On the evolution of patch-type dependent immigration

Mats Gyllenberg[a]
Éva Kisdi[b]
Helene C. Weigang[c*]
Department of Mathematics and Statistics
University of Helsinki
PO Box 68, FIN-00014 Finland
email: [a]mats.gyllenberg@helsinki.fi [b]eva.kisdi@helsinki.fi [c]helene.weigang@helsinki.fi
*corresponding author

This article has been published in the Journal of Theoretical Biology:
http://dx.doi.org/10.1016/j.jtbi.2016.01.042

Please cite as:
Gyllenberg M., É. Kisdi & H. C. Weigang. 2016. On the evolution of patch-type dependent immigration. J. theor. Biol. 395: 115-125.

Creative Commons CC BY NC ND license

Keywords: Dispersal, Kin Competition, Generalist-Specialist, Adaptive Dynamics, Settlement

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 (Matter and Roland, 2002; Schooley and Wiens, 2003; Zollner and Lima, 1999). Ultimately, individuals may base emigration and immigration decisions only on a specific cue inferred from the habitat type (Mitchell, 1977; Rees, 1969). Examples include scarce coppers which favour flower-rich patches (Schneider et al., 2003), or the butterfly species *P. 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 (Bonte et al., 2012; Edelaar et al., 2008; Travis 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 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 (Metz and Gyllenberg, 2001; Parvinen et al., 2012; Poethke et al., 2011; Saether et al., 1999), 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 Bonte et al., 2012; Clobert et al., 2009; Travis 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., 1998, 1990). 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 $f^j = (f_1^j, f_2^j)$ 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.

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

$$\begin{aligned} \Pi_i(f) &= \phi_i \rho f_i \int_0^T \mathrm{e}^{-(\sum\limits_{j=1}^{2} \rho\phi_j f_j + \nu)t - \mu_i(T-t)}\, dt \\ &= \phi_i \rho f_i \frac{\mathrm{e}^{-\mu_i T} - \mathrm{e}^{-(\sum\limits_{j=1}^{2} \rho\phi_j f_j + \nu)T}}{\sum\limits_{j=1}^{2} \rho\phi_j f_j + \nu - \mu_i}. \end{aligned} \tag{3}$$

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

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

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

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

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

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

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

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

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

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

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 (Kisdi, 2001; Levene, 1953).

3.1 Monomorphic singularities

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

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

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:

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

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

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

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

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:

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

In Prop. 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 $\frac{\partial w}{\partial f_i^m}\big|_{f^m=f} = \frac{\phi_i}{u}(\frac{k_i}{f_i} - \rho T \gamma(f_1, f_2))$ 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:

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

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

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

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 $\frac{k_1}{f_1^*} = \rho T \gamma(f_1^*, 1)$ respectively, then we call the strategy a *boundary singularity*. The boundary singularity $f^* = (1, f_2^*)$ is evolutionarily stable (ESS) if

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

is negative (Hofbauer and Sigmund, 1990; Maynard Smith and Price, 1973). 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

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

(Christiansen, 1991; Eshel, 1983), which always holds (see Prop. 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

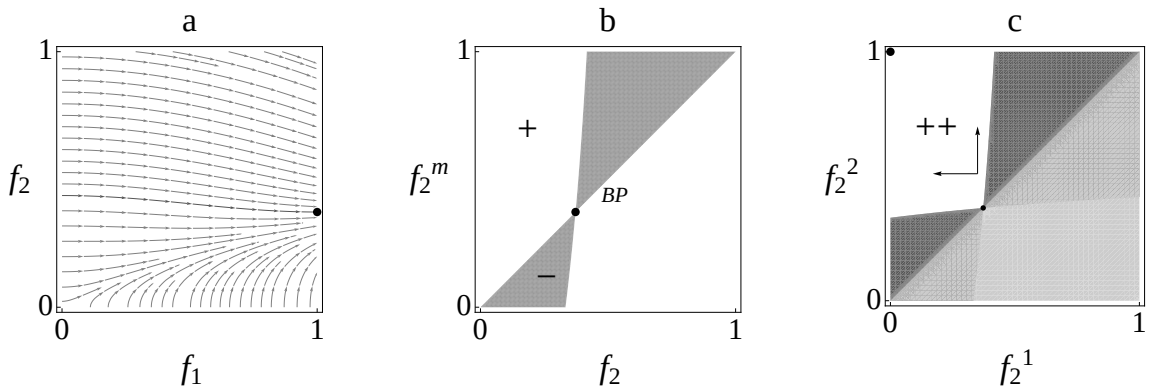

Figure 1: (a) The stream plot of the dynamics in the interior of trait space; evolution pushes the trait vector to the $(1, f_2)$-boundary of trait space. The dot marks the boundary singularity $(1, f_2^*)$. Parameters: $\phi_1 = 0.3$, $T = 1$, $\mu_1 = 100$, $\mu_2 = 40$, $k_1 = 0.8$, $k_2 = 0.1$, $\nu = 150$, $\rho = 100$. (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).

$\sum_{j=1}^{l} n_j \Pi_2(f^j)$, cf. Eq. (7)), which sets an upper limit to the number of coexisting strategies (Geritz et al., 1997; Levin, 1970). 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 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 $T, \rho, \nu, \mu_i, \phi_i$ and k_i. The selection gradient of trait f_2^* depending explicitly on one of the model parameters (ξ) is defined as usual as $D(f_2^*, \xi) = \partial w / \partial f_2^m \big|_{f^m = f = f^*} = 0$.

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

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

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 (i.e., $\text{sign}\big[\frac{df_2^*}{d\xi}\big]$=$\text{sign}\big[\frac{\partial D}{\partial \xi}\big]$). 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

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

Since $1 + \mathrm{e}^x(x-1)$ 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:

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

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

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

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 Boulinier and Danchin, 1997; Stamps

et al., 2005; Ward, 1987).

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^*:

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

The partial derivative is $\frac{\partial c_i}{\partial \nu}$ equals $Tc'(x_i)$. In Prop. 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 Barton et al., 2009; Doyle, 1975; Hanski and Mononen, 2011; Jones and Boulding, 1999; Ruxton and Rohani, 1998). 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

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

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

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

is negative. In Prop. 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 Boulinier and Danchin, 1997; Ward, 1987). 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^*

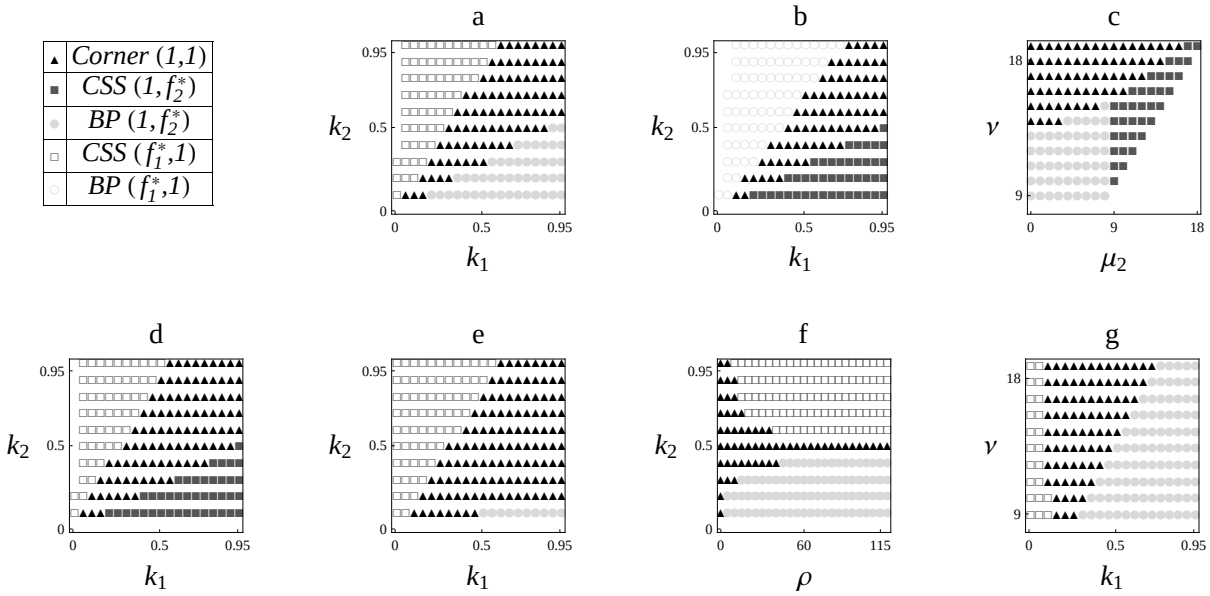

Figure 2: Two-parameter bifurcation diagrams. Plot markers indicate different evolutionary outcomes as described above. Evolution to the corner $(1,1)$ of trait space represents the evolution to a single generalist. If the outcome is a CSS, on one of the two boundaries, an intermediate specialist evolves with $(1, f_2^*)$, or $(f_1^*, 1)$. In this examples holds, that at the evolutionary BPs, the resulting coevolution leads to a generalist $(1,1)$ coexisting with a specialist $(1,0)$, or $(0,1)$ 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) $\rho = 11$, $\phi_1 = 0.4$, $\mu_1 = 9$, $\mu_2 = 3$, $k_2 = 0.2$.

decreases if

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

is negative. The derivative (21) is negative because the term in the brackets is positive (see proof of Prop. 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

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

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 the previous section 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 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 Prop. 6 in AppendixA). 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. Egas et al., 2004; Rausher, 1984; Rausher and Englander, 1987; Ravigné et al., 2009, 2004). 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 (Berdahl et al., 2015; Kisdi, 2002; Kisdi and Geritz, 1999; Levene, 1953; Meszéna et al., 1997; Ravigné et al., 2004; Ronce and Kirkpatrick, 2001), the competitive ability in different habitats (Egas et al., 2004; Haegeman and Loreau, 2014), or the efficiency of using different resources (Day, 2000; Nurmi and Parvinen, 2008, 2011; Rueffler et al., 2006). 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; Gyllenberg et al., 2011; Kisdi, 2004). 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 (Baker and Rao, 2004; Doyle, 1975; Stamps et al., 2005; Ward, 1987). 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 (Stamps, 2006; Stamps and Davis, 2006; Ward, 1987). 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; Clobert et al., 2009; Schaub et al., 2013; Stamps, 2006, 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.

Acknowledgments

We acknowledge financial support from the Finnish Doctoral Programme in Computational Sciences (FICS) and the Academy of Finland. We thank Chun Fang for discussions and three anonymous reviewers for comments.

A Appendix

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

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

From the definition of $c_j = \frac{1}{x_j} - \frac{1}{\mathrm{e}^{x_j}-1}$, 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,

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

□

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

$$\begin{cases} \frac{\partial w}{\partial f_1^m}\Big|_{f^m=f=f^*} = 0 \\ \frac{\partial w}{\partial f_2^m}\Big|_{f^m=f=f^*} = 0. \end{cases} \tag{22}$$

Proof. The system (22) can be rewritten as:

$$\begin{cases} \frac{k_1}{f_1^*} = \rho T \gamma(f_1^*, f_2^*) \\ \frac{k_2}{f_2^*} = \rho T \gamma(f_1^*, f_2^*) \end{cases} \quad \text{or, equivalently as} \quad \begin{cases} \frac{k_1}{f_1^*} = \rho T \gamma(f_1^*, f_2^*) \\ f_2^* = f_1^* \frac{k_2}{k_1}. \end{cases} \tag{23}$$

Assume that there exists a solution to the system (23). Using $c_j < 1/x_j$ and the definition of x_j, the term $\rho T \gamma(f_1^*, f_2^*)$ in system (23) can be written as

$$\begin{aligned} \rho T \gamma(f_1^*, f_2^*) = \rho T(\phi_1 k_1 c_1 + \phi_2 k_2 c_2) &< \rho T \Big(\frac{\phi_1 k_1}{x_1} + \frac{\phi_2 k_2}{x_2} \Big) \\ &< \frac{\phi_1 k_1 + \phi_2 k_2}{\phi_1 f_1^* + \phi_2 f_2^*}. \end{aligned}$$

By substituting $f_2^* = f_1^* \frac{k_2}{k_1}$ into the first line of system (23) we obtain

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

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

$$c'(x) = \frac{e^x - \eta(x)^2}{(e^x - 1)^2}. \tag{24}$$

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

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

which is negative. Hence, h is negative for all $x > 0$. Therefore, (24) 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:

$$-\phi_1 k_1 \rho \phi_2 T \frac{\partial c_1}{\partial f_2^*} - \phi_2 k_2 (\frac{1}{f_2^{*2}} + \rho \phi_2 T \frac{\partial c_2}{\partial f_2^*}) < 0. \tag{25}$$

We substitute the singularity condition Eq. (10), use Eq. (14), and rewrite condition (25):

$$f_2^* \rho \phi_2 T \sum_{i=1}^{2} \phi_i k_i \big(c_i (c_i - \frac{1}{f_2^* \rho \phi_2 T}) - H_i\big) < 0. \tag{26}$$

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 (26) and hence inequality (25) 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

$$\frac{k_2}{f_2^*} c_2 < k_1 c_1. \tag{27}$$

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 (27) and with some algebra we get:

$$\rho T (\phi_1 + \phi_2 f_2^*) c_2 < 1. \tag{28}$$

Since $\rho T(\phi_1 + \phi_2 f_2^*) < x_2$ and $c_2 < \frac{1}{x_2}$ we conclude that (28) is true, and hence (27) 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:

$$\begin{cases} \left.\frac{\partial w}{\partial f_1^m}\right|_{f^m=f=f^*} & = \frac{\phi k}{u f_1^*} - \frac{1}{u}\rho\phi T(\phi k c_1 + \phi k c_2) = 0 \\ \left.\frac{\partial w}{\partial f_2^m}\right|_{f^m=f=f^*} & = \frac{\phi k}{u f_2^*} - \frac{1}{u}\rho\phi T(\phi k c_1 + \phi k c_2) = 0. \end{cases} \tag{29}$$

Solving the system (29) we get: $f_1^* = f_2^*$. In Appendix A Prop. 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 $(1, 1)$. □

References

Andreassen, H. P., Ims, R. A., 2001. Dispersal in patchy vole populations: role of patch configuration, density dependence, and demography. Ecology 82 (10), 2911–2926.

Baker, M. B., Rao, S., 2004. Incremental Costs and Benefits Shape Natal Dispersal: Theory and Example with Hemilepistus reaumuri. Ecology 85 (4), 1039–1051.

Barton , K. A., Phillips, B. L., Morales, J. M., Travis, J. M. J., 2009. The evolution of an 'intelligent' dispersal strategy: Biased, correlated random walks in patchy landscapes. Oikos 118 (2), 309–319.

Berdahl, A., Torney, C. J., Schertzer, E., Levin, S. A., 2015. On the evolutionary interplay between dispersal and local adaptation in heterogeneous environments. Evolution 69 (6), 1390–1405.

Billiard, S., Lenormand, T., 2005. Evolution of migration under kin selection and local adaptation. Evolution 59 (1), 13–23.

Blanquart, F., Gandon, S., 2014. On the Evolution of Migration in Heterogeneous Environments. Evolution 68 (6), 1617–1628.

Bonte, D., Van Dyck, H., Bullock, J. M., Coulon, A., Delgado, M. M., Gibbs, M., Lehouck, V., Matthysen, E., Mustin, K., Saastamoinen, M., Schtickzelle, N., Stevens, V. M., Vandewoestijne, S., Baguette, M., Barto, K. A., Benton, T. G., Chaput-Bardy, A., Clobert, J., Dytham, C., Hovestadt, T., Meier, C. M., Palmer, S. C. F., Turlure, C., Travis, J. M. J., 2012. Costs of dispersal. Biological Reviews 87, 290–312.

Boulinier, T., Danchin, E., 1997. The use of conspecific reproductive success for breeding patch selection in terrestrial migratory species. Evolutionary Ecology 11 (5), 505–517.

Bowler, D. E., Benton, T. G., 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. Biological Reviews 80 (2), 205–225.

Cheptou, P.-O., Massol, F., 2009. Pollination Fluctuations Drive Evolutionary Syndromes Linking Dispersal and Mating System. The American Naturalist 174 (1), 46–55.

Christiansen, F., 1991. On Conditions for Evolutionary Stability for a Continuously Varying Character. The American Naturalist 138 (1), 37–50.

Clobert, J., Le Galliard, J.-F., Cote, J., Meylan, S., Massot, M., 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. Ecology Letters 12 (3), 197–209.

Conradt, L., Roper, T., Thomas, C., 2001. Dispersal Behaviour of Individuals in Metapopulations of Two British Butterflies. Oikos 95 (3), 416–424.

Cote, J., Clobert, J., 2007. Social personalities influence natal dispersal in a lizard. Proceedings of the Royal Society B: Biology 274 (1608), 383–390.

Day, T., 2000. Competition and the Effect of Spatial Resource Heterogeneity on Evolutionary Diversification. The American Naturalist 155 (6), 790–803.

Delgado, M. M., Barto, K. A., Bonte, D., Travis, J. M. J., 2014. Prospecting and dispersal: their eco-evolutionary dynamics and implications for population patterns. Proceedings of the Royal Society B: Biological Sciences 281.

Diekmann, O., Gyllenberg, M., Metz, J. A. J., Thieme, H. R., 1998. On the formulation and analysis of general deterministic structured population models. Journal of Mathematical Biology 36 (4), 349–388.

Diekmann, O., Heesterbeek, J., Metz, J. A. J., 1990. On the definition and the computation of the basic reproduction ratio R0 in models for infectious diseases in heterogeneous populations. Journal of Mathematical Biology 28, 365–382.

Doyle, R., 1975. Settlement of Planktonic Larvae: A Theory of Habitat Selection in Varying Environments. The American Naturalist 109 (966), 113–126.

Edelaar, P., Siepielski, A. M., Clobert, J., 2008. Matching habitat choice causes directed gene flow: A neglected dimension in evolution and ecology. Evolution 62, 2462–2472.

Egas, M., Dieckmann, U., Sabelis, M., 2004. Evolution restricts the coexistence of specialists and generalists: the role of tradeoff structure. The American Naturalist 163 (4), 518–531.

Ehlinger, T., 1990. Habitat Choice and Phenotype-Limited Feeding Efficiency in Bluegill: Individual Differences and Trophic Polymorphism. Ecology 71 (3), 886–896.

Eshel, I., 1983. Evolutionary and Continuous Stability. Journal of Theoretical Biology 103, 99–111.

Ezoe, H., Iwasa, Y., 1997. Evolution of Condition Dependent Dispersal: A Genetic Algorithm Search for the ESS Reaction Norm. Researches on Population Ecology 39 (2), 127–137.

Fretwell, S. D., Lucas, H. L., 1969. On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheoretica 19, 16–36.

Gaines, M. S., McClenaghan, L. R., 1980. Dispersal in Small Mammals. Annual Review of Ecology and Systematics 11 (1), 163–196.

Garant, D., Kruuk, L. E. B., Wilkin, T. A., McCleery, R. H., Sheldon, B. C., 2005. Evolution driven by differential dispersal within a wild bird population. Nature 433 (7021), 60–65.

Geritz, S. A. H., Kisdi, É., Meszéna, G., Metz, J. A. J., 1998. Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. Evolutionary Ecology 12 (1), 35–57.

Geritz, S. A. H., Metz, J. A. J., Kisdi, É., Meszéna, G., 1997. Dynamics of Adaptation and Evolutionary Branching. Physical Review Letters 78 (10), 2024–2027.

Gyllenberg, M., Kisdi, É., Utz, M., 2011. Body condition dependent dispersal in a heterogeneous environment. Theoretical Population Biology 79 (4), 139–54.

Gyllenberg, M., Metz, J. A. J., 2001. On fitness in structured metapopulations. Journal of Mathematical Biology 268 (6), 545–560.

Haegeman, B., Loreau, M., 2014. A Graphical-Mechanistic Approach to Spatial Resource Competition. The American Naturalist 185 (1), E1–E13.

Hamilton, W., May, R. M., 1977. Dispersal in Stable Habitats. Nature 269, 578–581.

Hanski, I., Gyllenberg, M., 1993. Two General Metapopulation Models and the Core-Satellite Species Hypothesis. The American Naturalist 142 (1), 17–41.

Hanski, I., Mononen, T., 2011. Eco-evolutionary dynamics of dispersal in spatially heterogeneous environments. Ecology Letters 14 (10), 1025–1034.

Hofbauer, J., Sigmund, K., 1990. Adaptive Dynamics and Evolutionary Stability. Applied Mathematics Letters 3 (4), 75–79.

Jones, K. M. M., Boulding, E. G., 1999. State-dependent habitat selection by an intertidal snail: the costs of selecting a physically stressful microhabitat. Journal of Experimental Marine Biology and Ecology 242 (2), 149–177.

Kisdi, É., 2001. Long-term adaptive diversity in Levene-type models. Evolutionary Ecology Research 3, 721–727.

Kisdi, É., 2002. Dispersal: risk spreading versus local adaptation. The American Naturalist 159 (6), 579–596.

Kisdi, É., 2004. Conditional dispersal under kin competition: extension of the Hamilton-May model to brood size-dependent dispersal. Theoretical Population Biology 66 (4), 369–380.

Kisdi, É., Geritz, S. A. H., 1999. Adpative Dynamics in Allele Space: Evolution of Genetic Polymorphism by Small Mutations in a Heterogeneous Environment. Evolution 53 (4), 993–1008.

Krebs, J. R., Davies, N. B., 1993. Economic Decisions and the Individual. In: An introduction to behavioural ecology. Vol. 3. Oxford: Blackwell Scientific Publications, Ch. 3, pp. 48–76.

Levene, H., 1953. Genetic equilibrium when more than one ecological niche is available. The American Naturalist 87 (836), 331–333.

Levin, S. A., 1970. Equilibria and Stability, and an Extension of the Competitive Exclusion Principle. The American Naturalist 104 (939), 413–423.

Matter, S., Roland, J., 2002. An experimental examination of the effects of habitat quality on the dispersal and local abundance of the butterfly Parnassius smintheus. Ecological Entomology 27, 308–316.

Maynard Smith, J., Price, G. R., 1973. The logic of animal conflict. Nature.

McNamara, J. M., Dall, S. R. X., 2011. The evolution of unconditional strategies via the 'multiplier effect'. Ecology letters 14 (3), 237–43.

Meszéna, G., Czibula, I., Geritz, S. A. H., 1997. Adaptive Dynamics in A 2-Patch Environment: A Toy Model For Allopatric and Parapatric Speciation. Journal of Biological Systems 5 (2), 265–284.

Metz, J. A. J., Gyllenberg, M., 2001. How should we define fitness in structured metapopulation models? Including an application to the calculation of evolutionarily stable dispersal strategies. Proceedings of the Royal Society B: Biological Sciences 268 (1466), 499–508.

Mitchell, N. D., 1977. Differential host selection by pieris brassicae (the large white butterfly) on brassica oleracea subsp. oleracea (the wild cabbage). Entomologia Experimentalis et Applicata 22 (1911), 208–219.

Morris, D. W., MacEachern, J. T., 2010. Active density-dependent habitat selection in a controlled population of small mammals. Ecology 91 (11), 3131–3137.

Nurmi, T., Parvinen, K., 2008. On the evolution of specialization with a mechanistic underpinning in structured metapopulations. Theoretical Population Biology 73 (2), 222–243.

Nurmi, T., Parvinen, K., 2011. Joint evolution of specialization and dispersal in structured metapopulations. Journal of Theoretical Biology 275 (1), 78–92.

Parvinen, K., 2002. Evolutionary branching of dispersal strategies in structured metapopulations. Journal of Mathematical Biology 45, 106–124.

Parvinen, K., Seppänen, A., Nagy, J. D., 2012. Evolution of complex density-dependent dispersal strategies. Bulletin of Mathematical Biology 74 (11), 2622–2649.

Poethke, H.-J., Gros, A., Hovestadt, T., 2011. The ability of individuals to assess population density influences the evolution of emigration propensity and dispersal distance. Journal of Theoretical Biology 282 (1), 93–99.

Rausher, M. D., 1984. The evolution of habitat preference in subdivided populations. Evolution 38 (3), 596–608.

Rausher, M. D., Englander, R., 1987. The Evolution of Habitat Preference II . Evolutionary Genetic Stability under Soft Selection. Theoretical Population Biology 31, 116–139.

Ravigné, V., Dieckmann, U., Olivieri, I., 2009. Live where you thrive: joint evolution of habitat choice and local adaptation facilitates specialization and promotes diversity. The American Naturalist 174 (4), E141–E169.

Ravigné, V., Olivieri, I., Dieckmann, U., 2004. Implications of habitat choice for protected polymorphisms. Evolutionary Ecology Research 6, 125–145.

Rees, C., 1969. Chemoreceptor specificity associated with choice of feeding site by the beetle, chrysolina brunsvicensis on tis foodplant, hypericum hirsutum. Entomologia Experimentalis et Applicata 12, 565–583.

Ronce, O., Kirkpatrick, M., 2001. When sources become sinks: migrational meltdown in heterogeneous habitats. Evolution; international journal of organic evolution 55 (8), 1520–1531.

Rosenzweig, M., 1981. A theory of habitat selection. Ecology 62 (2), 327–335.

Rousset, F., Gandon, S., 2002. Evolution of the distribution of dispersal distance under distance-dependent cost of dispersal. Journal of Evolutionary Biology 15 (4), 515–523.

Rueffler, C., Van Dooren, T. J. M., Metz, J. A. J., 2006. The evolution of resource specialization through frequency-dependent and frequency-independent mechanisms. The American Naturalist 167 (1), 81–93.

Ruxton, G. D., Rohani, P., 1998. Fitness-dependent dispersal in metapopulations and its consequences for persistence and synchrony. Journal of Animal Ecology 67, 530–539.

Saether, B.-E., Engen, S., Lande, R., 1999. Finite metapopulation models with density-dependent migration and stochastic local dynamics. Proceedings of the Royal Society B: Biological Sciences 266 (1415), 113–118.

Schaub, M., Jakober, H., Stauber, W., 2013. Strong contribution of immigration to local population regulation: Evidence from a migratory passerine. Ecology 94 (8), 1828–1838.

Schneider, C., Dover, J., Fry, G., 2003. Movement of two grassland butterflies in the same habitat network: the role of adult resources and size of the study area. Ecological Entomology 28, 219–227.

Schooley, R. L., Wiens, J. A., 2003. Finding habitat patches and directional connectivity. Oikos 102 (3), 559–570.

Shaw, A. K., Kokko, H., 2015. Dispersal Evolution in the Presence of Allee Effects Can Speed Up or Slow Down Invasions. The American Naturalist 185 (5), 631–639.

Stamps, J. A., 2006. The silver spoon effect and habitat selection by natal dispersers. Ecology Letters 9 (11), 1179–1185.

Stamps, J. A., Davis, J. M., 2006. Adaptive effects of natal experience on habitat selection by dispersers. Animal Behaviour 72 (6), 1279–1289.

Stamps, J. A., Krishnan, V., Reid, M., 2005. Search costs and habitat selection by dispersers. Ecology 86 (2), 510–518.

Travis, J. M. J., Mustin, K., Barto, K. A., Benton, T. G., Clobert, J., Delgado, M. M., Dytham, C., Hovestadt, T., Palmer, S. C. F., Van Dyck, H., Bonte, D., 2012. Modelling dispersal: an eco-evolutionary framework incorporating emigration, movement, settlement behaviour and the multiple costs involved. Methods in Ecology and Evolution 3 (4), 628–641.

Ward, S., 1987. Optimal habitat selection in time-limited dispersers. The American Naturalist 129 (4), 568–579.

Zollner, P., Lima, S., 1999. Illumination and the perception of remote habitat patches by white-footed mice. Animal Behaviour 58 (3), 489–500.