Coevolution of dispersal-related traits: modelling and analysis

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Academic dissertation

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Abstract

This thesis theoretically investigates dispersal evolution in a wider ecological context. It factors in ecological relevant dependencies e.g. trade-offs or spatial heterogeneity, and allows coevolutionary interactions between immigration and other traits. It extends well-known models to include more biological realism, reveals novel evolutionary mechanisms and helps to understand the complex dispersal patterns more accurately.

In particular, this work studies the evolution of dispersal, i.e., natal emigration when it is under a trade-off with fecundity. Furthermore, dispersal is divided into its three phases and hence studied as emigration, transfer and immigration. Emigration and immigration are made dependent on the local conditions experienced by the individuals: the patch types. The coevolution of patch-type dependent immigration is investigated alone, but also the coevolution of patch-type dependent immigration and patch-type dependent emigration or local adaptation is studied. The evolutionary framework was chosen to be adaptive dynamics, a way of describing the long-term evolutionary outcomes of single populations that can lead to evolutionary diversification of strategies.

List of Articles

The thesis consists of an introductory part and the following four articles:

Article *I* Helene Camilla Weigang & Éva Kisdi. 2015. **Evolution of dispersal under a fecundity-dispersal trade-off.** *Journal of Theoretical Biology* 371: 145-153.

Article *II* Mats Gyllenberg, Éva Kisdi & Helene Camilla Weigang. 2016. **On the evolution of patch-type dependent immigration.** *Journal of Theoretical Biology* 395: 115-125.

Article *III* Helene Camilla Weigang. **Coevolution of patch-type dependent emigration and patch-type dependent immigration.** *submitted in revised form to the Journal of Theoretical Biology.*

Article *IV* Mats Gyllenberg, Éva Kisdi & Helene Camilla Weigang. **Coevolution of patch-type dependent immigration and local adaptation.** *submitted to The American Naturalist.*

Following the tradition of mathematical literature, the authors of **Articles *II*** and ***IV*** are listed alphabetically. I had the leading role in the development, model analysis and writing part of all manuscripts.

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Contents

Chapter 1

Dispersal

Dispersal is defined as the movement of individuals or propagules from the natal patch to a breeding site (natal dispersal) or between consecutive breeding sites (breeding dispersal) (Bonte et al., 2012; Clobert et al., 2009; Hanski, 1999; Hanski and Gaggiotti, 2004; Hanski and Gilpin, 1997; Travis et al., 2012). It involves a decision to emigrate from a site, move and immigrate into a new breeding site. Dispersal, in contrast to migration (e.g. see Cote et al., 2016), can potentially lead to gene flow which is vital in adapting to heterogeneous and changing environments, especially under the increasing habitat fragmentation that many species experience today. It shapes the species diversity, distribution and abundance and is the key phenomenon that connects local populations in a metapopulation.

Dispersal has evolved because of various drivers. Individuals disperse to avoid competition or inbreeding with their kin, to escape spatio-temporal variation in the environment or from predators, to colonise new habitats and recolonise patches in which individuals went locally extinct (Clobert et al., 2009; Ronce, 2007). Dispersal can help to locally adapt to environments, but may also hinder local adaptation if well-adapted individuals are swamped by non-adapted dispersers (Lenormand, 2002). The costs that incur through dispersal exist at all stages. Before departure, energetic costs occur during the development of dispersal structures, e.g. wings or seed plumes (see Bonte et al., 2012, and citations therein). The costs for developing dispersal structures are then not only paid by dispersing individuals, but also by the non-dispersers. Further, the costs of information acquisition and the energy and time spent during transfer count to the negative effects of dispersal, not to forget the possibility of settling in an unsuitable habitat. If individuals evolve a strategy to alleviate some costs, constraints are experienced through trade-offs elsewhere. Trade-offs occur between dispersal and fecundity, survival during dispersal, competitive ability or resistance to natural enemies. However, the costs and trade-offs do generally not surpass the benefits of dispersal. One strategy that has evolved to alleviate some costs of dispersal, is a capability to perceive, sample and detect the experienced heterogeneous environments (Doyle, 1975; Ehlinger, 1990; Hey and Houle, 1987; Hoffmann, 1985; Jaenike, 1985; Jaenike and Holt, 1991; Matter and Roland, 2002; Schooley and Wiens, 2003; Zollner and Lima, 1999). This enables populations to base emigration and immigration decisions on the environmental cues (Mitchell, 1977; Rees, 1969) and match their local adaptations to the environment (Hanski, 2011; Klemme and Hanski, 2009; Myers et al., 1981). The environmental cues, for instance local population density or patch types, that affect dispersal decisions have long been recognised, but only recently studies have started to focus on the interaction between the emigration and immigration decisions (Bonte et al., 2012; Clobert et al., 2009; Jacob et al., 2015; Travis et al., 2012). Disentangling dispersal and splitting it up into its three phases is expected to substantially improve the understanding of the complex process.

This thesis theoretically investigates dispersal evolution in a wider ecological context. It factors in ecological relevant dependencies, e.g., trade-offs or spatial heterogeneity, and allows for coevolutionary interactions between immigration and other traits. It extends well-known models to include more biological realism, reveals novel evolutionary mechanisms and helps to understand the complex dispersal patterns more accurately. Article *I* studied the evolution of dispersal under commonly detected dispersal-fecundity trade-offs. Articles *II*, *III* and *IV* studied the evolution of immigration in heterogeneous environments (Article *II*), in coevolution with patch-type dependent emigration (Article *III*), or local adaptation (Article *IV*). Articles *I*, *II* and *III* are extensions of the discrete-time Hamilton-May model (Hamilton and May, 1977, see Sections 2.1 & 2.4). Article *IV* investigated a continuous-time metapopulation model, with explicit local population dynamics similarly to the models of Gyllenberg and Hanski (1992) and Hanski and Gyllenberg (1993) (see Section 2.5). Article *I* analysed the evolutionary dynamics in real time (see Section 2.2 & 2.3), whereas Articles *II*, *III* and *IV* derived a fitness proxy on a generation basis (see Section 2.3 & 2.6). A summary of all articles is presented in Section 2.7.

Chapter 2

Dispersal theory

2.1 Hamilton-May models

One of the most classical and fundamental models that investigated the evolution of dispersal is the Hamilton-May model (Hamilton and May, 1977). The Hamilton-May model works in discrete time, it is spatially implicit and assumes non-overlapping generations in a landscape with infinitely many patches connected through global dispersal. The life cycle of an annual, asexual and semelparous population in the Hamilton-May model is as follows: In the beginning of each year every patch is inhabited by one individual. In any of the M patches individuals produce a large number of offspring, B, and the mothers die immediately after. Then, the offspring disperses with probability p_i. The dispersers survive dispersal with probability π and settle in a new patch. After settlement, fair competition takes place with 1 individual surviving per patch. This model is deterministic if the number of patches M and number of offspring produced B are infinitely large.

The number of patches in year t that are occupied by individuals with dispersal strategy p_i is $N_i(t)$. The number of patches in the next year $t+1$ equals the number of offspring that is produced $N_i(t)B$ times the probability that the offspring conquers new patches and defends the natal patch. A non-dispersed individual competes in the natal site against all immigrants that arrive at the patch and the other non-dispersing siblings. An offspring that disperses and survives dispersal, encounters a patch where non-dispersing offspring of other mothers are present. In these patches a single individual competes against all non-dispersers and the immigrants that arrive at the patch. When there are several dispersal strategies p_j for $j = 1, \dots, l$ present in the landscape, $N_i(t)$ changes from year t to $t+1$ accordingly to the following dynamics

$$N_i(t+1) = N_i(t)B\Bigg(\frac{1-p_i}{(1-p_i)B + \sum_{j=1}^{l}\frac{N_j(t)}{M}\pi B p_j} \\ + \sum_{\iota=1}^{l}\frac{N_\iota(t)}{M}\frac{\pi p_i}{1+(1-p_\iota)B + \sum_{j=1}^{l}\frac{N_j(t)}{M}\pi B p_j}\Bigg). \tag{2.1}$$

2.1.1 Survival until maturation

The Hamilton-May model serves as a first investigation of kin competition and dispersal and has been extended in various ways (e.g. Comins et al., 1980; Johnson and Gaines, 1990; Kisdi, 2004). One simple and natural way of extending the Hamilton-May model is to assume that not all individuals that won competition survive until reproduction (e.g. Comins et al., 1980; Kisdi, 2004, Articles *I*, *II* and *III*). The individuals may not survive because of local catastrophes or deaths before reproduction. When it is assumed that only a fraction of individuals s survives until maturation the following variations are encountered in the ecological dynamics of Eq. (2.1). In only sM patches individuals survive until maturation. Hence, fewer individuals are produced in the landscape and the number of immigrants that arrive in any patch is then $\sum_{j=1}^{l}\frac{N_j(t)}{M}s\pi B p_j$. The individuals that did not survive until reproduction leave empty patches behind, which are filled by immigrants during dispersal. The fraction of patches with reduced competition is $1-s$ and the fraction of patches an individual wins of this type is $\frac{1-s}{1+\sum_{j=1}^{l}\frac{N_j(t)}{M}s\pi B p_j}$. Then, the population dynamics of the extended

Hamilton-May model with some deaths before reproduction is

$$\begin{aligned} N_i(t+1) = N_i(t)sB\Bigg(& \frac{(1-p_i)}{(1-p_i)B+\sum_{j=1}^{l}\frac{N_j(t)}{M}s\pi Bp_j}+ \\ & \sum_{\iota=1}^{l}\frac{N_\iota(t)}{M}\frac{s\pi p_i}{1+(1-p_\iota)B+\sum_{j=1}^{l}\frac{N_j(t)}{M}s\pi Bp_j}+\frac{(1-s)\pi p_i}{1+\sum_{j=1}^{l}\frac{N_j(t)}{M}s\pi Bp_j}\Bigg). \end{aligned} \tag{2.2}$$

2.1.2 Dispersal limitation

Dispersal is correlated with many other life-history traits and improvements in some traits induce disadvantages in other life-history traits. Most models incorporate dispersal costs as a fixed mortality during dispersal, or model it as a distance-dependent cost (e.g. see Bonte et al., 2010; Poethke et al., 2011; Rousset and Gandon, 2002). A fixed dispersal mortality, however, induces a strict trade-off between non-dispersing and dispersing individuals.

In reality, individuals evolved strategies to elude some mortality costs, but unavoidably face trade-offs at other stages. There exists evidence that energy constraints enforce a trade-off between dispersal and fecundity (Roff, 1977). The investments into dispersal structures during development increase the offspring's propensity to disperse. However, if more energy is used per offspring, the dispersal ability may be high but fewer individuals are born. Hence, reproducing individuals need to maximise the reproductive output by apportioning resources among the offspring and by controlling the dispersal strategy of their offspring. Such a dispersal-fecundity trade-off is faced by many species, e.g. in wing-dimorphic organisms and *Lepidoptera* (Gu and Danthanarayana, 1992; Gu et al., 2006; Hughes et al., 2003; Karlsson and Johansson, 2008; Mole and Zera, 1993; Roff, 1984, 1986; Stirling et al., 2001; Wratten, 1977; Zera, 1984; Zera and Denno, 1997).

The effect of a dispersal-fecundity trade-off in the Hamilton-May model was first analysed by Cohen and Motro (1989). However, the latter study investigated the effects of only one particular shape of the trade-off function, which again constrained the analysis to a special case. Since it is not clear from biological data which exact shape a dispersal-fecundity trade-off should have, it is of major importance to analyse models with an unspecified trade-off and classify the evolutionary outcomes in dependence of the trade-off shape (see Article I). If one assumes that dispersal is under a dispersal-fecundity trade-off, replace B with $B\beta(p_i)$. The function β is the trade-off function describing the antagonistic effect between dispersal and fecundity. It gives the fecundity of an individual with dispersal strategy p_i. Trade-offs introduce nonlinear dispersal costs which are expected to enrich the evolutionary dynamics and may lead to a diversification of dispersal strategies.

2.2 Fitness in unstructured environments

To study the evolutionary outcome of mutating traits a fitness concept was derived, the invasion fitness (Metz et al., 1992). The invasion fitness is the long-term exponential growth rate of a small mutant population in an environment set up by a resident population at equilibrium and is derived from the ecological dynamics. If the invasion fitness is positive the mutant population grows in abundance and replaces the resident population. The mutants become the new residents and their dynamics settles at a new equilibrium. The new residents shape the environment anew, which in turn alters the invasion fitness of mutants, i.e., an eco-evolutionary feedback is observed.

The invasion fitness of individuals with a mutated dispersal strategy in the extended Hamilton-May model with deaths before reproduction and a dispersal-fecundity trade-off (replace B with $B\beta(p_i)$) is derived from Eq. (2.2) for $l = 1$. By dividing both sides of Eq. (2.2) with M, frequencies rather than absolute numbers are being kept track of. Then, the invasion fitness of a small mutant population with strategy p^m, slightly different to the resident's strategy p, into an environment that is inhabited by the resident population is (see Eq.(2) in Article *I*):

$$w(p^m, p) = s\beta(p^m)$$
$$\left(\frac{1-p^m}{(1-p^m)\beta(p^m) + s\pi\beta(p)p} + \frac{s\pi p^m}{(1-p)\beta(p) + s\pi\beta(p)p} + \frac{(1-s)\pi p^m}{s\pi\beta(p)p}\right). \tag{2.3}$$

2.3 Adaptive dynamics

The theory that studies the long-term evolutionary outcome using invasion fitness is adaptive dynamics (Dieckmann and Law, 1996; Geritz et al., 1998; Metz et al., 1992). For large population sizes and small mutation rates with small effects the path of the trait substitution events, as explained in Section 2.2, can be approximated and deterministically described by the canonical equation of adaptive dynamics (Dieckmann and Law, 1996):

$$\frac{dp^*}{dt} = \frac{T_r}{T_s\sigma_e^2} m(p^*)N(p^*)\mathbf{C}(p^*)\left.\frac{\partial w(p^m, p)}{\partial p^m}\right|_{p^m=p=p^*}, \tag{2.4}$$

where T_r is the average age at reproduction, T_s is the average age at death of the individuals, σ_e^2 is a measure for the variability of their lifetime offspring production, $m(p^*)$ is the mutation probability per birth event, $N(p^*)$ is the equilibrium population density of individuals with strategy p^* and $\mathbf{C}(p^*)$ is the variance-covariance matrix. It is a symmetric and positive definite matrix that represents the mutational increments between traits. The last term of Eq. (2.4) is called the selection gradient. Note that in Section 2.2 the evolving trait is a scalar strategy p and Eq. (2.4) is formulated for finite dimensional traits. For infinite dimensional strategies a canonical equation has been derived in Dieckmann et al. (2006).

First I explain how the evolutionary outcome of scalar strategies is analysed, before I explain how it is done for finite and infinite dimensional traits. In one dimension the invasion fitness function provides all information to study the long-term evolution. A strategy that makes the selection gradient of the canonical equation vanish, is called a singular strategy, denoted by p^*. The strategy p^* solves:

$$\left.\frac{\partial w(p^m,p)}{\partial p^m}\right|_{p^m=p=p^*} = 0. \tag{2.5}$$

It is (locally) evolutionarily stable (a local ESS, or local fitness maximum) if

$$\left.\frac{\partial^2 w(p^m,p)}{\partial p^{m2}}\right|_{p^m=p=p^*} < 0.$$

The singular strategy p^* is an asymptotically stable fixed point of the canonical equation Eq. (2.4), i.e., attracting (locally convergence stable) if

$$\left.\frac{\partial^2 w(p^m,p)}{\partial p^{m2}} + \frac{\partial^2 w(p^m,p)}{\partial p^m \partial p}\right|_{p^m=p=p^*} < 0.$$

Strategies that are asymptotically stable and fitness minima, are evolutionary branching points, at which evolutionary diversification occurs. In one dimension, the branching criterion implies that mutants nearby the singularity can coexist (Geritz et al., 1998), which is not guaranteed in higher dimensions (Geritz et al., 2016). Attracting fitness maxima are called, continuously stable strategies or CSSs and strategies that are not attracting are repellors. If a strategy is a repellor and a fitness maximum, it is called a Garden of Eden point.

Evolving traits need not be scalars, but can well take values in a finite dimensional space. A singular vector-valued strategy solves the singularity condition (2.5) for every vector element. To analyse the stability of vector-valued singularities we need to remember the following: a real symmetric matrix $\mathbf{M}$ is positive definite if $x^\top \mathbf{M} x > 0$ for all non-zero vectors $x \in \mathbb{R}^n$, negative definite if $x^\top \mathbf{M} x < 0$ and indefinite if it is neither positive definite, negative definite, $x^\top \mathbf{M} x \geq 0$ nor $x^\top \mathbf{M} x \leq 0$. The evolutionary stability of a vector-valued singularity is investigated using the Hessian matrix $\mathbf{H}$ of the invasion fitness with elements $h_{ij} = \left.\frac{\partial^2 w}{\partial p_i^m \partial p_j^m}\right|_{p^m=p=p^*}$. The singular strategy is a fitness maximum if the Hessian matrix is negative definite. It is a minimum if the Hessian matrix is positive definite and a saddle of the invasion fitness function if the Hessian matrix is indefinite. The asymptotic stability of a vector-valued strategy is investigated using the Jacobian matrix of the selection gradient $\mathbf{J}$ (Geritz et al., 2016; Leimar, 2005, 2009). The Jacobian matrix can be written as $\mathbf{J} = \mathbf{H} + \mathbf{Q}$ and matrix $\mathbf{Q}$ has elements of the form: $q_{ij} = \frac{\partial^2 w}{\partial p_i^m \partial p_j}\Big|_{p^m = p = p^*}$. Note that the Jacobian matrix is usually not symmetric. We extend the classical definition of definiteness given above following Leimar (2009). The matrix $\mathbf{J}$ is negative definite, positive definite or indefinite if its symmetric part $(\mathbf{J} + \mathbf{J}^\top)/2$ is negative definite, positive definite or indefinite, respectively. The singular vector-valued strategy is strongly attracting, i.e., it is an asymptotically stable fixed point of the canonical equation for all symmetric and positive definite variance-covariance matrices $\mathbf{C}(p^*)$, if the Jacobian matrix is negative definite. In the remainder of the paragraph I focus on the strongly attracting case only. When the singularity is strongly attracting and a saddle or minimum of the fitness function, evolutionary branching may occur. In three or higher dimensions the coexistence of strategies is not implied by the branching condition, since the emerging branches locally around the singularity could possibly evolve out of the coexistence region with one branch going extinct. Hence, one needs to derive an additional condition to check if the emerging strategies stay in the coexistence set (see Geritz et al., 2016). If the emerging strategies remain in the coexistence set, strongly attracting fitness saddles or minima are then called sustainable evolutionary branching points.

There also exist, biologically more realistically, infinite dimensional traits of the form $p : \mathbb{R} \mapsto \mathbb{R}$. The tools of the theory of calculus of variations and Euler's equation (Euler-Lagrange equation) are useful to find singular function-valued strategies (Dieckmann et al., 2006; Parvinen et al., 2006). Function-valued singularities have not yet been fully classified. In particular, there exists no criterion for strong convergence stability. The calculus of variations theory provides tools to find the extremal p^* of a functional R_m that describes fitness, where $R_m(p) = \int_{\mathbb{R}} J(y, p(y))dy$. Assume that J

is differentiable with respect to p and assume that p is piecewise smooth. A necessary condition for p^* to be an extremal is that Euler's equation is satisfied: $\frac{\partial}{\partial p(y)} J(y, p^*(y)) = 0$ for all $y \in \mathbb{R}$. Note that this is a special case of Euler's equation, since J is not depending on p'. A sufficient condition for p^* to be a maximum is that J is concave with respect to p.

2.3.1 Adaptive dynamics in the Hamilton-May model

In the classical Hamilton-May model evolution leads to an attracting evolutionarily stable dispersal strategy $p^* = 1/(2-\pi)$ (a CSS, $s = 1$ and $\beta(p) = \beta$ in Eq. (2.3); Hamilton and May, 1977). It seems surprising that although dispersal is costly, the strategy evolves to let more than half of the offspring disperse from the natal patch. However, it is intuitively clear why such a high fraction of offspring disperse. If all individuals would stay at home, but only one individual can establish itself, then all other siblings would be lost during competition between themselves and the immigrants that arrive. If individuals, however, disperse although dispersal is costly, some dispersers survive dispersal and are given a chance to win a new site.

2.3.2 Critical function analysis

When there exists a constraint between the trait under selection and another trait, a trade-off function may be introduced in the model. Then, one should not limit the evolutionary analysis committing to a particular function, since from biological data it is hard to infer the exact trade-off shape. However, the evolutionary outcome may critically depend on the trade-off shape. The technique to analyse the evolutionary outcome with an unspecified trade-off function is called critical function analysis (de Mazancourt and Dieckmann, 2004; Kisdi, 2006). It takes the slope and curvature of the trade-off function as bifurcation parameters to identify the conditions of the different evolutionary outcomes.

The singular strategy needs to solve Eq. (2.5). The latter equation can be equivalently expressed as the slope of the trade-off function $\beta'(p^*)$ at the singularity (see Eq.(3) in Article *I*). For an initial value β_0 a function

$\beta_{crit}(p)$ solves the equation of $\beta'(p^*)$ and is called the *critical function*. Any point of β_{crit} is singular if one chooses a trade-off function tangentially to the critical function at that point. The curvature of the critical function and the trade-off function then give information about the local stability of a singular point. The singular strategy p^* of a trade-off function β with local curvature smaller than $\beta''_{crit}(p^*)$ is attracting, $\beta''(p^*) < \beta''_{crit}(p^*)$, and repelling if the opposite holds (de Mazancourt and Dieckmann, 2004; Kisdi, 2006, see Article *I*).

2.4 Structured Hamilton-May models

The classical Hamilton-May model and Article *I* assume no environmental heterogeneity and regard dispersal as an unconditional process although landscapes are clearly structured by many different quantities and dispersal decisions depend on the environmental factors. Articles *II* and *III* extend the Hamilton-May model to a heterogeneous landscape structured by patch types (also Article *IV* assumes a structured environment, but the underlying model is different). A heterogeneous landscape structure induces differences of the model parameters in the patches of different types and hence dispersal decisions are affected as well. Instead of simplistically focusing on a single parameter of patch-type dependent dispersal, the process can be decomposed in its three stages. Then, dispersal is not only seen as patch-type dependent emigration but consists of a transfer phase where individuals immigrate into a patch with a patch-type dependent settlement probability.

Dispersal in structured environments has been investigated when emigration depends on population density (Gyllenberg and Hanski, 1992; Hovestadt et al., 2010; Kun and Scheuring, 2006; Poethke and Hovestadt, 2002; Poethke et al., 2007; Travis et al., 1999) or immigration depends on density (Nonaka et al., 2013; Parvinen and Brännström, 2016), or both, emigration and immigration are density-dependent (Hanski and Gyllenberg, 1993; Metz and Gyllenberg, 2001; Parvinen et al., 2012; Poethke et al., 2011; Saether et al., 1999). Many other models that study dispersal evolution in structured habitats use a phenomenological approach of immigration, modelling it as a habitat choice trait. Habitat choice measures the fraction of individuals to settle in one habitat type, and the remainder of dispersers directly moves to the other type (Ravigné et al., 2009, and citations therein). These models neglect the details of the dispersal process. Other studies (Baker and Rao, 2004; Doyle, 1975; Stamps et al., 2005; Ward, 1987) as well as Articles *II* and *III* model the dispersal process mechanistically and explicitly incorporate a dispersal season in the model. The season is incorporated as a continuous-time transfer phase, during which individuals randomly encounter patches and settle in an encountered patch of certain type with a patch-type dependent settlement probability.

2.4.1 Dispersal season

When dispersal occurs in a structured landscape with patches of two different types with frequencies ϕ_1 and $\phi_2 = 1 - \phi_1$ and immigration is considered explicitly in a continuous-time season (see Articles *II-III*), the probability to survive dispersal is not fixed as in the Hamilton-May model and in Article *I*. The probability to survive dispersal and after settlement in a patch of type i is then given by $\Pi_i(f)$. It depends on the settlement strategies $f = (f_1, f_2)$, where f_i denotes the probability to settle in a patch of type i upon encounter. The $\Pi_i(f)$ is derived as follows: In the beginning of the dispersal season, individuals emigrate and join the dispersal pool. They leave the pool exponentially as they (i) settle in a patch upon encounter at the rate $\rho(\phi_1 f_1 + \phi_2 f_2)$, where ρ is the patch encounter rate. Dispersers may also leave the dispersal pool (ii) by dying in the dispersal pool, which happens at a rate ν. The probability that an individual is still in transit at time $t \in [0, T]$ is $e^{-(\rho(\phi_1 f_1 + \phi_2 f_2) + \nu)t}$. Given that the individual has not disappeared from the dispersal pool until time t, the probability that it encounters a patch of type i within the next time interval $(t, t + dt)$ is $\phi_i \rho dt$ and that it settles in the encountered patch of type i is f_i. If the individual settles it cannot move back to the dispersal pool. In the patch it survives until the end of the dispersal season, time T, with probability $e^{-\mu_i(T-t)}$, where the patch-death rate in a patch of type i is μ_i and $\nu > \mu_i$ for $i = 1, 2$

is assumed, since dispersal is usually more dangerous than residing in a patch. All dispersers that do not settle until the end of the dispersal season die. Integrating over t, the probability of surviving the dispersal season by dispersing and after settlement in the patch of type i until the end of the dispersal season is

$$\begin{aligned}
\Pi_i(f) &= \phi_i \rho f_i \int_0^T \mathrm{e}^{-(\rho(\phi_1 f_1+\phi_2 f_2)+\nu)t-\mu_i(T-t)}\,dt \qquad (2.6)\\
&= \phi_i \rho f_i \frac{\mathrm{e}^{-\mu_i T} - \mathrm{e}^{-(\ \rho(\phi_1 f_1+\phi_2 f_2)+\nu)T}}{\rho(\phi_1 f_1+\phi_2 f_2)+\nu-\mu_i}
\end{aligned}$$

(see Eq.(3) of Article *II*).

2.4.2 Projection matrix

The life cycle and population dynamics of the structured model as compared to the extended Hamilton-May model does not change as such, with the difference that all patches can be of two types. The probabilities to survive until maturation s_i and emigrate p_i as well as the relative fecundity β_i are then patch-type dependent. When several strategies are present in the landscape, p_i^j gives the emigration probability from patches of type i of individuals with strategy j. The relative frequency of patches of type i occupied by individuals with strategy j is ϕ_i^j where $\sum_j \phi_i^j = \phi_i$. Then, the average number of individuals of strategy j that emigrate from any of the patches is Bu_j, where $u_j = \sum_{i=1}^{2} \phi_i^j s_i \beta_i p_i^j$. The number of immigrants that arrive in a patch is $M \sum_{j=1}^{l} \frac{\Pi_i(f^j)}{\phi_i M} B u_j$, which is the analog to the unstructured Hamilton-May model with deaths before reproduction $\sum_{j=1}^{l} \frac{N_j}{M} s \pi B p_j$. The probability to survive the dispersal season as a non-disperser in the natal patch of type i is $\mathrm{e}^{-\mu_i T}$. Assume that individuals are characterised by the dispersal strategy $d^J = (p_1^J, p_2^J, f_1^J, f_2^J)$ and that l strategies d^j, $j = 1, \ldots, l$, occupy the landscape. The population dynamics of relative frequencies of patches occupied by an individual with strategy J changes in each patch type from one year to the next in a similar manner as derived in Eq. (2.2). The population dynamics of ϕ_1^J and ϕ_2^J in a structured environment can be written in vector form:

$$\begin{pmatrix} \phi_1^J(t+1) \\ \phi_2^J(t+1) \end{pmatrix} = \begin{pmatrix} l_{11}^J & l_{12}^J \\ l_{21}^J & l_{22}^J \end{pmatrix} \begin{pmatrix} \phi_1^J(t) \\ \phi_2^J(t) \end{pmatrix}, \tag{2.7}$$

where the matrix L is called the projection matrix. The matrix elements l_{ij}^J for $i \neq j$ give the expected frequency of offspring of strategy J that emigrates from a patch of type j, survives dispersal and the remainder of the season in a patch of type i and wins fair competition. The matrix elements l_{ii}^J denote the expected fraction of offspring of strategy J that defends the natal patch of type i against all immigrants and the fraction of patches of type i that are newly conquered by dispersers. The matrix elements from i-patches are

$$l_{ii}^J = s_i B \beta_i \left(\frac{(1-p_i^J)\mathrm{e}^{-\mu_i T}}{(1-p_i^J) B \beta_i \mathrm{e}^{-\mu_i T} + \sum_{\iota=1}^{l} \frac{\Pi_i(f^\iota)}{\phi_i} B u_\iota(t)} + p_i^J \Pi_i(f^J) V_i(\Phi(t), d^1, \ldots, d^l) \right)$$

and

$$l_{ij}^J = s_j B \beta_j p_j^J \Pi_i(f^J) V_i(\Phi(t), d^1, \ldots, d^l) \qquad \text{for } i, j = 1, 2 \text{ and } i \neq j$$

and $\Phi(t)$ is the vector that collects all relative frequencies of strategies in patches of type 1 and 2 in year t. Note that the first term of l_{ii}^J is similar to the first term in Eq. (2.1), with the difference that non-dispersers need to survive the dispersal season in a patch and the immigrants come from patches of both types. The V_i in l_{ii}^J and l_{ij}^J, gives the probability of winning fair competition in any of the non-natal patches of type i. It is similar to the second line of Eq.(2.2). The V_i is the sum of winning competition in a patch where non-dispersing individuals of type j were present and winning competition in the patches that were empty in the beginning of the dispersal season. In the latter patches, competition is less strong, since only immigrants are competing for the patch. For $B \to \infty$ the term BV_i is

$$V_i^+(\Phi, d^1, \ldots, d^l) = \lim_{B\to\infty} BV_i(\Phi, d^1, \ldots, d^l) =$$
$$\sum_{j=1}^{l} \frac{\phi_i^j(t)}{\phi_i} \frac{s_i}{(1-p_i^j)\beta_i \mathrm{e}^{-\mu_i T} + \sum\limits_{\iota=1}^{l} \frac{\Pi_i(f^\iota)}{\phi_i} u_\iota(t)} + \frac{1-s_i}{\sum\limits_{\iota=1}^{l} \frac{\Pi_i(f^\iota)}{\phi_i} u_\iota(t)}. \qquad (2.8)$$

2.5 Structured metapopulation models

Continuous-time structured metapopulation models, that allow for local dynamics in habitat patches connected through dispersal in a continuously structured environment were first derived in the late 1980's. Hastings and Wolin (1989) presented the first age-structured metapopulation model, whereas Gyllenberg and Hanski (1992) introduced the first size-structured metapopulation model, that used local population size as structuring variable (see also Hanski and Gyllenberg, 1993). The age-structured metapopulation model is presented here, but see the size-structured derivation in the Online Appendix A.1 of Article *IV*. These structured metapopulation models are spatially implicit and consider asexually reproducing individuals, but, more realistically and demanding then previous ones, assume a continuous distribution n of patch types $y \in Y$. Individuals disperse in a metapopulation that consists of patches that can inhabit more than one individual. Local catastrophes kill the individuals in patches at a rate μ, but dispersers recolonise empty patches and grow there if well-adapted and undisturbed by catastrophes. The time elapsed since the last catastrophe is denoted the age of a patch τ. The density of occupied patches of type y and age τ at time t is $q(t, \tau, y)$. It is normalised such that

$$\int_Y \int_0^\infty q(t, \tau, y)\, d\tau dy = 1$$

holds. The patch type distribution is normalised to 1 such that $\int_Y n(y)\,dy = 1$. Note that the integral of q over all patch ages yields:

$$\int_0^\infty q(t,\tau,y)\,d\tau = n(y).$$

In such metapopulation models, the change of the density of occupied patches can be written as a patch-balance equation of McKendrick type:

$$\frac{\partial q(t,\tau,y)}{\partial t} + \frac{\partial q(t,\tau,y)}{\partial \tau} = -\mu q(t,\tau,y). \tag{2.9}$$

The boundary condition of the patch-balance equation is:

$$q(t,0,y) = \int_0^\infty \mu q(t,\tau,y)\,d\tau.$$

The dynamics of the local population density in a patch of type y since the last catastrophe can be written as:

$$\frac{dN(\tau,y)}{d\tau} = g(N(\tau,y),y,\theta)\,N(\tau,y) - \gamma\,N(\tau,y) + \alpha\psi(y)D(t)\ \text{with}\ N(0,y) = 0.$$

The rate g accounts for the per capita growth of individuals with local adaptation trait θ in a patch of type y with density $N(\tau,y)$, the rate γ is the rate of emigration from a patch, and $\alpha\psi(y)D(t)$ is the number of immigrants settling in a patch per unit of time, where α is the encounter rate, $\psi(y)$ is the settlement probability upon encounter in a patch of type y and $D(t)$ is the density of dispersers at time t. In Article *VI*, the growth function was of the form:

$$g(N,y,\theta) = r\left(1 - \frac{N}{k}\right) - c(\theta - y)^2.$$

It gives the difference between the logistic function with per capita birth rate r and carrying capacity k, and a per capita maladaptation death rate in the patch of type y (see also Hanski and Mononen, 2011; Hanski et al., 2011; Lande and Shannon, 1996). The death rate depends on the local adaptation trait θ of an individual and is small when θ is close to the patch type y. The scalar c scales the strength of maladaptation and the local optimum in a patch is described by the patch type y.

The density of dispersers $D(t)$ at time t changes accordingly to the equation:

$$\frac{dD(t)}{dt} = -\big(\alpha \int_Y \psi(y)n(y)\,dy + \nu\big)D(t) + \int_Y \int_0^\infty \gamma N(\tau, y)q(t, \tau, y)\,d\tau\,dy. \tag{2.10}$$

The first term on the right hand side of Eq. (2.10) is the density of dispersers that leave the dispersal pool, by settling or dying (at a rate ν) and the influx of dispersers comes from the patches individuals emigrate from. Note that individuals are not able to reproduce during dispersal.

As the evolutionary dynamics is investigated later, one assumes that the metapopulation dynamics is at steady state. At steady state the density of occupied patches of certain age does not change in time. However, local catastrophes still occur, that kill all individuals in a single patch and the patches get recolonised by dispersers. The density of occupied patches $q(t, \tau, y)$ at steady-state is $\hat{q}(\tau, y)$. At steady-state Eq. (2.9) simplifies to

$$\frac{\partial \hat{q}(\tau, y)}{\partial \tau} = -\mu \hat{q}(\tau, y) \quad \text{with} \quad \hat{q}(0, y) = \int_0^\infty \mu \hat{q}(\tau, y)\,d\tau \tag{2.11}$$

for all y. Solve Eq. (2.11) and obtain:

$$\hat{q}(\tau, y) = \hat{q}(0, y)e^{-\tau\mu}.$$

Define $l(\tau) = e^{-\tau\mu}$ as the probability that no catastrophe occurred in a patch until τ. The expected lifetime of the patch of type y is then $\int_0^\infty l(\tau)d\tau = 1/\mu$. At metapopulation steady-state also the disperser density is at equilibrium, denoted by $\hat{D}$. It is

$$\hat{D} = \frac{\int_Y \int_0^\infty \gamma N(\tau, y)\hat{q}(\tau, y)\,d\tau\,dy}{\alpha\bar{\psi} + \nu}, \tag{2.12}$$

where the average settlement probability of the population with settlement strategy ψ is $\bar{\psi} = \int_Y \psi(y)n(y)\,dy$ and the probability to survive dispersal is $\frac{\alpha\bar{\psi}}{\alpha\bar{\psi}+\nu}$. Note that $N(\tau, y)$ contains $\hat{D}$ as well, so (2.12) is actually an equation from which $\hat{D}$ can be solved.

2.6 Fitness in structured environments

When the environment is unstructured, fitness can be described as the per-capita long-term exponential growth rate of a rare mutant population invading a resident population, given that the resident is at equilibrium (e.g. Eq. (2.3); see Section 2.2).

In structured environments it may be difficult to calculate invasion fitness, since mutants experience variable environmental conditions in different patches and the local differences in resident abundance may cause additional variabilities in how the environment is perceived. To avoid this problem a fitness proxy was developed for structured metapopulation models (Diekmann et al., 1998, 1990; Gyllenberg and Metz, 2001; Metz and Gyllenberg, 2001). It does not follow the births, i.e., growth rate, of individuals from year to year, but works on the basis of disperser generations. The operator that maps the number of dispersers from one generation to the next, during the lifetime of the disperser's relatives in the natal patch, is called next-generation operator (Diekmann et al., 1998, 1990). Its spectral radius R_m is defined as the basic reproduction ratio, or basic reproductive number and measures fitness on a generation basis (Gyllenberg and Metz, 2001; Metz and Gyllenberg, 2001). In the following sections I derive the invasion fitness proxies for the discrete-time models as in Articles *II* and *III* and for continuous-time models as in Article *IV*. Note, that it would be possible to derive a different fitness proxy directly from the dynamics given in (2.7) for the models of Articles *II* & *III* (see Metz and Leimar, 2011). For simplicity I chose to study the evolutionary dynamics in structured environments via the basic reproduction number of dispersers.

2.6.1 Fitness in structured Hamilton-May models

The discrete-time model of Article *II* investigated the evolution of patch-type dependent immigration and Article *III* extended the latter model to the coevolution of patch-type dependent immigration and emigration. Hence, I will derive the invasion fitness proxy for the evolutionary scenario with mutating emigration and immigration strategies. By setting the emigration probabilities constant, one obtains the fitness proxy of Article *II*.

The next-generation operator $\mathcal{G}$ of the discrete-time Hamilton-May model with structured environment and deaths before reproduction that maps the number of dispersers N with strategy $d = (p_1, p_2, f_1, f_2)$ of one generation to its next during the lifetime of the disperser's family is

$$\mathcal{G}(N) = Q^\top(d^1, \ldots, d^l, d)\mathbf{V}(d^1, \ldots, d^l)\Pi(f)N. \tag{2.13}$$

Note that $\Phi(t) = \Phi$ in $\mathbf{V}$ is suppressed here, since the ϕ_i^js are constant in a given resident environment. The operator counts the number of dispersers that survive dispersal, settle in the patches and produce new dispersers during all the years the natal patch of the focal dispersers is defended. The matrix $\mathbf{V}(d^1, \ldots, d^l)$ is a diagonal matrix with elements V_i and $\Pi_i(f)$ are the elements of the vector $\Pi(f)$. The detailed derivation of V_i and Π_i can be found in Section 2.4 and V_i and Π_i are given in Eqs (2.6) and (2.8), respectively. The elements $Q_i(d^1, \ldots, d^l, d)$ of $Q(d^1, \ldots, d^l, d)$ give the expected number of offspring dispersing from a patch of type i in a generation. The Q_is depend on the l strategies present in the landscape and on the focal strategy. It is the product of the expected number of years the natal patch is defended, $E_i(d^1, \ldots, d^l, d)$, times the number of individuals that are sent away every year from the conquered patches, Bk_i, where $k_i = \beta_i s_i p_i$, the expected reproductive output. The number of years the natal patch can be defended is derived as follows. The probability of non-dispersing individuals defending their natal patch of type i is

$$\frac{s_i B\beta_i(1-p_i)\mathrm{e}^{-\mu_i T}}{(1-p_i)B\beta_i\mathrm{e}^{-\mu_i T} + \sum\limits_{j=1}^{l} \frac{\Pi_i(f^j)}{\phi_i} B u_j}$$

(see first term of l_{ii}^{J}). Then, the expected number of years a family keeps its natal patch of type i occupied follows a geometric distribution with expectation

$$\begin{aligned}E_i(d^1,\dots,d^l,d) =& \frac{1}{1-\frac{s_iB\beta_i(1-p_i)\mathrm{e}^{-\mu_iT}}{(1-p_i)B\beta_i\mathrm{e}^{-\mu_iT}+\sum\limits_{j=1}^{l}\frac{\Pi_i(f^j)}{\phi_i}Bu_j}}\\ =& \frac{B\beta_i(1-p_i)\mathrm{e}^{-\mu_iT}+\sum\limits_{j=1}^{l}\frac{\Pi_i(f^j)}{\phi_i}Bu_j}{(1-s_i)(1-p_i)B\beta_i\mathrm{e}^{-\mu_iT}+\sum\limits_{j=1}^{l}\frac{\Pi_i(f^j)}{\phi_i}Bu_j}.\end{aligned}$$

Subsequently, I shorten the notation and write $E_i(p_i)$ instead of $E_i(d^1,\dots,d^l,d)$.

The next-generation operator from Eq. (2.13) is then:

$$\mathcal{G}(N)=\sum_{i=1}^{2}s_i\beta_ip_iE_i(p_i)\Pi_i(f)V_i^+(\Phi,d^1,\dots,d^l)N \tag{2.14}$$

(see Eq.(1) of Article *III*). With fixed emigration probabilities (see Article *II*) the next-generation operator simplifies to:

$$\mathcal{G}(N)=\left(\frac{\phi_1k_1\Pi_1(f)}{\sum\limits_{j=1}^{l}n_j\Pi_1(f^j)u}+\frac{\phi_2k_2\Pi_2(f)}{\sum\limits_{j=1}^{l}n_j\Pi_2(f^j)u}\right)N,$$

where the n_js are the frequencies of strategies $j=1,\dots,l$ in the dispersal pool and are assumed to be at equilibrium. Since the dispersal pool is unstructured the basic reproduction number is simply derived from Eq. (2.14). For a small mutant population with strategy d^m invading a resident population with frequency $\phi_i^r\approx\phi_i$ and strategy d, the basic reproduction number can be derived by dividing both sides of Eq. (2.14) with N. The number of resident strategies present in the metapopulation is 1. In the case where emigration and immigration are coevolving the basic reproduction number of a mutant population is

$$R_m(d^m, d) = \frac{\phi_1 s_1 \beta_1 p_1^m}{u_r} \frac{E_1(p_1^m)\Pi_1(f^m)}{E_1(p_1)\Pi_1(f)} + \frac{\phi_2 s_2 \beta_2 p_2^m}{u_r} \frac{E_2(p_2^m)\Pi_2(f^m)}{E_2(p_2)\Pi_2(f)}.$$

If the emigration probabilities are not mutating then the factors $E_i(p_i^j)$ cancel (see Article *II*). The fitness proxy R_m allows to investigate the joint evolutionary outcome of emigration strategies p_is and immigration strategies f_is (see Article *III*).

2.6.2 Fitness in structured metapopulation models

Here, I explain how the fitness proxy for continuous-time metapopulation models is derived (Gyllenberg and Metz, 2001; Gyllenberg et al., 2002; Metz and Gyllenberg, 2001; Parvinen, 2002, see also Article *IV*). When the settlement strategy ψ and the scalar local adaptation trait $\theta \in Y$ are assumed under natural selection, the invasion fitness of a mutant in continuous time is derived as follows: Assume that a mutant population was established in a patch of type y at patch age T. The mutant population $M(\tau, y)$ with trait (ψ^m, θ^m) increases if its per-capita growth rate $g(N(\tau, y), y, \theta^m)$ in a patch of type y with resident population density $N(\tau, y)$ is positive. Mutant individuals emigrate from the patch at a rate γ. The local dynamics of the mutant population in the patch of type y is

$$\frac{dM(\tau, y)}{d\tau} = \big(g(N(\tau, y), y, \theta^m) - \gamma\big)M(\tau, y). \tag{2.15}$$

In the initial phase of invasion, the number of mutant immigrants is negligible and mutants only interact with resident individuals. The number of mutants after growing for $\tau - T$ time, given that there is no catastrophe between T and τ, is obtained by solving Eq. (2.15):

$$M(\tau, y) = M(T, y)\mathrm{e}^{\int_T^\tau g(N(\zeta, y), y, \theta^m) - \gamma \, d\zeta}$$

(see Eq. (6) of Article *IV*). The probability that the local population is still alive at age τ given that it survived to age T is:

$$\frac{l(\tau)}{l(T)} = \mathrm{e}^{-\mu(\tau-T)}.$$

The expected number of mutant dispersers that emigrate from a patch of type y per one mutant that arrived at patch age T in a resident environment is

$$F(T, y, \theta^m, \psi(y)\hat{D}) = \int_T^\infty \mathrm{e}^{\int_T^\tau g(N(\zeta,y),y,\theta^m)-\gamma\, d\zeta} \mathrm{e}^{-\mu(\tau-T)} \gamma \, d\tau$$

(see Eq. (7) of Article *IV*). Note that F depends on $\psi(y)\hat{D}$ and θ via $N(\cdot, y)$. It is the product of the number of mutant individuals $M(\tau, y)$ that emigrate with a rate γ, where the patch is still alive with probability $\frac{l(\tau)}{l(T)}$, integrated over τ. Integrated over all times T the expected number of mutant emigrants from a patch of type y in an environment set up by the resident with strategies ψ, θ and $\hat{D}$ is:

$$\rho(y, \theta^m, \psi(y)\hat{D}) = \int_0^\infty \frac{q(T, y)}{n(y)} F(T, y, \theta^m, \psi(y)\hat{D}) \, dT$$

(see Eq. (8) of Article *IV*). The basic reproduction number counts mutant dispersers that survive dispersal, settle in patches of type $y \in Y$ where they establish local populations and produce new emigrants until the patch goes extinct, integrated over all patch types y. The fitness proxy in the continuous-time metapopulation model is

$$R_m(\psi^m, \theta^m, \psi, \theta) = \frac{\alpha \int_Y \psi^m(y) n(y) \rho(y, \theta^m, \psi(y)\hat{D}) \, dy}{\alpha \bar{\psi}_m + \nu}.$$

Note that for each resident the matching disperser number $\hat{D}$ needs to be derived by solving $R_m(\psi, \theta, \psi, \theta) = 1$, which necessarily holds when the resident equals the mutant. The joint adaptive dynamics of the function-valued trait ψ and scalar trait θ was analysed in Article *IV*.

2.7 Summary

Article I

Article *I* investigates dispersal evolution when it is under a commonly detected trade-off with fecundity. It extends the Hamilton-May model by including this trade-off and assumes that not all individuals survive until maturation. Instead of focusing on a single trade-off function, the adaptive dynamics is analysed using an unspecified trade-off function. That is, critical function analysis is employed, that classifies the evolutionary outcomes depending on the properties of the trade-off function. The model produces evolutionary branching, $CSSs$ and repellors, of which some singularities are not found in the classical Hamilton-May model. Furthermore, it finds that the opposing selection pressures of kin competition and natal patch defence on top of the trade-off can cause two alternative stable dispersal strategies to co-occur. In an example it observes a novel and counterintuitive pattern of dispersal evolution: The dispersal probability monotonically decreases with increased survival during dispersal. The increase of the probability to survive dispersal let more immigrants arrive at the natal patch. Hence in this example, competition is increased and individuals need to stay at home to defend the patch against the immigrants and the dispersal probability decreases.

Article II

In Article *II* the evolution of patch-type dependent immigration is investigated and modelled in a mechanistic way when all other life-history traits are depending on the patch type. Immigration is introduced as a settlement probability in a patch of certain type upon encounter. This article studies under which conditions individuals decide to settle in a new location. The population dynamics is kept track of via a next-generation operator that maps the number of dispersers of one generation to the next during the lifetime of the individual's family in the natal patch. From the next-generation operator the basic reproduction number is derived to study the adaptive dynamics of settlement strategies. The effects of the parameters are investigated by a bifurcation analysis. One interesting result obtained in this model is a decrease of the settlement probability into the patches of low reward (lower survival until reproduction, dispersal probability and relative fecundity) when patches of high reward become more unsafe during the dispersal season. Individuals reject patches of low reward to increase the chance to encounter a highly rewarding patch, since the high death rate in these patches kills competitors which increases the chances of establishment. The eco-evolutionary feedback incorporated in the model generates disruptive selection, such that evolutionary branching of the immigration strategy occurs in a wide parameter range. Evolutionary branching points are observed when the patches that guarantee a high reward are less safe during the dispersal season. After evolutionary branching the strategies of the coexisting populations are one that accepts every patch at first encounter, a generalist strategy, and one that only settles into the highly rewarding patches, a specialist.

Article III

Article *III* extends Article *II* by investigating the coevolution of patch-type dependent emigration and patch-type dependent immigration to understand under which conditions the individuals decide to move out of their natal patch and settle in a new location. The model is analogously set up as in Article *II*, and the basic reproduction number that measures fitness is derived. I present examples where patches with high local death rates during dispersal are always emigrated from in the beginning of the season, but during the dispersal season, individuals always immediately settle in them after encounter. When the patches with high survival until reproduction and high relative fecundity have a high local death rate during the dispersal season, the singularity is sometimes found at a saddle of the fitness landscape. These singular strategies are sustainable evolutionary branching points, i.e., the strategies are predicted to remain in the coexistence set as they diversify. In Article *II*, where only immigration evolves, evolutionary diversification is possible, but the condition is not restricted to singular emigration strategies. Hence, this study highlights that the coevolution of a higher dimensional trait still permits evolutionary diversification, but it occurs in restricted scenarios since the emigration probabilities need to be singular. To test the numerical predictions of evolutionary branching in higher dimensions and visualise the result, stochastic simulations are run. The presented simulations show that evolutionary branching is possible and the strategies remain coexisting after diversification.

Article IV

Since there exists increasingly more empirical evidence that individuals make dispersal decisions based on local patch types, which are distributed continuously, and the decisions to settle are influenced by the individuals' adaptations, Article *IV* investigates the coevolution of patch-type dependent immigration and local adaptation. A metapopulation model is constructed with explicit local population dynamics, when patch types are continuously distributed (similar to Gyllenberg and Hanski, 1992; Hanski and Gyllenberg, 1993). It models patch-type dependent immigration as a function-valued trait, that presents the settlement probability into a patch of a certain type upon encounter. Local adaptation is introduced as extra mortality rate due to maladaptation to a patch type. The coevolutionary outcome of patch-type dependent settlement and local adaptation is derived using the adaptive dynamics framework. The singular local adaptation trait matches the most frequent patch type and the settlement strategy has a hat-like shape. Individuals always settle in the patches they are highly adapted to. They settle into some patches with a intermediate probability, since the patches are crowded with more immigrants and rejects patches where maladaptation is high. When the patch type distribution is wide or bimodal, evolutionary branching of the local adaptation trait is shown. The evolutionary endpoints are presented in numerical examples, where the two strategies that are locally adapted to different patch types with a respective settlement strategy coexist.

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Article *I*

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Evolution of dispersal under a fecundity-dispersal trade-off

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HIGHLIGHTS

- We investigate dispersal evolution under a trade-off between dispersal and fecundity.
- The trade-off can generate branching if some individuals die before reproduction.
- Dispersal may monotonically decrease with increased survival during dispersal.
- Two stable strategies may exist and fold bifurcations lead to evolutionary catastrophes.

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ABSTRACT

Resources invested in dispersal structures as well as time and energy spent during transfer may often decrease fecundity. Here we analyse an extended version of the Hamilton–May model of dispersal evolution, where we include a fecundity-dispersal trade-off and also mortality between competition and reproduction. With adaptive dynamics and critical function analysis we investigate the evolution of dispersal strategies and ask whether adaptive diversification is possible. We exclude evolutionary branching for concave trade-offs and show that for convex trade-offs diversification is promoted in a narrow parameter range. We provide theoretical evidence that dispersal strategies can monotonically decrease with increasing survival during dispersal. Moreover, we illustrate the existence of two alternative attracting dispersal strategies. The model exhibits fold bifurcation points where slight changes in survival can lead to evolutionary catastrophes.

1. Introduction

Dispersal is an elementary driver of ecology and evolution, which fundamentally shapes the distribution, abundance and diversity of species, and plays a key role in their persistence in the face of habitat fragmentation, climate change, and other adverse environmental impacts. Dispersal helps to avoid crowding, kin competition and inbreeding, and to escape from natural enemies. However, dispersal has multifarious costs (reviewed by Bonte et al., 2012; Travis et al., 2012): investments into the ability to disperse (e.g., into flight muscles) imply energetic costs that are paid prior to dispersal and often concern all individuals, also those who eventually do not disperse. During transfer, there is typically a high risk of mortality and a risk of not arriving in any suitable habitat, which affects the individuals who do disperse. The transfer process itself has extra energetic costs, which may impinge on the condition of the individual, and it also needs time, whereby priority advantages may be lost. Upon settlement, immigrants may be affected by various costs related to loss of familiarity and social rank. Many of these costs depend also on the distance traversed during dispersal.

Despite the great variety and rich biological context of dispersal costs, most models consider only a fixed mortality cost (combining mortality during transfer and the risk of landing in an unsuitable habitat), a fixed cost for each dispersal distance (e.g., Rousset and Gandon, 2002), or a fixed mortality cost per movement step (e.g., Bonte et al., 2010; Poethke et al., 2011). Fixed mortality costs generate rigid trade-offs between the number of non-dispersed and successfully dispersed offspring. In reality, however, organisms have evolved many ways to alleviate mortality during dispersal; but this is unavoidably costly and induces trade-offs elsewhere. For example, investing resources into better sensory or flight capabilities reduces mortality during dispersal (Bonte et al., 2012; Travis et al., 2012), but the resources used to this end represent an energetic cost of dispersal.

More specifically, energetic costs of dispersal (e.g., investment into morphological structures such as flight muscles or energy spent during transfer) can easily enforce a trade-off with fecundity. Indeed, there is good empirical evidence for fecundity costs of dispersal ability in insects (Roff, 1977), especially in wing-dimorphic species (Wratten, 1977; Roff, 1984; Zera, 1984; Mole and Zera, 1993; Stirling et al., 2001;

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reviewed by Roff, 1986; Zera and Denno, 1997) and in *Lepidoptera* (Gu and Danthanarayana, 1992; Hughes et al., 2003; Gu et al., 2006; Karlsson and Johansson, 2008; but see Hanski et al., 2006). In plants, seed dispersal depends on plant height more than on seed size (Thomson et al., 2011), and investments into tall stems may cause a trade-off between dispersal ability and seed number when dispersal is facilitated by wind. Furthermore, dispersal may occur via the production of costly fruits, which also leads to a trade-off between dispersal and fecundity.

When fecundity is antagonistically interacting with dispersal, it is unclear what shape the trade-off function should be. Energy allocated to dispersal structures can be measured directly in terms of lost fecundity (e.g., the number of eggs energetically equivalent to the dispersal structure). The probability of dispersal is likely an increasing function of the energy allocated to dispersal structures (Roff and Fairbairn, 1991), but the exact shape of this function is unclear. Existing models assume some simple function without sufficient justification (e.g., Burton et al., 2010; King and Roff, 2010; but see Cohen and Motro, 1989). Other models assume that investment into dispersal-related traits reduces the mortality risk during transfer (Fronhofer et al., 2011; Travis et al., 2012). This improves the classic assumption of a fixed mortality cost, yet the function linking investment and risk is chosen only for its simplicity. Similar choices are made when seed dispersal is linked to seed size (Ezoe, 1998; Levin and Muller-Landau, 2000). These choices of functions amount to assuming *ad hoc* trade-offs between fecundity and (successful) dispersal. Importantly, seemingly minor details of the trade-off functions can change the qualitative predictions of a model (de Mazancourt and Dieckmann, 2004; Geritz et al., 2007). Hence assuming an arbitrary trade-off function, even if it is a biologically plausible function, can unjustifiably distort the results.

In this paper, we investigate the adaptive dynamics of dispersal (i.e., emigration) under a dispersal-fecundity trade-off. In Section 2, we include the trade-off in a generalised version of the model of Hamilton and May (1977) where some individuals may die before reproduction. In order to avoid *ad hoc* choices of trade-off functions, in Section 3 we analyse the model without committing to any particular trade-off shape.

In Section 3.1, we employ the technique of critical function analysis (de Mazancourt and Dieckmann, 2004; Kisdi, 2006, 2014). In critical function analysis, we identify the conditions under which various evolutionary outcomes are possible in terms of the local properties (such as the slope and the curvature) of the unspecified trade-off function. This technique differs from a traditional bifurcation analysis in treating the slope and the curvature of the trade-off function directly as bifurcation parameters, instead of first fixing a parameterised trade-off function and then analysing the model in terms of the parameters. In the present model, we show that all generic types of evolutionary singularities can occur, provided that there is some mortality between establishment and reproduction. In particular, dispersal may evolve to an evolutionarily stable level, may undergo evolutionary branching, or there may be a repelling singularity leading to multiple attractors of dispersal evolution. For comparison, we analyse the model also without the dispersal-fecundity trade-off (i.e., assuming constant fecundity; see Appendix A) and show that in this case, no evolutionary branching and no multiple attractors can occur.

In Section 3.2, we investigate how the evolutionary singularity changes with survival before reproduction and with survival during dispersal. For the latter, we find a novel pattern of dispersal evolution demonstrated in the example of Section 4: dispersal can monotonically decrease with increasing survival during dispersal over its entire range, or else (as found earlier, see Section 5) it may also increase or vary non-monotonically. In the example of Section 4, we also illustrate evolutionary branching, show an example for the co-evolution of divergent dispersal strategies after evolutionary branching, present examples for multiple attractors, and highlight the possibility of evolutionary catastrophes due to slight changes in survival probabilities at fold bifurcation points.

2. Model

Consider a semelparous population with non-overlapping generations that reproduces asexually and lives in a fragmented landscape. After competition between juveniles, each site is occupied by one individual that survives until reproduction with probability $s > 0$. We refer to s as adult survival (but note that this precedes the only time when the individual reproduces). At the time of reproduction a fraction $1-s$ of sites is empty. All individuals who survived to reproduction give birth to $B(x_i)$ offspring and die. The offspring disperse with probability x_i, join a global dispersal pool and survive dispersal with probability $p > 0$. The dispersers land on an empty site with probability $1-s$, or on an occupied site with probability s, where non-dispersed offspring are present (i.e. higher competition). After dispersal, one individual establishes at each site (fair competition) and survives until reproduction with probability s.

The production of offspring with dispersal morphologies is costly. Since resources are limited and energy finite, individuals who invest more into the dispersal apparatus of their offspring produce fewer offspring than individuals who invest little into dispersal structures. Hence, the number of offspring of the latter individuals is high compared to the former, but comes at a cost of reduced dispersal probability, which increases kin competition and decreases the chances of colonising new sites. We include such a fecundity-dispersal trade-off in the form $B(x_i) = \kappa b(x_i)$, where $b(x_i)$ describes the trade-off between the dispersal probability and fecundity. The function $b(x_i)$ is non-negative and decreasing for all $x_i \in [0, 1]$.

Let $n_i(t)$ be the fraction of M sites that adults with dispersal trait x_i occupy at time t. Assuming that both the number of individuals born in every patch and the number of patches is large ($M, \kappa \to \infty$), we can neglect stochastic effects. We then obtain $n_i(t+1)$ as the number of offspring produced ($n_i(t) s b(x_i)$) times the probability that the offspring wins a site. Offspring compete for sites in three ways: first, an offspring stays in the natal site and competes for the natal site; second, the offspring successfully disperses (i.e., emigrates and survives dispersal) and lands in a site where offspring have been born; and third, the offspring successfully disperses and lands in a site that was empty before immigration. In each case, the probability of winning the site is one over the number of competitors, but the number of competitors varies in different sites. This leads to the three terms of the discrete-time population model

$$n_i(t+1) = n_i(t) s b(x_i) \left(\frac{(1-x_i)}{spE_1 + (1-x_i) b(x_i)} + s x_i p E_2 + \frac{(1-s) x_i p}{spE_1} \right), \qquad (1)$$

where E_1 and E_2 are the environmental feedback variables given by $E_1 = \sum_{j=1}^{k} n_j(t) b(x_j) x_j$ and $E_2 = \sum_{l=1}^{k} (n_l(t)/((1-x_l) b(x_l) + spE_1))$ and k is the number of dispersal strategies. E_1 is the average number of individuals that disperse from a site, and E_2 gives the probability that a disperser establishes upon landing at an occupied site. Since feedback variables, of which we have two, set an upper limit to the number of coexisting strategies (Geritz et al., 1997) we conclude that at most two dispersal strategies coexist.

This model is an extension of the Hamilton–May model (Hamilton and May, 1977) with a trade-off between dispersal and fecundity (Cohen and Motro, 1989) and the possibility of death before reproduction.

3. Adaptive dynamics of dispersal

To determine the long-term evolution of dispersal we investigate a series of invasion-fixation events. We assume that (i) the ecological time-scale is faster than the evolutionary, (ii) mutations have small effects on the evolving dispersal trait, and (iii) the mutant population is initially small compared to the resident population. These assumptions allow us to use the adaptive dynamics toolbox (Geritz et al., 1998). The invasion fitness of a mutant population with trait y into an environment inhabited by a resident population with trait x is derived from Eq. (1) for $k=2$ and given by the following function:

$$w(x,y) = sb(y)\left(\frac{(1-y)}{b(x)xps + b(y)(1-y)} + \frac{yps}{b(x)xps + b(x)(1-x)} + \frac{yp(1-s)}{b(x)xps}\right). \tag{2}$$

Directional selection ceases at the singular strategy x^*, where $D(x^*) = \partial w/\partial y|_{y=x=x^*} = 0$. This is equivalent to

$$b'(x^*) = \frac{b(x^*)}{x^*}\left[\frac{ps^2x^*}{(1-s)(1-x^*)^2 + p^2s^2x^{*2} + 2ps(1-x^*)x^*} - 1\right]. \tag{3}$$

Note that when $s \to 0$ or $p \to 0$ (with $sM \to \infty$ and $sp\kappa \to \infty$), the singular dispersal strategy is the solution to

$$b'(x^*) = -\frac{b(x^*)}{x^*}.$$

In this limit, the number of immigrants arriving at the natal site becomes negligible and competition vanishes. In this case, any non-dispersed offspring can retain the natal site and the favoured strategy, i.e., the singular strategy, maximises the number of dispersers $xb(x)$.

A singular strategy is evolutionarily stable if

$$E = \left.\frac{\partial^2 w(x,y)}{\partial y^2}\right|_{x=y=x^*} < 0 \tag{4}$$

and attracting (convergence stable) if

$$E + M = \left.\frac{\partial^2 w(x,y)}{\partial y^2} + \frac{\partial^2 w(x,y)}{\partial x \partial y}\right|_{x=y=x^*} < 0 \tag{5}$$

(Eshel, 1983; Christiansen, 1991). In Appendix A we analyse the evolutionary dynamics without a trade-off (i.e., assuming that b is constant). In this case, the model always has a unique singular strategy that is both attracting and evolutionarily stable, i.e., a *CSS*.

3.1. Critical function analysis

Here we use critical function analysis (de Mazancourt and Dieckmann, 2004; Kisdi, 2006, 2014) to analyse evolutionary scenarios without pre-defining a specific trade-off shape. Let $b_{crit}(x)$ be a solution of the differential equation in (3) (note that there are infinitely many solutions with different initial values). The function $b_{crit}(x)$ is called the *critical function* and any point along the critical function can be made singular by choosing a trade-off tangential to the critical function at that point.

We obtain the critical function analytically with Mathematica (Wolfram Research, version 8.0.4.0)

$$b_{crit}(x) = \frac{b_0x_0}{x}\exp(f(x_0) - f(x))$$

for the initial condition $b(x_0) = b_0$, where

$$f(x) = \sqrt{s}\,\mathrm{ArcTanh}\left(\frac{x[(1-ps)^2 - s] - [(1-ps) - s]}{p\sqrt{s^3}}\right).$$

If the argument of the ArcTanh lies outside of $(-1,1)$, the function value is complex. For some parameter values of s and p the argument can be smaller than -1 for all x (see Appendix B.1). Then the imaginary part of $f(x)$ cancels with the imaginary part of $f(x_0)$ and the critical function remains real (see Appendix B.1). In Appendix B.2 we show that the critical function is convex. Singular strategies of trade-offs with local curvature smaller than $b''_{crit}(x)$ are attracting, and repelling if the opposite holds (de Mazancourt and Dieckmann, 2004).

Additionally, we determine the critical curvature for evolutionary stability. Since E (see inequality (4)) depends on the curvature of the trade-off function, we rewrite E as $b''(x^*) - e(x^*)$, where x^* is the point of tangent between the trade-off and a critical function. A singular strategy is an *ESS* if $E < 0$, i.e. the curvature of the trade-off function is smaller than the critical curvature of evolutionary stability $e(x^*)$. In Appendix B.3 we prove that $e(x^*)$ is positive.

The second term of inequality (5), M, is independent of the trade-off curvature but depends on the slope of the trade-off at x^*, which is determined by the slope of the critical function. If M is negative, evolutionary branching is possible by choosing the trade-off curvature such that E is positive but $E+M$ is negative, i.e., the singularity is an attractor (inequality (5) holds) but not evolutionary stable (the opposite of (4) holds; see details below). We find that M is negative if

$$\frac{p^2x^{*2}}{(1-x^*)^2} < \frac{1-s}{s^2} \tag{6}$$

and positive if the opposite holds. Note that for $s=1$, inequality (6) is never fulfilled and evolutionary branching is impossible (see Hamilton and May, 1977). Since M can be of both signs depending on the parameters s, p and on x^*, the point of tangent between the trade-off and a critical function (which can also be chosen freely by choosing an appropriate trade-off), it is possible to construct trade-offs that lead to any type of singularity. If x^* is chosen such that inequality (6) holds, then $e(x^*) < b''_{crit}(x^*)$, and hence trade-offs with an intermediate curvature, i.e., with $e(x^*) < b''(x^*) < b''_{crit}(x^*)$, lead to evolutionary branching, whereas trade-offs with $b''(x^*) < e(x^*)$ yield an attracting evolutionary stable strategy and trade-offs with $b''(x^*) > b''_{crit}(x^*)$ yield an evolutionary repellor. If x^* is chosen such that the opposite of inequality (6) holds, then $e(x^*) > b''_{crit}(x^*)$, and trade-offs with an intermediate curvature (i.e., with $b''_{crit}(x^*) < b''(x^*) < e(x^*)$) lead to so-called the Garden of Eden (*GoE*) points (Hofbauer and Sigmund, 1990; Geritz et al., 1998). A Garden of Eden point is an evolutionarily stable singularity, i.e., if the population is exactly at this point, then it stays there forever; but it is not attracting, i.e., starting with a dispersal strategy near but not exactly at the Garden of Eden point, the population evolves away from it.

The grey regions of Fig. 1 show where inequality (6) is fulfilled and the critical function is decreasing; i.e., where evolutionary branching is possible for realistic trade-offs. The different shades of grey indicate the normalised range of curvature $b''_{crit}(x^*)/\ b(x^*) - e(x^*)/b(x^*)$, where the trade-off yields evolutionary branching. For low adult survival s, this range is narrow (Fig. 1a). Increased adult survival only slightly increases the range in which the trade-off must lie for branching to occur (Fig. 1b). High adult survival and medium to high survival during dispersal increase the range further, but diversification of dispersal strategies remains unlikely (Fig. 1c). Further evolutionary branching can be excluded, since there exist only two environmental feedbacks (see Section 2).

Note that sufficiently convex trade-offs ($b''(x^*) > b''_{crit}(x^*)$) always yield evolutionary repellors. The boundary strategy $x=0$ is always repelling because of kin competition (see Appendix C). The strategy on the upper boundary $x=1$ is also always repelling (see Appendix C). At the upper boundary kin competition vanishes and all sites are equal (whether offspring have been born on the site or not), which means no selection is favouring dispersal. Dispersal is however selected against both because a dispersed offspring has a chance of dying and because of the loss of fecundity through the dispersal-fecundity trade-off, so that $x=1$ is repelling. Because the boundary strategies are repelling, a repellor in the interior implies that at least two attracting singularities exist in $(0,1)$, one on each side of the interior repellor. Convex trade-offs therefore readily lead to alternative stable dispersal

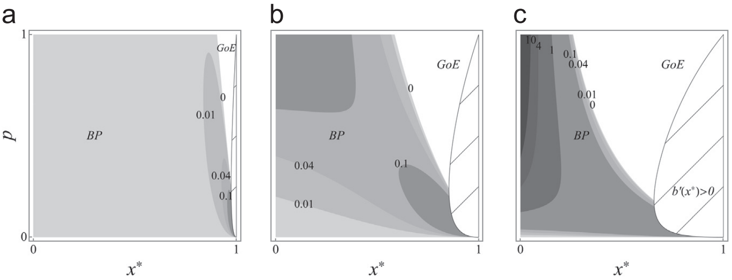

Fig. 1. The grey regions show where $M<0$, i.e., inequality (6) is satisfied and where the critical function is decreasing. The shades of grey indicate the width of the interval $(b''_{crit}(x^*)/b(x^*), e(x^*)/b(x^*))$, where evolutionary branching (*BP*) occurs. In white regions $b''_{crit}(x^*)/b(x^*)<e(x^*)/b(x^*)$ holds and trade-offs of intermediate curvature make singular strategies Garden of Eden points (*GoE*). In the dashed region, the critical function is increasing so that x^* could be singular only with an increasing trade-off function, which is not of biological interest. Parameters: (a) $s=0.1$, (b) $s=0.5$, (c) $s=0.9$.

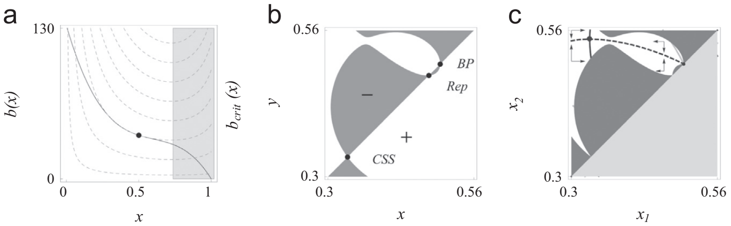

Fig. 2. (a) The trade-off function $b(x)=-369.3x^3+667.9x^2-430.915x+132.314$ (black) with a singular strategy at $x^*=0.5$ (dot). Dashed curves are critical functions for different initial values b_0. In the grey region, inequality (6) is violated so that evolutionary branching cannot occur with any trade-off (in this figure, the edge of the grey region seems to be at the minima of the critical functions, but this is a mere coincidence; see Fig. 1). Parameters: $s=0.8$, $p=0.2$. (b) The pairwise invasibility plot with parameters as given in (a). Abbreviations: *CSS*, attracting *ESS* (also known as continuously stable strategy); *Rep*, repellor; *BP*, branching point. Parameters as in (a). (c) The mutual invasibility plot with arrows indicating the direction of dimorphic coevolution. Without loss of generality, we assume $x_1<x_2$, hence the lower half of this figure is greyed out. The lines within the white area (the area of coexistence) are isoclines at which the selection gradient is zero in either the x_1-direction or x_2-direction (dashed); color indicates whether isoclines are evolutionarily stable (black) or not (grey). The intersection of lines correspond to the dimorphic evolutionary singularity. Parameters as in (a).

strategies. Concave trade-offs always lead to *CSS*s since $b''(x^*)$ is negative and smaller than $e(x^*)$ and $b''_{crit}(x^*)$, which are both positive.

3.2. Effect of adult survival and survival during dispersal on dispersal strategy

To study the effect of adult survival on the attracting singular strategy x^*, we implicitly differentiate the singularity condition $D(x^*)=\partial w/\partial y|_{y=x=x^*}=0$ with respect to s. Rearranging terms leads to

$$\frac{dx^*}{ds}=-\frac{\frac{\partial D}{\partial s}}{\frac{\partial D}{\partial x^*}}. \tag{7}$$

For attracting singular strategies the denominator on the right hand side is always negative. Therefore, the numerator determines whether the singular strategy is increasing or decreasing with changing adult survival. In Appendix D.1 we show that $\partial D/\partial s<0$ and therefore the attracting dispersal strategy always decreases with adult survival (note that this holds also for the special case where we assume that $b(x)=b$ is constant, i.e., for the model without a trade-off). When more adults survive until reproduction, more patches are occupied, which selects for a decrease in dispersal, since it is harder to conquer new patches. Furthermore, more competitors arrive at a natal patch which increases competition locally with strangers and selects for less dispersal to increase the chance of retaining the natal patch (Gandon and Michalakis, 1999). In other words, kin competition becomes weaker when more immigrants dilute the non-dispersed siblings, and therefore dispersal decreases. Next, we study the effect of survival during dispersal p on the attracting singular strategy x^*. Analogously to Eq. (7), x^* decreases with increasing p if $\partial D/\partial p<0$. In Appendix D.2 we show that the attracting strategy decreases with p if $p^2x^{*2}/(1-x^*)^2<(1-s)/s^2$. This condition is the same as inequality (6). When the probability of survival during dispersal increases, the dispersal strategy can decrease, increase or vary non-monotonically. As p increases, individuals' prospects to survive dispersal ameliorates, which selects for x^* to increase with p; but more competitors arrive at the natal site, selecting for x^* to decrease with p. Depending on the relative weight of these effects, one is dominating the other which makes all three scenarios possible (see the next section for examples). Without the trade-off (i.e., if b is constant), the attracting dispersal strategy is always a non-monotone function of p for $s<1$ (see Appendix D.2), whereas for $s=1$, we recover the result $x^*=1/(2-p)$ of Hamilton and May (1977), which is an increasing function of p.

4. Example

In this section we illustrate our general results with a numerical example. We choose the trade-off function $b(x)=\alpha x^3+\beta x^2+\gamma x+\delta$ with parameters such that the trade-off function is (i) decreasing, (ii) non-negative and with $s=0.8$ and $p=0.2$ it is (iii) tangential to a critical function at $x^*=0.5$ with (iv) intermediate convexity such that $e(x^*)<b''(x^*)<b''_{crit}(x^*)$ (Fig. 2a). Hence, x^* is an evolutionary branching point. Note that for the chosen values of s and p, branching is impossible in the grey region of Fig. 2a, because inequality (6) is violated.

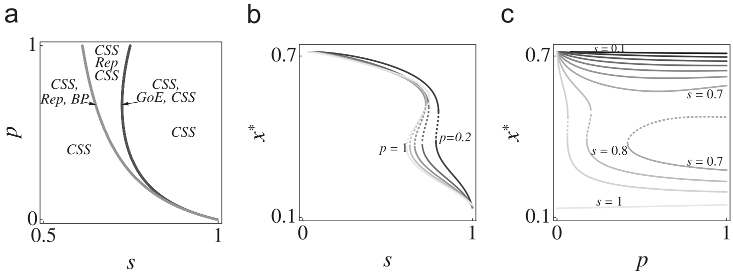

Fig. 3. (a) The two parameter bifurcation diagram of evolutionary singularities assuming the trade-off function as given in Fig. 2a. Abbreviation: *GoE*, Garden of Eden (convergence unstable *ESS*). Note that the areas "*CSS*, *Rep*, *BP*" and "*CSS*, *GoE*, *CSS*" are exceedingly narrow. (b) and (c) The bifurcation diagrams for s and p, respectively. Dotted lines indicate repellors. At the upper bifurcation points *GoE*s exist and at the lower *BP*s; the attractors are *CSS*s elsewhere. The lighter the lines, the higher the p and s value, respectively (p varies between 0.2 and 1 with steps of 0.2; s varies between 0.1 and 1 with steps of 0.1).

Fig. 2b shows the pairwise invasibility plot for the above example, obtained as a sign plot of the logarithm of the invasion fitness in Eq. (2). There are three evolutionary singularities: an attracting and evolutionarily stable strategy (*CSS*), an evolutionary repellor (*Rep*), and the branching point x^* (*BP*). The first two singularities correspond to points where the trade-off function is tangent to other critical functions not shown in Fig. 2a.

The adaptive dynamics after evolutionary branching is shown in Fig. 2c. Within the area of coexistence, the two resident dispersal strategies x_1 and x_2 evolve in the direction of their respective selection gradients (arrows). Evolution stops at the dimorphic singularity, the intersection of the isoclines of the selection gradients. The isoclines indicate the lines where the local fitness gradients vanish with respect to the x_1- or x_2-direction. We obtained the evolutionary isoclines by deriving the dimorphic invasion fitness $w(x_1, x_2, y)$ (Geritz et al., 1998). The dimorphic singularity is locally attracting (Leimar, 2009) and also evolutionarily stable. Since this model has two environmental feedback variables, branching into more than two strategies is impossible. Notice, however, that in the example of Fig. 2c, the evolutionary trajectory may easily leave the area of coexistence if x_1 (the strategy with lower dispersal) evolves faster than x_2. In this case, the strategy with higher dispersal goes extinct, and the remaining monomorphic population evolves to the *CSS*. Although the example in Fig. 2a–c demonstrates evolutionary branching, this appears to be an infrequent outcome. Fig. 3a shows the bifurcation diagram of evolutionary singularities under the trade-off in Fig. 2a, obtained by solving $D(x^*) = 0$ and evaluating the stability criteria in (4) and (5) numerically. For most values of s and p, the model exhibits a single convergence and evolutionarily stable dispersal strategy (*CSS*), but there is also a sizeable area of the parameter space with two *CSS*s separated by a repellor. In the latter area evolution leads to either of the two *CSS*s depending on the initial trait value. The light grey area of Fig. 3a is a very narrow region where one singularity is an evolutionary branching point. In a similarly narrow region (dark grey in Fig. 3a), the repellor between the two *CSS*s is a Garden of Eden strategy, i.e., a repellor that is evolutionarily stable. Fig. 3b shows that the attracting singularity always decreases with increasing adult survival, s (as proven in the previous section). In accordance with Fig. 3a, there may be alternative attractors of dispersal evolution when adult survival is relatively high. Fig. 3c demonstrates that the attracting dispersal strategy may increase or decrease with the probability of survival during dispersal (p), and in this example dispersal is monotonically decreasing over the entire range $0 < p < 1$ when adult survival is either low or high but still sufficiently smaller than 1. In Fig. 3b and c the dotted lines indicate repellors. Where a repellor collides with an evolutionary attractor, i.e., at fold bifurcation points, slight changes in the survival probabilities lead to an evolutionary catastrophe, whereby the former attractor disappears and the population evolves to another attractor at a very different dispersal probability.

5. Discussion

We have investigated the evolution of dispersal in an extended version of the Hamilton–May model (Hamilton and May, 1977), with a fecundity-dispersal trade-off and with mortality between competition and reproduction (i.e., a factor of adult survival in the semelparous life cycle). Here dispersal helps offspring to avoid kin competition and potentially escape to a site with fewer competitors (i.e., where there was no surviving parent and thus only immigrants compete), whereas the costs are reduced fecundity and a chance of mortality during dispersal. We have found that in this extended model, all generic types of evolutionary singularities can occur, including evolutionary branching and evolutionary repellors; the latter leads to multiple attractors of dispersal evolution. In contrast, when there is no trade-off (i.e., fecundity is constant), there is always a single attractor which is evolutionarily stable (Appendix A).

Evolutionary branching requires multiple dispersal strategies to coexist near an evolutionary singularity. Such coexistence is impossible in the Hamilton–May model, but becomes possible with adult mortality (see inequality (6)). Many metapopulation models of dispersal evolution assume that catastrophes may extinguish local populations (e.g., Comins et al., 1980; Olivieri et al., 1995; Gandon and Michalakis, 1999; Ronce et al., 2000a, 2000b; Parvinen et al., 2003). Adult survival in our model is analogous to surviving such a catastrophe, where the local "population" that survives the catastrophe is a single individual. Olivieri et al. (1995) showed that two dispersal strategies can coexist in a metapopulation model with catastrophes, although in their model the singular dispersal strategies are always *ESS*s.

When coexistence near an evolutionary singularity is possible, then the shape of the trade-off function determines whether evolutionary branching occurs. The importance of the trade-off shape was highlighted by Ronce and Olivieri (1997), who found an evolutionarily stable dimorphism in fecundity when it stands in a trade-off with parental survival according to a convex–concave trade-off function (similar to our example in Fig. 2) in a population with overlapping generations. Dispersal was linked to reproduction and branching in fecundity amounted to branching in dispersal, resulting in a strategy with a high fecundity, high dispersal and low parental survival and a strategy characterised by low fecundity, low dispersal and high parental survival. Many other models, however, assume only a fixed mortality cost of dispersal, which amounts to a linear trade-off between the number of dispersed and non-dispersed offspring; this rigid trade-off explains, for example, why evolutionary branching does not occur in the model of Olivieri et al. (1995). When the trade-off is flexible, as in case of a fecundity-dispersal trade-off, then given coexistence, one can always find trade-off functions that yield evolutionary branching (Kisdi, 2006, 2014). Whether these trade-offs are biologically realistic can be evaluated by empirical studies. In Fig. 3a, we show that any evolutionary outcome is possible in the present model with a decreasing trade-off function, which is a minimal requirement for biological realism when the trade-off derives from resource allocation between dispersal-related investments and fecundity.

Two previous models have been used to study the evolution of dispersal with arbitrary shapes of trade-offs. Cohen and Motro (1989) assumed a trade-off between dispersal and fecundity as in our model, but assumed 100% adult survival, such that coexistence was impossible in their model. They found that there is always at least one attracting singularity, and since dispersal implies a cost in fecundity, all singular dispersal strategies must be lower than the Hamilton–May solution. Note that this does not hold when there is adult mortality, since the empty sites generate an extra selective force promoting dispersal. Levin and Muller-Landau (2000) investigated the evolution of seed size, assuming that small seeds are more likely to disperse but are competitively inferior to large seeds. Varying seed size thus generates a trade-off between dispersal and potency, a combined measure of the number of seeds and their competitive weight. Four types of evolutionary singularities without coexistence can occur in this model (including the Garden of Eden scenario), but since 100% adult survival is assumed, coexistence and evolutionary branching is impossible. Asymmetric competition is known to facilitate evolutionary branching of seed size when some sites are empty before dispersal (Geritz et al., 1999).

Evolutionary branching of dispersal has been found in a number of models, but has not been linked to the shapes of trade-offs involved. Most of these models assume no trade-off (Doebeli and Ruxton, 1997; Mathias et al., 2001) or only the linear trade-off implied by a fixed mortality cost of dispersal (Parvinen, 1999, 2002; Parvinen and Metz, 2008; Massol et al., 2011). The simulation study of Fronhofer et al. (2011) found evolutionary branching in sexually reproducing populations under a fixed trade-off between fecundity and survival during dispersal in a model where temporal variability selects for dispersal. With the exceptions of Parvinen and Metz (2008) and Massol et al. (2011), models with evolutionary branching of dispersal also assumed large local populations where kin competition does not play a role.

The multiple attractors of dispersal evolution predicted by our model are intimately linked to the shape of the underlying trade-offs. One numerical example for multiple attractors was found by Levin and Muller-Landau (2000), when they assumed an *ad hoc* non-monotone relationship between dispersal and potency (the total competitive weight represented by the offspring). In our model, potency is given by $b(x)[1-(1-p)x]$, which is a monotone decreasing function of x whenever $b(x)$ is non-increasing (note, however, Levin and Muller-Landau, 2000 assumed that small seeds disperse better; in their model $b(x)$ is an increasing function of x). Our model demonstrates that the existence of an evolutionary repellor, and hence of multiple attractors, depends not on the monotonicity but on the curvature of the trade-off: when the trade-off is more convex than the critical function at the point of tangent, the singularity is a repellor (Fig. 2a; de Mazancourt and Dieckmann, 2004).

A fundamentally different mechanism leads to multiple attractors in the model of Billiard and Lenormand (2005). They assume genetic polymorphism in a locus involved in local adaptation to contrasting habitats in a heterogeneous landscape. When dispersal is low, the locally favoured allele is frequent in each local population, which selects against immigrants carrying the “wrong” allele and thereby stabilises low dispersal. In contrast, high dispersal homogenises the allele frequencies and thus reduces the disadvantage of dispersal, so that kin competition can maintain high dispersal. Also the joint adaptive dynamics of dispersal and a local adaptation trait readily leads to multiple attractors, but here selective forces on the trait under local adaptation play a major role (Kisdi, 2002; Nurmi and Parvinen, 2011).

Multiple attractors can also arise such that one attractor is an evolutionarily stable dispersal strategy and another is an evolutionarily stable dispersal dimorphism. The simultaneous existence of a monomorphic *ESS* and a dimorphic *ESS* is a generic feature of adaptive dynamics (Geritz et al., 1999). In our example, the region where a dimorphic *ESS* exists is small (see Fig. E5 in Appendix E), yet somewhat larger than the region where evolutionary branching occurs (Fig. 3a). In the part where a dimorphic *ESS* exists but branching does not occur, a population can evolve to the dimorphic *ESS* only if it starts dimorphic (e.g., by immigration).

In our model, the attracting dispersal strategy always decreases with adult survival. This is different from how dispersal changes with the catastrophe rate in structured metapopulations (Ronce et al., 200a,b; Parvinen et al., 2003), but agrees with metapopulation models that assume saturated local populations (Comins et al., 1980; Olivieri et al., 1995). Our model is analogous to the latter case since a site is saturated with one individual.

Contrastingly, the attracting dispersal strategy of our model may either increase or decrease with increasing survival during dispersal. Higher survival selects for dispersal as dispersal is then safer, but also selects against dispersal because more immigrants arrive at the natal site of the offspring and therefore more offspring need to stay in the natal patch in order to protect the site against competitors. These conflicting forces can lead to a non-monotonic relationship between dispersal and survival during dispersal (Comins et al., 1980; Gandon and Michalakis, 1999; Gandon, 1999; Heino and Hanski, 2001; Kisdi, 2004). Interestingly, in the example of Fig. 2, we also find a monotone decreasing relationship, i.e., here increasing the probability of survival during dispersal leads to even lower (and not higher) dispersal, which is a novel pattern in dispersal evolution.

Close to fold bifurcation points, i.e., at points where an attractor disappears via colliding with a repellor, slight changes in the probability of adult survival or in survival during dispersal may cause major shifts in the evolved dispersal strategies (see Fig. 2e and f). At such points, ‘evolutionary catastrophes’ occur and the population evolves rapidly to another attractor (Rand and Wilson, 1993).

The present results highlight the importance of the shape of trade-off in generating disruptive selection and hence polymorphisms or multiple attractors in dispersal evolution. However, we have made just one step in exploring the rich trade-off structure that determines the evolution of dispersal (Bonte et al., 2012; Travis et al., 2012). Most importantly, models should go beyond considering a single trade-off linking only two life-history parameters, and incorporate multiple trade-offs between interacting traits.

In the present model, we assumed that the probability of dispersal is a purely genetically determined trait. Even though dispersal is indeed a heritable trait (see Ronce, 2007; birds: Hansson et al., 2003; Doligez et al., 2009; plants: Clay, 1982; Venable and Burquez, 1989), in reality other factors such as the quality of the natal habitat, local population density, the strength of kin competition, and the competitive ability of the individual also influence dispersal (Benard and McCauley, 2008; Clobert et al., 2009). Function-valued dispersal strategies have been investigated in the context of density-dependent dispersal (e.g., Gyllenberg and Metz, 2001; Parvinen et al., 2012), kin competition (Ezoe and Iwasa, 1997; Ronce et al., 1998; Kisdi, 2004), and dispersal in relation to body condition (Gyllenberg et al., 2011a,b; Kisdi et al., 2012), but these models make only the simplest assumptions about the costs of dispersal. Integrating improved modelling of dispersal-related trade-offs with plastic dispersal strategies is an important step in exploring the role of plasticity and genetic diversification in the evolution of dispersal.

Acknowledgments

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Appendix A. Adaptive dynamics of dispersal without a trade-off

In this section we analyse the model assuming no trade-off, i.e., assuming constant fecundity ($b(x)=b$). The fitness function is then independent of fecundity and is given by

$$w(x,y)=s\left(\frac{(1-y)}{xps+(1-y)}+\frac{yps}{xps+(1-x)}+\frac{yp(1-s)}{xps}\right). \tag{A.1}$$

We derive the singular strategy by solving $D(x^*)=0$ and get

$$x^*=\frac{2-s\left(p(2-s)+2+\sqrt{p}\sqrt{4+s(ps-4)}\right)}{2-2s(p(2-ps)+1)}. \tag{A.2}$$

When $s=1$, the singular strategy simplifies to $1/(2-p)$, which has been obtained by Hamilton and May (1977). The singular strategy is evolutionarily stable if

$$\left.\frac{\partial^2 w(x,y)}{\partial y^2}\right|_{x=y=x^*}=-\frac{2ps^2x^*}{(1-x^*+psx^*)^3}<0,$$

which is always true. The singular strategy is convergence stable if

$$\left.\frac{\partial^2 w(x,y)}{\partial y^2}+\frac{\partial^2 w(x,y)}{\partial x\partial y}\right|_{x=y=x^*}$$
$$=-\frac{1-s}{x^{*2}}-\frac{ps^2(ps(1-x^*)+x^*(2(1-ps)+p^2s^2))}{(1-x^*+psx^*)^3}<0,$$

which is always true and therefore the singular strategy is a *CSS* when the trade-off function is constant.

Appendix B. Critical functions and curvatures

B.1. Imaginary part of ArcTanh

When the argument of ArcTanh lies outside of $(-1,\,1)$ the function value is complex. If $z\in\mathbb{R}$ with $z^2>1$, then we can write

$$\mathrm{ArcTanh}(z)=\alpha+i\beta,$$

where $\alpha=1/2\mathrm{Ln}[(z+1)/(z-1)]$ and $\beta=\pm\pi/2$. Note that the imaginary part of the ArcTanh is positive if $z<-1$ and negative if $z>1$. The argument of ArcTanh(z) is

$$z=\frac{x[(1-ps)^2-s]-[(1-ps)-s]}{p\sqrt{s^3}},$$

which is linear in x. Let us look at the values of z when $x=0$ and $x=1$. When x is at the lower boundary of trait space z simplifies to

$$z|_{x=0}=\frac{s(1+p)-1}{ps^{3/2}} \tag{B.1}$$

and when $x=1$, z is

$$z|_{x=1}=\frac{ps-1}{\sqrt{s}}. \tag{B.2}$$

The righthand sides of Eqs. (B.1) and (B.2) are always less than 1. If $p>1/s-\sqrt{1/s}$, then both (B.1) and (B.2) are greater than -1, so that the ArcTanh function evaluates to real numbers for all x. If the reverse inequality holds, then both (B.1) and (B.2) are less than -1, so that the ArcTanh function evaluates to a complex number with imaginary part $\beta=\pi/2$. Therefore when $f(x)$ is complex, then $f(x_0)$ is also complex and the imaginary parts cancel in $f(x_0)-f(x)$.

B.2. Curvature of the critical function

Here we investigate the curvature of the critical function $b_{crit}(x^*)$. We derive the second derivative and get

$$b''_{crit}(x)=\frac{b_{crit}(x)}{d(p,s,x)^2x^2}\Big[2(1-s)^2(1-x)^4+2ps(1-s)x(1-x)A$$
$$+p^2s^2x^2(4(1-x)^2(1-s)+B)\Big], \tag{B.3}$$

where

$$d(p,s,x)=p^2s^2x^2+(1-s)(1-x)^2+2spx(1-x), \tag{B.4}$$

which is positive. The term in square brackets on the right hand side of Eq. (B.3) has three terms, of which the first one is positive. The second term is positive whenever

$$A=(4(1-x)^2-s(1-2x))>0. \tag{B.5}$$

This always holds when $x>1/2$. If $x<1/2$, then A is decreasing in s. When taking the worst case $s=1$, inequality (B.5) simplifies to $4x^2-6x+3$, which is positive for all x. Hence, also the second term of Eq. (B.3) is positive. The last term of Eq. (B.3) is positive if B is positive, where

$$B=8-6s+s^2+C$$

and

$$C=2x(2-ps)((2-ps)x-4+2s). \tag{B.6}$$

Only C depends on x, in particular it is quadratic in x. The coefficient of the quadratic term of Eq. (B.6) is positive. The minimum value of C is reached when $x=(2-s)/(2-ps)$. Substituting the minimum into B gives $(2-s)s>0$, which is positive. Therefore Eq. (B.3) is positive and hence $b_{crit}(x)$ is convex.

B.3. Critical curvature for evolutionary stability

Here we show that $e(x^*)$, defined as the minimal value of $b''(x^*)$ that violates the evolutionary stability condition in Eq. (4) for the singularity x^*, is always positive. From its definition, we obtain

$$e(x^*)=\left(\frac{d(p,s,x^*)-ps^2x^*}{x^*d(p,s,x^*)}\right)^2$$
$$+\frac{ps^2[x^*-1+s(1-x^*(1+p))]^2(1-x^*+psx^*)}{x^*d(p,s,x^*)^3}, \tag{B.7}$$

where $d(p,s,x)$ is given by Eq. (B.4). Since the first term of Eq. (B.7) is strictly non-negative and the second term is positive, $e(x^*)$ is positive.

Appendix C. Stability on the boundary

The strategy located at the lower boundary of the trait space, $x=0$, is repelling if $D(0)>0$, which is equivalent to $1-s>0$. The strategy located at the upper boundary of the trait space, $x=1$, is repelling if

$$D(1)<0\quad\Leftrightarrow\quad 1-\frac{1}{p}+\frac{b'(1)}{b(1)}<0,$$

which is also true for decreasing trade-offs.

Appendix D. The effect of *s* and *p* on the attracting singular strategy

D.1. The effect of s on the attracting singular strategy

Here we investigate how the attracting singular strategy changes with increased adult survival. From Eq. (7) we have

$$\frac{\partial D}{\partial s}=-\frac{ps(1-x^*)[2psx^*+(1-x^*)(2-s)]}{d(p,s,x^*)(1-x^*+psx^*)^2}. \tag{D.1}$$

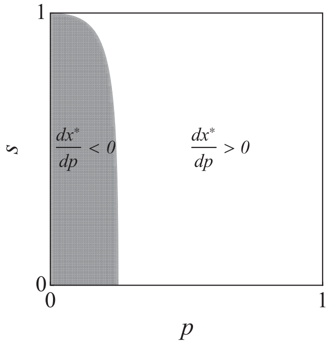

Fig. D4. A sign plot of dx^*/dp when the trade-off function is constant.

Since $d(p,s,x^*)$ as given in Eq. (B.4) is positive, the right-hand side of Eq. (D.1) is negative for attracting singular strategies. Hence Eq. (7) is negative and dispersal decreases with survival.

Next consider the case when the trade-off function is constant. In this case we can explicitly derive the singular strategy (see Eq. (A.2)). The singular strategy increases with adult survival if

$$\frac{\mathrm{dx}^*}{\mathrm{ds}} = \frac{\sqrt{p}(2(2-s)(s-1)+s^2p(4p+s-6))}{2\sqrt{4+s(\mathrm{ps}-4)}(1+s(p(\mathrm{ps}-2)-1))^2} + \frac{p((2-s)s+2(1-\mathrm{ps})^2)}{2(1+s(p(\mathrm{ps}-2)-1))^2} < 0. \tag{D.2}$$

With the command *Reduce* of Mathematica, we prove that inequality (D.2) is always fulfilled. Hence, the singular strategy decreases with increasing adult survival.

D.2. The effect of p on the attracting singular strategy

As shown in the main text, the sign of dx^*/dp coincides with the sign of

$$\frac{\partial D}{\partial p} = \frac{s^2(p^2s^2x^{*2}-(1-s)(1-x^*)^2)}{d(p,s,x^*)(1-x^*+psx^*)^2}. \tag{D.3}$$

We can see that the denominator is always positive. Therefore Eq. (D.3) is negative if $p^2s^2x^{*2}-(1-s)(1-x^*)^2 < 0$, which is equivalent to

$$\frac{p^2x^{*2}}{(1-x^*)^2} < \frac{1-s}{s^2}. \tag{D.4}$$

In particular, when $s=1$ then Eq. (D.4) simplifies to $p^2x^{*2} < 0$ which is never satisfied. Hence, the attracting singularity increases with p when all adults survive until reproduction. When inequality (D.4) is fulfilled dispersal decreases with increasing survival during dispersal.

Next, we analyse the change of the singular strategy as survival during dispersal increases in the case where the trade-off function is constant. The singular strategy as given in Eq. (A.2) decreases with increasing p if

$$\frac{\mathrm{dx}^*}{\mathrm{dp}} = \frac{s\left(s-2-\dfrac{\mathrm{ps}^2+4+s(\mathrm{ps}-4)}{2\sqrt{p}\sqrt{4+s(\mathrm{ps}-4)}}\right)}{2(1-s)+2\mathrm{ps}(\mathrm{ps}-2)} - \frac{s(\mathrm{ps}-1)(2-s(2-p(s-2)+\sqrt{p}\sqrt{4+s(\mathrm{ps}-4)}))}{(1+s(p(\mathrm{ps}-2)-1))^2} < 0. \tag{D.5}$$

Instead of analysing the sign change of Eq. (D.5), we show in Fig. D4 that the dx^*/dp changes sign for all $s<1$. Then, we can conclude that the singular strategy changes non-monotonically for all $s<1$.

Appendix E. Dimorphic ESS

See Fig. E5.

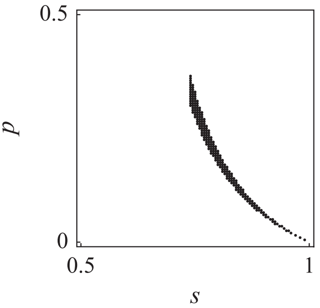

Fig. E5. The black region indicates the existence of a dimorphic *ESS* assuming the trade-off function as in Fig. 2. We numerically obtained the dimorphic *ESS* by setting the selection gradients $\partial w(x_1,x_2,y)/\partial y|_{y=x_1}$ and $\partial w(x_1,x_2,y)/\partial y|_{y=x_2}$ equal to zero. We then evaluated the stability criteria (analog to (4)) at the singular strategy numerically and checked if the equilibrium population densities were positive at that point.

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Article *II*

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On the evolution of patch-type dependent immigration.

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On the evolution of patch-type dependent immigration

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HIGHLIGHTS

- We analyse the evolution of immigration into two types of patches.
- Generalists settle in any patch, specialists settle only in good patches.
- A high death rate during the dispersal season in rewarding patches favours branching.
- Evolutionary branching may lead to a stable coexistence of a generalist & specialist.

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ABSTRACT

Empirical studies of dispersal indicate that decisions to immigrate are patch-type dependent; yet theoretical models usually ignore this fact. Here, we investigate the evolution of patch-type dependent immigration of a population inhabiting and dispersing in a heterogeneous landscape, which is structured by patches of low and high reward. We model the decision to immigrate in detail from a mechanistic underpinning. With the methods of adaptive dynamics, we derive both analytical and numerical results for the evolution of immigration when life-history traits are patch-type dependent. The model exhibits evolutionary branching in a wide parameter range and the subsequent coevolution can lead to a stable coexistence of a generalist, settling in patches of any type, and a specialist that only immigrates into patches of high reward. We find that individuals always settle in the patches of high reward, in which survival until maturation, relative fecundity and emigration probability are high. We investigate how the probability to immigrate into patches of low reward changes with model parameters. For example, we show that immigration into patches of low reward increases when the emigration probability in these patches increases. Further, immigration into patches of low reward decreases when the patches of high reward become less safe during the dispersal season.

1. Introduction

Dispersal is the key ecological process of individuals moving between and breeding in different habitats. Dispersal enables populations to thrive in a heterogeneous environment in which habitats differ in size, the geography and location in the landscape, quality, food availability, conspecific presence (Bowler and Benton, 2005; Travis et al., 2012) or the social environment (Cote and Clobert, 2007). Such environmental variations trigger dispersal decisions to be based on local circumstances and individuals come equipped with sophisticated receptors and cognitive or sensory abilities (Doyle, 1975; Ehlinger, 1990; Garant et al., 2005) to smell, detect or sample the environment (Zollner and Lima, 1999; Matter and Roland, 2002; Schooley and Wiens, 2003). Ultimately, individuals may base emigration and immigration decisions only on a specific cue inferred from the habitat type (Rees, 1969; Mitchell, 1977). Examples include scarce coppers which favour flower-rich patches (Schneider et al., 2003), or the butterfly species *Parnassius smintheus* which settles in habitats with high abundance of host plants and nectar flowers (Matter and Roland, 2002).

The number of theoretical studies on dispersal is staggering. Although the immigration decision is an important part of dispersal (Edelaar et al., 2008; Travis et al., 2012; Bonte et al., 2012), the greater body of literature focuses on emigration and avoids an explicit description of immigration. Most models assume that dispersers are evenly distributed over space (e.g. Hamilton and May, 1977) or travel to a certain distance (e.g. Rousset and Gandon, 2002). Models of habitat choice may treat the probability of entering a certain habitat directly as an evolving parameter, suppressing details of locating habitats during dispersal and making a decision on settlement (e.g. Ravigné et al., 2009). In models of

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structured populations, dispersers are often assumed to settle in the first patch they encounter (e.g. Parvinen, 2002). Some studies, however, have made immigration dependent on local population density (Saether et al., 1999; Metz and Gyllenberg, 2001; Poethke et al., 2011; Parvinen et al., 2012), also in combination with mate abundance (Shaw and Kokko, 2015), or preferred distance (Delgado et al., 2014), dependent on patch size (Hanski and Gyllenberg, 1993), or on expected fitness (Ruxton and Rohani, 1998). In this paper, we focus on immigration depending on the physical characteristics (but not on population density) of the target patch.

When dispersal is modelled, one has to consider the processes explicitly and model survival during the dispersal season, patch encounter and the decision on settlement in a mechanistic way, since it should be clear that it is the individual's behaviour that shapes the dynamics of the population as a whole. With a mechanistic underpinning of patch-type dependent immigration, it is possible to incorporate the individual's decision to settle more realistically. In this latter respect, our model is conceptually similar to the studies of Doyle (1975), Ward (1987), Baker and Rao (2004) and Stamps et al. (2005). These authors determined the optimal patch-dependent immigration behaviour when habitats differ in abundance and suitability, but (except for an attempt by Ward, 1987) neglected eco-evolutionary feedbacks from the immigration behaviour of individuals to the strength of competition experienced in different habitats.

Here, we derive a mechanistic underpinning for immigration of dispersing individuals, where we explicitly incorporate a continuous time dispersal season during which individuals randomly encounter patches. Upon encounter individuals settle in a patch with a patch-type dependent settlement probability (we follow the terminology of Clobert et al., 2009; Travis et al., 2012; Bonte et al., 2012). Habitat type affects survival during the dispersal season, survival from establishment to reproduction, fecundity and the probability of emigration of the offspring. We call individuals that settle in any patch generalists, whereas individuals that settle in patches of a specific type are called specialists. In this work, we study the eco-evolutionary dynamics of patch-type dependent immigration, i.e., the settlement strategy.

In Section 2 we derive the ecological model that incorporates the mechanistic derivation of the dispersal process of a population. In Section 3 we use the adaptive dynamics framework to study the long-term evolutionary behaviour of settlement strategies. In Section 3.1 we derive the monomorphic singularities and in Section 3.2 we investigate the stability conditions of the singular strategy. We give conditions when patch-type dependent settlement is prone to undergo evolutionary branching. We show an example where, after evolutionary branching, the coevolution of the two strategies leads to a stable coexistence of a specialist and a generalist strategy. In Section 3.3 we investigate the change (increase or decrease) of the settlement probability as we vary the model parameters. In Section 3.4 we focus on the effects of the parameters on the stability of evolutionary singularities of the different evolutionary outcomes. In Section 4 we discuss our results.

2. The model

We consider an asexual, annual, semelparous organism inhabiting a heterogeneous landscape of M patches of different types $i=1,2$ and frequencies ϕ_1 and $\phi_2 = 1-\phi_1$. Patches differ in death rates during the dispersal season once settled in the patch (patch safety or pre-competitive death), survival until reproduction (post-competitive survival), in relative fecundity, and the probability to emigrate (disperse). Individuals are characterised by their patch-type dependent settlement probability, the trait vector $f=(f_1,f_2)$, which is under natural selection. In the beginning of the year every patch is occupied by one individual. Each individual survives with a patch-type dependent survival probability s_i and gives birth to $B\beta_i$ offspring, where β_i is the relative fecundity in a patch of type i. We assume that the number of offspring B and the number of patches M are infinitely large, such that the model remains deterministic. Offspring disperse from a patch of type i with probability p_i and stay in the natal patch (of type i) with probability $1-p_i$. Every disperser joins the dispersal pool and may settle during a continuous-time dispersal season of length T. During the dispersal season dispersers encounter patches of type i at a rate $\phi_i\rho$ and settle in a patch of type i with probability f_i. Throughout the dispersal season every individual faces a risk of death (during dispersal and in the patches). We denote the death rate of individuals during transfer by ν and the death rate in a patch of type i by μ_i. We assume that the death rate in the dispersal pool is higher than the death rate in any of the patches during the dispersal season, i.e., $\nu > \mu_i$ for $i=1,2$. Dispersers who have not settled by the end of the dispersal season die. After the dispersal season the remaining individuals compete for one site per patch. All model parameters are summarised in Table 1.

To keep track of the dynamics of the model, we construct a disperser generation expansion (Diekmann et al., 1990, 1998). It follows the expected total offspring and their descendants of a single mother in the dispersal pool. The mother and her descendants are called a *family*. Let $\mathcal{G}$ be the next generation operator that maps the number of dispersers N of strategy f in one generation to the next during the lifetime of the disperser's family:

$$\mathcal{G}(N) = F(n,f^1,\ldots,f^l,f)N, \tag{1}$$

when the number of different settlement strategies present is l. The unit vector $n \in \mathbb{R}^l$, with entries n_j, describes the frequency of individuals characterised by the settlement trait vector f^j in the dispersal pool, where $f^j = (f^j_1, f^j_2)$ and $j=1,\ldots,l$. We assume that the population is either monomorphic, where all patches are occupied by individuals of a single settlement strategy ($n_1 = 1$), or in the polymorphic case it has reached its positive equilibrium. The function $F(n,f^1,\ldots,f^l,f)$ can be written as

$$F(n,f^1,\ldots,f^l,f) = Q^\top(n,f^1,\ldots,f^l)\mathbf{V}(n,f^1,\ldots,f^l)\Pi(f). \tag{2}$$

The entries $Q_i(n,f^1,\ldots,f^l)$ of the two-dimensional vector $Q(n,f^1,\ldots,f^l)$ describe the expected number of offspring that a family occupying a patch of type i contributes to the dispersal pool. The elements $V_i(n,f^1,\ldots,f^l)$ of the two-dimensional diagonal matrix $\mathbf{V}(n,f^1,\ldots,f^l)$ describe the probability of an individual winning a patch of type i. The two-dimensional vector $\Pi(f)$ has entries $\Pi_i(f)$ that describe the probability of a disperser settling in any of the patches of type i and surviving until the end of the dispersal season.

Table 1
Notation.

Variable	Definition
B	Number of offspring
β_i	Relative fecundity in patch of type i
$f=(f_1,f_2)$	Settlement trait vector
f_i	Settlement probability into patch of type i
$k_i = s_i\beta_i p_i$	Reward in patch of type i
M	Number of patches
μ_i	Death rate in patch of type i (patch safety)
ν	Death rate of dispersers
p_i	Emigration probability from patch of type i
ϕ_i	Frequency of patch of type i
ρ	Encounter rate
s_i	Survival until reproduction in patch of type i
T	Length of the dispersal season

We take a closer look at the factors in Eq. (2): to calculate the probability $\Pi_i(f)$, note that dispersers disappear from the dispersal pool exponentially as they encounter a patch where they settle at the rate $\sum_{j=1}^{2}\rho\phi_j f_j$ and they die in the dispersal pool at the rate ν. Hence the probability that a disperser is still in the dispersal pool at time $t \in [0,T]$ is $e^{-(\sum_{j=1}^{2}\rho\phi_j f_j+\nu)t}$. Given that the disperser is in the dispersal pool at time t, it encounters a patch of type i within the short time period $(t, t+dt)$ with probability $\phi_i\rho\,dt$, and settles in this patch with probability f_i. If this happens, the individual stays in patch i and survives until the end of the dispersal season with probability $e^{-\mu_i(T-t)}$. Integrating over t, we obtain the probability that a disperser settles in a patch of type i and survives there until the end of the dispersal season as

$$\Pi_i(f) = \phi_i\rho f_i \int_0^T \mathrm{e}^{-\left(\sum_{j=1}^{2}\rho\phi_j f_j+\nu\right)t-\mu_i(T-t)}\,dt$$
$$= \phi_i\rho f_i \frac{\mathrm{e}^{-\mu_i T}-\mathrm{e}^{-\left(\sum_{j=1}^{2}\rho\phi_j f_j+\nu\right)T}}{\sum_{j=1}^{2}\rho\phi_j f_j+\nu-\mu_i}. \tag{3}$$

To write $\Pi_i(f)$ neatly, let

$$\alpha = \sum_{j=1}^{2}\rho\phi_j f_j+\nu$$

denote the rate at which a disperser leaves the dispersal pool and define $\eta(x) = \frac{\mathrm{e}^x-1}{x}$ for $x>0$ and $\eta(0) = \lim_{x\to 0}\eta(x) = 1$. Then Eq. (3) is

$$\Pi_i(f) = \rho\phi_i T f_i \mathrm{e}^{-\alpha T}\eta((\alpha-\mu_i)T).$$

The average number of offspring emigrating from a patch is Bu with:

$$u = \sum_{j=1}^{2}\phi_j s_j\beta_j p_j. \tag{4}$$

For simplicity we define $k_j = s_j\beta_j p_j$. The expected number of dispersers settling during the dispersal season in a single patch of type i and surviving there is $MBu\sum_{j=1}^{l} n_j\frac{\Pi_i(f^j)}{\phi_i M}$. Note that $\Pi_i/(\phi_i M)$ is the probability of settling and surviving in a single patch of type i. The non-dispersed surviving fraction of offspring in a patch of type i is $\beta_i(1-p_i)\mathrm{e}^{-\mu_i T}$. At the beginning of the dispersal season, the fraction $1-s_i$ of the patches of type i is empty. Dispersers either arrive with probability $1-s_i$ at a site of type i in which the mother died before reproduction or, with probability s_i at a site where non-dispersing individuals are present. Hence, the probability of a single individual winning competition in a patch of type i is

$$V_i(n,f^1,\ldots,f^l) = \frac{s_i}{B\beta_i(1-p_i)\mathrm{e}^{-\mu_i T}+Bu\sum_{j=1}^{l} n_j\dfrac{\Pi_i(f^j)}{\phi_i}} + \frac{1-s_i}{Bu\sum_{j=1}^{l} n_j\dfrac{\Pi_i(f^j)}{\phi_i}}. \tag{5}$$

Next, we derive the expected number of years a family stays alive in its natal patch. The probability of non-dispersing individuals winning competition in a patch of type i is

$$\frac{s_i B\beta_i(1-p_i)\mathrm{e}^{-\mu_i T}}{B\beta_i(1-p_i)\mathrm{e}^{-\mu_i T}+Bu\sum_{j=1}^{l} n_j\dfrac{\Pi_i(f^j)}{\phi_i}}.$$

Hence, the expected number of years a family defends its natal patch is given by

$$E_i(n,f^1,\ldots,f^l) = \frac{1}{1-\dfrac{s_i B\beta_i(1-p_i)\mathrm{e}^{-\mu_i T}}{B\beta_i(1-p_i)\mathrm{e}^{-\mu_i T}+Bu\sum_{j=1}^{l} n_j\dfrac{\Pi_i(f^j)}{\phi_i}}}. \tag{6}$$

The vector entry $Q_i(n,f^1,\ldots,f^l)$ in Eq. (2) can be written as $Q_i(n,f^1,\ldots,f^l) = Bk_iE_i(n,f^1,\ldots,f^l)$. Using (5) and (6), the product $Q_i(n,f^1,\ldots,f^l)V_i(n,f^1,\ldots,f^l)$ simplifies to

$$Q_i(n,f^1,\ldots,f^l)V_i(n,f^1,\ldots,f^l) = Bk_iE_i(n,f^1,\ldots,f^l))V_i(n,f^1,\ldots,f^l)$$
$$= \frac{\phi_i k_i}{u\sum_{j=1}^{l} n_j\Pi_i(f^j)}.$$

We have derived all factors of the function $F(n,f^1,\ldots,f^l,f)$ in Eq. (2). Thus the next generation operator that maps the number of dispersing individuals N of one dispersal generation to the next is written as follows:

$$\mathcal{G}(N) = \left(\frac{\phi_1 k_1\Pi_1(f)}{u\sum_{j=1}^{l} n_j\Pi_1(f^j)} + \frac{\phi_2 k_2\Pi_2(f)}{u\sum_{j=1}^{l} n_j\Pi_2(f^j)}\right)N. \tag{7}$$

3. Evolutionary dynamics

Here, we analyse the long-term evolution of patch-type dependent settlement strategies. Assume that a *resident* population with settlement strategy $f=(f_1,f_2)$ is occupying almost all patches in the landscape, whereas an infinitesimal fraction of patches is occupied by *mutants*. The mutants characterised by a slightly different settlement strategy, the trait vector $f^m=(f_1^m,f_2^m)$, experience an environment that is set up by the resident. If the mutant's fitness is higher than the resident's, the mutant increases in numbers, outcompetes the resident and the ecological dynamics settles at a new population dynamical equilibrium. These assumptions permit the use of the adaptive dynamics framework (Geritz et al., 1998). We measure fitness as the basic reproduction number (Gyllenberg and Metz, 2001; Metz and Gyllenberg, 2001) and derive it from Eq. (7) for $l=2$. The fitness function is given by:

$$w(f^m,f) = \frac{\phi_1 k_1}{u}\frac{\Pi_1(f^m)}{\Pi_1(f)} + \frac{\phi_2 k_2}{u}\frac{\Pi_2(f^m)}{\Pi_2(f)}. \tag{8}$$

Eq. (8) has a Levene-type form (Levene, 1953; Kisdi, 2001).

3.1. Monomorphic singularities

Monomorphic evolution ceases at the singular strategy $f^*=(f_1^*, f_2^*)$ where:

$$\left.\frac{\partial w}{\partial f_i^m}\right|_{f^m=f=f^*} = \left.\frac{\phi_1 k_1}{u\Pi_1(f)}\frac{\partial\Pi_1(f^m)}{\partial f_i^m} + \frac{\phi_2 k_2}{u\Pi_2(f)}\frac{\partial\Pi_2(f^m)}{\partial f_i^m}\right|_{f^m=f=f^*}$$
$$= 0 \quad \text{for } i=1,2.$$

To write $\frac{\partial\Pi_j(f)}{\partial f_i}$ neatly, we define

$$c(x) = 1-\frac{\eta'(x)}{\eta(x)} = \frac{1}{x}-\frac{1}{\mathrm{e}^x-1},$$

and

$$x_j = (\alpha-\mu_j)T.$$

The function c is positive and we write $c(x_j)$ short as c_j. Note that $x_j>0$ since $\nu-\mu_j>0$ and α and therefore x_j are functions of the settlement strategy f.

With this notation, the derivatives of Π_j are written as follows:

$$\frac{\partial\Pi_j}{\partial f_i} = \begin{cases} -\rho\phi_i Tc_j\Pi_j & \text{for } i\neq j \\ \dfrac{\Pi_j}{f_j}-\rho\phi_j Tc_j\Pi_j & \text{for } i=j. \end{cases} \tag{9}$$

When $i\neq j$ the partial derivative in (9) is negative; when $i=j$ it is positive (see Proposition 1 in Appendix A).

The singularity condition for $i=1$ is thus:

$$\begin{aligned}\left.\frac{\partial w}{\partial f_1^m}\right|_{f^m=f=f^*} &= \left.\frac{\phi_1 k_1}{u\Pi_1(f)}\frac{\partial \Pi_1(f^m)}{\partial f_1^m}+\frac{\phi_2 k_2}{u\Pi_2(f)}\frac{\partial \Pi_2(f^m)}{\partial f_1^m}\right|_{f^m=f=f^*}\\ &=\frac{\phi_1 k_1}{u\Pi_1}\left(\frac{\Pi_1}{f_1^*}-\rho\phi_1 Tc_1\Pi_1\right)-\frac{\phi_2 k_2}{u\Pi_2}\rho\phi_1 Tc_2\Pi_2\\ &=\frac{\phi_1 k_1}{uf_1^*}-\frac{1}{u}\rho\phi_1 T(\phi_1 k_1 c_1+\phi_2 k_2 c_2)=0.\end{aligned}$$

We define $\gamma(f_1,f_2)=\phi_1 k_1 c_1+\phi_2 k_2 c_2$. Then, the singularity conditions are given by the system:

$$\begin{cases}\left.\dfrac{\partial w}{\partial f_1^m}\right|_{f^m=f=f^*}=0\\ \left.\dfrac{\partial w}{\partial f_2^m}\right|_{f^m=f=f^*}=0\end{cases}\quad \text{or, equivalently as}\quad \begin{cases}\dfrac{k_1}{f_1^*}=\rho T\gamma(f_1^*,f_2^*)\\ \dfrac{k_2}{f_2^*}=\rho T\gamma(f_1^*,f_2^*).\end{cases} \tag{10}$$

In Proposition 2 in Appendix A we prove that system (10) has no solution, i.e., there exists no singularity in the interior of trait space.

Suppose now that f_i is close to zero with f_j $(j\neq i)$ being arbitrary. The selection gradient $\left.\frac{\partial w}{\partial f_i^m}\right|_{f^m=f}=\frac{\phi_i}{u}\left(\frac{k_i}{f_i}-\rho T\gamma(f_1,f_2)\right)$ is then positive because $\frac{k_i}{f_i}\to\infty$ as $f_i\to 0$ and $\gamma(f_1,f_2)$ is bounded. It follows that the boundaries $(0,f_2)$ and $(f_1,0)$ of the trait space $[0,1]^2$ are repelling, and all evolutionary trajectories are attracted to the boundaries $(1,f_2)$ and $(f_1,1)$.

3.2. Stability of the boundary singularity

Without loss of generality, let us assume that the singular strategy is located on the boundary $(1,f_2)$, with $f^*=(1,f_2^*)$. Then the selection gradient with respect to $f_1{}^m$ is positive:

$$\left.\frac{\partial w}{\partial f_1^m}\right|_{f^m=f=f^*}>0\quad\text{or, equivalently}\quad k_1>\rho T\gamma(1,f_2^*), \tag{11}$$

which pushes the trait to the boundary $(1,f_2)$. The singularity condition for $f^*=(1,f_2^*)$ reduces to a single equation:

$$\left.\frac{\partial w}{\partial f_2^m}\right|_{f^m=f=f^*}=0 \tag{12}$$

or, equivalently to $\frac{k_2}{f_2^*}=\rho T\gamma(1,f_2^*)$. In particular, at the singular strategy $k_1>k_2/f_2^*$ holds. We call patches of type 1 highly rewarding if $k_1>k_2$, i.e., the product of survival until maturation, relative fecundity and emigration probability in patches of type 1 is higher than the same product in patches of type 2. Individuals always settle in patches of the highly rewarding type.

If there exists no solution to Eq. (12) and neither a solution to $\frac{k_1}{f_1^*}=\rho T\gamma(f_1^*,1)$, then selection pushes both traits to 1. We call the strategy $(1,1)$ *corner singularity*. Individuals exhibiting such a settlement behaviour are generalists, who settle in the first patch they encounter.

If there exists a solution to Eq. (12) or to $\frac{k_1}{f_1^*}=\rho T\gamma(f_1^*,1)$, then we call the strategy a *boundary singularity*. The boundary singularity $f^*=(1,f_2^*)$ is evolutionarily stable (*ESS*) if

$$E=\left.\frac{\partial^2 w(f^m,f)}{\partial f_2^{m2}}\right|_{f^m=f=f^*}=\left.\frac{\phi_1 k_1}{u\Pi_1}\frac{\partial^2\Pi_1^m}{\partial f_2^{m2}}+\frac{\phi_2 k_2}{u\Pi_2}\frac{\partial^2\Pi_2^m}{\partial f_2^{m2}}\right|_{f^m=f=f^*} \tag{13}$$

is negative (Maynard Smith and Price, 1973; Hofbauer and Sigmund, 1990). To write the derivatives in Eq. (13) explicitly, we have to investigate the derivative of c_j:

$$\frac{\partial c_j}{\partial f_i}=\rho\phi_i T(-c_j^2+H_j), \tag{14}$$

where H_j is a short notation for $H(x_j)=\frac{x_j(\mathrm{e}^{x_j}+1)-2(\mathrm{e}^{x_j}-1)}{x_j(\mathrm{e}^{x_j}-1)^2}$, which is positive for all x_j. Using (9) and (14) and substituting $(f_1^*,f_2^*)=(1,f_2^*)$ from (12), the condition for evolutionary stability can be rearranged with some algebra into

$$\frac{(\rho T\phi_2)^2}{u}(2\phi_1 k_1 c_1(c_1-c_2)-(\phi_1 k_1 H_1+\phi_2 k_2 H_2))<0. \tag{15}$$

If $c_2\geq c_1$, then this condition holds and the boundary singularity is a fitness maximum. The inequality $c_2\geq c_1$ is equivalent to $\mu_2\geq\mu_1$. Therefore, the boundary singularity is an *ESS* if the patches of high reward are safer during the dispersal season than the patches of low reward. If the death rate in patches of type 1 is sufficiently higher than in patches of type 2, then E may be positive so that boundary singularity is a fitness minimum (see example below).

The boundary singularity is attracting (convergence stable) if

$$\left.\frac{\partial^2 w(f^m,f)}{\partial f_2^{m2}}+\frac{\partial^2 w(f^m,f)}{\partial f_2\partial f_2^m}\right|_{f^m=f=f^*}<0 \tag{16}$$

(Eshel, 1983; Christiansen, 1991), which always holds (see Proposition 4 in Appendix A). Since the singularity is always convergence stable, we conclude that the singularity is also unique.

In summary, the boundary singularity $(1,f_2^*)$ or $(f_1^*,1)$ is either an attracting fitness maximum (*CSS*) or minimum (*BP*). At a *CSS* evolution reaches its long-term evolutionary endpoint. At a *BP*, branching point, evolutionary diversification occurs and two divergent strategies appear. To explore what happens after evolutionary branching, the dimorphic invasion fitness is derived from Eq. (1) for $l=3$ and at equilibrium $\mathcal{G}(N)=N$ for the two residents. The frequencies of the two coexisting resident subpopulations $n_1(f^1,f^2)$ and $n_2(f^1,f^2)$ are derived by solving $F(n,f^1,f^2,f^i)=1$ for $i=1,2$. We substitute the relative frequencies into the dimorphic fitness function $F(n,f^1,f^2,f^m)$ and investigate the evolutionary dynamics for rare mutants with trait $f^m=(f_1^m,f_2^m)$ (Geritz et al., 1998). Further evolutionary branching can be excluded since the number of environmental feedback variables is two $(\sum_{j=1}^{l}n_j\Pi_1(f^j)$ and $\sum_{j=1}^{l}n_j\Pi_2(f^j)$, cf. Eq. (7)), which sets an upper limit to the number of coexisting strategies (Levin, 1970; Geritz et al., 1997). If the partial derivative of the dimorphic fitness function $\partial F(n,f^1,f^2,f^m)/\partial f_1^m|_{f_1^m=f_1^1=f_1^2=1,f_2^i=f_2^m}$ is positive for $i=1,2$, the settlement probability f_1^* remains 1.

In Fig. 1 we present an example of the monomorphic evolution and dimorphic coevolution of patch-type dependent settlement. We chose parameters such that patches of type 1 are highly rewarding $(k_1>k_2)$ but less safe during the dispersal season $(\mu_1>\mu_2)$. Fig. 1a shows the adaptive dynamics in a monomorphic population that leads to a boundary singularity at $(1,f_2^*)$ (dot in Fig. 1). Fig. 1b shows the pairwise invadability plot for the trait f_2. It is a sign plot of the logarithm of the fitness function given in Eq. (8). There exists one singular strategy, an evolutionary branching point (*BP*). At this point the monomorphic population branches into two subpopulations. In Fig. 1c the adaptive dynamics of the coevolution of strategies is presented by a mutual invadability plot. The strategies coexist in the white area of this figure and evolve towards the corner $(f_2^1,f_2^2)=(0,1)$. The arrows indicate the vector field of the selection gradient $\partial F(n,f^1,f^2,f^m)/\partial f_2^m|_{f_1^m=f_1^1=f_1^2=1,f_2^i=f_2^m}$ for $i=1,2$. The dimorphic selection gradient with respect to $f_1{}^m$ remains positive at $f_1^*=1$. Hence, the coevolution of two subpopulations leads to the strategies $(f_1^{1*},f_2^{1*})=(1,1)$ and $(f_1^{2*},f_2^{2*})=(1,0)$. This implies that a generalist, which settles in all patches, and a specialist, which settles only in patches of type 1, coexist. Note, that the

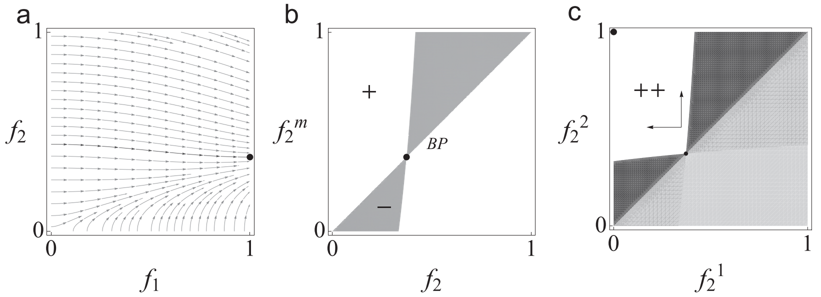

Fig. 1. (a) The stream plot of the dynamics in the interior of trait space; evolution pushes the trait vector to the $(1,f_2)$-boundary of trait space. The dot marks the boundary singularity $(1,f_2^*)$. Parameters: $\phi_1=0.3$, $T=1$, $\mu_1=100$, $\mu_2=40$, $k_1=0.8$, $k_2=0.1$, $\nu=150$, $\rho=100$. (b) Pairwise invadability plot of the dynamics of the trait f_2; the boundary singular strategy $(1,f_2^*)$ is an evolutionary branching point (*BP*). Parameters as in (a). (c) Mutual invadability plot with coexistence within the white area. Arrows indicate the direction of the dimorphic coevolution to the upper left corner (big dot). The dimorphic selection gradient $\partial F(n,f^1,f^2,f^m)/\partial f_1^m|_{f_1^m=f_1^1=f_1^2=1 f_2^i=f_2^m}$ with $i=1,2$ remains positive; and hence $f_1^*=1$. The two strategies evolve to $(f_2^1,f_2^2)=(0,1)$. Parameters as in (a).

strategy $(1,0)$ can evolve only after branching in coexistence with a second sub-population.

3.3. Effects of model parameters on the settlement probability

Here, we investigate the effects of model parameters on the patch-type dependent settlement probability. We assume that the reward in patches of type 1 is high, i.e., $f_1^*=1$, and investigate how the singular strategy $f^*=(1,f_2^*)$, in particular how f_2^*, varies with changing parameters T,ρ,ν,μ_i,ϕ_i and k_i. The selection gradient of trait f_2^* depending explicitly on one of the model parameters (ξ) is defined as usual as $D(f_2^*,\xi)=\partial w/\partial f_2^m|_{f^m=f=f^*}=0$.

To study the effects of the model parameters, we implicitly differentiate this equation with respect to ξ. Rearranging terms leads to

$$\frac{df_2^*}{d\xi}=-\frac{\dfrac{\partial D}{\partial \xi}}{\dfrac{\partial D}{\partial f_2^*}},$$

which has to be evaluated at the singular strategy. As we have seen in the previous section, the singular strategy is a convergence stable strategy, making $\frac{\partial D}{\partial f_2^*}$ negative. Thus the sign of $\frac{\partial D}{\partial \xi}$ determines the sign of change of the singular strategy $\left(\text{i.e., sign}\left[\frac{df_2^*}{d\xi}\right]=\text{sign}\left[\frac{\partial D}{\partial \xi}\right]\right)$. In the next paragraphs we investigate the effects of each parameter of the model on the singular trait f_2^* by deriving the sign of the partial derivatives of $D(f_2^*,\xi)$.

The effect of the dispersal season length and encounter rate: First, we investigate how the dispersal season length and encounter rate affects the settlement probability of patches of type 2. With some algebra, the partial derivative of D with respect to T simplifies to

$$\frac{\partial D}{\partial T}=-\frac{\rho\phi_2}{u}\left(\frac{\phi_1 k_1(1+e^{x_1}(x_1-1))}{(e^{x_1}-1)^2}+\frac{\phi_2 k_2(1+e^{x_2}(x_2-1))}{(e^{x_2}-1)^2}\right).$$

Since $1+e^x(x-1)$ is positive for all $x>0$, $\frac{\partial D}{\partial T}$ is negative and f_2^* decreases with increasing length of the dispersal season.

When ρ is varied we get:

$$\frac{\partial D}{\partial \rho}=-\frac{T}{u}(\phi_2\gamma(1,f_2^*)+\partial_2\gamma(1,f_2^*)(\phi_1+\phi_2 f_2^*)), \tag{17}$$

where $\partial_2\gamma(1,f_2^*)=\frac{\partial\gamma(f_1,f_2)}{\partial f_2}\Big|_{(f_1,f_2)=(1,f_2^*)}$ is negative. Rewriting Eq. (17), we get:

$$\frac{\partial D}{\partial \rho}=\frac{\phi_2 T}{u}\rho T(\phi_1+\phi_2 f_2^*)\sum_{i=1}^{2}\phi_i k_i\left(c_i(c_i-\frac{1}{\rho T(\phi_1+\phi_2 f_2^*)})-H_i\right). \tag{18}$$

Because $c_i<\frac{1}{x_i}$ and $\frac{1}{x_i}<\frac{1}{\rho T(\phi_1+\phi_2 f_2^*)}$ we conclude that $c_i-\frac{1}{\rho T(\phi_1+\phi_2 f_2^*)}<0$ holds for $i=1,2$. So (18) is negative and the settlement strategy f_2^* decreases with increased encounter rate.

The higher the encounter rate or the longer the dispersal season, the smaller the probability to settle in the patches of low reward because the number of encounters during the dispersal season increases, which increases the chance to find a highly rewarding patch. Therefore, the patches of low reward are more often rejected (see also Ward, 1987; Boulinier and Danchin, 1997; Stamps et al., 2005).

The effect of death rates during the dispersal season: Second, we investigate the effect of the death rate in the dispersal pool on the singular trait f_2^*:

$$\frac{\partial D}{\partial \nu}=-\frac{\rho\phi_2 T}{u}\left(\phi_1 k_1\frac{\partial c_1}{\partial \nu}+\phi_2 k_2\frac{\partial c_2}{\partial \nu}\right). \tag{19}$$

The partial derivative of $\frac{\partial c_i}{\partial \nu}$ equals $Tc'(x_i)$. In Proposition 3 in Appendix A we prove that $c'(x)$ is negative. So we can conclude that (19) is positive. When dispersal becomes more dangerous, the probability to settle increases. Individuals also settle in the worse patches with higher probability because the risk of death in the dispersal pool increases (see also Doyle, 1975; Ruxton and Rohani, 1998; Jones and Boulding, 1999; Barton et al., 2009; Hanski and Mononen, 2011). Contrastingly, an increasing patch-dependent death rate during the dispersal season μ_i decreases the settlement probability in patches of type i, for both types $i=1,2$. The derivative

$$\frac{\partial D}{\partial \mu_i}=-\frac{\rho\phi_2 T}{u}\left(\phi_1 k_1\frac{\partial c_1}{\partial \mu_i}+\phi_2 k_2\frac{\partial c_2}{\partial \mu_i}\right)$$

is negative because $\partial c_j/\partial\mu_i=0$ for $i\neq j$ and $\partial c_i/\partial\mu_i>0$ for $i=1,2$.

When patches of low reward become less safe, individuals reject such patches more often because conditions become more hostile (see also Metz and Gyllenberg, 2001). Still, f_2^* remains positive, since survival in the patch is higher than in the dispersal pool and settling pays off because of reduced competition.

When safety decreases in the patches of high reward, individuals reject the patches of low reward more often, to increase the probability of encountering a highly rewarding patch. The high death rate in the patches causes a decrease in the number of competitors which increases the chances of establishing in a patch of high reward.

The effect of the patch-type distribution: Third, we investigate the effect of the patch-type distribution. Using $\phi_2=1-\phi_1$, the singular trait f_2^* decreases with increased ϕ_1 when

$$\frac{\partial D}{\partial \phi_1} = \frac{\rho \phi_2 T}{u}\left(k_2 c_2 - k_1 c_1 - \frac{1-f_2^*}{\phi_2}\partial_2 \gamma(1,f_2^*)\right) \tag{20}$$

is negative. In Proposition 5 in Appendix A we prove that (20) is always negative. When patches of type 1 become more frequent, or patches of type 2 less frequent, the probability to settle when encountering a patch of type 2 decreases (see also Ward, 1987; Boulinier and Danchin, 1997). When the frequency of patches of type 2 is high, the chances to encounter a patch of high reward is low; settlement in the patches of low reward is favoured since the chance of not encountering the highly rewarding patches at all is high and dispersal remains costly.

The effect of survival until reproduction, relative fecundity and emigration: Last, we investigate the effects of survival until reproduction s_i, relative fecundity β_i and emigration probability p_i on the settlement probability f_2^*, i.e., we study the effect of the parameter $k_i = s_i \beta_i p_i$ for $i=1,2$. If patches of type 1 become more rewarding, the singular trait f_2^* decreases if

$$\frac{\partial D}{\partial k_1} = -\frac{\phi_1 \phi_2 k_2}{u^2}\left(\rho \phi_2 T c_1 + \left[\frac{1}{f_2^*} - \rho \phi_2 T c_2\right]\right) \tag{21}$$

is negative. The derivative (21) is negative because the term in the brackets is positive (see proof of Proposition 1 in Appendix A). The probability to settle in a patch of type 2 decreases as k_1 increases because the highly rewarding patches become more rewarding and therefore individuals discriminate more strongly against patches of low reward.

The parameter k_2 increases the singular trait f_2^* if

$$\frac{\partial D}{\partial k_2} = \frac{\phi_2 \phi_1 k_1}{u^2}\left(\rho \phi_2 T c_1 + \left[\frac{1}{f_2^*} - \rho \phi_2 T c_2\right]\right)$$

is positive, which always holds. When the probability of survival until reproduction, relative fecundity and emigration increase in patches of type 2, individuals settle in patches with higher probability.

3.4. Effects of parameters on the stability of different evolutionary outcomes

Here, we investigate the effects of model parameters on the stability of the boundary singularity and the evolutionary outcome. We present two-parameter bifurcation plots of different varying parameters (Fig. 2). From Section 3.2 we know that the singular strategy is either a *CSS* or *BP* boundary singularity, or a corner strategy. To obtain the two-parameter bifurcation diagrams we numerically solved Eq. (12) and checked if inequality (11) is fulfilled. If there exists no solution to Eq. (12) we solved the singularity condition for f_1 and checked if the fitness gradient with respect to f_2 is positive. If neither of the gradients vanish, the singular strategy is a corner singularity. At boundary singularities we numerically evaluated the stability criterion (13) to determine the evolutionary stability of the singular strategy. When the boundary singularity is a *BP* on the boundary $(1,f_2^*)$, we checked if the fitness gradient of the dimorphic fitness function with respect to $f_2{}^i$ evaluated at the point $(f_2^1, f_2^2) = (0,1)$ is negative for $i=1$ and positive for $i=2$ and if the dimorphic fitness gradient of f_1 is positive at 1. If so, the point $(f_2^1, f_2^2) = (0,1)$ in the dimorphic trait space is locally stable and a generalist and a specialist can coexist. If the boundary singularity lies on the other boundary, we proceeded analogously to check whether $(f_1^1, f_1^2) = (0,1)$ is locally stable and if $\partial F(n, f^1, f^2, f^m)/\partial f_2^m|_{f_1^i = f_1^m f_2^1 = f_2^2 = f_2^m = 1} > 0$ for $i=1,2$. In Fig. 2 coevolution always leads to such a coexistence. Note however, that the point $(f_2^1, f_2^2) = (0,1)$ may be locally unstable for different parameter values and coevolution after branching may halt at two mixed strategies $(1, f_2^{1*})$ and $(1, f_2^{2*})$, or $(f_1^{1*}, 1)$ and $(f_1^{2*}, 1)$, respectively.

In Fig. 2a we show that generalists evolve if $k_1 \approx k_2$ since both patches are equally rewarding, even though in this example, the patch-specific death rates differ. When k_2 increases the settlement probability f_1^* decreases and the singularity moves from the corner onto the boundary $(f_1, 1)$. Individuals always settle in patches of type 2 when they become more rewarding (survival until maturation, relative fecundity and emigration probability increase), whereas the patches of the other type may sometimes get rejected. On the other hand, if survival until maturation, relative fecundity and emigration probability increase in patches of type 1, the

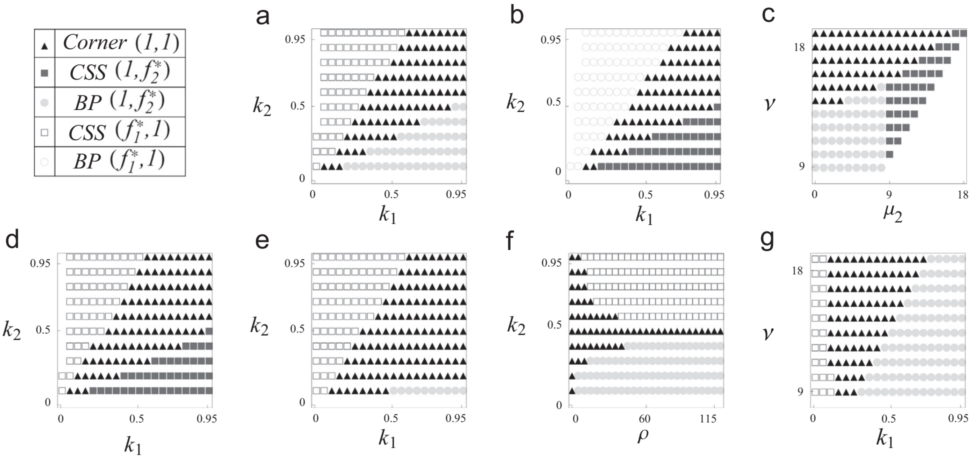

Fig. 2. Two-parameter bifurcation diagrams. Plot markers indicate different evolutionary outcomes as described above. Evolution to the corner $(1,1)$ of trait space represents the evolution to a single generalist. If the outcome is a *CSS*, on one of the two boundaries, an intermediate specialist evolves with $(1, f_2^*)$, or $(f_1^*, 1)$. When evolutionary branching (BP) occurs at $(f_1^*, 1)$ or $(1, f_2^*)$, the ensuing coevolution of the two branches leads, at least in these examples, to a generalist $(1,1)$ coexisting with a specialist (0,1) or (1,0), respectively. Parameters: $T=1$. (a) $\rho=11$, $\nu=10$, $\phi_1=0.4$, $\mu_1=9$, $\mu_2=3$; (b) $\rho=11$, $\nu=10$, $\phi_1=0.4$, $\mu_1=3$, $\mu_2=9$; (c) $\rho=11$, $\phi_1=0.4$, $\mu_1=9$, $k_1=0.5$, $k_2=0.2$; (d) $\rho=11$, $\nu=10$, $\phi_1=0.5$, $\mu_1=5$, $\mu_2=5$; (e) $\rho=11$, $\nu=10$, $\phi_1=0.1$, $\mu_1=9$, $\mu_2=3$; (f) $\nu=10$, $\phi_1=0.4$, $\mu_1=9$, $\mu_2=3$, $k_1=0.5$; (g) $\rho=11$, $\phi_1=0.4$, $\mu_1=9$, $\mu_2=3$, $k_2=0.2$.

settlement probability f_2^* decreases and the singular strategy is located at the $(1,f_2)$-boundary. In this example $\mu_1 > \mu_2$ holds and the strategy is then a branching point (see explanation below Eq. (15)). The two-parameter plot in Fig. 2b shows the effect of patch death rates when k_1 and k_2 are varied. In this figure patches of type 1 are safer than patches of type 2 (in Fig. 2a: $\mu_1 > \mu_2$). Hence, if k_1 is sufficiently higher than k_2, then the singular strategy is an evolutionary maximum. If $k_2 > k_1$, the singular strategy is a branching point on the $(1,f_2)$-boundary, instead of a *CSS* as in Fig. 2a. In Fig. 2c we varied the death rate in patches of type 2 and death rate during dispersal. As mentioned earlier we assume $\nu > \mu_2$ and in particular greater than $\mu_1 = 9 < \nu$. In this plot $k_1 > k_2$ holds and the singular strategy is located at the corner or at the boundary $(1,f_2)$. For a relatively low death rate during dispersal and when $\mu_2 < \mu_1$, the singular strategy is an evolutionary branching point because the highly rewarding patches are unsafe. As μ_2 increases the singular strategy becomes a fitness maximum. When dispersal becomes very costly, natural selection favours a generalist. In Fig. 2d we studied the effect of k_1 and k_2, when all other parameters are patch-type independent and when the abundance of patches of low reward equals the abundance of the highly rewarding ones. If k_1 is much greater than k_2, the settlement probability f_2 decreases and the singularity is located on the $(1,f_2)$-boundary. Since death rates are patch-type independent the boundary singularity is always a *CSS* (cf. inequality (15)). If k_2 is greater than k_1, the *CSS* is $(f_1^*, 1)$. If $k_i = k$ for $i=1,2$, but $\mu_1 \neq \mu_2$, then generalists are favoured (see Proposition 6 in Appendix A). In Fig. 2e the frequency of patches of type 1 is less than in Fig. 2a. Since f_2^* increases with decreased ϕ_1 and γ increases as well, Eq. (12) is less often fulfilled and hence the singular strategy moves from the boundary to the corner which increases the area of corner singularities. Fig. 2f shows the effects of varying ρ and k_2. Increased ρ generally decreases the settlement probability and hence the area of generalists decreases as ρ increases. When k_2 is higher than $k_1 = 0.5$, the singular strategy is either in the corner (for low ρ), or on the $(f_1, 1)$-boundary (for high ρ). In this example $\mu_1 > \mu_2$ holds and the boundary singularity is a *CSS*. When $k_2 < 0.5$ the strategy is either a corner singularity or a branching point boundary singularity on the $(1,f_2)$-boundary. In Fig. 2g the parameters k_1 and ν are varied and $\mu_1 > \mu_2$ holds. When $k_1 < k_2 = 0.2$ evolution pushes the strategy towards the corner or a *CSS* on the $(f_1, 1)$-boundary. When k_1 increases, f_2^* decreases; patches of type 1 become more rewarding and selection starts to push the singular strategy towards the other boundary. Since the death rates are higher in patches of type 1, the boundary singularity $(1,f_2^*)$ is a branching point.

4. Discussion

In this paper, we considered a population that inhabits a heterogeneous environment with two types of patches, and analysed the evolution of patch-type dependent immigration, i.e., the decision to settle in a patch upon encountering it. Models of habitat choice often suppress the details of searching for a suitable patch, and assign only a fixed probability to settle in a certain type of habitat (e.g. Rausher, 1984; Rausher and Englander, 1987; Egas et al., 2004; Ravigné et al., 2004, 2009). In particular, early studies considered the evolution of habitat selection in a cost-free movement environment, leading to an arrangement of species in ideal free distribution (Fretwell and Lucas, 1969; Rosenzweig, 1981). In contrast, we have modelled the dispersal process mechanistically, assuming that in each generation after emigration, dispersal is possible up to a certain length of time, i.e., in the dispersal season, during which individuals encounter patches randomly and must decide whether they accept the patch or keep searching (non-randomness is discussed by Conradt et al., 2001). Movement is costly because the death rate of searching individuals (i.e., the death rate in the dispersal pool) is higher than the death rate in any of the patches during the dispersal season, and individuals not settled by the end of the dispersal season die. These assumptions exclude an ideal free distribution, and also underpin a nontrivial relationship between the probabilities that an individual is alive and settled in a patch of type 1 versus patch of type 2 at the end of the dispersal season (i.e., Π_1 vs Π_2).

We have found that evolutionary branching may lead to the coexistence of a generalist strategy that settles in every patch and a specialist strategy that settles only in the highly rewarding patches. We must emphasise that our current use of “generalist” and “specialist” differs from the literature. Specialisation is commonly defined in terms of the probability of survival during viability selection or fecundity in contrasting habitats (Levene, 1953; Meszéna et al., 1997; Kisdi and Geritz, 1999; Ronce and Kirkpatrick, 2001; Kisdi, 2002; Ravigné et al., 2004; Berdahl et al., 2015), the competitive ability in different habitats (Egas et al., 2004; Haegeman and Loreau, 2014), or the efficiency of using different resources (Day, 2000; Rueffler et al., 2006; Nurmi and Parvinen, 2008, 2011). These definitions are all based on the notion that a specialist has high fitness but only in a certain habitat, whereas a generalist does reasonably well in every habitat. Consistence with this common notion led Cheptou and Massol (2009) to consider outcrossing plants (which have high fitness but only in habitats where pollinators are available) specialists and selfing plants (which have more modest fitness but independently of the presence of pollinators) generalists. Our present terminology, however, relies on where a certain strategy is found (generalists in all patches, specialists only in certain patches), and not on its habitat-specific fitness.

Despite this difference, our model yields a fitness function that is mathematically equivalent to fitness in the Levene model (Levene, 1953), with Π_1 and Π_2 replacing the within-habitat fitnesses of a strategy (see Eq. (8)). The Levene model predicts evolutionary branching when the within-habitat fitnesses are traded off according to a convex function (Kisdi, 2001). In the present model, Π_1 and Π_2 depend on two traits, i.e., the probabilities of settling in the patches of high and low reward. Since selection always keeps the probability of settling in the highly rewarding patch equal to 1, the relevant trade-off between Π_1 and Π_2 is generated by varying the probability of settling in the patches of low reward. The present model yields evolutionary branching when the resulting trade-off between Π_1 and Π_2 is convex in the neighbourhood of the singular strategy. It is always the probability of settling in the patch of low reward that undergoes branching, and hence we never have specialisation to the worse patch type or two specialists each using one patch type.

When the trade-off between Π_1 and Π_2 is concave, the probability of settling in the patches of low reward evolves to a *CSS*. We find that the settlement probability in patches of low reward increases with increasing emigration from these patches: the expected number of years a family defends its natal patch E_i (see Eq. (6)) is decreasing with an increase in the emigration probability. In contrast, the probability of a single individual winning competition in a patch V_i (see Eq. (5)) is increasing with increasing emigration probability. The effects of emigration cancel in the two factors (E_i and V_i) of the fitness function and the emigration probability p_i remains only in the product $k_i = s_i \beta_i p_i$ for $i=1,2$. Higher emigration from the patches of low reward guarantees higher contribution to the next generation and hence also settlement into them pays off.

In case emigration was evolving, the emigration probability of mutants p_i^m would not cancel with the emigration probability of the residents p_i in the above mentioned terms and kin selection effects would matter. In our present model kin competition plays no role since dispersing mutants never compete (they are rare and do not interact during transit and neither after settlement). If emigration probabilities are allowed to mutate, individuals may evolve patch-type dependent emigration probabilities keeping the locally optimal competitive weight at home and sending away the rest (Ezoe and Iwasa, 1997; Kisdi, 2004; Gyllenberg et al., 2011). Furthermore, we expect emigration to be higher in low quality patches (Gyllenberg et al., 2011). If patch-type dependent settlement is allowed to coevolve with emigration, highly rewarding patches are characterised as habitats with high survival until reproduction and high relative fecundity. Full acceptance of highly rewarding patches may evolve and low emigration from them. On the contrary, the settlement into patches of low reward is conjectured to evolve to a positive but low optimum, and emigration to a high one.

Here, we assumed that individuals are simple organisms that are unaware of time in the dispersal season. Some studies have incorporated time dependency of settlement decisions mechanistically (Doyle, 1975; Ward, 1987; Baker and Rao, 2004; Stamps et al., 2005). In these papers, as also shown in our study, individuals should always settle in the most suitable habitat (see also Poethke et al., 2011; for empirical evidence see Matter and Roland, 2002; Schneider et al., 2003). In time-dependent models a time threshold evolved at which individuals no longer discriminate against bad quality patches, but settle in any patch they encounter; i.e., individuals become less choosy as time passes by (Ward, 1987; Stamps, 2006; Stamps and Davis, 2006). If individuals are aware of time we expect that specialists change their behaviour towards the end of the dispersal season and become generalists. Individuals would not need to make a compromise between choosing one or the other strategy, and we expect to lose the possibility of branching.

For simplicity, we assumed that individuals can ascertain the types of patches they encounter without mistakes. In reality, however, patch type can be mistaken. McNamara and Dall (2011) have shown that if the information available about the future type of a patch is less than fully reliable, it may be best to ignore it when a decision on emigration is made. This is because the existence of an individual in a certain patch is a signal that the patch was likely good in the past, and with positive temporal autocorrelation it will likely be a favourable patch also in the future (the “multiplier effect” of McNamara and Dall, 2011). In our model, the evolving trait is expressed only if the individual has emigrated from its natal patch, and hence the “multiplier effect” does not play a role. However, uncertainties about patch types will have an effect on the adaptive dynamics of immigration strategies. In our model, an individual rejects a patch of low reward to have a chance to encounter and settle in a highly rewarding one. If patches of different types cannot be distinguished by the individuals, then there is no reason to reject the patch first encountered. By continuity, the more uncertain is the cue that signals a patch of low reward, the less likely the patch should be rejected. We thus expect that mistakes in judging patch types will shift the singular strategy towards settling in all patches, or, in our current terminology, towards a generalist strategy.

The present study further ignored density-dependence in the settlement behaviour. It assumed that individuals are incapable of sensing more than the type of the patch although there exists evidence that some species select habitats depending on local population density (Andreassen and Ims, 2001; Stamps, 2006; Clobert et al., 2009; Schaub et al., 2013, but see Gaines and McClenaghan, 1980). However, it has been indicated that density does not always affect individual's patch selectivity (Jones and Boulding, 1999; I. Hanski, personal communication) and that habitat use and active selection of patches may increase with patch quality (Morris and MacEachern, 2010).

The present model can be compared to general optimal foraging theory (Krebs and Davies, 1993). Optimal foraging theory predicts that individuals consume the less nutritious prey if the probability to find the better prey is small. In any case the consumption of a prey is a pure gain for the individual, but prey of higher nutritional value is favoured. Similarly, in our model individuals settle in patches of low reward more likely if the probability of encountering patches of high reward is small or dispersal costly. Still, a decision to settle in a highly rewarding patch may be accompanied by high competition if other individuals choose the same strategy; i.e., settling in the highly rewarding patch is not necessarily a pure benefit for the individual. Frequency-dependence in our model acts as a driver to settle in the patches of low reward, even if the probability to find a rewarding patch is relatively high.

We have also assumed that the patches have fixed characteristics in terms of patch-specific fecundity, emigration, pre-reproductive survival and death rate during the dispersal season. This excludes not only temporal variation in the environment, but also the possibility that adaptation to local environmental conditions would change the patch-specific demographic parameters. The evolution of a trait involved in local adaptation (such as thermal adaptation or drought resistance) would change how rewarding a certain patch is, and therefore the evolution of local adaptation would interact with the evolution of the immigration strategy. If the local adaptation trait becomes dimorphic such that some individuals find patch type 1 more rewarding whereas others find patch type 2 more rewarding, then two specialist immigration strategies may also evolve such that individuals adapted to patch 1 settle only in patch 1 and individuals adapted to patch 2 settle only in patch 2.

One intriguing aspect of the joint dynamics of local adaptation and dispersal is the possibility of multiple evolutionary attractors. Billiard and Lenormand (2005) found that emigration may evolve either to a high or to a low value when a locus responsible for local adaptation is polymorphic (they assumed that the alleles of this polymorphism do not change; see also Blanquart and Gandon, 2014). At low dispersal, each habitat contains mostly the locally adapted allele, and since dispersers typically carry the alternative allele, dispersal is selected against. At high dispersal, there is little difference in the frequencies of local adaptation alleles between the habitats, and therefore selection against dispersal is relaxed. By analogy, we expect that the immigration strategy may also have multiple evolutionary attractors. Suppose the resident population contains two specialists, each adapted to one patch type and immigrating only in patches to which it is adapted (as described in the previous paragraph). In this case, each patch contains only the locally adapted allele, and the alternative allele is strongly selected against. In this resident population, a generalist immigration strategy that settles in every patch would settle also in patches where the local adaptation allele (whichever it was carrying) is mismatched with the patch type, and therefore the generalist immigration strategy would be selected against. Conversely, if the resident population follows a generalist immigration strategy, then every patch contains every allele, and the mismatched allele is less strongly selected against. This relaxes selection against the generalist immigration strategy, and since it suffers less from dispersal-related mortality, the generalist immigration strategy may be at an advantage over specialists. Investigating the coevolution of immigration and other traits in mechanistic models should be a next step to reveal novel mechanisms of dispersal syndromes.

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Appendix A

In this appendix we give detailed proofs of six auxiliary results needed in the main text.

Proposition 1. *The partial derivative of Π_j with respect to f_j is positive.*

Proof. The derivative

$$\frac{\partial \Pi_j}{\partial f_j} = \frac{\Pi_j}{f_j} - \rho\phi_j T c_j \Pi_j \quad \text{is positive iff } f_j \rho \phi_j T c_j < 1.$$

From the definition of $c_j = \frac{1}{x_j} - \frac{1}{e^{x_j}-1}$, we know that $c_j < 1/x_j$ and $x_j = (\rho\phi_1 f_1 + \rho\phi_2 f_2 + \nu - \mu_j)T$ and $\nu - \mu_j > 0$. Therefore,

$$f_j\rho\phi_j T c_j < f_j \rho \phi_j T \frac{1}{x_j} < 1. \square$$

Proposition 2. *There exists no solution to the system of equations*:

$$\begin{cases} \left.\dfrac{\partial w}{\partial f_1^m}\right|_{f^m = f = f^*} = 0 \\ \left.\dfrac{\partial w}{\partial f_2^m}\right|_{f^m = f = f^*} = 0. \end{cases} \tag{A.1}$$

Proof. The system (A.1) can be rewritten as:

$$\begin{cases} \dfrac{k_1}{f_1^*} = \rho T \gamma(f_1^*, f_2^*) \\ \dfrac{k_2}{f_2^*} = \rho T \gamma(f_1^*, f_2^*) \end{cases} \quad \text{or, equivalently as} \quad \begin{cases} \dfrac{k_1}{f_1^*} = \rho T \gamma(f_1^*, f_2^*) \\ f_2^* = f_1^* \dfrac{k_2}{k_1}. \end{cases} \tag{A.2}$$

Assume that there exists a solution to the system (A.2). Using $c_j < 1/x_j$ and the definition of x_j, the term $\rho T \gamma(f_1^*, f_2^*)$ in system (A.2) can be written as

$$\rho T\gamma(f_1^*, f_2^*) = \rho T(\phi_1 k_1 c_1 + \phi_2 k_2 c_2) < \rho T\left(\frac{\phi_1 k_1}{x_1} + \frac{\phi_2 k_2}{x_2}\right) < \frac{\phi_1 k_1 + \phi_2 k_2}{\phi_1 f_1^* + \phi_2 f_2^*}.$$

By substituting $f_2^* = f_1^* \frac{k_2}{k_1}$ into the first line of system (A.2) we obtain

$$\frac{k_1}{f_1^*} = \rho T \gamma\left(f_1^*, f_1^* \frac{k_2}{k_1}\right) < \frac{\phi_1 k_1 + \phi_2 k_2}{\phi_1 f_1^* + \phi_2 f_1^* \frac{k_2}{k_1}} = \frac{k_1}{f_1^*},$$

which is a contradiction. Hence, there exists no solution to the system (no interior singularity).□

Proposition 3. *The function c is decreasing.*

Proof. The function $c(x) = \frac{1}{x} - \frac{1}{e^x - 1}$ is decreasing if $c'(x)$ is negative. The derivative is

$$c'(x) = \frac{e^x - \eta(x)^2}{(e^x - 1)^2}. \tag{A.3}$$

It is negative if $e^x - \eta(x)^2 < 0$, which is equivalent to

$$h(x) = x^2 e^x - (e^x - 1)^2$$

being negative. At the origin $h(0) = 0$ holds. The derivative of $h(x)$ is

$$h'(x) = 2e^x\left(1 + x + \frac{x^2}{2} - e^x\right),$$

which is negative. Hence, h is negative for all $x > 0$. Therefore, (A.3) is negative and c is a decreasing function. □

Proposition 4. *The boundary singularity is convergence stable.*

Proof. After rewriting Eq. (16), the convergence stability condition is:

$$-\phi_1 k_1 \rho \phi_2 T \frac{\partial c_1}{\partial f_2^*} - \phi_2 k_2 \left(\frac{1}{f_2^{*2}} + \rho\phi_2 T \frac{\partial c_2}{\partial f_2^*}\right) < 0. \tag{A.4}$$

We substitute the singularity condition Eq. (10), use Eq. (14), and rewrite condition (A.4):

$$f_2^* \rho \phi_2 T \sum_{i=1}^{2} \phi_i k_i \left(c_i\left(c_i - \frac{1}{f_2^* \rho \phi_2 T}\right) - H_i\right) < 0. \tag{A.5}$$

Since $c_i < 1/x_i$ and $1/x_i < 1/(f_2^* \rho\phi_2 T)$, also $c_i - \frac{1}{f_2^* \rho \phi_2 T} < 0 \ \forall i$. Then inequality (A.5) and hence inequality (A.4) are fulfilled and the boundary singularity is convergence stable.□

Proposition 5. *The singular strategy f_2^* decreases with increased frequency of patches of type 1, ϕ_1.*

Proof. The right hand side of Eq. (17) is negative (see proof in main text below Eq. (17)). Then it follows that $-\partial_2\gamma(1, f_2^*) < \gamma(1, f_2^*)\frac{\phi_2}{(\phi_1 + \phi_2 f_2^*)}$. Using this inequality, it is straightforward to show that f_2^* decreases with increased ϕ_1, i.e., (20) is negative if

$$\frac{k_2}{f_2^*} c_2 < k_1 c_1. \tag{A.6}$$

The singularity condition Eq. (12) can be rewritten as follows:

$$c_1 = \frac{k_2}{\phi_1 k_1 f_2^* \rho T} - \frac{\phi_2 k_2 c_2}{\phi_1 k_1}.$$

We substitute c_1 in (A.6) and with some algebra we get:

$$\rho T(\phi_1 + \phi_2 f_2^*) c_2 < 1. \tag{A.7}$$

Since $\rho T(\phi_1 + \phi_2 f_2^*) < x_2$ and $c_2 < \frac{1}{x_2}$ we conclude that (A.7) is true, and hence (A.6) holds and (20) is negative. The singular strategy f_2^* is decreasing with increased ϕ_1.□

Proposition 6. *The singular strategy is a corner singularity if $\mu_1 \neq \mu_2$ and all other parameters are patch-type independent ($s_i = s$, $k_i = k$, $\phi_i = \phi$).*

Proof. The system of singularity conditions can be written as:

$$\begin{cases} \left.\dfrac{\partial w}{\partial f_1^m}\right|_{f^m = f = f^*} = \dfrac{\phi k}{u f_1^*} - \dfrac{1}{u}\rho\phi T(\phi k c_1 + \phi k c_2) = 0 \\ \left.\dfrac{\partial w}{\partial f_2^m}\right|_{f^m = f = f^*} = \dfrac{\phi k}{u f_2^*} - \dfrac{1}{u}\rho\phi T(\phi k c_1 + \phi k c_2) = 0. \end{cases} \tag{A.8}$$

Solving the system (A.8) we get $f_1^* = f_2^*$. In Appendix A Proposition 2 we proved that the singular strategy can never be in the interior.

Hence, independent of the death rates during the dispersal season the evolved strategy is (1,1). □

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Article *III*

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Coevolution of patch-type dependent emigration and patch-type dependent immigration.

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Coevolution of patch-type dependent emigration and patch-type dependent immigration

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Abstract

Dispersal can be divided in three phases: emigration, transfer and immigration. All phases are clearly intertwined and emigration and immigration decisions depend on patch types. Despite the inevitable fact of the complexity of the dispersal process, patch-type dependencies of dispersal decisions modelling emigration and immigration are usually missing in theoretical dispersal models. Here, I investigate the coevolution of patch-type dependent emigration and patch-type dependent immigration in an extended Hamilton-May model. The dispersing population inhabits a landscape structured into many patches of two types and disperses during a continuous-time season. The trait under selection is a four dimensional strategy vector. Using the adaptive dynamics approach I show that four qualitatively different dispersal strategies may evolve, including a counterintuitive strategy, where patches of one type are fully dispersed from but nevertheless always settled into during the dispersal phase. I present examples of evolutionary branching in a wide parameter range, when the patches with high local death rate during the dispersal season guarantee a high expected disperser output. I find that two dispersal types can coexist after diversification and that stochastic simulations agree with the novel result. Since evolutionary branching is also found when immigration evolves alone, the present study is adding coevolutionary constraints on the emigration traits and hence finds that the coevolution of a higher dimensional trait sometimes hinders evolutionary diversification.

Keywords: Dispersal, Kin Competition, Adaptive Dynamics, Settlement, Evolutionary branching

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1. Highlights

- I analyse the coevolution of patch-type dependent emigration and immigration.
- A high during-season death rate in patches with high disperser output favours branching.

- Patches may be initially fully dispersed from, but always settled in during transfer.
- Sustainable evolutionary branching is found in three dimensions.
- Higher dimensional traits sometimes hinder diversification.

2. Introduction

Dispersal is a widely studied life-history trait that evolved because of many selective pressures (Ronce, 2007). Although it has been studied for decades, only recently studies have emphasised that dispersal has three phases: emigration, transience and immigration (Metz and Gyllenberg, 2001; Clobert et al., 2009; Travis et al., 2012; Bonte et al., 2012; Jacob et al., 2015) and that all phases interact on different levels. Understanding the complex dispersal behaviour is becoming increasingly more important as the vast majority of species experiences threats by global warming and climate change. Timing (Cote et al., 2016), costs (Bonte et al., 2012), patch-type dependent conditions, e.g., host plants or resource availability (Matter and Roland, 2002; Schneider et al., 2003), or various other cues (Bowler and Benton, 2005), e.g., indirect information (Cote and Clobert, 2007; Clobert et al., 2009), all influence the non-random decisions to move and stop moving in heterogeneous environments. In turn, individuals have evolved ways to perceive and assess the local conditions of the environment (Doyle, 1975; Ehlinger, 1990; Zollner and Lima, 1999; Matter and Roland, 2002; Schooley and Wiens, 2003; Garant et al., 2005) and base their dispersal decisions on the triggers and cues they encounter (Rees, 1969; Mitchell, 1977; Myers et al., 1981; Hey and Houle, 1987; Jaenike and Holt, 1991; Hanski et al., 2002; Hanski, 2011).

The empirical literature is jaded with condition dependencies at the three different dispersal stages, but mathematical models seldom incorporate such complexity. The only relative well-studied dependency is density-dependence: Many theoretical studies have investigated density-dependent emigration (Travis et al., 1999; Poethke and Hovestadt, 2002; Kun and Scheuring, 2006; Poethke et al., 2007; Hovestadt et al., 2010), or predator- or prey-density-dependent emigration (Sjödin et al., 2014, 2015), whereas only very few have touched upon the evolution of density-dependent emigration and immigration (Saether et al., 1999; Metz and Gyllenberg, 2001; Poethke et al., 2011; Parvinen et al., 2012), or on density-dependent immigration (Nonaka et al., 2013; Parvinen and Brännström, 2016). These studies focused on density dependency, but did neglect other characteristics of the patch. Some studies allowed emigration decisions based on density and on the number of immigrants (immigrant-dependent dispersal; see Chaine et al., 2013), or on body-condition and patch-type (Bonte and De La Peña, 2009; Gyllenberg et al., 2011a,b), but ignored dependencies of immigration decisions.

Studies that modelled immigration patch-type dependently, implemented it as a mechanistic settlement probability upon encounter (Doyle, 1975; Ward, 1987; Baker and Rao, 2004; Stamps et al., 2005; Gyllenberg et al., 2016, submitted), or as a phenomenological habitat choice trait (Levins, 1963; Rausher and Englander, 1987; Castillo-Chavez et al., 1988; Beltman and Metz, 2005; Ravigné et al., 2009), but disregarded the coevolution with patch-type dependent emigration.

Splitting up the dispersal process in a model will improve our knowledge on the coevolutionary forces and costs and benefits at each phase. It will inform us on how selection acts on the different life stages from a theoretical point of view. Hence, the multi-causal effects of patch-type dependency are studied in this paper. Dispersal is decomposed into its three stages and the joint evolution of emigration and immigration when both decisions depend on the physical characteristics of the patch, the patch types, is investigated. Emigration is handled as the natal dispersal probability of leaving a patch of certain type in the beginning of the dispersal season. Immigration is modelled as the settlement probability (Clobert et al., 2009; Travis et al., 2012; Bonte et al., 2012) of an individual into a patch upon encounter during a continuous-time dispersal season, i.e., in a mechanistic way. With the analytic methods of adaptive dynamics and complemented by numerical investigations and simulations I analyse the eco-evolutionary model to investigate how the selection pressures shape the dispersal decisions.

I find four qualitatively different evolutionary outcomes, including strategies that do not differentiate between the habitat types at settlement, and a strategy that fully emigrates from patches of one type in the beginning of the dispersal phase but nevertheless settles in the patches of equal type with full probability during the dispersal season. I highlight that when emigration is allowed to coevolve with immigration evolutionary branching can occur and the two emerging subpopulations remain coexisting after diversification. Stochastic simulations agree with the theoretical predictions and show evolutionary branching. The coevolutionary constraint that is induced through an additional evolutionary trait, the patch-type dependent emigration probability, sometimes hinders evolutionary diversification as compared to scenarios where only immigration is evolving (see

Gyllenberg et al., 2016).

In Section 3 I set up the ecological model deriving the next-generation operator. Section 4 derives the fitness proxy of the model. In Section 4.1 I derive the monomorphic singularity, explain how to derive the stability conditions (Section 4.2) and analyse the 4 qualitatively different evolutionary outcomes (Section 4.3), before investigating the effects of some parameters on the evolutionary outcome (Section 4.4). In Section 5 the implementation and results of the stochastic simulations are presented, followed by Section 6 where I discuss the novel results.

3. The model

Here, the life cycle of the annual, asexual and semelparous population is described (see equivalent setting in Gyllenberg et al., 2016). The landscape is structured in M patches of two types with frequencies ϕ_1 and $\phi_2 = 1 - \phi_1$, respectively. Each individual carries a heritable dispersal trait $d = (p_1, p_2, f_1, f_2)$, a *vector-valued* strategy, where p_i is the (natal) emigration probability from and f_i the settlement probability into a patch of type i for $i = 1, 2$. I sometimes write $f = (f_1, f_2)$. In the beginning of the year each patch is inhabited by one individual. It survives until maturation in a patch of type i with probability s_i. If it survives in the patch of type i it produces $B\beta_i$ offspring, where B is the offspring number and β_i denotes the relative fecundity in a patch of type i. After reproduction all mothers die. Then, the life cycle is continued by a continuous-time season during which individuals disperse or stay in the patch. In the beginning of the season, individuals instantaneously emigrate from a patch of type i with probability p_i and join the dispersal pool. During the season the dispersing individuals die at a rate ν. Dispersers encounter, i.e., arrive at, a patch of type i at a rate $\phi_i\rho$, where ρ is the patch encounter rate and ϕ_i is the frequency of patches of type i. Upon encounter individuals immigrate into, i.e., settle in, a patch of type i with probability f_i. If the individual does not settle in the patch it has encountered, it moves back into the dispersal pool, where, if the dispersal season has not ended yet, it may encounter another patch during the next time step, or may die. Once an individual has decided to settle, it cannot change its decision later on. Non-dispersed individuals die during the season sedentary in a patch at a rate μ_i (patch safety), as do the newly settled immigrants in the patch of type i during the remainder of the season. I assume that the death rate in the dispersal pool is higher than in any of the patches, i.e., $\nu > \mu_i$ for $i = 1, 2$. The dispersal season ends at time T and dispersers that are

Table 1: Notation

Variable	Definition
B	number of offspring
β_i	relative fecundity in patch of type i
$d = (p_1, p_2, f_1, f_2)$	dispersal trait vector (evolving)
f_i	settlement probability into patch of type i (evolving)
M	number of patches
μ_i	death rate in patch of type i (patch safety)
ν	death rate in dispersal pool
p_i	emigration probability from patch of type i (evolving)
ϕ_i	relative frequency of patch of type i
ρ	patch encounter rate
s_i	survival until reproduction in patch of type i
T	length of dispersal season

still in the dispersal pool die. Then competition takes place with one individual surviving per patch (fair competition). To end up with a deterministic model, I assume that the number of patches M and the offspring number B are infinitely large. All parameters are summarised in Table 1. Note that present model is an extension of the Hamilton-May model (Hamilton and May, 1977) and the model of Gyllenberg et al. (2016).

I keep track of the population dynamics via a next-generation map of the dispersers. The next-generation operator $\mathcal{G}$ maps the number of dispersers N with strategy $d = (p_1, p_2, f_1, f_2)$ of one disperser generation to its next during the lifetime of the *family*, that is, all kin and kin's kin of the dispersing individuals in the natal patch (Diekmann et al., 1990, 1998). Hence, the disperser generations are not measured in real time, but operate during years the focal individual's kin and descendants remain in the natal patch (Gyllenberg and Metz, 2001; Metz and Gyllenberg, 2001). The next-generation operator of the present model is:

$$\mathcal{G}(N) = Q^\top(D, d)\mathbf{V}(D)\Pi(f)N,$$

given that l competing dispersal strategies $d^j = (p_1^j, p_2^j, f_1^j, f_2^j)$ with $j = 1, \dots, l$ are present at population dynamical equilibrium and where $D = (d^1, \dots, d^l)$. The elements $Q_i(D, d)$ of the vector $Q(D, d)$ give the expected number of offspring dispersers with strategy d that emigrate from a patch of type i in one generation, i.e. during the years the individuals of the same strategy defend the natal patch. It is the product of the number of years the patch can be defended against the competing strategies $j = 1, \dots, l$ times the number of emigrants that can be produced each year. The elements V_i of the diagonal matrix $\mathbf{V}(D)$ are the probability of a disperser winning a patch of type i, by winning fair competition against the competing strategies $j = 1, \dots, l$, which are present in the patch of type i. The probabilities are independent of the focal strategy d. The terms $\Pi_1(f)$ and $\Pi_2(f)$ are the elements of the vector $\Pi(f)$ and each $\Pi_i(f)$ accounts for the probability to survive dispersal and after settlement in any of the patches of type i until the end of the dispersal season. The derivation of $\Pi_i(f)$ is as follows (see also Gyllenberg et al., 2016): In the beginning of the dispersal season, offspring emigrates and joins the dispersal pool. An individual leaves the dispersal pool at an exponential rate as it either (i) dies in the dispersal pool at a rate ν or (ii) settles in a patch upon encounter with rate $\rho(\phi_1 f_1 + \phi_2 f_2)$, where ρ is again the patch encounter rate. The probability of an individual still being in the dispersal pool at time $t \in [0, T]$ is $e^{-(\rho(\phi_1 f_1+\phi_2 f_2)+\nu)t}$ and that it encounters a patch of type i within the next time interval $(t, t + dt)$ is $\phi_i \rho dt$. It settles in the patch with probability f_i and once settled its decision is irreversible. Once settled, the individual survives in the patch of type i until the end of the dispersal season with probability $e^{-\mu_i(T-t)}$. Integrating over t yields the probability to survive the dispersal season in the dispersal pool and after settlement in the patch of type i:

$$\Pi_i(f) = \rho\phi_i T f_i \mathrm{e}^{-\alpha T}\eta((\alpha - \mu_i)T),$$

where $\alpha = \rho(\phi_1 f_1 + \phi_2 f_2) + \nu$ is the rate at which individuals disappear from the dispersal pool (die or settle) and $\eta(x) = \frac{\mathrm{e}^x - 1}{x}$ for $x > 0$. The term $\alpha - \mu_i$ is positive, since I assume that the dispersal death rate ν is higher than each of the patch-type dependent death rates μ_i for $i = 1, 2$. Note that α depends on the settlement strategies f_1 and f_2.

The average number of emigrants with strategy j dispersing from any patch is Bu_j, where $u_j = s_1\beta_1\phi_1^j p_1^j + s_2\beta_2\phi_2^j p_2^j$. The ϕ_i^j denotes the relative frequency of patches of type i that are occupied by strategy j and $\phi_i = \sum_{j=1}^{l} \phi_i^j$ holds. Hence, the relative number of immigrants settling in a patch of type i and surviving until the end of the dispersal season is $\sum_{j=1}^{l} u_j \frac{\Pi_i(f^j)}{\phi_i}$.

Since a next-generation fitness proxy is used, the expected number of years a family with strategy d stays alive in its natal patch of type i needs to be derived. The probability of non-dispersing individuals winning competition in a patch of type i is

$$\frac{s_i\beta_i(1-p_i)\mathrm{e}^{-\mu_i T}}{\beta_i(1-p_i)\mathrm{e}^{-\mu_i T}+\sum\limits_{j=1}^{l} u_j\frac{\Pi_i(f^j)}{\phi_i}}.$$

Hence, the expected number of years a family defends its natal patch is given by

$$E_i(D,d)=\frac{1}{1-\frac{s_i\beta_i(1-p_i)\mathrm{e}^{-\mu_i T}}{\beta_i(1-p_i)\mathrm{e}^{-\mu_i T}+\sum\limits_{j=1}^{l} u_j\frac{\Pi_i(f^j)}{\phi_i}}}=\frac{\beta_i(1-p_i)\mathrm{e}^{-\mu_i T}+\sum\limits_{j=1}^{l} u_j\frac{\Pi_i(f^j)}{\phi_i}}{(1-s_i)\beta_i(1-p_i)\mathrm{e}^{-\mu_i T}+\sum\limits_{j=1}^{l} u_j\frac{\Pi_i(f^j)}{\phi_i}},$$

where u_j and f^j are the strategies of the residents $j=1,\ldots,l$. I slightly change notation and write $E_i(D,d)$ as $E_i(p_i)$.

The vector element $Q_i(D,d)$ describes the expected relative per-generation offspring number a family occupying a patch of type i contributes to the dispersal pool. The element is $Q_i(D,d)=k_iE_i(D,d)$, where $k_i=\beta_i s_i p_i$ is the (yearly) expected relative reproductive disperser output.

The probability of winning a patch of type i is $V_i(D)$. The product $BV_i(D)$ for $B\to\infty$ is:

$$V_i^+(D)=\lim_{B\to\infty}BV_i(D)=\sum_{j=1}^{l}\frac{\phi_i^j}{\phi_i}\frac{s_i}{\beta_i(1-p_i^j)\mathrm{e}^{-\mu_i T}+\sum\limits_{\iota=1}^{l} u_\iota\frac{\Pi_i(f^\iota)}{\phi_i}}+\frac{1-s_i}{\sum\limits_{\iota=1}^{l} u_\iota\frac{\Pi_i(f^\iota)}{\phi_i}}.$$

It is the probability to win a patch of type i where non-dispersers with strategy j are present, summed over j, and the probability to win a patch of type i that was empty in the beginning of the dispersal season, i.e., where an established individual died before reproduction.

As mentioned before, the relative frequency of patches of type i occupied by an individual with strategy j is given by ϕ_i^j. At the population dynamical equilibrium the relative frequencies ϕ_i^j equilibrate and solve the fixed point equations for all $i=1,2$ and strategies $j=1,\ldots,l$:

$$\phi_i^j=\phi_i^j\frac{s_i\beta_i(1-p_i^j)\mathrm{e}^{-\mu_i T}}{\beta_i(1-p_i^j)\mathrm{e}^{-\mu_i T}+\sum\limits_{\iota=1}^{l} u_\iota\frac{\Pi_i(f^\iota)}{\phi_i}}+u_j\Pi_i(f^j)V_i^+(D).$$

The frequency of patches of type i occupied by an individual with strategy j equals the frequency of patches that had been occupied before and are defended by non-dispersers and the new patches that are conquered by dispersers.

Thus, the next-generation operator is written as follows:

$$\mathcal{G}(N) = \big(s_1\beta_1 p_1 E_1(p_1)\Pi_1(f)V_1^+(D) + s_2\beta_2 p_2 E_2(p_2)\Pi_2(f)V_2^+(D)\big)N. \tag{1}$$

4. Evolution

Here, I analyse the adaptive dynamics (Geritz et al., 1998; Leimar, 2009; Geritz et al., 2016) of patch-type dependent dispersal, i.e., patch-type dependent emigration and patch-type dependent settlement, the coevolution of p_1, p_2, f_1 and f_2. Assume that a *resident* population with dispersal strategy $d^r = (p_1^r, p_2^r, f_1^r, f_2^r)$ is at its population dynamical equilibrium and occupies almost all patches in the landscape $\phi_1^r \approx \phi_1$ and an infinitesimal fraction of patches is occupied by *mutants.* The mutants are characterised by a slightly different dispersal strategy, the trait vector $d^m = (p_1^m, p_2^m, f_1^m, f_2^m)$, experience an environment that is set up by the resident. If the mutant's fitness is higher than the resident's, the mutant increases in numbers, outcompetes the resident and the ecological dynamics settles at a new population dynamical equilibrium. I measure fitness of a mutant with vector-valued strategy d^m in an environment set up by the resident as the basic reproduction number derived from the next-generation operator (Gyllenberg and Metz, 2001; Metz and Gyllenberg, 2001). From Eq. (1) with one resident with strategy d^r and abundance $\phi_1^r \approx \phi_1$ and one invading mutant strategy d^m, the fitness proxy is:

$$R_m(d^m, d^r) = \frac{\phi_1 s_1 \beta_1 p_1^m}{u_r}\frac{E_1(p_1^m)\Pi_1(f^m)}{E_1(p_1^r)\Pi_1(f^r)} + \frac{\phi_2 s_2 \beta_2 p_2^m}{u_r}\frac{E_2(p_2^m)\Pi_2(f^m)}{E_2(p_2^r)\Pi_2(f^r)}.$$

Sometimes I write $\Pi_i(f^m) = \Pi_i^m$, etc.

4.1. Monomorphic singularities

Monomorphic evolution ceases at the singular strategy $d^* = (p_1^*, p_2^*, f_1^*, f_2^*)$ where the selection gradient vanishes:

$$\begin{cases} \left.\frac{\partial R_m}{\partial p_i^m}\right|_{d^m=d^r=d^*} = \frac{\phi_i s_i \beta_i}{u_* E_i(p_i^*)}\big(E_i(p_i^*) + p_i^* E_i'(p_i^*)\big) = 0 \quad \text{for} \quad i = 1, 2, \\ \frac{\partial R_m}{\partial f_i^m} = \left.\frac{\phi_1 k_1^m E_1(p_1^m)}{u_r \Pi_1(f^r) E_1(p_1^r)}\frac{\partial \Pi_1(f^m)}{\partial f_i^m} + \frac{\phi_2 k_2^m E_2(p_2^m)}{u_r \Pi_2(f^r) E_2(p_2^r)}\frac{\partial \Pi_2(f^m)}{\partial f_i^m}\right|_{d^m=d^r=d^*} = 0 \quad \text{for} \quad i = 1, 2. \end{cases} \tag{2}$$

The term $E_i'(p_i^*)$ is a short notation for $\frac{\partial E_i}{\partial p_i^m}\big|_{d^m=d^r=d^*}$. I define the function c as

$$c(x) = 1 - \frac{\eta'(x)}{\eta(x)} = \frac{1}{x} - \frac{1}{\mathrm{e}^x - 1},$$

write $c_i = c(x_i T)$ where $x_i = (\alpha - \mu_i)$ for $i = 1, 2$ and define $\gamma(f_1, f_2) = \phi_1 k_1 c_1 + \phi_2 k_2 c_2$. Note that $\gamma(f_1, f_2)$ also depends on p_1 and p_2.

In Proposition 1 of AppendixA.1 I show that system (2) has no solution and that the singularity is $d^* = (p_1^*, p_2^*, f_1^*, 1)$ that solves:

$$\begin{cases} p_1^* = -\frac{E_1(p_1^*)}{E_1'(p_1^*)}, \\ p_2^* = -\frac{E_2(p_2^*)}{E_2'(p_2^*)}, \\ \frac{k_1^*}{f_1^*} = \rho T \gamma(f_1^*, 1) \end{cases} \tag{3}$$

with $\frac{\partial R_m}{\partial f_2^m}\big|_{f_2^m=f_2^r=f_2^*=1,*} > 0$. I call the singularity $d^* = (p_1^*, p_2^*, f_1^*, 1)$ a *three dimensional singularity.* Note that at the singular emigration strategy the expected per-generation disperser output $p_i^m E_i(p_i^m)$ gets maximised in the mutant direction. In Proposition 2 of AppendixA.1 I show that the emigration probability p_i evolves to 1 if the relative frequency of offspring born in a patch of type i that survive in the patch until the end of the dispersal season is smaller than the relative frequency of dispersers that survive dispersal and in a patch of type i until the end of the dispersal season. In Gyllenberg et al. (2016) we proved that the settlement strategy stays bounded away from 0. In Proposition 3 of AppendixA.1 I show further that non of the emigration probabilities can evolve to zero. For notational simplicity I omit the * in k_i^* and u_* in the remainder of the paper.

4.2. Stability of the singular strategy

Evolutionary stability of singular strategies in higher dimensions is analysed using the Hessian matrix of the invasion fitness $\mathbf{H} = [h_{ij}]$ that describes the local shape of the fitness landscape around the singularity. The singular strategy is a fitness maximum, locally evolutionarily stable, if the Hessian matrix is negative definite, a minimum if the matrix is positive definite and a saddle if indefinite. The elements of the Hessian matrix are

$$h_{ij} = \frac{\partial^2 R_m}{\partial d_i^m \partial d_j^m}\bigg|_{d^m=d^r=d^*},$$

for $i, j = 1, 2, 3$ where $\partial d_1^m = \partial p_1^m$, $\partial d_2^m = \partial p_2^m$ and $\partial d_3^m = \partial f_1^m$. Evaluated at the singularity the Hessian matrix is a diagonal matrix:

$$\mathbf{H} = \begin{pmatrix} h_{11} & 0 & 0 \\ 0 & h_{22} & 0 \\ 0 & 0 & h_{33} \end{pmatrix}.$$

In Proposition 4 of AppendixA.1 I prove that the eigenvalues h_{11} and h_{22} are negative. The third eigenvalue h_{33} is

$$h_{33} = \frac{\phi_1 k_1^m}{u_r \Pi_1^r} \frac{\partial^2 \Pi_1^m}{\partial f_1^{m2}} + \frac{\phi_2 k_2^m}{u_r \Pi_2^r} \frac{\partial^2 \Pi_2^m}{\partial f_1^{m2}} \bigg|_{d^m = d^r = d^*} = \frac{(\rho \, T \, \phi_1)^2}{u} \big(2 \, \phi_2 \, k_2 \, c_2 \, (c_2 - c_1) - (\phi_1 k_1 H_1 + \phi_2 k_2 H_2) \big) \tag{4}$$

(see (15) in Gyllenberg et al., 2016, with indices 1 and 2 interchanged), where H_j is $H(x_j T) = \frac{x_j T(\mathrm{e}^{x_j T}+1) - 2(\mathrm{e}^{x_j T}-1)}{x_j T(\mathrm{e}^{x_j T}-1)^2}$, which is positive for all $x_j T$ and in this case $x_j = (\rho \phi_1 f_1^* + \rho \phi_2 + \nu - \mu_j)$. Note that c_i and H_i are also evaluated at the singularity but I omit the * in the notation. If $c_1 \geq c_2$ or equivalently $\mu_1 \geq \mu_2$, then Eq. (4) is negative, which makes the Hessian matrix negative definite and the singularity a maximum of the fitness landscape. If the death rate in patches of type 2 is sufficiently higher than in patches of type 1, i.e., $\mu_2 > \mu_1$, then $c_2 > c_1$ and h_{33} may be positive such that the Hessian matrix is indefinite (see Fig. 1). An indefinite Hessian matrix makes the singularity invadable in some directions of trait space.

Whether a singular point is gradually reached by evolution, is determined by the Jacobian matrix of the selection gradient $\mathbf{J}$ (Leimar, 2005, 2009). It is derived by adding the matrix $\mathbf{Q}$ to the Hessian matrix $\mathbf{H}$. The elements of $\mathbf{Q}$ are

$$q_{ij} = \frac{\partial^2 R_m}{\partial d_i^m \partial d_j^r} \bigg|_{d^m = d^r = d^*}.$$

In the present model the Jacobian matrix $\mathbf{J} = \mathbf{H} + \mathbf{Q}$ is non-symmetric and real. The matrix $\mathbf{J}$ is negative definite, if its symmetric part $(\mathbf{J} + \mathbf{J}^\top)/2$ is negative definite. The singularity is strongly convergence stable if the Jacobian is negative definite (Leimar, 2009). If $\mathbf{J}$ is indefinite, convergence to the singular strategy depends on the mutational covariance matrix (Leimar, 2009). A singularity with a positive definite Jacobian matrix is repelling.

When the strongly convergence stable singularity is a saddle or minimum of the fitness function evolutionary branching may occur, i.e., two strategies emerge. In higher dimensions, it is not automatically guaranteed that the emerging strategies coexist. The coexistence of the emerging strategies is sustainable if the strategies can mutually invade each other and remain in the coexistence area (Geritz et al., 2016). I assume that the mutational covariance matrix is the identity matrix **Id**. To derive the sustainability condition after branching, derive the eigenvector z of $\mathbf{H}$ corresponding to the positive eigenvalue h_{33}. Normalise the eigenvector $z = (0, 0, 1)$ of h_{33} such that $z^\top \mathbf{Q} z = -2$. The eigenvector is $z = (0, 0, \sqrt{2}\sqrt{-q_{33}}/q_{33})$, which is real since $q_{33} = -\frac{1}{p_1\phi_1 + p_2\phi_2} \sum_{i=1}^{2} \frac{p_i\phi_i(\partial \Pi_i(f_1,1)/\partial f_1)^2}{\Pi_i(f_1,1)^2}\big|_{d^*}$ is negative. Further derive λ_1, the largest eigenvalue of $(\mathbf{Id} + 1/2\mathbf{Q}zz^\top)\mathbf{J}$. The two emerging strategies can persist, i.e., branching is evolutionary sustainable (the two coevolving strategies stay in the coexistence region) if

$$h_{33} > \lambda_1 \tag{5}$$

(Geritz et al., 2016).

4.3. Evolutionary outcomes

There exists no guarantee that system (3) has a solution of the form $d^* = (p_1^*, p_2^*, f_1^*, 1)$ with $0 < p_1^*, p_2^*, f_1^* < 1$. If system (3) has no solution, selection might push some traits to 1. Then, there may exist singularities of the form $d^* = (p_1^*, p_2^*, 1, 1)$ or $d^* = (1, p_2^*, f_1^*, 1)$ (or, $(p_1^*, 1, 1, f_2^*)$), *two dimensional singularities*, where the selection gradient of the traits that are 1 is positive at d^*. If even more traits are selected to be 1, there might exist a *one dimensional singularity* $d^* = (1, p_2^*, 1, 1)$ or $d^* = (p_1^*, 1, 1, 1)$, given that the selection gradient of the traits that are 1 is positive at d^*. Depending on the parameter values of the model all possible combinations occur. In the next sections I investigate the stability conditions of the four qualitatively different outcomes of the model analytically and add missing information through numerical investigations, which I present in Fig. 1.

4.3.1. Evolutionary outcome $(p_1^*, p_2^*, f_1^*, 1)$

System (3) may have a solution of the form $d^* = (p_1^*, p_2^*, f_1^*, 1)$. The three dimensional singularity occurs, inter alia, in regions where $\mu_2 > \mu_1$, i.e., where the patches with high expected disperser output are unsafer during the dispersal season (see Figs 1b-c). In Proposition 5 of AppendixA.1

I exclude that a unique three dimensional singularity of the form $d^* = (p_1^*, p_2^*, f_1^*, 1)$ occurs when $\mu_1 \geq \mu_2$. The stability conditions of d^* are derived by investigating the three dimensional Hessian and Jacobian matrix as explained in Section 4.2. Analytic results from Section 4.2 show that the Hessian matrix is either negative definite or indefinite at the singularity. In all numerical examples the three dimensional singularity is a unique and strongly convergence stable saddle of the fitness landscape, i.e., the Hessian matrix is indefinite and the Jacobian matrix negative definite. All explored examples fulfill (5) and hence branching is predicted sustainable (Geritz et al., 2016). Since, these examples are the first cases that predict sustainable branching in three dimensions, I investigated the evolutionary dynamics further using numerical simulations (see Section 5).

4.3.2. Evolutionary outcome $(p_1^*, p_2^*, 1, 1)$

As mentioned above, a two dimensional singularity $d^* = (p_1^*, p_2^*, 1, 1)$ may exist. Then the Hessian matrix reduces to a two-by-two diagonal matrix with elements h_{11} and h_{22}. In such scenarios the Hessian is negative definite ($h_{ii} < 0$ for $i = 1, 2$, see Proposition 4 in AppendixA.1) and hence the singularity is evolutionarily stable. The symmetric part of the Jacobian matrix evaluated at the singularity has a negative trace $(h_{11} + q_{11} + h_{22} + q_{22})/2 < 0$. The latter inequality is equivalent to

$$\sum_{i=1}^{2} -\frac{s_i\beta_i\phi_i\big((1-s_i)\beta_i\phi_i(2u + (1-p_i^*)s_i\beta_i\phi_i) + e^{T\mu_i}u(2p_j^* s_j\beta_j\phi_j + s_i\beta_i\phi_i)\Pi_i(1,1)\big)}{p_i^* u^2\left((1-p_i^*)(1-s_i)\beta_i\phi_i + e^{T\mu_i}u\Pi_i(1,1)\right)} < 0$$

with $i \neq j$. Since the trace of the symmetric part of the Jacobian is negative, the Jacobian can be negative definite or indefinite. In all scenarios of Fig. 1 where $(p_1^*, p_2^*, 1, 1)$ is singular the Jacobian is negative definite. Hence, for such scenarios the singularity is a strongly attracting fitness maximum.

4.3.3. Evolutionary outcome $(1, p_2^*, f_1^*, 1)$

If $d^* = (1, p_2^*, f_1^*, 1)$ is singular, then the Hessian matrix has diagonal elements h_{22} and h_{33}. The Hessian is negative definite as long as $\mu_1 \geq \mu_2$, since then also $c_1 \geq c_2$ holds (see Eq. (4)). In all examples presented in Fig. 1 the singularity $d^* = (1, p_2^*, f_1^*, 1)$ occurred in a region where $\mu_1 > \mu_2$ and therefore it is a fitness maximum. In Proposition 6 of AppendixA.1 I prove that the trace of the symmetric part of the Jacobian is negative. In the numerical examples presented in Fig. 1 the Jacobian is negative definite. Hence, also in this scenario the singularity is a strongly attracting fitness maximum.

4.3.4. Evolutionary outcome $(1, p_2^*, 1, 1)$

If a singularity is of the form $d^* = (1, p_2^*, 1, 1)$, then it is possible to derive an explicit expression for p_2^*, but for brevity I do not present it here. A scalar trait is locally evolutionarily stable, an local ESS, if the second derivative of fitness with respect to the mutant trait is negative, i.e., $h_{22} < 0$ (Geritz et al., 1998), which holds (see Proposition 4 in AppendixA.1). The singular emigration strategy from patches of type 2 is convergence stable (attracting) if $h_{22} + q_{22} < 0$ (Geritz et al., 1998). This is the case if

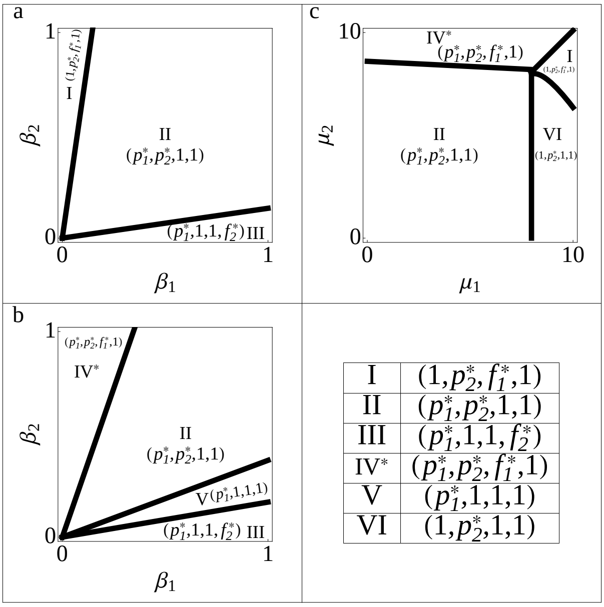
$$\begin{aligned} & h_{22} + q_{22}\big|_{f_1^*=f_2^*=p_1^*=1, p_2^m=p_2^r=p_2^*} = \\ & = -\frac{s_2\beta_2\phi_2(\beta_2\phi_2(1-s_2)e^{-T\mu_2}(\beta_2\phi_2 s_2(1-p_2^*)+2u)+u\Pi_2(1,1)(s_2\beta_2\phi_2+2s_1\beta_1\phi_1))}{p_2^* u^2((1-p_2^*)(1-s_2)\beta_2\phi_2 e^{-T\mu_2}+u\Pi_2(1,1))} < 0. \end{aligned}$$

Hence, when both settlement strategies and the emigration probability from patches of type 1 are 1 the singular emigration strategy from patches of type 2 is convergence stable and evolutionarily stable.

4.4. Effects of parameters β_i *and* μ_i

In this section I investigate the effects of the parameters β_i and μ_i on the evolutionary outcome and present them in two-parameter bifurcation diagrams (Fig. 1). I numerically solve system (3) and check if $\frac{\partial R_m}{\partial f_2^m}\big|_{f_2^m=f_2^r=f_2^*=1,^*} > 0$. From Proposition 1 of AppendixA.1 it is known that the patches with highest expected reproductive disperser output are always settled in, since no better patches can be encountered. If latter inequality is not fulfilled I check if $f_1^* = 1$ and $f_2^* < 1$, or if the singularity is two- or one-dimensional, making sure that all other gradients are positive at 1. Next, I derive the eigenvalues of the Hessian and Jacobian matrices. In regions I,II,III,V,VI of Fig. 1 singularities are strongly convergence fitness maxima and in region IV, sustainable evolutionary branching points.

First, I analyse the evolutionary outcomes in a constrained setting (see Fig.1a). Therefore I set the probabilities to survive until maturation, both patch-type death rates and the patch type frequencies equal ($s_1 = s_2$, $\mu_1 = \mu_2$ and $\phi_1 = \phi_2 = 0.5$), but vary the relative fecundities $\beta_1 \neq \beta_2$. When $\beta_1 \approx \beta_2$ the singularity is $(p_1^*, p_2^*, 1, 1)$. Individuals settle in the first patch they encounter, since the expected reproductive disperser outputs are similar. When $\beta_1 > \beta_2$ the singularity $p_1^* < p_2^*$, i.e., the higher the relative fecundity, the lower emigration from the patch. When β_2 increases the



I	$(1,p_2^*,f_1^*,1)$
II	$(p_1^*,p_2^*,1,1)$
III	$(p_1^*,1,1,f_2^*)$
IV*	$(p_1^*,p_2^*,f_1^*,1)$
V	$(p_1^*,1,1,1)$
VI	$(1,p_2^*,1,1)$

Figure 1: Two-parameter bifurcation diagrams for varied relative fecundities (a,b) and patch-death rates (c). Roman numbers as described in the lower right panel indicate the different evolutionary singularities. The singularities $(p_1^*, p_2^*, f_1^*, 1)$ are sustainable evolutionary branching points. The singularities $(p_1^*, p_2^*, 1, 1)$, $(1, p_2^*, f_1^*, 1)$ and $(p_1^*, 1, 1, f_2^*)$ are strongly convergence stable fitness maxima and the strategies $(1, p_2^*, 1, 1)$ and $(p_1^*, 1, 1, 1)$ are convergence stable maxima. Parameter values: $\rho = 3.3$, $T = 3$, $\nu = 10$, $s_1 = s_2 = 0.5$, $\phi_1 = 0.5$. a: $\mu_1 = \mu_2 = 2$; b: $\mu_1 = 2$, $\mu_2 = 8$. c: $\beta_1 = 0.1$, $\beta_2 = 0.25$;

settlement probability f_1^* decreases and p_1^* increases. The singularity is $d^* = (1, p_2^*, f_1^*, 1)$. All individuals emigrate from the patches of type 1. The relative frequency of offspring born in a patch of type 1 that survive in the patch until the end of the dispersal season is smaller than the relative frequency of dispersers that survive dispersal and in a patch of type 1 until the end of the dispersal season. Nevertheless individuals settle in the patches of type 1 with probability f_1^* upon encounter, since the expected reproductive disperser output is somewhat positive. If few individuals settle in the patches of type 1 competition is lower in the end of the dispersal season and the chance to establish in this patch is higher. Individuals emigrate from the patches of type 2 with a smaller probability, but always settle ($f_2^* = 1$) into patches of equal type. When parameters are chosen such that the relative fecundity in patches of type 1 is high and β_2 low the singular strategy is $d^* = (p_1^*, 1, 1, f_2^*)$, which is the opposite singularity of $d^* = (1, p_2^*, f_1^*, 1)$.

Scenarios where $s_1 \neq s_2$ with all other parameters set equal for all patches were also investigated, but a figure is not presented here since it does not qualitatively differ from Fig. 1a.

In scenarios where the patch-type dependent death rates μ_1 and μ_2 vary but all other parameters are equal the singular strategy is always $(p_1^*, p_2^*, 1, 1)$ (figure not shown). The p_i^* is higher in patches with higher μ_i and individuals settle in the first encountered patch, independently of how safe the patches are, since again k_1 and k_2 are similar and in the patches with high death rate during the dispersal season competition is lower at the end of the season.

Next, I consider scenarios where the β_is are varied and $\mu_1 \neq \mu_2$ (Fig. 1b). The asymmetries introduced through unequal μ_is create all qualitatively different outcomes. In Fig. 1b the regions II and III with singularities $d^* = (p_1^*, p_2^*, 1, 1)$ and $(p_1^*, 1, 1, f_2^*)$, respectively exist. With unequal μ_is and $\beta_2 > \beta_1$, p_2^* is sometimes bigger than p_1^*. A high μ_2 increases the chance of dying during the season in the patches with high expected disperser output and therefore more individuals emigrate from these patches. In region IV of Fig. 1b the patches with high expected reproductive disperser output have a high death rate during the dispersal season. The singularity is $(p_1^*, p_2^*, f_1^*, 1)$ (compare with Fig. 1a where a three dimensional singularity was absent) and a sustainable evolutionary branching point, where evolutionary diversification occurs. In region V of Fig. 1b the singularity is $(p_1^*, 1, 1, 1)$ (compare also with Fig. 1a where a one dimensional singularity was absent). Individuals emigrate from the patches of type 2 with probability 1 but nevertheless settle immediately into patches of any type upon encounter. Patches of type 1 are fully dispersed from and fully settled into, since individuals want to escape from the unsafe patches to gain a chance to encounter patches with high safety during the dispersal season.

Figures with varying β_is, unequal μ_is, s_is and ϕ_is are not shown, since also here the outcomes do not differ qualitatively as compared to Fig. 1b.

In Fig. 1c the μ_is are varied and $\beta_1 \neq \beta_2$. Regions I, II and IV are again encountered. When $f_1^* < 1$ the border between region I and IV is along the diagonal. When μ_1 in region IV increases and eventually exceeds μ_2, the emigration probability p_1^* moves to 1 (see Proposition 5 in AppendixA.1). In region VI the patches of type 1 are highly unsafe and the death rate of patches of type 2 low ($\mu_2 << \mu_1 < \nu$) and the singularity is $(1, p_2^*, 1, 1)$ (see Fig. 1c), which is the opposite singularity to $(p_1^*, 1, 1, 1)$.

5. Simulations

Simulations are performed for the following two reasons: (i) to test analytical/numerical predictions derived using Geritz et al. (2016) and (ii) to investigate the mono/dimorphic evolutionary outcome. That is, I investigate whether branching is sustainable in the simulations and explore which trait values evolve. Instead of running individual based simulations I iterate the metapopulation dynamics and infrequently insert mutants. Note that the simulations follow single individuals and mutant clans are not considered.

The establishment probability π_i of a mutant individual emerging from a patch of type i is (Durinx et al., 2008):

$$\pi_i(D, d^m) \approx \left[\frac{2 \log R_0}{\mathcal{B}} v_i\right]_+ ,$$

where R_0 is the dominant eigenvalue of the matrix $\mathbf{L} = [l_{ij}]$ that maps the metapopulation dynamics in real time, i.e., it maps the relative frequencies ϕ_i^j from one year to the next. The vectors u and v are the right and left eigenvectors of $\mathbf{L}$ belonging to its dominant eigenvalue R_0. The eigenvectors are normalised such that $\sum_{i=1}^2 u_i = 1$ and $v^\top u = 1$. The term $\mathcal{B}$ as given in Durinx et al. (2008) is $\mathcal{B} = \sum_{j,\,m,\,n=1}^2 u_j v_m v_n \mathbb{E}\big[\xi_{mj}(\xi_{nl} - \delta_{mn})\big]$. The matrix elements l_{ij} denote the expected number of offspring born in a patch of type i that are produced by an individual born in a patch of type j.

Since the habitat is structured in two different patch types the matrix is a 2x2-matrix:

$$\mathbf{L} = \begin{pmatrix} l_{11} & l_{12} \\ l_{21} & l_{22} \end{pmatrix},$$

where

$$l_{ii} = \frac{s_i \beta_i (1 - p_i^m) \mathrm{e}^{-\mu_i T}}{\beta_i (1 - p_i^m) \mathrm{e}^{-\mu_i T} + \sum\limits_{\iota=1}^{l} u_\iota \frac{\Pi_i(f^\iota)}{\phi_i}} + \beta_i s_i p_i^m \Pi_i(f^m) V_i^+(D)$$

and

$$l_{ij} = \beta_j s_j p_j^m \Pi_i(f^m) V_i^+(D) \qquad \text{for } i, j = 1, 2 \text{ and } i \neq j.$$

Note that I assume that B the number of offspring produced is large and I use V_i^+ instead of BV_i. The elements of the matrix $\mathbf{L}$ are the expectations of the random variables ξ_{ij}, the number of offspring born in a patch of type i that are produced by an individual born in a patch of type j, i.e., $\mathbb{E}(\xi_{ij}) = l_{ij}$. A focal single mutant individual in a patch of type i can have surviving offspring in two ways: (i) one of its non-dispersed offspring wins the natal site and becomes the single occupant there. Since there is only one natal site, the random variable is a Bernoulli-distributed random variable with parameter σ_i, and (ii) its dispersed offspring win k sites of type j elsewhere, where k is a Poisson distributed random variable with parameter ω_{ji}. Hence, the expectations of each of the diagonal elements of $\mathbf{L}$ is then $l_{ii} = \sigma_i + \omega_{ii}$ and the expectations of the off-diagonal elements are $l_{ij} = \omega_{ij}$ for $i \neq j$ and $i, j = 1, 2$ respectively. The term $\mathcal{B}$ can be rearranged to:

$$\begin{aligned} \mathcal{B} = \sum_{j,m,n=1}^{2} & u_j v_m v_n \mathbb{E}\big[\xi_{mj}(\xi_{nl} - \delta_{mn})\big] = \\ & v_1^2 \Big(u_1 \Big(\mathrm{Var}\big[\xi_{11}\big] + (l_{11} - 1) l_{11} \Big) + u_2 \Big(\mathrm{Var}\big[\xi_{12}\big] + (l_{12} - 1) l_{12} \Big) \Big) + 2 \Big(u_1 l_{11} l_{21} + u_2 l_{12} l_{22} \Big) v_1 v_2 \\ & + v_2^2 \Big(u_1 \Big(\mathrm{Var}\big[\xi_{21}\big] + (l_{21} - 1) l_{21} \Big) + u_2 \Big(\mathrm{Var}\big[\xi_{22}\big] + (l_{22} - 1) l_{22} \Big) \Big), \end{aligned}$$

with δ_{mn} being the Kronecker delta. The variances of the Bernoulli and Poisson distributed random variables in the above terms are $\mathrm{Var}\big[\xi_{ii}\big] = \sigma_i(1-\sigma_i)+\omega_{ii}$ for $i = 1, 2$ and $\mathrm{Var}\big[\xi_{ij}\big] = \omega_{ij}$ for $i, j = 1, 2$ and $i \neq j$, respectively.

In AppendixA.2 I describe how the simulations are implemented.

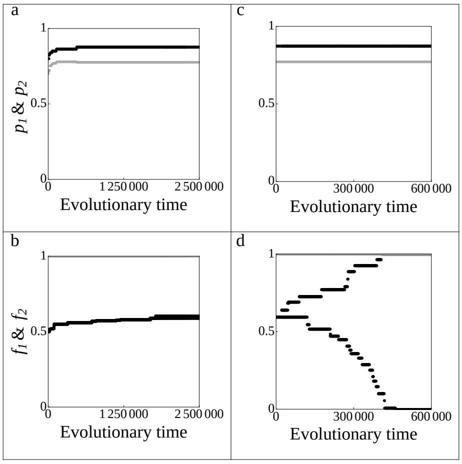


Figure 2: Simulations of the evolutionary dynamics of the patch-type dependent emigration and immigration traits. The black lines show the strategy p_1 (a,c) and f_1 (b,d), respectively. The grey lines show the strategy p_2 (a,c) and f_2 (b,d), respectively. The singularity is $d^* = (p_1^*, p_2^*, f_1^*, f_2^*) = (0.874, 0.774, 0.595, 1)$. In panel a & b the simulations started at $(p_1, p_2, f_1, f_2) = (0.8, 0.7, 0.5, 0.9)$ and mutations are distributed uniformly from the interval $[-0.012, 0.012]$. In panel c & d the simulations started at d^* and mutations are uniformly picked from $[-0.048, 0.048]$. Parameters: $\mu_1 = 2$, $\mu_2 = 8$, $s_1 = 0.5$, $s_2 = 0.8$, $\phi_1 = 0.35$, other parameters as in Fig. 1c.

5.1. Simulation results

Two representative simulation runs are presented in Fig. 2. The first analysis examined the theoretical predictions of the monomorphic evolution: I checked if a strategy with random initial values converges to the singularity $d^* = (p_1^*, p_2^*, f_1^*, f_2^*) = (0.874, 0.774, 0.595, 1)$, a sustainable evolutionary branching point (see figure legend of Fig. 2 for parameter values). Figs 2a and b show one representative example of the evolution of the emigration probabilities p_1 and p_2 (Fig. 2a) and settlement probabilities f_1 and f_2 (Fig. 2b) towards the singularity d^*.

Next, I started simulations at the singularity d^*, the sustainable evolutionary branching point and checked whether evolutionary diversification is sustainable. That is, both of the emerging branches remain in the coexistence region as they diversify, i.e., the population undergoes branching. The singularities of region IV derived in Section 4.4 all had a positive eigenvalue h_{33}. Therefore, I expect that if branching occurs, the settlement strategy f_1 diversifies. In the simulations the strategy f_1 always branched, which agrees with the theory of Geritz et al. (2016). Neither of the branches went extinct later on (Fig. 2d). When mutations are uniformly drawn from the interval $[-0.048, 0.048]$, evolutionary diversification of the settlement probability f_1 occurred relatively fast

(Fig. 2d). When mutations step sizes were small (uniformly drawn from $[-0.012, 0.012]$), evolutionary branching took a long time (see Fig. A.1 in AppendixA.3). The settlement probability into patches of type 2 remained 1 and the coevolving emigration strategies did not diversify (Figs 2c-d). The numerically derived coevolutionary outcome lead to two distinct populations with strategies $d_1^* = (p_1^{*d}, p_2^{*d}, f_1^{*d1}, f_2^{*d}) = (0.872, 0.776, 0, 1)$, a strategy never settling in patches of type 1 and the strategy $d_2^* = (p_1^{*d}, p_2^{*d}, f_1^{*d2}, f_2^{*d}) = (0.872, 0.776, 1, 1)$ accepting any type after encounter (dimorphic strategies are indicated with ^{d}; see Fig. 2c-d). Note that Fig. 2c shows constant emigration probabilities, $p_1 = 0.874$ and $p_2 = 0.774$. Here, the fitness landscape is relatively flat close by the singularity and stochasticity in the invasion process prevented mutants with different $p_i s$ from invasion during the 600.000 evolutionary time steps.

6. Discussion

The present study focused on a dispersing population inhabiting many patches of two types and investigated the coevolutionary outcome of patch-type dependent emigration and patch-type dependent immigration. It acts as an extension to the model of Gyllenberg et al. (2016), where emigration was fixed. Emigration is modelled as natal dispersal probability from a patch (p_i), but is allowed to mutate. Immigration is introduced as a mechanistic trait: a settlement probability upon encounter of a patch (f_i). The present study and Gyllenberg et al. (2016) are extensions of the Hamilton-May model (Hamilton and May, 1977) with three additional features: (i) the landscape is structured by many patches of two types, (ii) some individuals die before reproduction (s_i) and (iii) dispersal occurs in a continuous time season of certain length, during which immigration events are considered explicitly.

Dispersal is costly because of a high death rate in the dispersal pool (higher than in a patch) and since dispersers who do not settle until the end of the season die. Furthermore, the encounter of the desired patch is not guaranteed during the dispersal season (arrival is random, settlement not) and competitive weight of non-dispersers may be lacking to defend the natal patch. Dispersal however decreases kin competition in the patch and enables individuals to conquer new habitats with a high expected disperser output. Also empty patches (individuals in the preceding year did not survive until maturation) generate a selective driver promoting dispersal, as well as patches with low competition through high local patch-death rates during the season.

6.1. Evolution of emigration

In Gyllenberg et al. (2016) we expected the singular emigration strategy to keep the local optimal competitive weight at home and send away the remainder of the offspring (Ezoe and Iwasa, 1997; Kisdi, 2004; Gyllenberg et al., 2011a). In the present model fitness measures the number of mutant dispersers during a generation. I find that the singular strategy evolves to optimise the expected per-generation disperser output $p_i^* E_i(p_i^*)$ in the mutant direction. To conquer new habitat from which new offspring can be produced, individuals need to emigrate from the natal patch. The more individuals are sent away in one year the higher the chances of conquering new habitat. At the same time, the non-dispersers need to defend the natal patch (E_i is decreasing with the mutant dispersal strategy) so that new offspring's offspring gain an attempt to acquire more habitats from the natal patch. The attempts to conquer more habitats is repeated during all the years the natal patch is defended, i.e. during one generation.

Weigang and Kisdi (2015) investigated the evolution of dispersal in an unstructured Hamilton-May model when dispersal is under a trade-off with fecundity and not all individuals survive until reproduction. The study uses a fitness proxy in real time and finds that the singular emigration strategy optimally weights the number of non-dispersers and dispersers to defend the natal patch and win new patches, respectively (Weigang and Kisdi, 2015). In a special case, when (i) the probability to survive dispersal or (ii) until maturation is going to zero, competition vanishes in the natal site since no immigrants arrive. Then any positive number of non-dispersers defends the natal patch and hence the number of dispersers is solely optimised. The singular emigration strategy p^* is smaller than 1 because of the dispersal-fecundity trade-off and goes to 1 if the trade-off function is assumed constant. The present model agrees with their results for each patch of type i. Since here no trade-off is assumed, if (i) $s_i \to 0$, the expected number of years a family can defend its natal patch is 1. Then p_i is solely optimised resulting in all offspring emigrating from these patches, i.e., $p_i^* = 1$. When (ii) the dispersal death rate tends to infinity ($\nu \to \infty$) the probability to survive dispersal is zero and the term $E_i(p_i^*) \to 1/(1-s_i)$, which is the expected number of years individuals can defend their natal patch by surviving until maturation (no arriving competitors since they all die during dispersal). In this scenario p_i^* again evolves to a value that goes to 1, for the same reason as stated for the model of Weigang and Kisdi (2015) above. When $p_i^* = 1$, the expected number of years the patch is maintained is 1.

6.2. Evolutionary singularities

I showed that four qualitatively different evolutionary outcomes can occur in this model, including evolutionary branching points and strongly convergence stable fitness maxima. Dispersers always settle in the habitat with highest expected reproductive disperser output (assume in patches of type 2, i.e., $f_2^* = 1$). If other strategies choose to also settle in the same habitat, competition may be high and settlement in these habitats does not necessarily sheerly benefit the immigrants. Frequency dependence drives individuals to settle also in the patches with low expected reproductive disperser output, since competition may be lower there (patches less crowded). The emigration probabilities are always positive because of kin competition. The singularities are then either $(p_1^*, p_2^*, f_1^*, 1)$, or $(1, p_2^*, f_1^*, 1)$. If the expected reproductive disperser outputs are similar individuals settle in the first patch they encounter and the singularities are $(p_1^*, p_2^*, 1, 1)$ or, $(1, p_2^*, 1, 1)$. The latter strategy seems counterintuitive. When the patches have a relatively low β_1 and high μ_1 individuals all emigrate from such patches, but nevertheless accept them with full probability. Emigration is highest, since the relative frequency of offspring born in a patch of type 1 that survive in the patch until the end of the dispersal season is smaller than the relative frequency of dispersers that survive dispersal and in a patch of type 1 until the end of the dispersal season. They want to avoid the patches of poor type and gain a chance to encounter patches of best type. A high emigration probability increases the expected reproductive disperser output such that it is similar to the output in the best patches (i.e., $k_1 \approx k_2$). When the k_is are similar, strategies with full settlement into both patch types are singular.

In unstructured Hamilton-May models (Hamilton and May, 1977; Comins et al., 1980) emigration only evolves to 1 when the dispersal survival probability is 1, but trade-offs (Weigang and Kisdi, 2015) or a coevolving local adaptation trait (Kisdi, 2002) can select against full dispersal. However, in extensions of the Hamilton-May model where the landscape is structured in a continuous distribution of patch types and emigration is patch-quality and body-condition dependent, emigration is either 0 or 1 (Gyllenberg et al., 2011a,b). In case body-conditions were neglected in the latter models, intermediate emigration probabilities would evolve since then instead of sending individuals with particular body-conditions away, a fraction of ‘average individuals’ disperse.

6.3. Evolutionary branching

As mentioned above, when the patches with high disperser output are less safe than the patches with low disperser output and one settlement strategy is smaller than 1, the singularity is a saddle of the fitness landscape. Then, other strategies are fitter in some directions of trait space and the singularity is invadable. Using the novel criterion of Geritz et al. (2016), I find that all invadable singularities of the model are sustainable evolutionary branching points (see Fig. 1b & c), i.e., condition (5) is fulfilled. Sustainability guarantees that strategies remain in the coexistence region as they diversify (Geritz et al., 2016). Sustainable evolutionary branching points in three dimensions have never been exemplified before. To test the analytical/numerical predictions of the novel theory of Geritz et al. (2016), simulations were run. The settlement trait exhibits branching and the branches evolve to $(p_1^{*d}, p_2^{*d}, 0, 1)$ and $(p_1^{*d}, p_2^{*d}, 1, 1)$, respectively (see Fig. 2d). The settlement strategies of the dimorphic population (dimorphic strategies are indicated with ^{d}) evolved to the same values as in Gyllenberg et al. (2016) (see Gyllenberg et al., 2016, for further discussion), with one strategy settling only in the patches with high expected reproductive disperser output and the other strategy settling in any patch upon encounter. The emigration probabilities do not diversify since also in the dimorphic scenario $p_i^* E_i(p_i^*)$ is optimised in the mutant direction, independently of the individuals' settlement strategy. It is independent of how individuals got into a certain patch, but once present in a patch it is only important to make the optimal emigration choice. Note that the emigration probabilities of the dimorphic singularity are similar to the emigration probabilities of the monomorphic singularity (see Fig. 2c): The relative competitive weight of immigrants that arrives at every patch of type i in the monomorphic scenario ($l = 1$) is $u_r \frac{\Pi_i(f^r)}{\phi_i}$. The competitive weight in the dimorphic scenario is $\sum_{j=1}^{2} u_j \frac{\Pi_i(f^j)}{\phi_i}$. In the presented example of Fig. 2c-d the competitive weight of the dimorphic scenario is similar to the monomorphic weight and hence the function E_i varies little. Therefore, the singular emigration probabilities of the dimorphic scenario remain at similar values as compared to the monomorphic scenario. In Fig. 2c the small changes of the values of the emigration probabilities are not observed. The stochasticity in the invasion process prevented mutants from invasion during the first 600.000 evolutionary time steps.

The condition for a fitness saddle (positive righthand side of Eq.(4)) is similar to the branching condition (15) in Gyllenberg et al. (2016), with interchanged indices 1 and 2, where only immigration was evolving. However, in this model Eq. (4) is restricted to cases with singular emigration probabilities. Hence, the coevolution of a higher dimensional trait constrains the condition for fitness saddles and therefore sometimes hinders diversification. Note however that the fitness saddle needs to be sustainable in order for strategies to remain coexisting as they diversify. Doebeli and Ispolatov (2010), Svardal et al. (2014) and Débarre et al. (2014) claimed that the chance of diversification increases with trait dimensions. They investigated the eigenvalues of the Hessian matrix and showed that the occurrence of a positive eigenvalue increases with trait dimensions. A positive eigenvalue makes the singularity invadable at least in some directions of trait space. However, it does not necessarily lead to sustainable diversification. Hence, these studies should be revisited and the condition for sustainability derived. From the present study one can conclude that if trait dimensions increase starting from a scalar evolutionary branching point, higher trait dimensions constrain the conditions for (sustainable) branching and may make diversification scenarios less likely.

6.4. Sensing mistakes and density-dependent dispersal

The present study ignored time-dependent settlement decisions and assumed dispersal decisions without mistakes (see Gyllenberg et al., 2016, for further discussion). With sensing mistakes I expect the emigration probabilities of my model to be similar ($p_1^* \approx p_2^*$) since patch-types can then not be trusted much. The settlement probability f_1^* may however increase with inaccuracies, since it is still better to settle in a bad patch than to die in the dispersal pool.

Here, I disregarded density-dependent immigration and emigration. In a different metapopulation model with large patches, the patch state moving according to a deterministic dynamics in continuous time and connected through density-dependent emigration and settlement, bang-bang strategies are found (Metz and Gyllenberg, 2001). Full emigration occurs when the population density in the patch exceeds the carrying capacity and is 0 when the patch density is below carrying capacity. Settlement occurs only when patches are below carrying capacity. The singular density-dependent strategy is of the form $p^* = 1 - f^*$. In an extension of the metapopulation model of Metz and Gyllenberg (2001) with small-size patches settlement is again 1 if patches are below carrying capacity and 0 if above carrying capacity (Parvinen et al., 2012). However, emigration is changing in a non-monotonic way, where for some densities smaller than the carrying capacity the singularity is $p^* = 1$ and $f^* = 1$ (kin cooperation makes the individuals disperse from patches with densities below carrying capacity). Bang-bang strategies cannot occur in the present model, since only a single decision is allowed for each patch type and further every patch is infinitely good if no one settles ($B \to \infty$), which excludes $f_i = 0$ as part of a bang-bang strategy. The present study nevertheless finds scenarios with full emigration ($p_i^* = 1$) and full immigration ($f_i^* = 1$) into the patches with lower relative reproductive output (see discussed in Sect. 6.2).

The simulation study by Enfjäll and Leimar (2009) suggests a negative density-dependent dispersal relationship in a structured metapopulation model of Ricker-type with patches of different carrying capacities and nearest-neighbour dispersal. In their model high local growth beyond carrying capacity kills all individuals in a patch when the neighbouring mothers send too many individuals to the patch. High dispersal makes related individuals overcrowd patches and hence, dispersal is selected against. The study expects that negative density-dependent effects are lost if dispersal occurs randomly over the whole metapopulation, causing a decrease in kin competition of neighbours. In the present study dispersal is global, settlement is non-random and densities are above carrying capacities before competition. My model nevertheless indicates a negative relationship of emigration and relative densities: Emigration evolves to a high value when relative fecundity and survival until maturation are low (resulting in low densities after reproduction), i.e., scenarios where the strategy $(1, p_2^*, f_1^*, 1)$ is singular.

Recently, density-dependent and independent dispersal strategies were compared (Poethke et al., 2011). They find lower emigration and settlement in a density-dependent setting (see also Parvinen et al., 2012, for decreased emigration). The dispersers uninformed about densities settle in the first encountered habitat, unless dispersal mortality is close to zero. Another study showed that habitat-quality dependent emigration is higher than density-dependent emigration (Enfjäll and Leimar, 2009), but that a density- or quality-independent emigration probability evolves to highest values. In this paper the patch-independent emigration probability p^* is expected to be a weighted average of the probabilities p_1^* and p_2^*, and can hence be higher or lower than the patch-type dependent strategies.

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AppendixA.

AppendixA.1. Propositions

In this section the proofs of the analytical results are presented.

Proposition 1. *There exists no solution to the system*

$$\begin{cases} \frac{\partial R_m}{\partial p_i^m}\Big|_{d^m=d^r=d^*} = \frac{\phi_i s_i \beta_i}{u E_i(p_i^*)}\big(E_i(p_i^*) + p_i^* E_i'(p_i^*)\big) = 0 \quad for \quad i = 1,2, \\ \frac{\partial R_m}{\partial f_i^m} = \frac{\phi_1 k_1^m E_1(p_1^m)}{u_r \Pi_1(f^r) E_1(p_1^r)} \frac{\partial \Pi_1(f^m)}{\partial f_i^m} + \frac{\phi_2 k_2^m E_2(p_2^m)}{u_r \Pi_2(f^r) E_2(p_2^r)} \frac{\partial \Pi_2(f^m)}{\partial f_i^m}\Big|_{d^m=d^r=d^*} = 0 \quad for \quad i = 1,2 \end{cases} \tag{A.1}$$

and the singularity solves

$$\begin{cases} p_1^* = -\frac{E_1(p_1^*)}{E_1'(p_1^*)}, \\ p_2^* = -\frac{E_2(p_2^*)}{E_2'(p_2^*)}, \\ \frac{k_1^*}{f_1^*} = \rho T \gamma(f_1^*, 1) \end{cases} \tag{A.2}$$

with $\frac{\partial R_m}{\partial f_2^m}\Big|_{f_2^m=f_2^r=f_2^*=1,^*} > 0.$

Proof. The singularity condition for f_i^* from system (A.1) can be simplified to:

$$\frac{\partial R_m}{\partial f_i^m}\Big|_{d^m=d^r=d^*} = \frac{\phi_i s_i \beta_i p_i^*}{u f_i^*} - \frac{1}{u}\rho \phi_i T \gamma(f_1^*, f_2^*) = 0,$$

where γ was defined in the main text (see section 4).

Using the latter notations, I rewrite system (A.1) and obtain:

$$\begin{cases} p_1^* = -\frac{E_1(p_1^*)}{E_1'(p_1^*)}, \\ p_2^* = -\frac{E_2(p_2^*)}{E_2'(p_2^*)}, \\ \frac{k_1^*}{f_1^*} = \rho T \gamma(f_1^*, f_2^*), \\ \frac{k_2^*}{f_2^*} = \rho T \gamma(f_1^*, f_2^*). \end{cases} \tag{A.3}$$

The two singularity conditions for the singular settlement strategies f_1^* and f_2^* of system (A.3) have the same form as system (10) in Gyllenberg et al. (2016). In Gyllenberg et al. (2016) we showed that at least one of the two singular settlement strategies is 1 (see details in Gyllenberg et al. (2016)). Without loss of generality assume that $f_2^* = 1$. Then, the selection gradient with respect to f_2^m is positive at 1, i.e., $\frac{\partial R_m}{\partial f_2^m}\big|_{f_2^m=f_2^r=f_2^*=1,*} > 0$. The latter inequality is equivalent to $k_2^* > \rho T\gamma(f_1^*, 1)$ and at the singularity $k_2^* > k_1^*/f_1^* = \rho T\gamma(f_1^*, 1)$ is fulfilled. Then the singular strategy is of the form $d^* = (p_1^*, p_2^*, f_1^*, 1)$. It solves the system (A.2) (given that the gradient of the fitness function with respect to f_2^m for $f_2^m = f_2^r = f_2^*$ is positive at $f_2^* = 1$). ☐

Proposition 2. *The emigration probability evolves to one if the relative frequency of offspring born in a patch of type i that survive in the patch until the end of the dispersal season is smaller than the relative frequency of dispersers that survive dispersal and in a patch of type i until the end of the dispersal season.*

Proof. The emigration probability evolves to one if the gradient of p_i^m is positive at $p_i^m = p_i^r = 1$, i.e., $\frac{\partial R_m}{\partial p_i^m}\Big|_{p_i^m=p_i^r=1,*} > 0$. This is equivalent to

$$e^{-T\mu_i} s_i\beta_i\phi_i < u\,\Pi_i(f_1^*, f_2^*).$$

☐

Proposition 3. *The emigration probability p_i^* for $i = 1, 2$ cannot evolve to zero.*

Proof. Suppose that the emigration trait p_i is close to zero and the remaining traits are arbitrary. In the limit of $p_i \to 0$ the selection gradient of p_i^m is $\lim_{p_i\to 0} \frac{\partial R_m}{\partial p_i^m}\Big|_{p_i^m=p_i^r=p_i} = \frac{s_i\beta_i\phi_i}{s_j\beta_j\phi_j p_j}$ and positive for both $i, j = 1, 2$ and $i \neq j$. Hence, the emigration strategy cannot evolve to zero. ☐

Proposition 4. *The eigenvalues of the Hessian matrix are negative.*

Proof. The eigenvalues of the Hessian matrix are the elements from the diagonal, i.e., h_{11} and h_{22}. For $i = 1, 2$ the eigenvalue h_{ii} is of the form

$$h_{ii} = \frac{s_i\beta_i\phi_i(2\frac{\partial E_i^m}{\partial p_i^m} + p_i\frac{\partial^2 E_i^m}{\partial p_i^{m2}})}{u_r E_i^r}\Bigg|_{d^m=d^r=d^*}, \tag{A.4}$$

where the expression in parentheses of Eq. (A.4) is

$$2\frac{\partial E_i^m}{\partial p_i^m} + p_i \frac{\partial^2 E_i^m}{\partial p_i^{2m}}\bigg|_{d^m=d^r=d^*} = -\frac{2e^{T\mu_i} u\, s_i\, \beta_i\, \phi_i\, \Pi_i(f_1^*,1)\big((1-s_i)\beta_i\phi_i + e^{T\mu_i}\, u\,\Pi_i(f_1^*,1)\big)}{\big((1-p_i^*)(1-s_i)\beta_i\phi_i + e^{T\mu_i}\, u\,\Pi_i(f_1^*,1)\big)^3},$$

which is negative for $i = 1, 2$. Hence, both eigenvalues are negative. $\square$

Proposition 5. *There cannot exist a unique three dimensional strategy of the form* $(p_1^*, p_2^*, f_1^*, 1)$ *when* $\mu_1 \geq \mu_2$.

Proof. Assume that the settlement probability into patches of type 2 is 1, that f_1^* is singular and that $\mu_1 \geq \mu_2$. The selection gradient with respect to p_1^m is positive at $p_1^m = p_1^r = 1$ whenever:

$$\frac{\partial R_m}{\partial p_1^m}\bigg|_{p_1^m=p_1^r=1, p_2^*, f_1^*, f_2^*=1} > 0 \Leftrightarrow \frac{e^{-T\mu_1} s_1 \beta_1 \phi_1}{u \Pi_1(f_1^*, 1)} < 1.$$

I substitute the singularity condition of $f_1^* = \frac{k_1^*}{\gamma(f_1^*,1)\rho T}$ into the latter inequality and with some algebra I obtain

$$x_1 T \gamma(f_1^*, 1) < (1 - e^{-T x_1}) u, \tag{A.5}$$

where $x_1 = \rho(\phi_1 f_1^* + \phi_2) + \nu - \mu_1$. Use the definition of $\gamma(f_1^*, 1) = c_1\phi_1 k_1 + c_2 \phi_2 k_2$ and rewrite inequality (A.5):

$$x_1 T(c_1\phi_1 k_1 + c_2\phi_2 k_2) < (1 - e^{-T x_1}) u.$$

Since $\mu_1 \geq \mu_2$, also $c_1 \geq c_2$. Then

$$x_1 T(c_1\phi_1 k_1 + c_2\phi_2 k_2) < x_1 T(c_1\phi_1 k_1 + c_1\phi_2 k_2) = x_1 T c_1 u < (1 - e^{-T x_1}) u.$$

Latter inequality is fulfilled since $x_1 T c_1$ is smaller than $1 - e^{-T x_1}$ for positive $x_1 T$ and the selection gradient is positive at $p_1 = 1$. Hence, a unique strategy $(p_1^*, p_2^*, f_1^*, 1)$ cannot be singular. $\square$

Proposition 6. *The trace of the symmetric part of the Jacobian evaluated at the singularity* $d^* = (1, p_2^*, f_1^*, 1)$ *is negative.*

Proof. The trace of the symmetric part of the Jacobian at d^* is negative if

$$\frac{h_{22} + q_{22}}{2} + \frac{h_{33} + q_{33}}{2} < 0. \tag{A.6}$$

The first term of (A.6) can be rewritten as:

$$\frac{h_{22}+q_{22}}{2} = -\frac{s_2\beta_2\phi_2((1-s_2)\beta_2\phi_2(2u+(1-p_2^*)s_2\beta_2\phi_2) + e^{T\mu_2}u(2s_1\beta_1\phi_1 + s_2\beta_2\phi_2)\Pi_2(f_1^*,1))}{2p_2^* u^2((1-p_2^*)(1-s_2)\beta_2\phi_2 + e^{T\mu_2}u\Pi_2(f_1^*,1))},$$

which is negative.

The second term of (A.6) is negative if

$$\frac{h_{33}+q_{33}}{2} = -\frac{T^2\rho^2(H_1k_1^2\phi_1^4 + \phi_2(c_1k_1\phi_1(2c_2k_2 + c_1k_1\phi_1(1+\phi_1)) + k_2(c_2^2(k_2-k_1\phi_1^2) + H_2k_1\phi_1^2)\phi_2))}{2k_1u\,\phi_1} < 0. \tag{A.7}$$

Inequality (A.7) is fulfilled if $k_2 - k_1\phi_1^2 > 0$. Since f_1^* is singular and $f_2^* = 1$, i.e., $k_2 > \rho T\gamma(f_1^*, 1)$, it follows that

$$k_2 > k_1\phi_1^2 = f_1^*\rho T\gamma(f_1^*,1)\phi_1^2$$

is fulfilled since $1 > f_1^*\phi_1^2$. Hence, the trace of the symmetric part of the Jacobian is negative. □

AppendixA.2. Simulation details

To follow the theory of Geritz et al. (2016) closely, mutations arise in the population in line with the Lande's equation and not the canonical equation. For a given set of resident strategies, I iterate the metapopulation dynamics, i.e., the matrix $\mathbf{L}$, 200 times, such that the system reaches its steady state. I remove the strategies that decreased in relative frequency below 0.005 and repeat these two steps a second time. I randomly pick a resident strategy j with probability $1/l$, where l is the number of strategies present in the population and randomly pick one entry of the strategy vector $d = (p_1^j, p_2^j, f_1^j, f_2^j)$. The mutation step size is uniformly drawn from the interval $[-0.012, 0.012]$ or $[-0.048, 0.048]$ (see Fig. 2). If the mutated trait has a value higher than 1 or smaller than 0, I set it to 1 or 0, respectively. Next, I pick a random number from the unit interval. If this number is smaller than the frequency of strategy j in patches of type 1 relative to its total frequency $(\phi_1^j/(\phi_1^j + \phi_2^j))$ the mutant appears in patches of type 1 and the establishment probability $\pi_1(D, d^m)$ is derived. If the random number is bigger, the mutant appears in patches of type 2 and the establishment probability $\pi_2(D, d^m)$ is derived. If a random number from the unit interval is smaller than the probability $\pi_i(D, d^m)$, the mutant is allowed to invade and its frequencies are set to $0.1\phi_1^j$ in patch 1 and $0.1\phi_2^j$ in patch 2. The frequency of the resident strategy j gets reduced to $0.9\phi_1^j$ and $0.9\phi_2^j$, respectively. Then, the metapopulation dynamics is iterated twice as explained above before a new mutation occurs in the population. This procedure is iterated 600.000 to 12.000.000

times and denoted the evolutionary time scale.

AppendixA.3. Figure

See Fig. A.1.

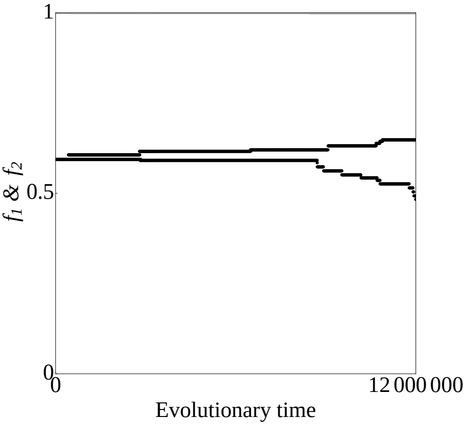

Figure A.1: Simulations of the evolutionary dynamics of the patch-type dependent emigration strategies. The black lines show the branching strategy f_1 and the grey line shows the strategy f_2. The simulation started at the singularity $d^* = (p_1^*, p_2^*, f_1^*, f_2^*) = (0.874, 0.774, 0.595, 1)$. Mutations are uniformly picked from $[-0.012, 0.012]$. Parameters: $\mu_1 = 2$, $\mu_2 = 8$, $s_1 = 0.5$, $s_2 = 0.8$, $\phi_1 = 0.35$, other parameters as in Fig. 1c.

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Article *IV*

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Coevolution of patch-type dependent immigration and local adaptation.

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Coevolution of patch-type dependent immigration and local adaptation

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† This paper is dedicated to the memory of Ilkka Hanski.

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Abstract

Landscapes are structured in a continuous distribution of patch types and dispersers choose to immigrate into patches where they are viable and locally adapt to the conditions they experience. Many theoretical dispersal models, however, assume that individuals can choose between two different patch types only, do not consider the mechanistic underpinning of immigration and neglect effects of adaptation. To study the coevolution of patch-type dependent immigration and local adaptation we construct a structured metapopulation model with explicit local population dynamics. Immigration is modelled as the settlement probability after encounter into a patch of certain type and assumed to be a function-valued trait. Local adaptation is implemented via an extra mortality rate representing maladaptation to the patch type. We derive the singular patch-type dependent immigration strategy and show that the population always accepts the patches it is best adapted to, settles with an intermediate probability in patches that would get overcrowded and rejects patches where maladaptation is high. We use the techniques of adaptive dynamics to predict evolutionary branching of the local adaptation trait. We present examples of the monomorphic and dimorphic evolutionary singularities, where two subpopulations with respective patch-type dependent immigration functions are locally adapted to different patch types.

Introduction

There are many reasons why natural selection, under certain conditions, favours dispersal. For instance, in heterogenous and fragmented landscapes dispersing individuals can track suitable local conditions and gain an advantage over sedentary ones by dispersing to a more favourable location. The decisions to emigrate and immigrate may depend on, for instance, resource availability, predator abundance, or habitat quality. Dispersal may also contribute to avoiding kin competition. Natural selection favours dispersal decisions that increase the individual's local adaptation.

Most theoretical work on dispersal assumes that dispersers choose their new habitat patch at random (Cohen and Motro, 1989; Comins et al., 1980; Hamilton and May, 1977). However, biological studies provide increasingly more evidence that immigration is non-random (Bowler and Benton, 2005; Clobert et al., 2009; Jacob et al., 2015). For instance, individuals of the Glanville fritillary butterfly (*Melitaea cinxia*) are adapted to lay their eggs on two different host plants and they base their settlement decisions on patch types (Hanski, 2011; Klemme and Hanski, 2009). Individuals of the moth species *Cactoblastits cactorum* investigate the resource quality of the patches into which they could potentially immigrate before they make a decision to land (Myers et al., 1981). Explicit habitat choice has led to spatially heterogeneous adaptations and genomic structures in e.g. Drosophilia. (Hey and Houle, 1987; Hoffmann, 1985; Jaenike, 1985; Jaenike and Holt, 1991).

The coevolution of local adaptation and dispersal, especially habitat choice, has long been studied theoretically. However, most published models are simply assuming movement between only two different habitats (see Ravigné et al., 2009, and the references therein). They assume that individuals carry one trait determining the local performance and a habitat choice trait measuring the preference for one patch type over the other. Habitat choice then describes the fraction of individuals settling in one habitat. In some models it is assumed that immigration depends on expected fitness (Armsworth and Roughgarden, 2005, 2008; Ruxton and Rohani, 1998), which could in principle be influenced by local adaptation. One-, two- or multilocus models have been used to investigate the interaction between genotype dependent habitat selection and within habitat fitness with patches of two types (Beltman and Haccou, 2005; Castillo-Chavez et al., 1988; de Meeûs et al., 1993; García-Dorado, 1986; Holt and Gomulkiewicz, 1997; Jaenike and Holt, 1991; Kawecki, 1997; Levins, 1963; Rausher, 1984; Rausher and Englander, 1987), when habitat choice depends on niche frequency (Hedrick, 1990), or includes assortative mating (Johnson et al., 1996). Habitat learning in a two patch scenario with a genetic habitat preference has been studied by Beltman and Metz (2005). There are some studies that model patch-type dependent immigration mechanistically (Baker and Rao, 2004; Doyle, 1975; Gyllenberg et al., 2016; Stamps et al., 2005; Ward, 1987; Weigang, submitted), but nevertheless structure the landscape only into two different patch types. So, almost all of the above mentioned studies either used a phenomenological approach to settlement, neglecting the phase of transience and search for a habitat or focused on two discrete patch types instead of a continuous patch-type distribution.

In this article we analyse the joint evolution of patch-type dependent immigration and local adaptation in an environment that is structured by a continuous distribution of patch types. We construct a structured metapopulation model which explicitly incorporates local population dynamics in the spirit of Gyllenberg and Hanski (1992), Hanski and Gyllenberg (1993) and Gyllenberg et al. (1997) (see also Gyllenberg and Metz, 2001; Gyllenberg et al., 2002; Parvinen, 2002; Parvinen and Seppänen, 2016). Immigration is modelled mechanistically as a probability to settle (Bonte et al., 2012; Clobert et al., 2009; Travis et al., 2012) in a patch upon encounter; it is a function-valued trait. Local adaptation is modelled via an additional mortality rate representing maladaptation to the local patch type. We use a basic reproduction number based fitness proxy and derive the monomorphic and dimorphic singularities of the function-valued patch-type dependent immigration trait, i.e., settlement probability, and the local adaptation strategy.

Ecological setting

We describe the dynamics of a population of asexually reproducing individuals living and dispersing in a heterogeneous and fragmented environment and subject to local catastrophes using the notion of a structured metapopulation (Gyllenberg and Hanski, 1992, 1997; Gyllenberg et al., 1997; Gyllenberg and Metz, 2001; Gyllenberg et al., 2002; Hanski and Gyllenberg, 1993; Parvinen, 2002). The landscape is assumed to consist of habitat patches of different types. The structuring variables are the type y of the patch and the size N of the local population inhabiting the patch. A local population is thus characterized by the pair (N, y) and the state of the metapopulation is, by definition, the distribution p of local population sizes and patch types. We assume that local catastrophes killing all the individuals in a patch happen at a given constant rate μ. Thus we can, and will, use the population age τ, defined as the time elapsed since the last catastrophe, as structuring variable instead of N. The corresponding distribution of local population age and patch type is denoted by q. The reason for choosing μ constant and not depending on patch type y and local population size N is twofold. Firstly, the phenomena that we want to explain by the model can be reproduced for constant μ and one should not make a model more complicated that necessary. Secondly, if μ is constant, then the age distribution of local populations is exponentially with the same parameter μ independently of the trait and type of the patch they are inhabiting. This considerably facilitates both the notation and the analysis.

The set Y of all admissible patch types is sometimes called the *niche axis* or *niche range*. We take Y as an interval of the real line.

In the Online appendix A.1 we present the structured metapopulation model that forms the starting point of our investigation and derive the corresponding metapopulation steady states. Here we only give the basic modelling assumptions and present the equations for the steady states. It is assumed that the local population does not affect the patch type and thus the patch-type distribution, denoted by n, is a given entity that does not change with time. We denote the per capita growth rate due to births and deaths by $g(N, y, \theta)$ and assume, as is clear from the notation, that it depends on the local population size N, the patch type y and a local adaptation trait θ. Patches are connected by dispersal. We assume that individuals leave their patch and enter the dispersal pool at a constant per capita emigration rate γ. Dispersing individuals may die at a per capita rate ν and they encounter patches for potential immigration at a rate α. Once they have encountered a patch they make a decision, based on the type y of the patch, to either settle down at the patch or to continue dispersal. This decision making is modelled by prescribing the probability $\psi(y)$ to settle down at a patch of type y upon encountering such a patch. The distribution of local population age and patch type at steady state is given by

$$q(\tau, y) = \mu n(y) l(\tau),$$

where

$$l(\tau) = e^{-\mu\tau}$$

is the probability that a local population has not been wiped out by a catastrophe until age τ. The immigration rate into a patch of type y at steady state is

$$I(y) = \frac{\alpha\psi(y)\hat{E}}{\alpha\bar{\psi} + \nu}, \tag{1}$$

where

$$\bar{\psi} = \int_Y \psi(y) n(y) dy$$

is the average probability of settlement upon encountering a patch in a population and

$$\hat{E} = \int_{Y} \int_{0}^{\infty} \gamma \, N(\tau, y) \, q(\tau, y) \, d\tau \, dy. \tag{2}$$

is the over-all emigration rate at steady state and $D = \frac{\hat{E}}{\alpha \bar{\psi} + \nu}$ gives the density of dispersers at steady state.

The size of a population of age τ inhabiting a patch of type y at metapopulation steady state is obtained by solving the ordinary differential equation

$$\frac{dN}{dt} = g(N, y, \theta) \, N - \gamma \, N + I(y) \tag{3}$$

describing local population growth with initial condition

$$N(0, y) = 0. \tag{4}$$

Notice that because $I(y)$ depends on $\hat{E}$ by (1), the same is true for the solution of (3) & (4). So substituting this solution into (2) one obtains an equation for $\hat{E}$. Once this equation has been solved, all the other formulas involving $\hat{E}$ become explicit expressions.

We now make the following choice for the growth function g:

$$g(N, y, \theta) = r\left(1 - \frac{N}{k}\right) - c(\theta - y)^2.$$

In words: we assume that, neglecting dispersal, local populations grow logistically with an extra death rate representing local maladaptation and large k. Recall that θ is the local adaption trait and the patch type y is thus identified as the local optimum of this trait.

The landscape may be inhabited by individuals playing different strategies. When there exist two subpopulations with densities $N_1(\cdot, y)$ and $N_2(\cdot, y)$ and strategies (ψ_1, θ_1) and (ψ_2, θ_2), respectively, the coupled local population dynamics at metapopulation steady state are given by

$$\begin{cases} \frac{dN_1(\tau,y)}{d\tau} = g(N(\tau,y),y,\theta_1)N_1(\tau,y) - \gamma N_1(\tau,y) + I_1(y), \\ \frac{dN_2(\tau,y)}{d\tau} = g(N(\tau,y),y,\theta_2)N_2(\tau,y) - \gamma N_2(\tau,y) + I_2(y). \end{cases} \tag{5}$$

The total population density in a patch of type y is $N(\tau,y) = \sum_{j=1}^{2} N_j(\tau,y)$, the initial conditions are $N_i(0,y) = 0$, the immigration rates are $I_i(y) = \frac{\alpha\psi_i(y)\hat{E}_i}{\alpha\bar{\psi}_i+\nu}$ and the densities of dispersers are $D_i = \frac{\hat{E}_i}{\alpha\bar{\psi}_i+\nu}$ for $i = 1,2$. The average number of emigrants per unit of time per patch of each of the two subpopulations are solutions to the equations:

$$\begin{cases} \hat{E}_1 = \int_Y \int_0^\infty \gamma N_1(\tau,y)q(\tau,y)\,d\tau\,dy, \\ \hat{E}_2 = \int_Y \int_0^\infty \gamma N_2(\tau,y)q(\tau,y)\,d\tau\,dy. \end{cases}$$

For our specific choice of g, the nonlinear system (5) of ordinary differential equations can actually be solved explicitly (see Online appendix A.2).

The most important parameters and variables of the model are listed in Table **??**.

Evolution

In this section we analyse the long-term eco-coevolution of patch-type dependent settlement and local adaptation within the framework of adaptive dynamics. The patch-type dependent settlement strategy is a function-valued strategy, viz. a function $\psi : Y \to [0,1]$, whereas the local adaptation trait is a number θ in Y. The trait is thus the pair (ψ,θ).

We assume that the resident metapopulation with trait (ψ,θ) has reached a steady state with over-all emigration rate $\hat{E}$. Assume now that a small mutation occurs, altering the trait to (ψ_m,θ_m). The mutant population finds itself in the environment shaped by the resident and may grow or decline, depending on its trait and the environmental conditions set by the resident.

The outcome of natural selection through mutations in a metapopulation is determined by the basic reproduction number (Gyllenberg and Metz, 2001; Metz and Gyllenberg, 2001), which is derived as follows: Assume that a mutant has arrived in a patch of type y and age T, the time since the last catastrophe, and initiates a local mutant population. The mutant population $M(\tau, y)$ grows in a patch of type y at rate $g(N(\tau, y), y, \theta_m)$, which depends on the resident population density and the mutated trait θ_m, and emigrates from the patch at a rate γ. The dynamics of the local mutant population is

$$\frac{dM(\tau, y)}{d\tau} = \big(g(N(\tau, y), y, \theta_m) - \gamma\big)M(\tau, y). \tag{6}$$

As long as the mutant is globally rare, immigration by more mutants is negligible and locally mutants interact with resident individuals only. Solving Eq. (6) we obtain the local mutant population

$$M(\tau, y) = M(T, y)\mathrm{e}^{\int_T^\tau (g(N(\zeta,y),y,\theta_m)-\gamma)d\zeta},$$

assuming no catastrophes between age T and τ. The probability that the local population still exists at age τ given that it survived to age T is:

$$\frac{l(\tau)}{l(T)} = \mathrm{e}^{-\mu(\tau - T)}.$$

The expected number of mutant dispersers that emigrate from a patch of type y per one mutant that arrived at patch age T in an environment set up by the resident is denoted by $F(T, y, \theta_m, \psi(y)D)$. It is the product of the probability that no catastrophe occurred between T and τ times the number of mutant emigrants produced during this time, integrated over τ:

$$F(T, y, \theta_m, \psi(y)D) = \int_T^\infty \mathrm{e}^{\int_T^\tau (g(N(\zeta,y),y,\theta_m)-\gamma-\mu)d\zeta}\gamma \, d\tau, \tag{7}$$

where F depends on $\psi(y)D$ via $N(\cdot, y)$. Note that F depends also on the resident θ via $N(\cdot, y)$, but this we suppress for brevity. The quantity

$$\rho(y, \theta_m, \psi(y)D) = \int_0^\infty \frac{q(T, y)}{n(y)} F(T, y, \theta_m, \psi(y)D)\, dT \tag{8}$$

is the expected number of mutant emigrants from a patch of type y in an environment set up by the resident with strategies ψ, θ and D.

The basic reproduction number of a mutant disperser is the probability that it survives dispersal until it enters a patch times the expected number of mutant dispersers produced over the lifetime of the patch:

$$R_m(\psi_m, \theta_m, \psi, \theta) = \frac{\alpha \int_Y \psi_m(y) n(y) \rho(y, \theta_m, \psi(y)D)\, dy}{\alpha \bar{\psi}_m + \nu}.$$

It measures the mutant's dispersing offspring and offsprings' offspring of a single mutant that initiated a mutant family in a patch that has not yet been destroyed by a local catastrophe. A mutant can invade if its basic reproduction number, i.e., *fitness*, is greater than 1. Note that for each resident, one needs to find the matching disperser number D using the condition that the basic reproduction number when the resident equals the mutant must equal 1, i.e., $R_m(\psi, \theta, \psi, \theta) = 1$.

In the next two sections we analyse the evolution of each trait separately and derive the dimorphic fitness measure, before we present examples of the monomorphic and dimorphic coevolutionary singularities in separate sections.

Evolution of patch-type dependent settlement

Let us assume that the settlement function ψ mutates and that $\theta_m = \theta$ is fixed. To find the singular immigration strategy we first assume that D is known.

We call a patch of type $y \in Y$ *not worthwhile* if $\rho(y, \theta, 0) < 1$ and denote the set of all such patch types by Y_0. An individual entering such a patch would not replace itself in the dispersal pool even in the absence of competition, because it suffers from maladaptation to the patch type, and therefore these patches should not be settled in. The set Y_0 depends on θ, but does not depend on the resident settlement strategy ψ.

In the remaining *worthwhile* patches, that is, patches of type $y \in Y \setminus Y_0$, the expected number of new dispersers in the absence of competition is $\rho(y,\theta,0) \geqslant 1$. It is easy to see that the expected number of mutant offspring from a patch ρ decreases with the immigration rate into a patch $\psi(y)D$: The function F depends on the resident strategy via $\psi(y)D$ hidden in $N(\cdot,y)$. At a fixed time T, the change of the local population density $N(T,y)$ increases with the immigration rate $\psi(y)D$ and hence the per-capita growth rate g decreases with $\psi(y)D$. As a result F decreases with $\psi(y)D$. From this follows that ρ decreases with $\psi(y)D$.

Some of the worthwhile patches are overcrowded if individuals settle with probability 1 such that the expected number of offspring produced from these patches declines below 1 ($\rho(y,\theta,D) < 1$). In the Online appendix A.3 we prove that in patches of this type that are in the set $Y_f := \{y : \rho(y,\theta,0) > 1 \,\&\, \rho(y,\theta,D) < 1\}$ an intermediate settlement strategy $0 < \psi(y) < 1$ is selected that solves $\rho(y,\theta,\psi(y)D) = 1$, and we denote the function that solves the latter equation by $f(y)$. The worthwhile patches of types in the set Y_f are *moderately beneficial* since a single individual is expected to produce only one emigrant after settlement.

Finally, there exists a second subset of worthwhile patches $Y_1 := \{y : \rho(y,\theta,D) > 1\}$. Individuals are most well adapted to patches of type $y \in Y_1$ and settle into them with probability 1. Therefore, we call these worthwhile patches *highly beneficial*. Note that the sets Y_1 and Y_f depend on the choice of the resident strategy ψ and its matching D.

In the Online appendix A.3 we prove that the resident with the strategy

$$\psi^*(y) = \begin{cases} 1 & \text{if } y \in Y_1, \\ f(y) & \text{if } y \in Y_f, \\ 0 & \text{if } y \in Y_0, \end{cases} \tag{9}$$

where the function f solves $\rho(y,\theta,f(y)D) = 1$ for $y \in Y_f$ and with D fulfilling $R_m(\psi^*,\theta,\psi^*,\theta) = 1$, is singular and a weak ESS. The shape of the singular settlement strategy is *hat*-like (see figs 1C-

E). Evolution selects for populations to settle in the patches that fit their optimum θ and reject the patches in which maladaptation is high.

Evolution of local adaptation

Let us assume that the local adaptation trait θ mutates and $\psi_m = \psi$ is fixed. We write fitness for short as $R_m(\theta_m, \theta)$ and assume further that D fulfils $R_m(\theta, \theta) = 1$. Since θ is a scalar we use the classical adaptive dynamics tools to derive the singular strategy and its stability properties (Geritz et al., 1998). Monomorphic evolution ceases at the singular strategy where

$$\left.\frac{\partial R_m(\theta_m, \theta)}{\partial \theta_m}\right|_{\theta_m=\theta=\theta^*} = \left.\frac{\alpha \int_Y \psi(y) n(y) \frac{\partial \rho(y,\theta_m,\psi(y)D)}{\partial \theta_m}\, dy}{\alpha \bar{\psi} + \nu}\right|_{\theta_m=\theta=\theta^*} = 0. \tag{10}$$

The singular strategy θ^* is a (local) fitness maximum (local ESS) if

$$\left.\frac{\partial^2 R_m(\theta_m, \theta)}{\partial \theta_m^2}\right|_{\theta_m=\theta=\theta^*} = \left.\frac{\alpha \int_Y \psi(y) n(y) \frac{\partial^2 \rho(y,\theta_m,\psi(y)D)}{\partial \theta_m^2}\, dy}{\alpha \bar{\psi} + \nu}\right|_{\theta_m=\theta=\theta^*} \tag{11}$$

is negative.

The singular strategy is locally convergence stable (attracts) if

$$\left.\frac{\partial^2 R_m(\theta_m, \theta)}{\partial \theta_m^2} + \frac{\partial^2 R_m(\theta_m, \theta)}{\partial \theta_m \partial \theta}\right|_{\theta_m=\theta=\theta^*} < 0. \tag{12}$$

A singularity violating the convergence stability condition is a repellor (Rep) and evolution leads away from such a singular point. If the singularity is an fitness maximum and convergence stable it is an attracting fitness maximum (CSS), an evolutionary endpoint. A singularity violating the local ESS condition but not the convergence stability condition is an evolutionary branching point (BP) (Geritz et al., 1998). Once the singularity of local adaptation has been found, ψ^* can be determined. Iterating the process to find θ^* to the given ψ^* the evolutionary singularity (ψ^*,θ^*) is obtained.

Dimorphic evolution

At a BP of the monomorphic evolution, evolutionary diversification of the local adaptation trait may occur and two subpopulations with densities $N_1(\cdot, y)$ and $N_2(\cdot, y)$ and strategies (ψ_1, θ_1) and (ψ_2, θ_2), respectively emerge. Furthermore the subpopulations come along with their matching disperser number D_1 and D_2 respectively and we write ρ as $\rho(y, \theta_m, \psi_1(y)D_1, \psi_2(y)D_2)$, where ρ also depends on θ_1 and θ_2 through the local population dynamics (cf. Eq. (7)). When the landscape is inhabited by two residents the dimorphic invasion fitness measure is:

$$R_m(\psi_m, \theta_m, \psi_1, \theta_1, \psi_2, \theta_2) = \frac{\alpha \int_Y \psi_m(y) n(y) \rho(y, \theta_m, \psi_1(y)D_1, \psi_2(y)D_2)\, dy}{\alpha \bar{\psi}_m + \nu}. \tag{13}$$

When we assume that the ψ_i functions are fixed the coevolutionary singularities θ_1^* and θ_2^* solve the equations:

$$\left. \frac{\partial R_m(\psi_i, \theta_m, \psi_1, \theta_1, \psi_2, \theta_2)}{\partial \theta_m} \right|_{\theta_m = \theta_i = \theta_i^*, \theta_j = \theta_j^*} = \left. \frac{\alpha \int_Y \psi_i(y) n(y) \frac{\partial \rho(y, \theta_m, \psi_1(y)D_1, \psi_2(y)D_2)}{\partial \theta_m}\, dy}{\alpha \bar{\psi}_i + \nu} \right|_* = 0, \tag{14}$$

where $|_*$ means evaluated at the singularity and are fitness maxima if:

$$\left. \frac{\partial^2 R_m(\psi_i, \theta_m, \psi_1, \theta_1, \psi_2, \theta_2)}{\partial \theta_m^2} \right|_* < 0 \tag{15}$$

for $i = 1$ and $i = 2$, where $i \neq j$, hold.

When the ψ_i functions are evolving, the singular strategies are found similarly to the monomorphic scenario, and the above conditions for the singular local adaptation strategies need also to be fulfilled.

Monomorphic evolutionary singularities

In the previous sections we presented conditions to derive the patch-type dependent settlement strategy ψ^*, the singular local adaptation strategy θ^* and find the matching disperser number D.

At the singular strategy of the settlement function the fitness measure $R_m(\psi^*, \theta, \psi^*, \theta) = 1$, which we rewrite as:

$$\int_{Y_1} n(y)(\rho(y, \theta, D) - 1)\, dy = \frac{\nu}{\alpha}. \tag{16}$$

In the following paragraphs we explain how to derive the monomorphic evolutionary singularities and present numerical examples. We discretised the patch-type space Y using a Chebyshev discretisation, assumed $Y = [-3, 3]$ and evaluated the integrals in Eq. (7) and (8) numerically assuming a maximum patch lifetime $T_{max} = 140$. The probability that a patch avoids a catastrophe until T_{max} is very small and therefore the numerical error caused by this truncation is negligible. The patch type distribution was chosen either a truncated Gaussian unimodal or bimodal curve (see fig. 1). The procedure to derive the eco-evolutionary singularities is as follows:

1. Pick a local adaptation trait value θ and an arbitrary value D.
2. For the given values θ and D find the set of highly beneficial patches Y_1.
3. Solve Eq. (16) for D numerically. Iterate step 2. and 3. until the matching pair D and Y_1 is found for the given value of θ.
4. Derive the set of moderately beneficial patch types Y_f and the function f by solving $\rho(y, \theta, f(y)D) = 1$ for $f(y)$ at every point $y \in Y_f$. Then ψ^* is known for the derived D and chosen θ.
5. With ψ^* known, solve Eq. (10) to find the singular local adaptation trait θ^*. If θ^* differs from θ, replace θ by θ^* and iterate the procedure (steps 1.-5.) to find the evolutionary singularity (ψ^*,θ^*).

Then, evaluate the stability conditions (11) and (12) at the singular local adaptation strategy θ^*. Note that we only look at the stability and evolutionary attraction of θ^* when ψ^* is fixed. We did not consider the coevolutionary dynamics of both traits simultaneously.

To begin with, we analysed the evolution of local adaptation only (fig. 1A), assumed that individuals settle in the first patch they encounter, independently of its type ($\psi(y) = 1$) and

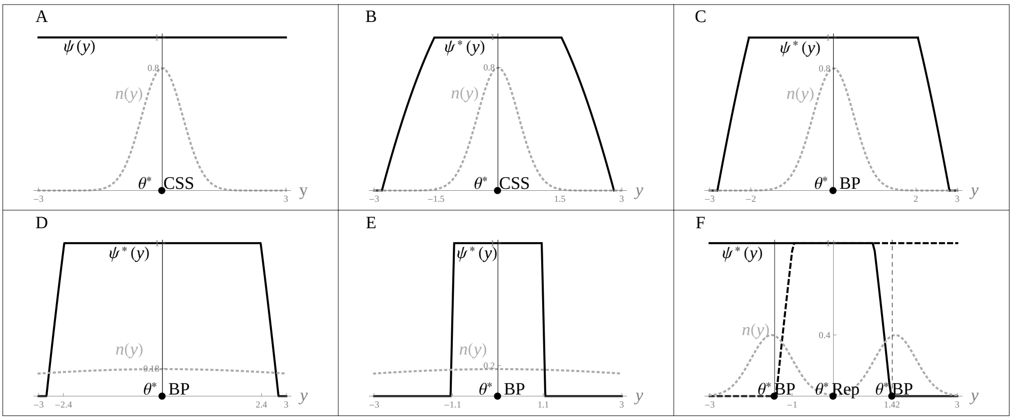

Figure 1: Numerical examples of the evolution of local adaptation θ^* (dots & vertical lines) where $\psi(y) = 1$ (black line) (A) and the evolutionary singularity of local adaptation θ^* and patch-type dependent settlement ψ^* (black lines, black dashed lines) (B-F). The dotted grey lines indicate the patch-type distribution $n(y)$. The singular patch-type dependent settlement strategy is a weak ESS for fixed θ^* and the singular local adaptation strategy $\theta^* = 0$ for the fixed ψ^* can be a CSS, evolutionary branching point (BP), or repellor (Rep). In F there exist two more singular local adaptation traits $\theta^* = \pm 1.42$, which are BPs. The patch-type distribution is a truncated Gaussian unimodal curve in A-E: $n(y) = \mathrm{e}^{-y^2/(2\sigma^2)} / \int_{-3}^{3} \mathrm{e}^{-\tilde{y}^2/(2\sigma^2)}\, d\tilde{y}$ and bimodal in F: $n(y) = (\mathrm{e}^{-(\tilde{y}+1.5)^2/(2\sigma^2)} + \mathrm{e}^{-(\tilde{y}-1.5)^2/(2\sigma^2)}) / \int_{-3}^{3} (\mathrm{e}^{-(\tilde{y}+1.5)^2/(2\sigma^2)} + \mathrm{e}^{-(\tilde{y}-1.5)^2/(2\sigma^2)})\, d\tilde{y}$. Parameter values: $\alpha = 1$, $k = 80$, $\mu = 0.1$, $\nu = 1$, $r = 8$, $Y = [-3, 3]$. A. $c = 1$, $\gamma = 2$, $\psi(y) = 1$, $\sigma = 0.5$, yielding $\hat{E} = 130.4$; B. $c = 1$, $\gamma = 2$, $\sigma = 0.5$, yielding $\hat{E} = 109.6$; C. $c = 1$, $\gamma = 0.5$, $\sigma = 0.5$, yielding $\hat{E} = 17.9$; D. $c = 1$, $\gamma = 2$, $\sigma = 5$, yielding $\hat{E} = 47.1$; E. $c = 6$, $\gamma = 2$, $\sigma = 5$, yielding $\hat{E} = 22.8$; F. $c = 1$, $\gamma = 2$, $\sigma = 0.5$, yielding $\hat{E} = 68.4$ (of $\theta^* = \pm 1.42$).

that patch-type abundance is unimodal. With the parameters used for fig. 1A the singular local adaptation trait θ^* matches the most abundant patch type and is a CSS, a stable evolutionary endpoint. When the encounter rate α is decreased the singular local adaptation strategy θ^* becomes an evolutionary branching point (BP) (fig. not shown). When the patch encounter rate α is low most dispersers die before encountering a patch and hence few individuals settle. Gene flow (mixing of individuals with different local adaptations) is reduced and therefore the individuals are selected to specialise.

The following examples allow patch-type dependent settlement to coevolve with local adaptation (see figs 1 B-F). The singular local adaptation strategy remains at the patch-type abundance peak (but see fig. 1F). Individuals with the singular strategy ψ^* always accept patches sufficiently similar to the patch type they are best adapted to (θ^*) and never accept patches that are too different from θ^*, with narrow patch type ranges in-between, in which they settle with an intermediate probability. Note that in some examples almost all patches are accepted (figs 1B-D; but see figs 1E-F).

The singular local adaptation trait θ^* is an evolutionary endpoint (CSS) in the example of fig. 1B, but a evolutionary branching point (BP) in fig. 1C. The difference between these examples is that in fig. 1C, the per capita emigration rate is lower. The population then branches because a lower emigration rate means a longer time in the same patch and also less gene flow from elsewhere, which selects against locally maladapted individuals and favours specialisation.

When individuals are confronted with a wider patch-type distribution (the width σ of the truncated Gaussian patch-type distribution is high, see fig. 1D) the evolved settlement strategy ψ^* accepts more patch types with probability 1 as compared to ψ^* that evolved for a narrow patch-type distribution. When the patch-type distribution is wider, fewer patches exist where adaptation is close to perfect (compare figs 1B & D). Hence, the over-all emigration rate from the patches decreases ($\hat{E} = 109.6$ in fig. 1B; $\hat{E} = 47.1$ in fig. 1D) and fewer patches are overcrowded, which selects for an increase in the settlement probability in these patches. The singular strategy θ^* is an evolutionary branching point (fig. 1D). The change of σ of the truncated Gaussian patch-type distribution changes the relative frequencies of patch types but does not change whether a patch is worthwhile. Hence, for the fixed θ^* the set of patches rejected by the weak ESS settlement strategy remains the same.

In fig. 1E the value of c is higher relative to fig. 1D and therefore the mortality of individuals increases faster with the difference between their trait θ and the within-patch optimum y. In such a case, the singular ψ^* is much narrower than in the other examples. More patch types are not worthwhile and hence do not get accepted by the individuals. The singular local adaptation strategy is a evolutionary branching point.

In addition, we analysed the effects of a bimodal patch-type distribution on the evolution of settlement and local adaptation (fig. 1F). In this scenario there exist three singularities. Two are attracting fitness minima (BP) and the middle one is an evolutionary repellor (Rep). At either of the evolutionary branching points the population may split into two subpopulations with different traits. When the population has the singular local adaptation trait value of the left singularity the evolved singular settlement strategy ψ^* settles in patches of type $y < 0$, accepts some types of patches $y > 0$ with intermediate probability, but patches of types $y >> 0$ are rejected and vice versa, the settlement strategy that belongs to the singularity on the right accepts the patches of type $y > 0$ and patches of types $y << 0$ are rejected, with a negative patch range where settlement is of intermediate probability. Notice that the non-zero singularities occur slightly off the peak of resource abundance. The singularities are shifted towards the centre, such that more patches are worthwhile.

In the above, BP denotes a singularity where the local adaptation trait undergoes evolutionary branching if the settlement function is held fixed at ψ^* for both emerging branches. In reality, the branches evolve their own settlement functions, and by doing so, they could in principle evolve such that one branch goes extinct while the branches are still in the vicinity of the singularity, which is not possible when only one trait evolves (see Geritz et al., 2016, for this ”failed branching” in trait spaces of finite dimensions). Here we do not pursue this problem but determine the possible endpoints of the joint evolution of local adaptation and the settlement strategy in dimorphic populations.

Dimorphic evolutionary singularities

We found the dimorphic singularity (ψ_1^*, θ_1^*) and (ψ_2^*, θ_2^*) with a numerical algorithm analogous to the monomorphic case (see the section “Monomorphic evolutionary singularities”) by using the equations $R_m(\psi_1^*, \theta_1, \psi_1^*, \theta_1, \psi_2^*, \theta_2) = 1$ and $R_m(\psi_2^*, \theta_2, \psi_1^*, \theta_1, \psi_2^*, \theta_2) = 1$ to obtain D_1 and D_2 and Eq. (14) to obtain the singular values of the local adaptation traits θ_1^* and θ_2^*. To investigate whether the singular local adaptation traits are evolutionarily stable we evaluate condition (15)

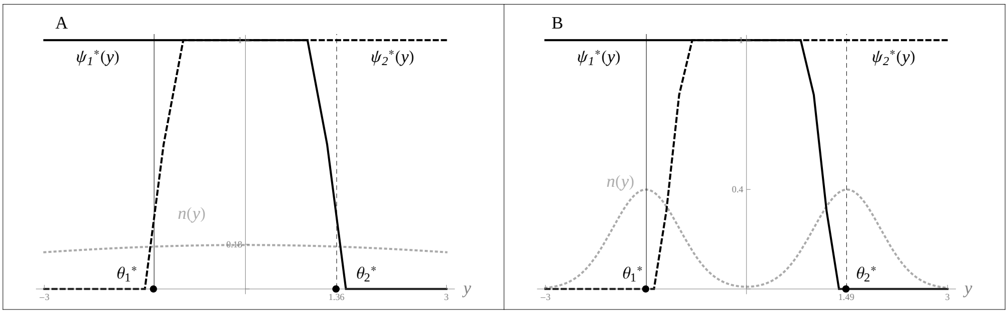

Figure 2: Numerical examples of the dimorphic coevolutionary singularity. The singular local adaptation traits are at the points θ_1^* and θ_2^* (dots & vertical lines) each subpopulation with the respective coevolved patch-type dependent immigration strategies ψ_1^* and ψ_2^*, respectively. A. $\theta_1^* = -1.36, \theta_2^* = 1.36$, yielding $\hat{E}_1 = \hat{E}_2 = 58.1$; B. $\theta_1^* = -1.49, \theta_2^* = 1.49$, yielding $\hat{E}_1 = \hat{E}_2 = 63.7$. All parameter values as in figs 1D & F, respectively.

for both $i = 1, 2$.

We present two examples of the coevolutionary singularities in figure 2. In fig. 2A we derived the dimorphic singularity of the example presented in fig. 1D. The monomorphic population did not settle in every patch, because of maladaptation. In the dimorphic scenario, however, every patch gets settled into by at least one subpopulation. The local adaptation trait of subpopulation 1 is $\theta_1^* < 0$ and therefore the subpopulation always settles into patches of type $y < 0$, since these are the patches it is most well adapted to. The patches that are of slight positive type are still always accepted. There exists a range of patch types individuals settle into with an intermediate probability and patches of type $y >> 0$ are never accepted. The competing subpopulation 2 behaves symmetrically. Around patch types $y = 0$ both subpopulations settle. The range of highly beneficial patch types for subpopulation 1 around the trait θ_1^* are moderately beneficial for the second subpopulation and therefore get accepted with a settlement probability smaller than 1. The singular local adaptation traits θ_1^* and θ_2^* are fitness minima and therefore the population may undergo further branching. The computation of higher order polymorphic singularities was computationally too demanding and therefore this type of *co-ESS* was not examined further.

The dimorphic singularity with a bimodal patch-type distribution population is shown in fig. 2B. Note that whereas in fig. 1F the ψ^* functions were alternative singularities in fig. 2B the strategies are both present in the metapopulation. The singular local adaptation trait θ_1^* is located left of the monomorphic singularity and its patch-type dependent settlement function shifted slightly to the left, as compared to the left monomorphic ψ^* function in fig. 1F. The local adaptation trait θ_2^* of the second subpopulation settled close to the second peak of the bimodal patch-type distribution. The ψ_i^* functions are of similar shape as explained in the example of fig. 2A with the difference that types of patches population 1 is most well adapted to are rejected by the competing subpopulation. In this scenario the singular local adaptation traits θ_1^* and θ_2^* are fitness maxima.

Discussion

In the present paper we derived the evolutionary singularity of local adaptation and patch-type dependent immigration in a continuous time metapopulation model with explicit local dynamics. Local adaptation was incorporated into the model via an extra mortality representing maladaptation, such that individuals were best adapted to a single patch type. Immigration was modelled mechanistically as the settlement probability after the encounter of a random patch. Patch types were continuously distributed making settlement a function-valued trait. Individuals evolved a strategy to settle in and exploit the types of patches they are well adapted to (Edelaar and Bolnick, 2012; Edelaar et al., 2008). The population always settles in patches where the expected number of disperser production exceeded 1. In some patches settlement evolves to an intermediate probability, because patches become overcrowded if too many individuals settle. In all other types of patches individuals are poorly adapted making the patches not worthwhile to accept and the settlement probability is 0, i.e., such patches get rejected and the individuals are absent from them. The range of not worthwhile patch types depends on the decrease of within-patch fitness when moving away from the local patch type optimum y (see Hanski and Mononen, 2011; Hanski et al., 2011; Lande and Shannon, 1996), i.e., on the costs of maladaptation.

Sharp limits of species' ranges in heterogeneous environments can be caused also by gene flow from central ranges that swamp the populations on the periphery leading to local maladaptation and local absence (Haldane, 1956; Kirkpatrick and Barton, 1997; Polechová and Barton, 2015). There has been empirical evidence, however, that random immigration can sometimes improve the ability to adapt to changing environments (Lawrence et al., 2016). Nevertheless, we expect non-random gene flow implemented as patch-type dependent settlement to decrease the swamping effect and allow the species' range to expand to more niches. If individuals that experience strong maladaptation, i.e., are distributed on a narrow range (see fig. 1E), were able to adapt better such that the strength of maladaptation is lowered (small c, see fig. 1D), the settlement strategy expands to a wider range (compare figs 1D-E).

Many studies have examined immigration incorporating habitat choice as one way of settlement after dispersal (de Meeûs et al., 1993; Ravigné et al., 2009). Habitat choice was modelled as the fraction of individuals sent to one patch or the other, or as a habitat preference, neglecting the costs of transfer and explicit patch encounters, and usually assumed that the spatially heterogeneous environment consists of two distinct patch types only. In some scenarios then individuals would fully exploit one habitat and leave the other completely empty (Ravigné et al., 2009). When settlement is a function-valued trait more types, where maladaptation is little, get accepted (see figs 1B-F). Whereas in habitat choice models individuals arrive where they want to be, in the present study it is not guaranteed that individuals encounter the patches they are most well adapted to, because of the mechanistic dispersal process and hence choose to settle in a continuous distribution of types. Holt and Barfield (2008) however, assumed that habitat selection depends on the phenotype and emigration occurs only when the expected conditions in the alternative habitat improve. When the environment is structured in a continuous distribution as presented here, instead of two discrete habitats as in Holt and Barfield (2008), it seems hard to predict before emigration which patch quality or type will be encountered, though it seems clear that the chance to encounter a more abundant type is higher.

In our model the patch-type abundance affects the singular local adaptation strategy, which evolves to match the unimodal patch-type distribution peak. Individuals settle into a patch only if the expected number of offspring produced is adequately high ($\geqslant 1$). Hence, even when the not worthwhile patches are relatively abundant, individuals reject such patches. In Hedrick (1990), however, habitat choice was made dependent on patch-type abundance, where patches of low abundance were chosen less likely. With our mechanistic approach of dispersal, not-worthwhile patches are always rejected independent of how frequent they are.

It is well known that a local adaptation trait branches or a polymorphism is protected (de Meeûs et al., 1993; Kisdi, 2002) when patches are of sufficiently different types or when mixing is hindered (low gene flow), i.e., when individuals experience a coarse grained environment (Levins, 1968; MacArthur and Levins, 1964) (see figs 1C-F). We assumed that if the local adaptation trait branches the settlement function becomes dimorphic as well and present examples of a coevolved dimorphism. With a continuous patch-type distribution as presented here we get a scenario in which every niche is accepted at least by one subpopulation. In patches where both populations are present competition may be higher, but local catastrophes set densities to zero and recolonisation, i.e., settlement, pays off. However, some patch ranges are accepted by only one strategy (see figs 2). In Ravigné et al. (2009) the dimorphic evolution leads to complete local adaptation of one population to one and another population to the other environment and habitat-choice evolved either to an intermediate value for both subpopulations (see Levene-type (Levene, 1953) and type 3 (Ravigné et al., 2004) model of Ravigné et al. (2009)), or individuals only settled in the patch they were adapted to and did therefore not interact (Dempster model (Dempster, 1955) of Ravigné et al. (2009)). Hence, in one of their models individuals did interact, whereas in another model they did not. When we have a dimorphism, however, the patch type ranges of the two subpopulations partially overlap, with ranges where each of the subpopulations occurs alone. Also in models that focused on patch-type dependent immigration (Gyllenberg et al., 2016) or emigration and immigration (Weigang, submitted) in a landscape with two types, the dimorphic coevolution lead both subpopulations to always settle in the best patch types, whereas one solely settled in the patches of worse type.

The season during which individuals are dispersing is time-limited and dispersal *per se* costs energy. Some studies have modelled how the acceptance of different habitats varies with time (Baker and Rao, 2004; Doyle, 1975; Levins, 1963; Stamps et al., 2005; Ward, 1987). They found that when niche acceptance is time-limited, individuals always accept the better type and also settle in the worse type as the dispersal time increases. These studies limit the investigation to two patch types and disregard the coevolution of local adaptation. If patch-type dependent settlement also depends on flight time a, the dispersal pool was age-structured, and the dispersal death rate increases with flight time $\nu(a)$, we expect the singular patch-type and flight-age dependent settlement probabilities to increase with flight age in patches where maladaptation is high. Once dispersal becomes too costly, i.e., survival in the dispersal pool is smaller than the expected number of dispersers emigrating from the encountered patch, individuals accept the patch to reset the dispersal flight time. So instead of dying in the dispersal pool, individuals settle even in patches where maladaptation is high and reproduce. Although the expected number of dispersers produced can be below one, the few newly produced dispersers may reach the dispersal pool and gain a chance to encounter a more worthwhile patch. Hence we expect the width of the *hat*-shape of the singular patch-type and flight-age dependent settlement strategy to expand and individuals to accept more patch types with flight age.

In the present paper we dealt with the coevolution of patch-type dependent immigration and local adaptation but neglected patch-type dependent emigration. In a model that investigated the coevolution of emigration and host-plant preference, the evolutionary outcome of emigration alone was not much affected when the coevolution of both traits were investigated (Hanski and Heino, 2003). This hints that emigration should also be considered under selection and made patch-type dependent. Then we expect emigration to evolve as a density-dependent bang-bang strategy (Gyllenberg and Metz, 2001). The bang-bang threshold of a density- and patch-type dependent emigration strategy may then be higher in better patch types.

Furthermore, future studies should bring phenotypic variability into focus, since it has been shown that body-condition variability in dispersal evolution causes differences in dispersal patterns of strong and weak individuals (Gyllenberg et al., 2008, 2011*a*,*b*). Such a body-condition context for immigration and habitat types are expected to greatly enrich our results. Body-condition could, e.g., be influenced by the match of the local adaptation trait of the individual and the patch type. In turn silver spoon effects may occur when body-conditions affect the competitive ability in the patch and strong dispersers settle in high quality patches (Stamps, 2006). Body-conditions could also affect the patch encounter rate, such that strong individuals have more chances to encounter patches during a season (Stamps, 2006). It does not seem straightforward to implement such variations and should be subject of further investigations. Diversification of local adaptation, however, seems likely since then more subpopulations could specialise and produce strong competitors.

Acknowledgments

This paper is dedicated to the memory of Ilkka Hanski who was an inspiration for us all and a collaborator of M.G. for almost thirty years. The research presented in this paper was initiated by discussions with Ilkka. We thank Hans Metz and Åke Brännström for comments on the manuscript. We acknowledge financial support by the Finnish Doctoral Programme in Computational Sciences (FICS), the Doctoral Programme in Mathematics and Statistics and the Academy of Finland.

Online appendix A

In this appendix we present the structured metapopulation model in detail and derive the steady state equations. We also show how to solve the dimorphic population dynamics and derive the singular settlement function ψ^*.

Online appendix A.1

We formulate the structured metapopulation along the lines of Gyllenberg and Hanski (1992) and Hanski and Gyllenberg (1993).

The patch-type distribution n is normalised by

$$\int_Y n(y)\,dy = 1. \tag{A.1.1}$$

Consistency requires that

$$\int_0^\infty p(t,N,y)dN = n(y)$$

for all time t and all $y \in Y$.

The assumptions about dispersal and immigration given in the main body of the text leads to the following expression for the immigration rate $I(t,y)$ at time t into a patch of type y:

$$I(t,y) = \alpha\psi(y)D(t).$$

Here $D(t)$ is the density of dispersers at time t.

The verbal description of the local population dynamics in a patch of type y given in the main body of the text translates into the following ordinary differential equation:

$$\frac{dN}{dt} = g(N,y,\theta)\,N - \gamma\,N + I(t,y). \tag{A.1.2}$$

Given the local population dynamics and the immigration rule above, the dynamics of the metapopulation is described by the following partial differential equation for the size distribution of local populations:

$$\frac{\partial}{\partial t}p(t,N,y)+\frac{\partial}{\partial N}\left(\left(g(N,y,\theta)\,N-\gamma\,N+I(t,y)\right)\right)p(t,N,y)\right)=-\mu p(t,N,y). \tag{A.1.3}$$

This equation has to be supplemented by the boundary condition

$$p(t,0,y)=\mu\int_0^\infty p(t,N,y)dN, \tag{A.1.4}$$

which simply states that when a catastrophe occurs the local population size in that patch is reset to zero.

Note that because the patch type distribution n is assumed to be fixed, y is not a dynamical variable but merely a label in Eq. (A.1.3) and the accompanying boundary condition (A.1.4).

The dynamics of the dispersers is given by

$$\frac{d}{dt}D(t)=\int_Y\int_0^\infty \gamma Np(t,N,y)dNdy-\left(\alpha\int_Y \psi(y)n(y)dy+\nu\right)D, \tag{A.1.5}$$

where ν is the per capita death rate of dispersers.

The equations (A.1.1) – (A.1.5) constitute the ecological model which is the starting point of our investigation.

Steady state solutions, that is, solutions independent of time, are found by putting the time derivatives in (A.1.3) and (A.1.5) equal to zero. This gives

$$D=\frac{\hat{E}}{\alpha\bar{\psi}+\nu} \tag{A.1.6}$$

for the density of dispersers at steady state and hence

$$I(y)=\frac{\alpha\psi(y)\hat{E}}{\alpha\bar{\psi}+\nu} \tag{A.1.7}$$

for the immigration rate into a patch of type y at steady state. Here

$$\bar{\psi} = \int_Y \psi(y)n(y)dy$$

is the average probability of settlement upon encountering a patch in a population where the individuals play settlement strategy ψ and

$$\hat{E} = \int_Y \int_0^\infty \gamma N p(N,y) dN dy \tag{A.1.8}$$

is the over-all emigration rate at steady state.

Finally, the steady state of the local population size and patch type distribution is

$$p(N,y) = \frac{1}{g(N,y,\theta)N + \gamma N + I(y)} e^{-\int_0^N \frac{\mu d\xi}{g(\xi,y,\theta)\xi + \gamma\xi + I(y)}}. \tag{A.1.9}$$

Recall from (A.1.7) that $I(y)$ depends on $\hat{E}$. So when the expression (A.1.9) for p is substituted into (A.1.8) one gets an equation for $\hat{E}$. Once this has been solved, (A.1.6), (A.1.7), and (A.1.9) become explicit expressions.

We now switch to use population age, that is, the time τ elapsed since the last catastrophe, as structuring variable instead of local population size N. The local population size $N = N(\tau, y)$, as a function of population age and patch type, is obtained by solving the ordinary differential equation (A.1.2) with initial condition $N(0,y) = 0$ and I given by (A.1.7). The equation for $\hat{E}$ becomes

$$\hat{E} = \int_Y \int_0^\infty \gamma \, N(\tau,y) \, q(\tau,y) \, d\tau \, dy,$$

where, as in the main text, $q(\tau, y)$ is the population age and patch type distribution at steady state.

With the choice

$$g(N,y,\theta) = r\left(1 - \frac{N}{k}\right) - c(\theta - y)^2 \tag{A.1.10}$$

for the local growth function g we get the following explicit expression for the size of local population of age τ inhabiting a patch of type y:

$$N(\tau,y) = \frac{2\, I(y)\sqrt{k}}{\sqrt{4I(y)r + k\beta(\theta,y)^2}\left(1 + \frac{2}{e^{\tau\frac{\sqrt{4I(y)r+k\beta(\theta,y)^2}}{\sqrt{k}}} - 1}\right) - \sqrt{k}\beta(\theta,y)}.$$

Here $\beta(\theta,y) = r - \gamma - c(\theta - y)^2$.

Online appendix A.2

Here, we derive the solution of the dimorphic local population dynamics. Since we focus on the dynamics of a single patch of type y, we shorten the notation $N_i(\tau,y)$, $I_i(y)$ and $N(\tau,y)$ to $N_i(\tau)$, I_i and $N(\tau)$, respectively.

The system of two non-linear ordinary differential equations is:

$$\begin{cases} \frac{dN_1(\tau)}{d\tau} = g(N(\tau),y,\theta_1)N_1(\tau) - \gamma N_1(\tau) + I_1, \\ \frac{dN_2(\tau)}{d\tau} = g(N(\tau),y,\theta_2)N_2(\tau) - \gamma N_2(\tau) + I_2, \end{cases} \tag{A.2.1}$$

with

$$\begin{cases} N_1(0) = 0, \\ N_2(0) = 0, \end{cases}$$

where $N(\tau) = \sum_{i=1}^{2} N_i(\tau)$ and g is the logistic growth rate as given in the main text (see also Eq. (A.1.10)). Let us shorten the notation further by writing $\beta_i = r - \gamma - c(\theta_i - y)^2$ for $i = 1,2$ and $\delta = \frac{r}{k}$:

$$\begin{cases} \frac{dN_1(\tau)}{d\tau} = (\beta_1 - \delta N(\tau))N_1(\tau) + I_1, \\ \frac{dN_2(\tau)}{d\tau} = (\beta_2 - \delta N(\tau))N_2(\tau) + I_2. \end{cases} \tag{A.2.2}$$

If we assume that $N(\tau)$ is known, we can solve the two equations and get:

$$\begin{cases} N_1(\tau) = I_1 \int_0^\tau \mathrm{e}^{\beta_1(\tau - s)} \mathrm{e}^{-\delta \int_s^\tau N(\sigma)\, d\sigma} ds, \\ N_2(\tau) = I_2 \int_0^\tau \mathrm{e}^{\beta_2(\tau - s)} \mathrm{e}^{-\delta \int_s^\tau N(\sigma)\, d\sigma} ds. \end{cases} \tag{A.2.3}$$

Then the total population size in a patch at time τ is:

$$N(\tau) = \int_0^\tau \left(I_1 \mathrm{e}^{\beta_1(\tau - s)} + I_2 \mathrm{e}^{\beta_2(\tau - s)} \right) \mathrm{e}^{-\delta \int_s^\tau N(\sigma)\, d\sigma} ds.$$

We define

$$\begin{aligned} K(\tau) &= I_1 \mathrm{e}^{\beta_1 \tau} + I_2 \mathrm{e}^{\beta_2 \tau} \quad \text{and} \\ X(\tau) &= \mathrm{e}^{\delta \int_0^\tau N(\sigma)\, d\sigma} ds. \end{aligned} \tag{A.2.4}$$

It follows that $\frac{dX(\tau)}{d\tau} = \delta N(\tau) X(\tau)$ with $X(0) = 1$ and

$$N(\tau) = \int_0^\tau K(\tau - s) \frac{X(s)}{X(\tau)}\, ds.$$

We substitute the latter into the derivative of Eq. (A.2.4) and get

$$\frac{dX(\tau)}{d\tau} = \delta \int_0^\tau K(\tau - s) X(s)\, ds. \tag{A.2.5}$$

Then we take the Laplace transform on both sides of Eq. (A.2.5) and write the Laplace transform as $\hat{X}(\lambda)$. We get:

$$\lambda \hat{X}(\lambda) - X(0) = \delta \left(\frac{I_1}{\lambda - \beta_1} + \frac{I_2}{\lambda - \beta_2} \right) \hat{X}(\lambda),$$

which we solve for $\hat{X}(\lambda)$:

$$\hat{X}(\lambda) = \frac{1}{\lambda - \delta\left(\frac{I_1}{\lambda-\beta_1} + \frac{I_2}{\lambda-\beta_2}\right)} = \frac{(\lambda-\beta_1)(\lambda-\beta_2)}{\lambda(\lambda-\beta_1)(\lambda-\beta_2) - \delta I_1(\lambda-\beta_2) - \delta I_2(\lambda-\beta_1)}. \tag{A.2.6}$$

Since the Laplace transform is a rational function in λ, its inverse can be calculated explicitly. It is

$$X(\tau) = \frac{\mathrm{e}^{\tau\lambda_1}(\lambda_1-\beta_1)(\lambda_1-\beta_2)}{(\lambda_1-\lambda_2)(\lambda_1-\lambda_3)} - \frac{\mathrm{e}^{\tau\lambda_2}(\lambda_2-\beta_1)(\lambda_2-\beta_2)}{(\lambda_1-\lambda_2)(\lambda_2-\lambda_3)} + \frac{\mathrm{e}^{\tau\lambda_3}(\lambda_3-\beta_1)(\lambda_3-\beta_2)}{(\lambda_1-\lambda_3)(\lambda_2-\lambda_3)},$$

where λ_i are the roots of the denominator of Eq. (A.2.6). The roots are real because I_1 and I_2 are positive rates. We write $\mathrm{e}^{-\delta\int_s^\tau N(\sigma)\,d\sigma} = \frac{X(s)}{X(\tau)}$ and using the latter we rewrite system (A.2.3) and get

$$\begin{cases} N_1(\tau) = I_1 \int_0^\tau \mathrm{e}^{\beta_1(\tau-s)} \frac{X(s)}{X(\tau)} ds, \\ N_2(\tau) = I_2 \int_0^\tau \mathrm{e}^{\beta_2(\tau-s)} \frac{X(s)}{X(\tau)} ds. \end{cases}$$

Hence, the solution to the dimorphic local population dynamics, system (A.2.2), is:

$$\begin{cases} N_1(\tau) = \frac{I_1(\mathrm{e}^{\lambda_1\tau}(\lambda_1-\beta_2)(\lambda_2-\lambda_3) - \mathrm{e}^{\lambda_2\tau}(\lambda_2-\beta_2)(\lambda_1-\lambda_3) + \mathrm{e}^{\lambda_3\tau}(\lambda_3-\beta_2)(\lambda_1-\lambda_2))}{\mathrm{e}^{\lambda_1\tau}(\lambda_1-\beta_1)(\lambda_1-\beta_2)(\lambda_2-\lambda_3) - \mathrm{e}^{\lambda_2\tau}(\lambda_2-\beta_1)(\lambda_2-\beta_2)(\lambda_1-\lambda_3) + \mathrm{e}^{\lambda_3\tau}(\lambda_3-\beta_1)(\lambda_3-\beta_2)(\lambda_1-\lambda_2)}, \\ N_2(\tau) = \frac{I_2(\mathrm{e}^{\lambda_1\tau}(\lambda_1-\beta_1)(\lambda_2-\lambda_3) - \mathrm{e}^{\lambda_2\tau}(\lambda_2-\beta_1)(\lambda_1-\lambda_3) + \mathrm{e}^{\lambda_3\tau}(\lambda_3-\beta_1)(\lambda_1-\lambda_2))}{\mathrm{e}^{\lambda_1\tau}(\lambda_1-\beta_1)(\lambda_1-\beta_2)(\lambda_2-\lambda_3) - \mathrm{e}^{\lambda_2\tau}(\lambda_2-\beta_1)(\lambda_2-\beta_2)(\lambda_1-\lambda_3) + \mathrm{e}^{\lambda_3\tau}(\lambda_3-\beta_1)(\lambda_3-\beta_2)(\lambda_1-\lambda_2)}. \end{cases}$$

Using the definitions of β_i and δ, we can explicitly write the solutions of system (A.2.1).

Online appendix A.3

We assume that there exists a positive density of any type of patch $n(y) > 0$ for all $y \in Y$. We focus on the settlement strategy ψ, assume that $\theta_m = \theta$ is fixed, write ρ as $\rho(y, \psi(y)D)$ and $R_m(\psi_m, \theta, \psi, \theta)$ as $R_m(\psi_m, \psi)$. Recall the definitions from the main text: $Y_0 := \{y : \rho(y, 0) < 1\}$ is the set of not worthwhile patches, $Y_f := \{y : \rho(y, 0) > 1 \,\&\, \rho(y, D) < 1\}$ is the set of worthwhile but moderately beneficial patches and $Y_1 := \{y : \rho(y, D) > 1\}$ is the worthwhile and highly beneficial patch type set for a resident with strategy ψ and dispersal number D.

Proposition 1. *The patch-type dependent settlement strategy*

$$\psi^*(y) = \begin{cases} 1 & \text{if } y \in Y_1, \\ f(y) & \text{if } y \in Y_f, \\ 0 & \text{if } y \in Y_0, \end{cases} \tag{A.3.1}$$

where f solves $\rho(y, f(y)D) = 1$ for all $y \in Y_f$ and D solves $R_m(\psi^*, \psi^*) = 1$, is a weak ESS.

Proof. The fitness of the mutant with strategy $\psi + h$ in an environment set up by the resident with strategy ψ and dispersal number D is:

$$R_m(\psi + h, \psi) = \frac{\int_Y \alpha(\psi(y) + h(y))n(y)\rho(y, \psi(y)D)\, dy}{\alpha \int_Y (\psi(y) + h(y))n(y)\, dy + \nu}.$$

The mutant invades if $R_m(\psi + h, \psi) - R_m(\psi, \psi) > 0$. So, invasion is possible if:

$$\begin{aligned}
&R_m(\psi + h, \psi) - R_m(\psi, \psi) = \\
&\quad = \frac{\alpha \int_Y (\psi(y) + h(y))n(y)\rho(y, \psi(y)D)\, dy}{\alpha(\bar{\psi} + \bar{h}) + \nu} - \frac{\alpha \int_Y \psi(y)n(y)\rho(y, \psi(y)D)\, dy}{\alpha\bar{\psi} + \nu} = \\
&\quad = \frac{(\alpha\bar{\psi} + \nu)\alpha \int_Y \psi(y)n(y)\rho(y, \psi(y)D)\, dy - (\alpha(\bar{\psi} + \bar{h}) + \nu)\alpha \int_Y \psi(y)n(y)\rho(y, \psi(y)D)\, dy}{(\alpha(\bar{\psi} + \bar{h}) + \nu)(\alpha\bar{\psi} + \nu)} \\
&\qquad + \frac{\alpha \int_Y h(y)n(y)\rho(y, \psi(y)D)\, dy}{\alpha(\bar{\psi} + \bar{h}) + \nu} = \\
&\quad = \frac{-\alpha\bar{h}}{\alpha(\bar{\psi} + \bar{h}) + \nu} \underbrace{\frac{\alpha \int_Y \psi(y)n(y)\rho(y, \psi(y)D)\, dy}{\alpha\bar{\psi} + \nu}}_{=1} + \frac{\alpha \int_Y h(y)n(y)\rho(y, \psi(y)D)\, dy}{\alpha(\bar{\psi} + \bar{h}) + \nu} = \\
&\quad = \frac{-\alpha \int_Y h(y)n(y)\, dy}{\alpha(\bar{\psi} + \bar{h}) + \nu} + \frac{\alpha \int_Y h(y)n(y)\rho(y, \psi(y)D)\, dy}{\alpha(\bar{\psi} + \bar{h}) + \nu} = \\
&\quad = \frac{\alpha \int_Y h(y)n(y)(\rho(y, \psi(y)D) - 1)\, dy}{\alpha(\bar{\psi} + \bar{h}) + \nu} > 0
\end{aligned} \tag{A.3.2}$$

with $\bar{\psi} = \int_Y \psi(y)n(y)\, dy$ and $\bar{h} = \int_Y h(y)n(y)\, dy$. The denominator of (A.3.2) is always strictly positive (h is admissible only if $\psi(y) + h(y)$ is non-negative for all y). Hence the condition for invasion being possible is equivalent to

$$\int_Y h(y)n(y)(\rho(y, \psi(y)D) - 1)\, dy > 0, \tag{A.3.3}$$

for D being the matching disperser number of the resident.

1. Suppose that $\int_{Y_0} \psi(y)n(y)\, dy > 0$, i.e., the resident accepts some of the non-worthwhile patches. Let a mutant arise with strategy $\psi + h$ where

   $$h(y) = \begin{cases} -\epsilon\psi(y) & \text{if } y \in Y_0, \\ 0 & \text{otherwise.} \end{cases}$$

   This choice represents an admissible mutant strategy ($\psi(y) + h(y) \geqslant 0$ for all y). Substituting into the left hand side of (A.3.3) yields

   $$-\epsilon \int_{Y_0} \psi(y)n(y)(\rho(y, \psi(y)D) - 1)\, dy. \tag{A.3.4}$$

   Since $\rho(y, 0) < 1$ for all $y \in Y_0$ and ρ is decreasing in its second argument $\rho(y, \psi(y)D) - 1 < 0$ for all $y \in Y_0$. It follows that (A.3.4) is positive, i.e., the mutant can invade and the resident cannot be an ESS. Mutants with smaller settlement probabilities in patches of type $y \in Y_0$ invade and the strategy evolves to 0 in the not worthwhile patches.

2. Suppose that $\int_{Y_1} (1 - \psi(y))n(y)\, dy > 0$, i.e., the resident rejects, or only sometimes settles in some of the highly beneficial patches. Take the mutant strategy that has the following strategy: $\psi_m = \psi + h$ with

   $$h(y) = \begin{cases} \epsilon\big(1 - \psi(y)\big) & \text{if } y \in Y_1, \\ 0 & \text{otherwise.} \end{cases}$$

This choice represents an admissible mutant strategy ($\psi(y) + h(y) \leqslant 1$ for all y). Substituting h into the left hand side of (A.3.3) yields

$$\epsilon \int_{Y_1} (1 - \psi(y))n(y)(\rho(y, \psi(y)D) - 1)\, dy. \tag{A.3.5}$$

Since for highly beneficial patches $\rho(y, D) > 1$ holds and ρ is decreasing in its second argument: $\rho(y, \psi(y)D) \geqslant \rho(y, D) > 1$. It follows that (A.3.5) is positive, i.e., the mutant can invade and the resident cannot be an ESS. Mutants invade that accept the highly beneficial patches with a higher probability and the settlement strategy evolves to 1 in these patches.

3. Let us define the set $Y_{f,1} := \{y : \rho(y, \psi(y)D) > 1 \,\&\, \rho(y, D) < 1\}$ and assume that $\int_{Y_{f,1}} n(y)\, dy > 0$ holds. Hence, the resident accepts the moderately beneficial patches with probability $\psi(y) < f(y)$ for $y \in Y_{f,1}$. Take a mutant with strategy $\psi + h$ where

$$h(y) = \begin{cases} \epsilon(1 - \psi(y)) & \text{if} \quad y \in Y_{f,1}, \\ 0 \quad \text{otherwise.} \end{cases}$$

Substituting h into (A.3.3) yields:

$$\epsilon \int_{Y_{f,1}} (1 - \psi(y))n(y)(\rho(y, \psi(y)D) - 1)\, dy. \tag{A.3.6}$$

Since $\rho(y, \psi(y)D) > 1$ holds for all $y \in Y_{f,1}$, the expression (A.3.6) is positive. A mutant with a slightly higher settlement strategy can invade and the resident cannot be an ESS.

Let us define the set $Y_{f,2} := \{y : \rho(y, 0) > 1 \,\&\, \rho(y, \psi(y)D) < 1\}$ and assume that $\int_{Y_{f,2}} n(y)\, dy > 0$ holds. Hence, the resident accepts the moderately beneficial patches with probability

$\psi(y) > f(y)$ for $y \in Y_{f,2}$. Take a mutant with strategy $\psi + h$ where

$$h(y) = \begin{cases} -\epsilon\psi(y) & \text{if} \quad y \in Y_{f,2}, \\ 0 & \text{otherwise.} \end{cases}$$

Substituting h into (A.3.3) yields:

$$-\epsilon \int_{Y_{f,2}} \psi(y)n(y)(\rho(y, \psi(y)D) - 1)\, dy. \tag{A.3.7}$$

Since $\rho(y, \psi(y)D) < 1$ holds for all $y \in Y_{f,2}$, expression (A.3.7) is positive and the mutant can invade. In patches of type $y \in Y_{f,2}$, mutants invade that decrease the settlement probability into the patch. So, mutants can invade that increase $\psi(y)$ in $y \in Y_{f,1}$ and decrease $\psi(y)$ in $y \in Y_{f,2}$ until $\psi(y) = f(y)$.

Assume now that the resident has the strategy ψ^* as given in system (A.3.1). Take a mutant with any $h(y)$ (such that $\psi + h$ remains admissible) for all $y \in Y_f$ and zero otherwise and substitute h into (A.3.3). The invasion criterion

$$\int_{Y_f} h(y)n(y)(\rho(y, f(y)D) - 1)\, dy$$

is zero since $\rho(y, f(y)D) = 1$ for $y \in Y_f$. It follows that the resident strategy cannot be invaded, but any mutant that differs from the strategy (A.3.1) only in Y_f has the same fitness as the resident. Hence, the resident with strategy ψ^* is a *weak* ESS. □

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