_2)t_{11}(\theta'))\\ FDC(\theta, \theta) &= w(\theta, [I_1(\theta), I_2(\theta)]) - w(\theta, [\bar{I}(\theta), \bar{I}(\theta)])\\ &= f(D_f(\bar{I})t_{22}(\theta) - D_f(\hat{N}_1)t_{22}(\theta) + D_f(\bar{I})t_{11}(\theta) - D_f(\hat{N}_2)t_{11}(\theta))\end{aligned}$$

The fitness benefit for a mutant compared to that of the resident is given by the difference of the two frequency-dependent components:

$$\begin{aligned}\Delta FDC(\theta', \theta) &= FDC(\theta', \theta) - FDC(\theta, \theta)\\ &= f[(t_{11}(\theta) - t_{11}(\theta'))(D_f(\hat{N}_2) - D_f(\bar{I})) + (t_{22}(\theta) - t_{22}(\theta'))(D_f(\hat{N}_1) - D_f(\bar{I}))].\end{aligned}$$

From the first paragraph follows

$$\theta \lesseqgtr 0.5 \Longleftrightarrow [\hat{N}_1(\theta) \gtreqless \bar{I}(\theta) \wedge \hat{N}_2(\theta) \lesseqgtr \bar{I}(\theta)]$$

and from our trade-off parameterisation equation (3) we know

$$\theta \lesseqgtr \theta' \Longleftrightarrow [t_{11}(\theta) \gtreqless t_{11}(\theta') \wedge t_{22}(\theta) \lesseqgtr t_{22}(\theta')].$$

From these equivalencies follows $\theta \lesseqgtr \theta' \lesseqgtr 0.5 \Longleftrightarrow \mathit{\Delta} FDC(\theta', \theta) > 0$.

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Table 1 Combinations of evolving traits (columns) and density regulated traits (rows) for which we found an optimisation criterion based on traits, where $k, l, m, n, p, q \in \{1, 2\}$ with $k \neq l$, $m \neq n$ and $p \neq q$. The numbers in the cells of the table refer to the numbered list in section 3.2 where necessary conditions for optimisation are stated. If the conditions are not met, then $\dim(\boldsymbol{I}) > 1$ and optimisation is not possible. A "7" indicates that under sufficient symmetry conditions the results from section 4 can be applied.

evolving traits regulated traits	t'_{kl} & f'_{kl}	a'_{kk} & a'_{pq}	a'_{11} & a'_{22}	a'_{12} & a'_{21}
single	1	1, 4, 5	1, 4	1, 3, 4
all	2, 6	2, 6	6, 7	3, 6, 7
$\tilde{a}_{kl}$, $\tilde{a}_{11}$ & $\tilde{a}_{22}$	2	-	-	3
$\tilde{a}_{kk}$ & $\tilde{a}_{mn}$	2	2	-	3
$\tilde{a}_{ll}$ & $\tilde{a}_{mn}$	2	5	-	3
$\tilde{a}_{12}$ & $\tilde{a}_{21}$	2	5	4	3, 7
$\tilde{a}_{11}$ & $\tilde{a}_{22}$	2	-	7	4

Table 2 Classification of evolutionarily singular traits θ^* with $I_1 = I_2$. The given signs of the frequency-dependent and frequency-independent component have to hold for all mutant and resident trait values from within some neighbourhood $B = (\theta^* - r, \theta^* + r)$, with $r \in \mathbb{R} > 0$ and $\theta < \theta' < \theta^*$ or $\theta^* < \theta' < \theta$. See section 4 for details.

	$\Delta DDC(\theta', \theta) > 0$	$\Delta DDC(\theta', \theta) < 0$
$\Delta FDC(\theta', \theta) > 0$	CSS	$\Delta DDC(\theta',\theta)+\Delta FDC(\theta',\theta)>0$ Branching Point
		$\Delta DDC(\theta',\theta)+\Delta FDC(\theta',\theta)<0$ Repeller
$\Delta FDC(\theta', \theta) < 0$	$\Delta DDC(\theta',\theta)+\Delta FDC(\theta',\theta)>0$ CSS	Repeller
	$\Delta DDC(\theta',\theta)+\Delta FDC(\theta',\theta)<0$ Garden of Eden	

Fig. 1 Life-cycle with two states. The parameters t_{kl} indicate the transition probability of individuals in state l at time t to state k at time $t+1$. The terms f_{kl} indicate the number of surviving offspring that enter state k and are born to an individual in state l.

Fig. 2 Trade-off curves illustrating the relationship between two traits that are traded-off. Parameterisation according to equation (3). The number next to each curve is the parameter z determining the curvature (strength) of the trade-off. The trade-off curve is parameterised in the coefficient θ that lies between zero and one. Filled circles half way on the trade-off curve correspond to $\theta = 0.5$.

Fig. 3 Bifurcation of singular points for the example of an age-structured population with bifurcation parameter z. Trade-off between f_{11} and t_{12} where f_{11} is decreasing in θ while t_{12} is increasing in θ. Solid black lines: CSS; hatched lines: evolutionary repeller. (a) Fecundities decrease in $N_1 + N_2$ ($D_{f_{11}} = 1/(1 + N_1 + N_2) = D_{f_{12}}$), (b) & (c) $\tilde{f}_{11}$ is decreasing in N_1 while $\tilde{f}_{12}$ is decreasing in N_2 ($D_{f_{11}} = 1/(1+N_1)$, $D_{f_{12}} = 1/(1+N_2)$). Other parameter-values: (a-c) $f_{11\max} = 5$, $t_{21\max} = 0.8$, (a) & (b) $f_{12} = 10$, $t_{22} = 0.5$, (c) $f_{12} = 3$, $t_{22} = 0$.

Fig. 4 Bifurcation of singular points for the example of a size-structured population with bifurcation parameter z. Trade-off between f_{12} and t_{22} where f_{12} is decreasing in θ while t_{22} is increasing in θ. (a) Fecundity decreases with total population size ($D_{f_{12}} = 1/(1 + N_1 + N_2)$), (b) new-born survival decreases with density of small individuals ($D_{f_{12}} = 1/(1 + N_1)$) and survival of large individuals decreases with density in this size class ($D_{t_{22}} = 1/(1+N_2)$. Other parameter-values: $f_{12\max} = 10$, $t_{22\max} = 0.8$, $t_{11} = 0.5$, $t_{21} = 0.5$.

Fig. 5 Bifurcation of singular points for the example of a spatially structured population with bifurcation parameter z. Trade-off between t_{11} and t_{22} where t_{11} is decreasing in θ while t_{22} is increasing in θ. Solid grey lines: evolutionary branching point. (a) All fecundities decrease in $N_1 + N_2$ ($D_{f_{kl}} = 1/(1 + N_1 + N_2)$ for $i, j \in \{1, 2\}$), (b) $\tilde{f}_{11}$ and $\tilde{f}_{12}$ are decreasing functions of N_1 ($D_{f_{11}} = 1/(1+N_1) = D_{f_{12}}$) while $\tilde{f}_{22}$ and $\tilde{f}_{21}$ are decreasing functions of N_2 ($D_{f_{22}} = 1/(1+N_2) = D_{f_{21}}$). Other parameter-values: $t_{11\max} = 0.7 = t_{22\max}$, $f_{11} = f_{22} = f_{21} = f_{12} = 10$.

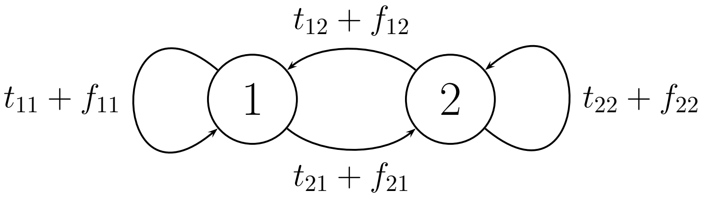

Figure (1)

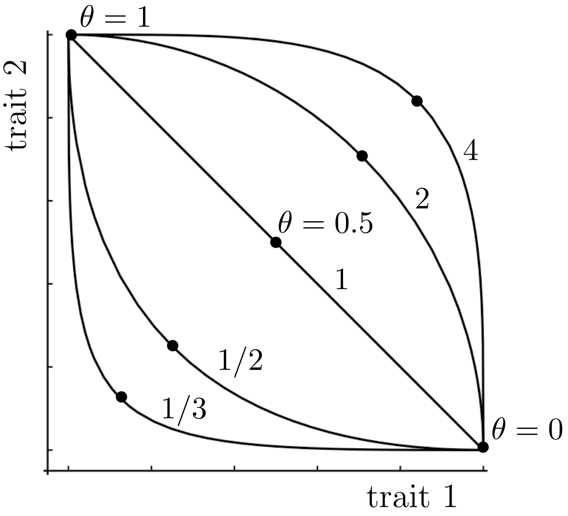

Figure (2)

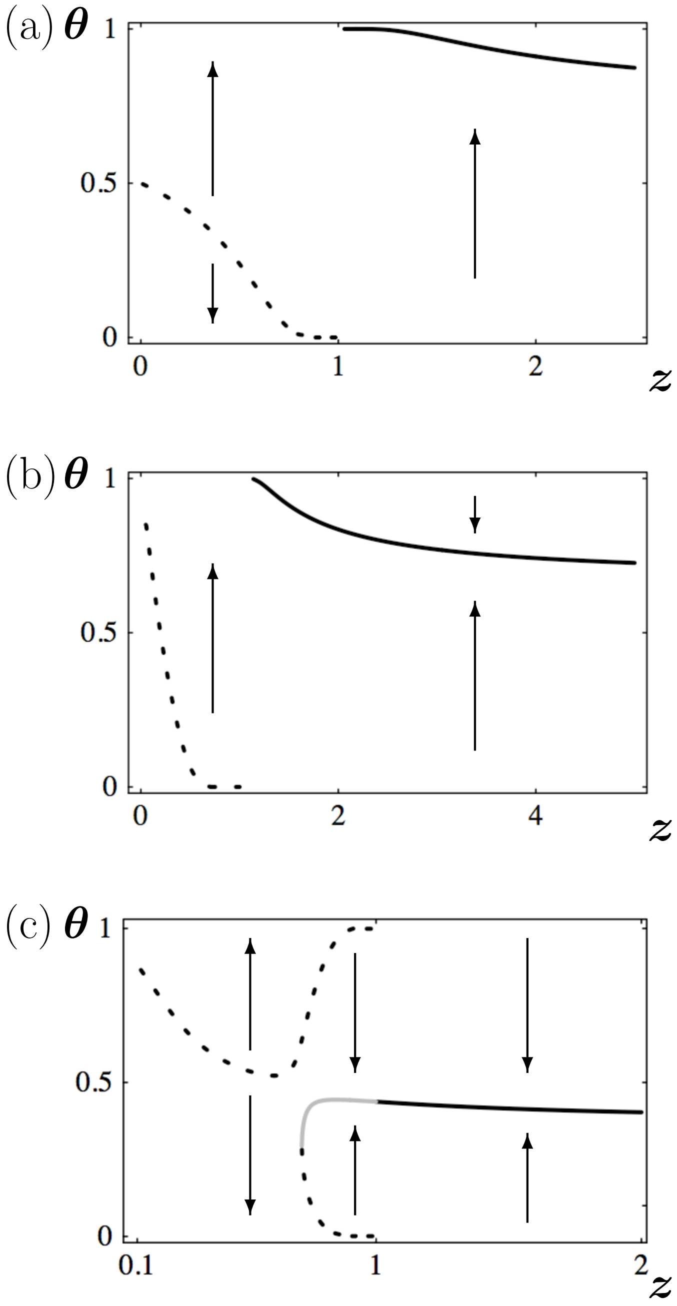

Figure (3)

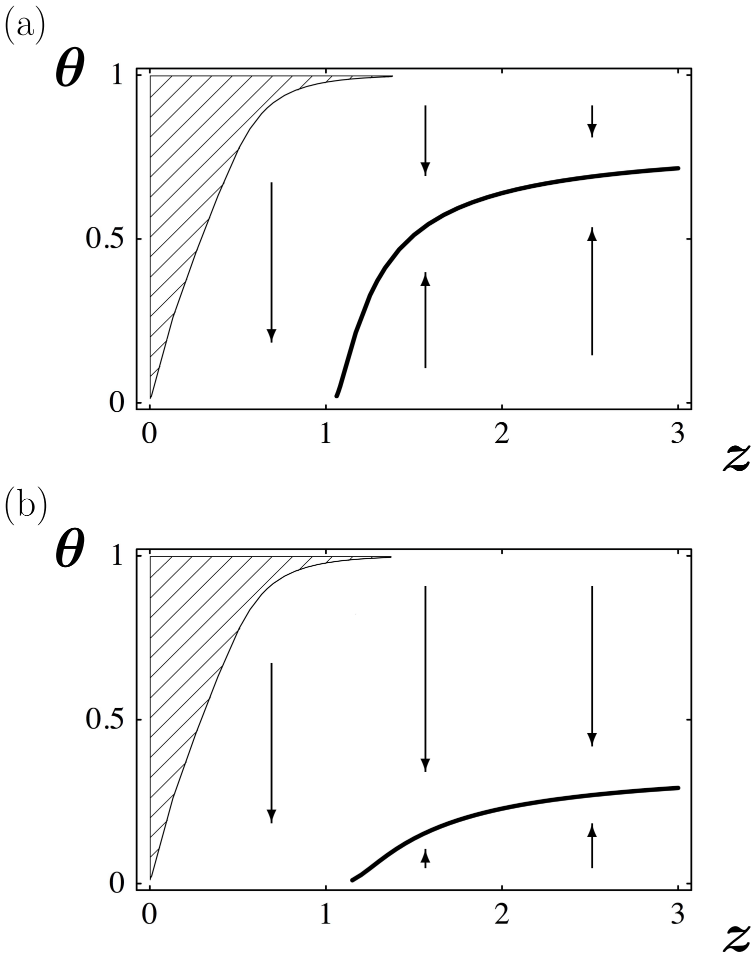

Figure (4)

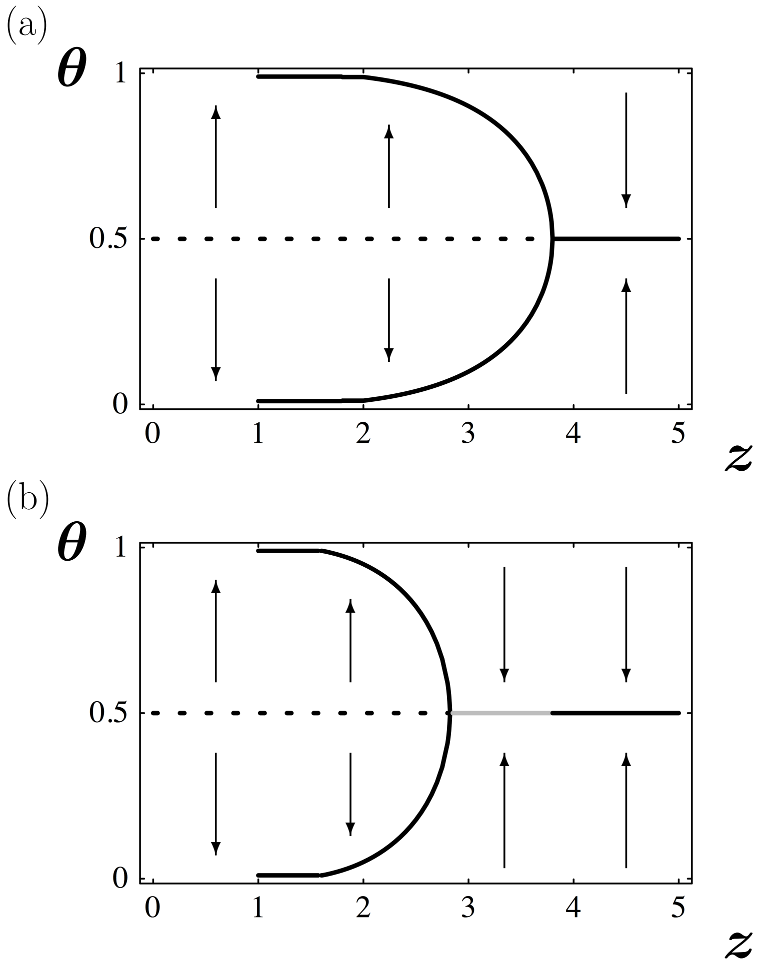

Figure (5)