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Abstract

Habitat loss and climate change are responsible for abrupt changes in selection patterns and connectivity in natural landscapes with direct consequences on biodiversity, but their joint effect on both population demography and evolution has received limited attention so far. We propose a new theoretical framework, combining demography and genetics, to study how abrupt changes in connectivity or habitat heterogeneity among local populations of a given species may affect patterns of local adaptation and favor specialist or generalist strategies. In a two-patch, iteroparous microscopic model, using adaptive dynamics, we demonstrate that when migration does not depend on the trait under selection, a single specialist or generalist strategy is favored by evolution, and we provide an explicit trait value for the equilibria, depending on migration and selection parameters. We also prove that, with non-zero migration, there is no pure specialist stable equilibrium. In addition, in some stable monomorphic equilibria commonly interpreted as generalist strategies, individuals are actually specialized on one of the patches due to demographic asymmetries. Finally, our analysis indicates that minor environmental changes in connectivity or environmental variance may drastically change adaptation patterns without causing discontinuities in equilibrium population sizes.

1 Introduction

Among the factors shaping adaptation patterns, spatial and temporal variations in the environment have received much theoretical attention (e.g. Johst et al. 2002, Ravigné et al. 2009 and references therein, Débarre and Gandon 2010). Spatial variation implies that one or several environmental parameters are heterogeneous in space, leading to spatial variation in fitness for a given genotype.

Classical work has shown that patterns of heterogeneity in space drive resource use along a specialist-generalist dichotomy (Futuyma and Moreno 1988, Wilson and Yoshimura 1994). Ecological specialization usually describes the niche width of a species, i.e. the range of environmental conditions it can tolerate or the variety of resources it can use. If there are only two resources, a specialist species is generally defined as one that maximize its efficiency on one type of resource, regardless on how poorly it performs on the other while a complete generalist species performs equally well on both resources. Theoretical work suggests that (1) as spatial environmental heterogeneity increases (i.e. selective trade-offs among locations become stronger), specialist strategies are favored; (2) in the absence of habitat choice, high and constant dispersal rates favor generalist strategies (Brown and Pavlovic 1992); (3) habitat choice as well as dispersal rates and patterns can be under selection, which greatly affects the evolution of specialization (Morris 2003, Ronce 2007, Rueffler et al. 2007, Ravigné et al. 2009, Nurmi and Parvinen 2011).

In addition to spatial variation, the evolution of specialization is also driven by temporal environmental variation, with stochastic and deterministic components. Stochastic temporal variations of the environment are known to favor generalist strategies (see Wilson and Yoshimura 1994), while deterministic changes, reflecting directional changes in environmental conditions, have received much less attention. Global changes associated with human activities are considered a major source of abrupt environmental change (see e.g. Sanderson et al. 2002). With respect to ecological specialization, one may distinguish among (1) changes that are expected to modify (increase or decrease) the environmental distances between habitat patches, such as climate change, land use changes or pollution (Adler et al. 2001; Seixas 2000); and (2) changes that are expected to affect both connectivity and environmental distance such as habitat destruction and fragmentation, which result in longer average geographic distances between patches of habitat (e.g., Adren and Delin 1994, Fahrig 2003). At the scale of populations or metapopulations (several discrete, usually interconnected subpopulations, Hanski and Simberloff 1997), climate and land use changes may therefore lead to abrupt changes in the quality, quantity and connectivity of habitats, which in turn may affect selective trade-offs, dispersal and the evolution of ecological specialization in fragmented landscapes. Despite numerous works on the evolution of metapopulations facing spatially heterogeneous conditions (see e.g. Parvinen and Egas 2004, Nurmi and Parvinen 2008), there is still no general framework to forecast the effect of abrupt changes in connectivity between habitat patches (but see Ronce and Kirkpatrick 2001; Gyllenberg et al. 2002) and changes in selective trade-offs among habitat types (e.g., Beltman and Metz 2005) on adaptation patterns. Yet general tools are urgently needed in the frame of scenarios of biodiversity response to global changes (Pereira et al. 2010; Morris et al. 2011). Here we use a two-patch model to examine the evolution of an iteroparous species in a heterogeneous environment, while accounting for varying population size, dispersal and intra-patch competition. We present a new approach to study how abrupt changes in connectivity or environmental differences among subpopulations of a given species may affect patterns of local adaptation and favor specialist vs. generalist strategies. This model allows us to track ecological and demographic changes simultaneously while providing a flexible framework that can be adapted to more realistic ecological scenarios.

2 Methods

The model is derived in three steps. First, we build a microscopic stochastic model describing the demographic parameters of individuals characterized by a heritable trait controlling their fitness. Second, we rescale this microscopic model to obtain a stochastic trait process describing population evolution. Finally, we approximate the stochastic process by a deterministic process, which we ultimately study.

2.1 The microscopic stochastic model

We first consider a two-patch, stochastic (individual-based) continuous-time birth and death process. This microscopic model allows us to examine patterns of adaptation in an iteroparous population with overlapping generations, while accounting for varying population size, dispersal and intra-patch competition.

Using an adaptive dynamics framework, we consider a single trait that can take an unrestricted number of quantitative values. We assume clonal inheritance of parental trait values, with possible mutation at each generation in each new zygote on the basis of a random Markovian mutation process (see details below). We assume that the fecundity of each individual depends on the interaction between its trait value x (representing an "optimal" environment for reproduction) and the local environment. The environment in each patch is characterized by a quantitative parameter that can capture one or several features of the patch (temperature, height, acidity, moisture...). Patch 1 has value $E_1 \in \mathbb{R}$ and patch 2 has value $E_2 > E_1$. For simplicity of notation, we assimilate the value of the optimal phenotypic trait to the value of the environment, e.g. in environment 1, the optimal phenotypic trait is of value E_1. Individuals with trait value x closer to the environmental value of the patch they live in have higher fecundity, so that the fecundity of an individual with trait value x on patch i is

$$b_i(x) = K\left(\left(\frac{x - E_i}{\sigma}\right)^2\right), \tag{1}$$

where K is a smooth positive decreasing function. Here we use $K(X) = \exp(-X)$ and $K(X) = 4 - X$ but any other smooth positive decreasing function is suitable. The shape of b_i is chosen so that fecundity decays symmetrically away from E_i, yielding a bell shaped curve. Hence, the fecundity of an individual is maximum at $b_i(E_i) = K(0)$, and decreases when the trait value gets further from the optimal environmental value, at a rate given by $\frac{1}{\sigma}$, i.e. the strength of environmental selection on the population (cf fig. A.1 in Appendix A). Consequently, σ also characterizes the fertility trade-off between the two patches.

In a generic landscape, E_1 and E_2 need not be the most different environments, i.e. we do not expect E_2 to be the worst possible trait value for individuals living in patch 1.

Hence, to ensure we are not in such a degenerate case, we assume that:

$$\min_{x\in\mathbb{R}} b_1(x) < b_1(E_2) \text{ and so by symmetry } \min_{x\in\mathbb{R}} b_2(x) < b_2(E_1) \tag{2}$$

This condition implies that the cost of reproducing in a non-optimal patch increases with the difference between the optimal environment of an individual and the patch environment, so that individuals with different suboptimal trait values cannot reproduce « equally badly » in a given patch.

We define

$$A = \frac{(E_1 - E_2)^2}{\sigma^2}$$

as the phenotypic distance between the two patches, i.e. the reduction in fertility of individuals with trait value E_1 that reproduce in patch 2. A is large whenever the two patches exhibit contrasting environments (i.e. $E_1 - E_2$ is large) or when the environment is highly selective (σ is small).

2.2 Model dynamics

The microscopic model is a continuous-time birth and death process with migration and competition: an individual with trait value x on patch i gives birth to a new individual on patch i with rate $b_i(x)$. The offspring retains the parental trait value with probability $(1-p)$ or mutates with probability p. In the latter case, the new trait value is randomly drawn from a distribution centered on x with unit variance.

At any time during its life, every individual can switch habitat at a constant rate m which does not depend on its location nor on its trait value for now (this assumption is relaxed in Section 3.5.2).

We assume intraspecific competition for limited resources within each patch (space, light, food, water, shelter...), which is modeled via a density-dependent death rate: if there are N individuals in a patch, each individual in this patch dies at rate αN. This allows a regulation of population size and captures the effect of selection without imposing a maximum population size or other extrinsic mechanisms. With these assumptions, we obtain a logistic growth in which the carrying capacity of each patch is the ratio of the maximal fertility rate on the compound death rate, $\frac{K(0)}{\alpha}$.

Alternatively, it is possible to distinguish intrinsic mortality (at rate d) from competition-induced mortality, so that individuals in a patch with total population N would die at rate $d + \alpha(N-1)$. However, as long as all sources of mortality are independent of genotypes, selection patterns are not affected by such change in the mortality parameters.

2.3 *Rescaling of the model*

2.3.1 The trait substitution sequence

Starting from an initially dimorphic population (see below), we investigate which trait values are found in the population after a long time. The microscopic model described above allows coexistence of numerous trait values in the population at a given time, so that we cannot track adaptation without further assumptions. Following the adaptive dynamics approach (Metz et al. 1992; Dieckmann and Law 1996) we assume large population size and rare mutations, which is required to derive a deterministic approximation of the adaptation process. Large populations are modelled by changing the compound death rate α to $\alpha_S = \frac{\alpha}{S}$ and the carrying capacity to $S\frac{K(0)}{\alpha}$, so that subpopulations in each patch become large when S tends to infinity. The large population assumption is required to prevent extinction by random events and to ensure that genetic drift is negligible compared to selection. Rare mutations are modeled by rescaling the frequency of mutation events from p to p_S with $p_S \to 0$ when $S \to \infty$ so that mutations appear in the population one at a time. Between mutation events, the resident population is at equilibrium, meaning that if the population is dimorphic with trait values x and y the population sizes on each patch satisfy:

$$\begin{cases} [b_1(x) - \alpha(n_{1,x}(x,y) + n_{1,y}(x,y))]\, n_{1,x}(x,y) + m(n_{2,x}(x,y) - n_{1,x}(x,y)) = 0 & \text{(3a)} \\ [b_2(x) - \alpha(n_{2,x}(x,y) + n_{2,y}(x,y))]\, n_{2,x}(x,y) + m(n_{1,x}(x,y) - n_{2,x}(x,y)) = 0 & \text{(3b)} \\ [b_1(y) - \alpha(n_{1,x}(x,y) + n_{1,y}(x,y))]\, n_{1,y}(x,y) + m(n_{2,y}(x,y) - n_{1,y}(x,y)) = 0 & \text{(3c)} \\ [b_2(y) - \alpha(n_{2,x}(x,y) + n_{2,y}(x,y))]\, n_{2,y}(x,y) + m(n_{1,y}(x,y) - n_{2,y}(x,y)) = 0 & \text{(3d)} \end{cases}$$

where $n_{i,x}(x,y)$ is the number of individuals with trait value x in patch i when the two resident trait values in the population are (x,y).

In each line of Equation (3), the leftmost term compares the fertility of individuals with a given trait value in a given patch (trait value x in patch 1 for (3a) for example) to the strength of competition in this patch. The rightmost term measures the difference in the flows of migrants entering and leaving the patch. Each resident size is therefore deduced from a balance between growth rates and migration flows.

With this rescaling of the microscopic process, combined with an appropriate rescaling of time, one can prove with the same arguments as in Champagnat (2006) that the dynamics of the trait values in the population are described accurately by a Markov jump process called the *trait substitution sequence* (Metz et al. 1992, Metz et al. 1996, Champagnat 2006).

The trait substitution sequence was first introduced by Metz et al. (1996) and studied mathematically in a single patch monomorphic population by Champagnat (2006).

The dynamics of the trait substitution sequence are driven by the probability of a mutant to invade and go to fixation in the population, $g_i(z; x, y)$ where $i = 1, 2$ is the patch the mutant was born in, z is the mutant trait value and x, y are the resident trait values (see Appendix A.2 for a more mathematically accurate definition).

Here, we examine whether there is a privileged direction for evolution and whether the evolutionary dynamics can reach an equilibrium.

2.3.2 Small mutations

The in-depth study of the trait substitution sequence in a two-patch model is not of our immediate concern; instead, we are interested in identifying privileged directions for evolution and possible evolutionarily stable equilibria. To this end, we approximate the stochastic process by a deterministic process, which requires a third assumption of small-effect mutations.

This is achieved again by rescaling mutation effects with a small parameter ϵ. We then choose a new mutation kernel such that all mutation effects are multiplied by ϵ, close to zero, and are therefore of much smaller amplitude.

Finally, we accelerate time to fit the new mutation scale (cf Champagnat et al. 2011). With these assumptions, the dynamics of $(x(t), y(t))$, the vector describing the two trait values in the population at time t are given by the following ordinary differential equation, a two-dimensional variant of the *canonical equation of adaptive dynamics*(Dieckmann and Law 1996):

$$\begin{cases} \dot{x} & = p[b_1(x)n_{1,x}(x,y)\partial_1 g_1(x;x,y) + b_2(x)n_{2,x}(x,y)\partial_1 g_2(x;x,y)] \\ \dot{y} & = p[b_1(y)n_{1,y}(x,y)\partial_1 g_1(y;x,y) + b_2(y)n_{2,y}(x,y)\partial_1 g_2(y;x,y)] \end{cases} \tag{4}$$

Equation (4) can be understood as follows: a mutation event introduces a new trait value z in a population with resident values x and y. For $i = 1, 2$, $g_i(z; x, y)$ is the probability that a trait value originally appearing in patch i invades in the population (see Appendix A.2).

Individuals with mutant trait values born from parents with trait value x are produced at rate $pb_i(x)n_{i,x}(x, y)$ in patch i. The gradient of the survival probability $\partial_i g_i(x; x, y)$ captures the direction and strength of evolutionary forces on x for patch i. Hence the variation imposed to trait value x by individuals in patch i is $pb_i(x)n_{i,x}(x, y)\partial_i g_i(x; x, y)$. The total change in x is the sum of such forces over both patches. Note that although the migration rate m does not explicitly appear in Equation (4), all population sizes $n_{i,.}$ as well as survival probabilities depend on m and are obtained by solving Equation (3)

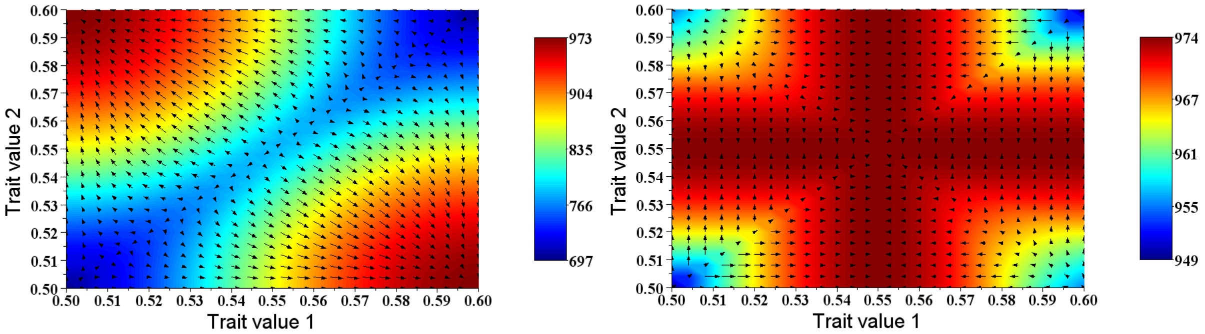
We further show in Appendix A.2 that Equation (4) can eventually be simplified to:

$$\begin{cases} \dot{x} & = h_1(x,y) = b_1'(x)(n_{1,x}(x,y))^2 + b_2'(x)(n_{2,x}(x,y))^2 \\ \dot{y} & = h_2(x,y) = b_1'(y)(n_{1,y}(x,y))^2 + b_2'(y)(n_{2,y}(x,y))^2 \end{cases}. \tag{5}$$

We begin by considering a dimorphic population with trait values (x^0, y^0), such that the two subpopulations are initially at equilibrium. We identify all possible equilibria and examine their stability.

2.4 *Test of the generality of the model*

After a thorough mathematical analysis of the basic model, we examined whether our results were robust to a variety of alternative assumptions. In most cases, the alternative models were not analytically tractable and were explored with numerical tools. We specifically addressed three assumptions with potentially significant impact on the results: (a) *Life-cycle of the modeled species*: we demonstrate (see Appendix B.1) that our results are qualitatively the same for a semelparous life cycle, which will not be discussed further. (b) *Patch symmetry*: apart from their environmental characteristic, the two patches are identical in all respects. We broke this symmetry by considering that the two patches had different carrying capacities or different strength of selection. In the former case, we introduced a new parameter $r_\kappa \geq 1$ so that the two carrying capacities satisfy: $\frac{K(0)}{\alpha_2} = r_\kappa \frac{K(0)}{\alpha_1}$. (c) *Variable migration rate*: Our framework allows us to track how adding or modifying microscopic mechanisms affects adaptation patterns. Because the movements of individuals can be triggered by the quality of the environment or their reproductive



(A) $\sigma = 0.3$, $m = 0.1$

(B) $\sigma = 0.1$, $m = 0.015$

Figure 1: Vector field of Equation (5) for two contrasting pairs of values of migration rate and strength of selection (m, σ). Starting from any couple of trait values in $[E_1, E_2]$, evolution follows the field lines of (5), i.e. the direction of arrows. The background color represents total population size, red indicating the more abundant populations. Other parameter values are $E_1 = 0.5$, $E_2 = 0.6$, $\alpha = 0.01$, $K(X) = exp(-X)$.

success in a patch (e.g. Ravigné et al. 2009), we examined a model in which the trait x under selection also modified the migration rate, which became $m(x)$. This changed the form of the canonical (4) and simplified equations (5) (see Equation (13) in Section 3.5.2). The full analysis of this new model is more complicated because the favored strategy can depend on the shape of the migration rate function. Nevertheless, we provide insights into how evolution is modified by a selection-dependent migration.

3 Results

We show that the model yields two extreme types of equilibria (Fig.1), the stability of which depends on the migration rate and on the between-patch phenotypic distance. With large migration rates and/or a small phenotypic distance, evolution leads to a monomorphic population, with a single trait value that is the mean of the two optimal trait values $x^* = \frac{E_1+E_2}{2}$ (Fig.1A). In addition, the figure shows that any pair (x, x^*) or (x^*, x) is attracting, because at these points the population is in fact monomorphic with trait value x^*. Alternatively, with little migration or a large phenotypic distance, the population eventually converges towards an equilibrium close to (E_1, E_2) (Fig.1B). In this case, the pair (x^*, x^*) is an unstable equilibrium. In both cases, there is a single stable equilibrium towards which the population converges from almost any point of the trait value space. We demonstrate below that this is always the case under weak assumptions, and we examine further how demographic and selection parameters favor monomorphic vs. dimorphic equilibria. It should be noted that there cannot be any equilibrium outside $[E_1, E_2]^2$ (cf Appendix A.3).

These two types of stable equilibria can be interpreted in terms of the specialist/generalist concept; hereafter, we use the following ad hoc definitions (which will be discussed further in Section 3.5.1):

A "generalist" equilibrium is a monomorphic stable equilibrium (x^*, x^*) (where $x^* = \frac{E_1+E_2}{2}$), in which all individuals have similar fitness in both habitats. A "pure specialist" equilibrium is a dimorphic stable equilibrium (E_1, E_2), in which individuals are perfectly adapted to patch 1 or patch 2. A "partial specialist" equilibrium is any dimorphic stable equilibrium not satisfying the condition above

3.1 *Explicit solution in the linear case*

Choosing $K : x \mapsto \lambda - x$ for the shape of the fertility rate (with λ large enough for $b_1(E_2)$ to be strictly positive) allows us to describe the equilibria explicitly. The symmetry of our system leads us to consider equilibria of the form $(x, \bar{x})$ where $\bar{x} = E_1 + E_2 - x$ is the symmetric of x with respect to x^*, such that an individual with trait value x in patch 1 is as fit as an individual of trait value $\bar{x}$ in patch 2 i.e.

$$b_1(x) = b_2(\bar{x}) \text{ and } b_2(x) = b_1(\bar{x}). \tag{6}$$

We show in Appendix A.7 that $(x, \bar{x})$ is an equilibrium of (5) if and only if

$$w(x) = b_1(x) - b_2(x) + m\left(\sqrt{\frac{-b_1'(x)}{b_2'(x)}} - \sqrt{\frac{-b_2'(x)}{b_1'(x)}}\right) = 0 \tag{7}$$

Using the explicit form of b_i yields a second degree polynomial equation (see Appendix A.8). Solving this equation shows that if $A < 2m$, $w(x) = 0$ has no solution on $[E_1, x^*[$, and (x^*, x^*) is the only stable equilibrium of (5) ; if $A > 2m$ then (x^*, x^*) is an unstable equilibrium and the unique stable equilibrium is obtained by solving $w(x) = 0$:

$$\begin{aligned} x &= x^* - \frac{(E_2 - E_1)}{2}\sqrt{1 - \frac{4m^2}{A^2}} \\ \bar{x} &= x^* + \frac{(E_2 - E_1)}{2}\sqrt{1 - \frac{4m^2}{A^2}}. \end{aligned} \tag{8}$$

The equilibria are driven to generalism when $\frac{2m}{A}$ gets closer to 1, i.e when the migration rate increases or the *phenotypic distance* decreases. If $\frac{2m}{A}$ goes to 0, the equilibria are close to full specialization, with first order estimates being

$$\begin{aligned} x &= E_1 + \frac{(E_2 - E_1)m^2}{A^2} = E_1 + \frac{\sigma^4 m^2}{(E_2 - E_1)^3} \\ \bar{x} &= E_2 - \frac{(E_2 - E_1)m^2}{A^2} = E_2 - \frac{\sigma^4 m^2}{(E_2 - E_1)^3} \end{aligned}. \tag{9}$$

For intermediate values of $\frac{2m}{A}$, the equilibrium lies between specialization and generalism. We will now show that these results are fairly general and can be extended to a wide class of functions K

3.2 *Condition for a generalist equilibrium*

We show that (x^*, x^*) is always an equilibrium of (5) for every m, σ and K: at this point $b_1'(x^*) = -b_2'(x^*)$ and $n_{1,x^*}(x^*, x^*) = n_{2,x^*}(x^*, x^*)$ (cf Appendix A.4 for the latter). However, this *generalist equilibrium* is a stable equilibrium of (5) if and only if

$$b_2''(x^*) + \frac{(b_2'(x^*)^2)}{m} < 0. \tag{10}$$

which yields

$$A\left(\frac{K'^2(A/4)}{m}+K''(A/4)\right)+2K'(A/4)<0 \tag{11}$$

An intuitive explanation is that individuals with trait value x^* have a moderate fertility in each patch, but do not suffer from fertility decay when they change habitat. When A is small (i.e. both patches have similar environments or selection is weak), $A\left(\frac{K'^2(A/4)}{m}+K''(A/4)\right)+2K'(A/4)\approx 2K'(A/4)<0$ because K is decreasing. Similarly, $A\left(\frac{K'^2(A/4)}{m}+K''(A/4)\right)+2K'(A/4)$ is decreasing with m ensuring that Condition (11) is more likely to be satisfied when m is large.

3.3 *There is no pure specialist equilibrium*

We show that with migration ($m \neq 0$), (E_1, E_2) is not an equilibrium of (5). The proof is based on a capital feature of our model: with migration, a given trait value always occurs in both patches (for example, if $m \neq 0$, taking $n_{1,x}(x,y)=0$ in the first equation from (3) implies that $n_{2,x}(x,y)=0$ and conversely).

Thus, at (E_1, E_2), the derivatives with respect to time of the two trait values are

$$\dot{x}=b_2'(E_1)[n_{2,E_1}(E_1,E_2)]^2$$

and

$$\dot{y}=b_1'(E_2)[n_{1,E_2}(E_1,E_2)]^2.$$

It is easy to check that $b_2'(E_1)=-b_1'(E_2)$. Both are different from 0 by hypothesis. Hence if (E_1,E_2) is an equilibrium ($\dot{x}=\dot{y}=0$), we have

$$n_{2,E_1}(E_1,E_2)=n_{1,E_2}(E_1,E_2)=0$$

which then implies

$$n_{1,E_1}(E_1,E_2)=n_{2,E_2}(E_1,E_2)=0$$

But the resident population cannot be zero. Hence $(\dot{x},\dot{y})(E_1,E_2)\neq(0,0)$ and (E_1,E_2) is not an equilibrium.

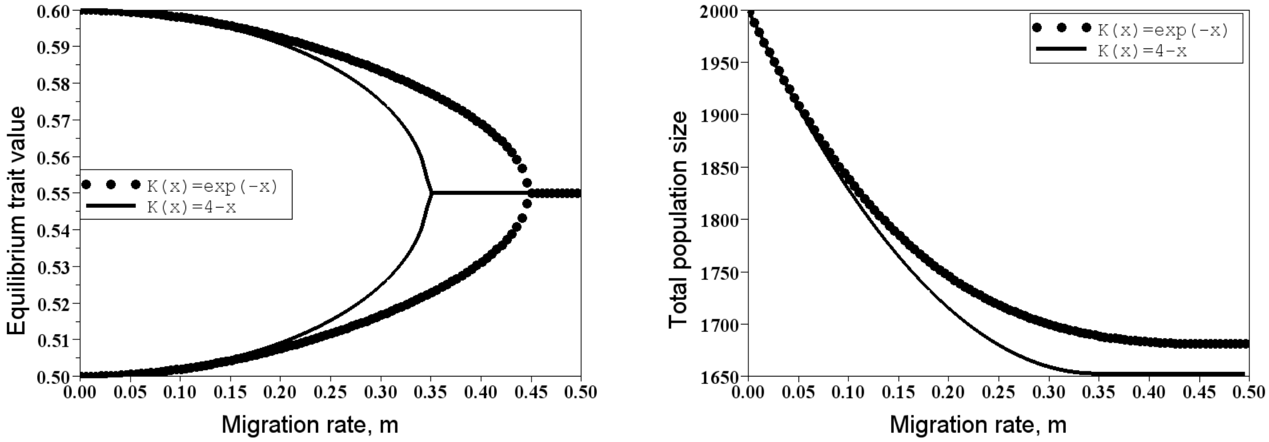
It should be noted that this result remains true even when relaxing the assumptions of symmetrical demography in the two patches (i.e., identical competition parameters) and iteroparity (cf. 3.5). However, « pure specialist » stable equilibria can be obtained with covariance of fertility and migration rates (see 3.5.2).

3.4 *Existence of a symmetrical equilibrium*

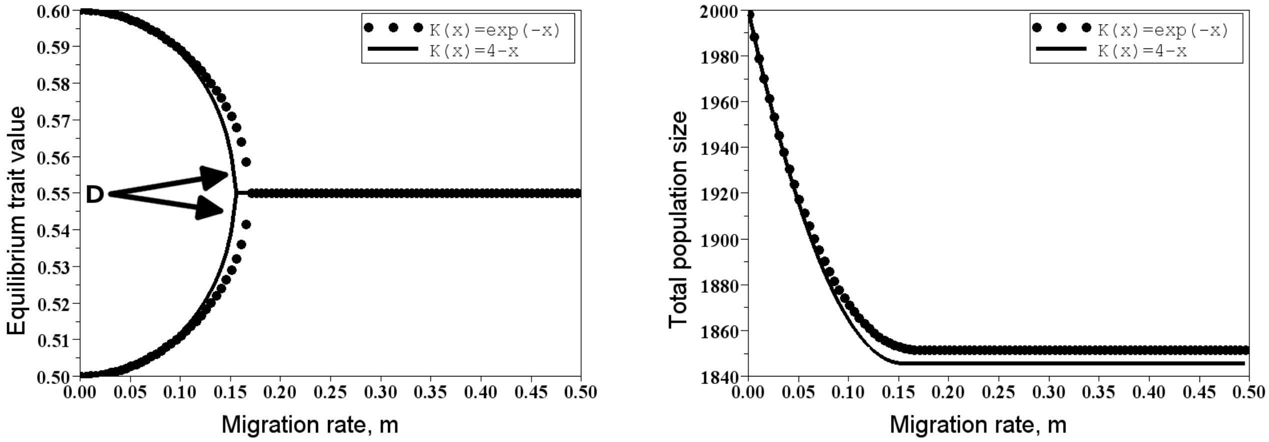
In situations where the generalist equilibrium is unstable we investigate other equilibria of the form $(x,\bar{x})$ (see Section 3.1).

To identify the condition of existence of such an equilibrium, one can check that if

$$b_2''(x^*)+\frac{b_2'(x^*)^2}{m}>0 \tag{12}$$

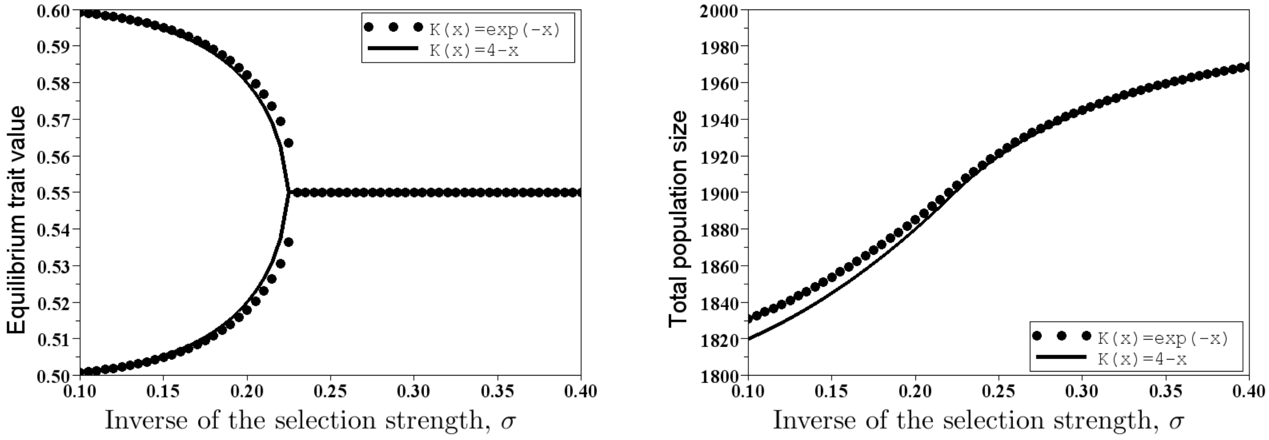


(A) $\sigma = 0.12$

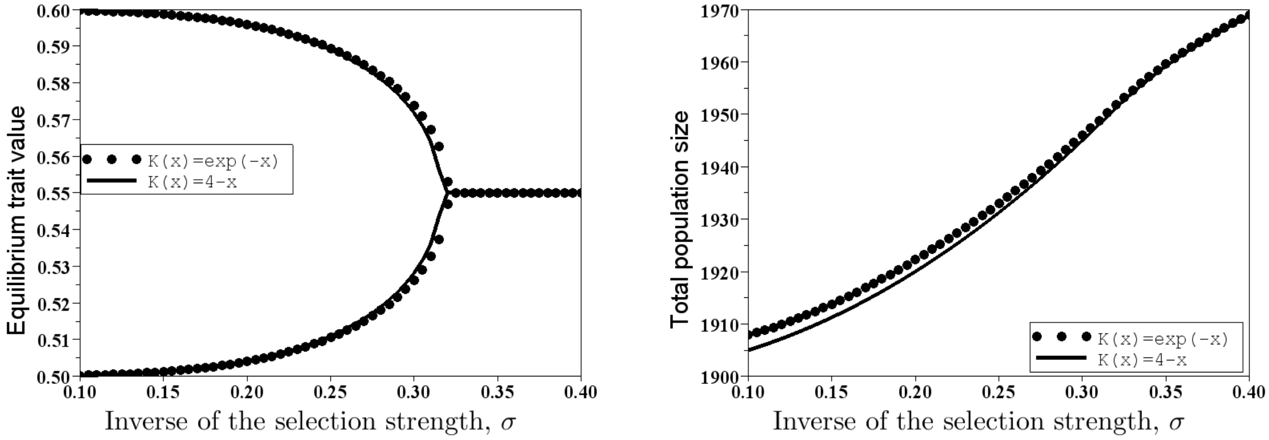


(B) $\sigma = 0.18$

Figure 2: Effect of migration rate m on equilibrium trait values and associated population sizes for two values of the inverse strength of selection σ and two shapes of the fertility function. On Panel B, the arrows labelled D indicate a specific dimorphic equilibrium : see Discussion for details. Other parameters: $E_1 = 0.5$, $E_2 = 0.6$, $\alpha = 0.001$.



(A) $m = 0.1$



(B) $m = 0.05$

Figure 3: Effect of inverse selection strength σ on equilibrium trait values and associated population sizes for two different values of the migration rate m and two shapes of the fertility function. Other parameters: $E_1 = 0.5$, $E_2 = 0.6$, $\alpha = 0.001$.

then there exists $x \in [E_1, E_2]$ so that $(x, \bar{x})$ is a stable equilibrium (cf Appendices A.5 and A.6). This dimorphic equilibrium is unique and depends on m and σ only (see Fig. 2)

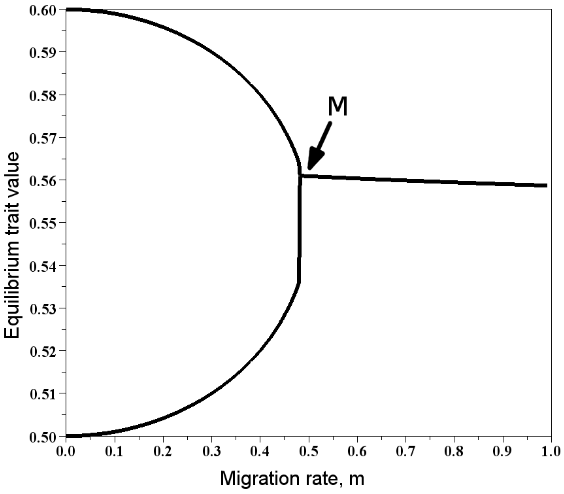
Note that when Condition (10) for the existence of a stable generalist equilibrium is not met, i.e. when the phenotypic distance A is large enough or the migration rate m small enough then Condition (12) is true: when the generalist equilibrium is unstable, another stable equilibrium always exists. Moreover, we show that with mild additional assumptions on the function K, there is always exactly one stable equilibrium (cf Appendix A.7).

Figure 2 and 3 summarize the effect of migration rate m and selection strength σ on equilibrium trait values and total population sizes. When m or σ are low enough, the population is characterized by a partial specialist strategy, with two distinct trait values. As m or σ increase, these values converge up to the point where they eventually collapse into the generalist strategy. Hence in all panels, there is a continuum of equilibria ranging from (E_1, E_2) to (x^*, x^*). The range of migration rates (respectively strengths of selection) allowing a stable dimorphic equilibrium decreases when σ increases (Figure 2) (respectively when m increases- see Figure 3). The critical point where symmetric and generalist equilibria merge is characterized by $b_2''(x^*) + \frac{b_2'(x^*)^2}{m} = 0$. At this point, we show that the derivative with respect to m is infinite (see (8) in Section 3.1 for a particular K), so that even a small variation of m around this point can have dramatic consequences in terms of the maintenance of a stable specialist strategy.

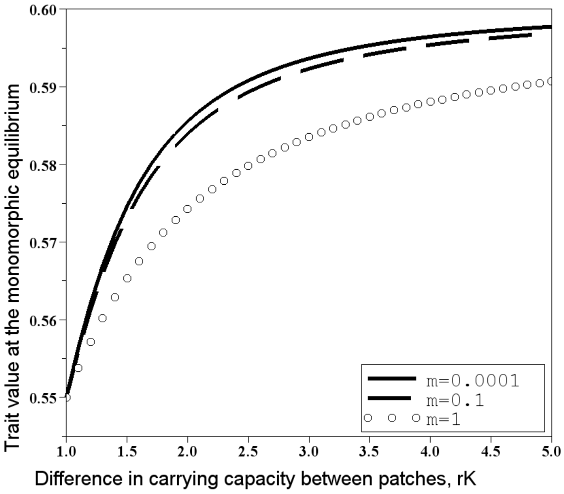
3.5 *Robustness of the model*

We now introduce slight changes in our model in order to analyze its robustness, mostly with numerical tools.

3.5.1 Asymmetry between the two patches



(A) $\frac{K(0)}{\alpha_1} = 100$, $r_\kappa = 1.25$

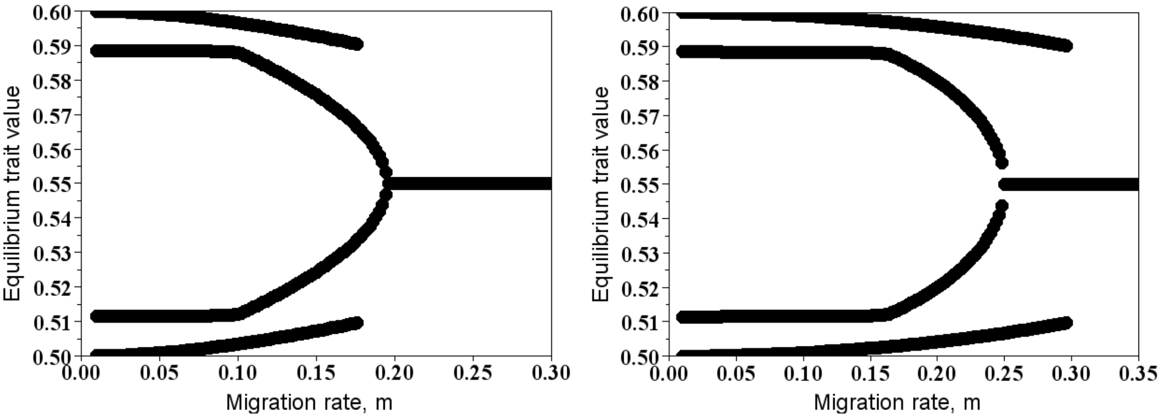


(B) $\frac{K(0)}{\alpha_1} = 100, \frac{K(0)}{\alpha_2} = r_\kappa \frac{K(0)}{\alpha_1}$

Figure 4: Influence of an asymmetry in the carrying capacities of patches on specialization. Panel A shows how the pattern of equilibrium trait values is modified by asymmetry while Panel B shows how the value of the monomorphic equilibrium varies with asymmetry. On Panel A, M indicates a specific monomorphic equilibrium : see Discussion for details. Other parameters: $\alpha_1 = 0.01$, $\sigma = 0.1$, $K(X) = \exp(-X)$

When the two patches have different carrying capacities, we still observe a unique dimorphic strategy that eventually collapses into a monomorphic equilibrium under large migration rates (Fig. 4A) or weak selection. Note that the lower curve exhibit a nearly vertical slope close to the critical value of m. In contrast to the symmetrical case, however, the trait value of the monomorphic strategy is biased toward the patch with the largest carrying capacity. Hence, from an ecological perspective, this equilibrium is no longer generalist in the strict sense. This bias increases with smaller migration rate m, stronger selection (smaller σ) or larger asymmetry of the two carrying capacities (cf. Fig. 4B). Similarly, when the strength of selection differs between the two patches, the general properties of our model are preserved and the monomorphic strategy is biased towards the trait value that is favored in the most selective patch, with a pattern very similar to fig 4. See Appendix B.2 for more details.

3.5.2 Covariance of fecundity and migration rate



(A) $K(X) = \exp(-X)$

(B) $K(X) = 4 - X$.

Figure 5: Effect of the maximum migration rate on evolutionarily stable trait values when migration covaries with the trait under selection. Here, migration is a sigmoid-like function that is symmetrical with respect to x^* so that $m(x) = m(\bar{x})$. Panels A and B show coexistence of stable strategies, depending on the shape of the fertility function. Other parameters $E_1 = 0.5$, $E_2 = 0.6$, $\sigma = 0.1$, $\alpha = 0.001$

Accounting for fitness-dependent migration yields more substantial changes to the outcomes of our model. Computing the derivative of the new survival probabilities as in Appendix A.2 yielded the new simplified equation :

$$\begin{cases} \dot{x} &= b_1'(x)(n_{1,x}(x,y))^2 + b_2'(x)(n_{2,x}(x,y))^2 + m'(x)[n_{2,x}(x,y) - n_{1,x}(x,y)]^2 \\ \dot{y} &= b_1'(y)(n_{1,y}(x,y))^2 + b_2'(y)(n_{2,y}(x,y))^2 + m'(y)[n_{2,y}(x,y) - n_{1,y}(x,y)]^2. \end{cases} \tag{13}$$

First, "pure specialist" equilibria (E_1, E_2) are now observed under the following condition:

$$m'(E_1) = -\frac{b_2'(E_1)[n_{2,E_1}(E_1, E_2)]^2}{[n_{2,E_1}(E_1, E_2) - n_{1,E_1}(E_1, E_2)]^2}. \tag{14}$$

This constrains the derivative of the migration rate at E_1 to be negative ($m'(E_1) < 0$), so that a "pure specialist" equilibrium can only emerge when the migration rate is larger at E_1 than for trait values $x > E_1$ but close to E_1. The generalist equilibrium (x^*, x^*) still exists (the new term of the equation depending on m cancels out at this point, because

$n_{1,x^*}(x^*, x^*) = n_{2,x^*}(x^*, x^*)$) and its stability depends on $m(x^*)$ only, not on the shape of $m(x)$ (cf Appendix A.9).

In addition to pure specialist and generalist equilibria, other equilibria are found which are expected to depend greatly on the shape of the function m. If we consider e.g. a migration function m that is symmetrical with respect to x^*, we can search equilibria of the form $(x, \bar{x})$ which are the roots of the following real function (see Appendix A.7 for the proof of this claim when m is constant):

$$\tilde{w}(x) = b_1'(x)(n_{1,x}(x, \bar{x}))^2 + b_2'(x)(n_{2,x}(x, \bar{x}))^2 + m'(x)[n_{2,x}(x, \bar{x}) - n_{1,x}(x, \bar{x})]^2. \qquad (15)$$

When the last term is large enough to modify the patterns of adaptation as compared to constant m, i.e $m'(x) = 0$, several dimorphic equilibria can be observed simultaneously. As an illustration, both panels of Figure 5 exhibit coexistence of stables strategies. In panel 5A where $K(X) = \exp(-X)$, we observe two dimorphic strategies; in panel 5B where $K(X) = 4 - X$, we observe either two dimorphic strategies or one monomorphic and one dimorphic strategy . More generally, when m is not symmetrical with respect to x^*, equilibria do not remain of the form $(x, \bar{x})$ and new monomorphic equilibria can be observed (see Fig.B.3 in Appendix B).

4 Discussion

Our theoretical approach provides a new framework to address the evolution of ecological specialization when deterministic temporal changes in the environment modify habitat connectivity or spatial heterogeneity among habitats (measured here as the phenotypic distance among the two patches). Our modelling framework allows in particular a variety of life history strategies and ecological processes to be considered, including varying population sizes, local competition and iteroparity with both natal and breeding dispersal. Note that, as in numerous previous theoretical works, we assume that decreased connectivity leads to decreased dispersal rates, i.e. a smaller probability of departure from a patch. In contrast, in natural populations departure rates might not be affected at an ecological timescale, but the cost of dispersal can be greatly increased. Both mechanisms cause decreased effective migration rates, but have contrasting impacts on demography.

4.1 *Changes in connectivity and the evolution of specialization*

Our results indicate that with constant migration rates a single strategy (specialist or generalist) is favored at equilibrium. As expected, the stable equilibrium depends on the opposing forces of migration (high migration rates favor the generalist strategy, Brown and Pavlovic 1992; Meszéna et al. 1997; Day 2000) and selection heterogeneity (Meszéna et al. 1997). The latter depends on the intrinsic selection parameter σ and on the environmental distance between habitat patches (which define together the phenotypic distance, see Hereford 2009). In the simplest cases we provide an explicit value for the equilibria, depending on migration and selection parameters. The strength of the selective trade-off among patches was deemed critical elsewhere in the evolution of specialization (see Ravigné et al. 2009, Nurmi and Parvinen 2011): here we demonstrate that characterizing this parameter by the convexity of the relationship $b_2 = f(b_1)$ is not necessarily relevant, as (i) the evolutionary endpoints depend solely on the selection parameter; (ii) one can prove that for any model with a bell-shaped fecundity, the trade-off is always locally concave close to the points $b_1(E_1)$ and $b_2(E_2)$. Importantly, the sensitivity of the equilibrium trait value to migration or selection parameters is high around transition areas between monomorphic and dimorphic populations. In these areas, a small increase in migration or a slightly softer selection can cause a collapse of a polymorphism in habitat use (Day 2000). In contrast, a small reduction in connectivity (i.e. of migration) or a small increase of environmental distance (which can both result from habitat destruction) may drastically change the evolutionary equilibrium from a generalist to a specialist regime (Fig. 2 and 3). Recent evidence indicates that geographic isolation in a heterogeneous environment may promote adaptive divergence within species (see e.g. Konuma et al. 2011, for an example of adaptive divergence of external morphology in carabid beetles). Although our results suggest that environmental changes of small magnitude may lead to abrupt evolutionary changes, we cannot assess the actual speed of these changes within our framework. Nevertheless, evolution is known to happen on short time scales such as ecological time scales (Stockwell et al. 2003)and rapid evolutionary responses to global change are already known to occur, as well exemplified by the evolution of resistance to pesticides in mosquitoes (e.g. Berticat et al. 2008), local adaptation to acidity in moor frogs (Räsänen et al. 2003) and adaptation to climate change in fruit flies (review in Merilä 2012).

4.2 *The importance of the demography-genetics interaction*

Using a two-patch « toy-model », Meszéna et al. (1997) obtained similar qualitative effects of migration rates and environmental distance on adaptive patterns (and subsequent work allowed to generalize these results to spatially continuous environments, see Débarre and Gandon 2010). However, Meszéna et al. (1997) could not assess the demographic costs associated with various strategies (soft selection model). With the present model, reducing connectivity or increasing environmental distance both shift a stable generalist equilibrium to a specialist equilibrium but these two mechanisms have contrasted effects on population sizes. Reducing connectivity increases average population size (i.e. a decrease of maladaptation, Fig. 2), while increasing environmental distance decreases population size (i.e. an increase of maladaptation). This implies that, although migration and selection seem to play symmetrical roles in adaptive patterns, they are associated with different costs, which is difficult to assess under pure soft selection models (i.e., when maladaptation has no consequences on population sizes). Under our assumption of rare mutations (Metz et al. 1996), abrupt shifts in stable equilibrium with change in migration rate are paradoxically associated with smooth and continuous changes in equilibrium population sizes (see Figs 2 and 3). Relaxing the assumption of rare mutations may lead to more complex evolutionary patterns due to irreversible interacting effects of demography and genetics, as illustrated by the migrational meltdown process, in which increasing migration may lead maladaptation and shrinking population size to mutually reinforce. Such processes may lead not only to abrupt shifts in evolutionary equilibrium along a migration gradient (as in our case) but also to abrupt and hysteretic decrease in population size at some migration threshold value (Ronce and Kirkpatrick 2001).

4.3 *On the ecological and evolutionary concepts of specialization*

Although it can be considered across ecological levels (from populations to communities), ecological specialization is primarily defined at the individual level, as the process by which individual genotypes become adapted to an increasingly narrow subset of their possible environments and persists in an increasingly narrow range of habitats (Futuyma and Moreno 1988; Poisot et al. 2011). In most theoretical population level studies on the evolution of specialization in heterogeneous environments, monomorphic strategies are considered as generalist strategies and polymorphic (dimorphic in our case) strategies, in which different genotypes are adapted to different environments, are considered as specialist strategies. This definition is consistent with the statement of Bolnick et al. (2003) suggesting that many apparently generalist species are in fact composed of a range of ecologically variable, individual specialists (see also Poisot et al. 2011). Some of our results however raise concerns on considering monomorphic (resp. polymorphic) equilibria as generalist (resp. specialist) strategies. Our results illustrate in particular that in most realistic situations (i.e., with non-zero migration rates and asymmetrical patch sizes), monomorphic equilibria cannot be considered as generalist strategies and polymorphic (dimorphic) equilibria generally do not correspond to pure specialist strategies. First, our analysis suggests that including some asymmetry in patch carrying capacities or in selection parameters does not affect the qualitative effects of selection and migration on monomorphic and dimorphic stable equilibria. However, asymmetry biases adaptation toward the largest/most selective patch (see Holt 1996), resulting in monomorphic equilibria in which individuals are in fact "specialized" on one of the patches (compare e.g., populations D and M , indicated by arrows on Figs 2B and 4A respectively: although D corresponds to a dimorphic equilibrium, individuals from the D population are less "specialized" on one of the two habitats than individuals from the M, monomorphic population). Second, in contrast with previous theoretical studies (in particular resource-consumption models, Nurmi and Parvinen 2008), we demonstrate that there is no pure specialist stable equilibrium (i.e. a dimorphic stable equilibrium in which individuals are perfectly adapted to either patch) as long as the migration rate is non-zero. Hence, in heterogeneous patchy environments, only completely isolated subpopulations are perfectly locally adapted. We further showed that (1) although theory predicts that specialist genotypes are more likely to coexist when they experience a single environment throughout their life cycle (Levins 1968), the absence of pure specialists is not a consequence of iteroparity and holds in case of semelparity as well; (2) if the migration rate covaries with the fertility rate, some pure specialist equilibrium can be obtained, but only under restrictive conditions.

4.4 *Limitations*

Future works on operational biodiversity scenarios (Pereira et al. 2010) will require consideration of transitory evolutionary states (not only equilibrium states). This entails estimating transitory costs of adaptation from an equilibrium state to another and assessing the speed of adaptation (as well as its associated extinction risk), which is generally not achieved in theoretical works on adaptation. With the present model, such quantitative approach on adaptation cannot be performed without adding complexity, e.g. in terms of the genetic architecture or the ecological processes modeled. From a quantitative genetics point of view, this includes considerations of large numbers of loci, realistic distributions of mutational additive effects, genetic linkage and epistatic interactions (Hill 2010), as well as constraints that can slow down or prevent evolutionary processes, such as the lack of genetic variation or the non-independence of traits (genetic correlations). While lack of genetic variation represents an absolute constraint that prevents adaptation, genetic correlations can reduce the rate of adaptation (e.g. Davis et al. 2005, Teplitsky et al. 2011; Morrissey et al. 2012). Future models should then consider several traits under selection, along with pleiotropic effects, and genetic correlations that can affect the pace but also the direction of the response to selection (in this context, we plan to develop further the model to examine cases in which fecundity and migration are controlled by separate loci). From an ecological point of view, consideration of (directional and stochastic) temporal environmental variation is of primary importance to the study of operational scenarios on adaptation, as (i) environmental noise strongly affects adaptive patterns in spatially heterogeneous environment (Wilson and Yoshimura 1994); (ii) biodiversity scenarios are in essence based on scenarios of environmental changes over time. Although our model is fairly simplified, the microscopic model can easily be improved to incorporate new mechanisms without artificially adding any term to Equation (3), but rather computing how the new feature changes it. This plasticity makes our model an efficient framework to study evolutionary dynamics in two-patch models, although extending the model to a more general context (more patches, disruptive selection, sexual reproduction, and most importantly, incorporation of temporal environmental variation) would require extension of the mathematical theorems on which this approach relies.

A Online Appendix: Mathematical proofs

For the proofs here it is assumed that $\alpha = 1$. We can revert to any α by taking $m \leftrightarrow \frac{m}{\alpha}$ and $b_i(x) \leftrightarrow \frac{b_i(x)}{\alpha}$.

We write

$$N_1(x,y) = n_{1,x}(x,y) + n_{1,y}(x,y) \text{ and } N_2(x,y) = n_{2,x}(x,y) + n_{2,y}(x,y) \tag{16}$$

the total population sizes on patches 1 and 2 when the resident population has trait values x and y.

A.1 Growth rate

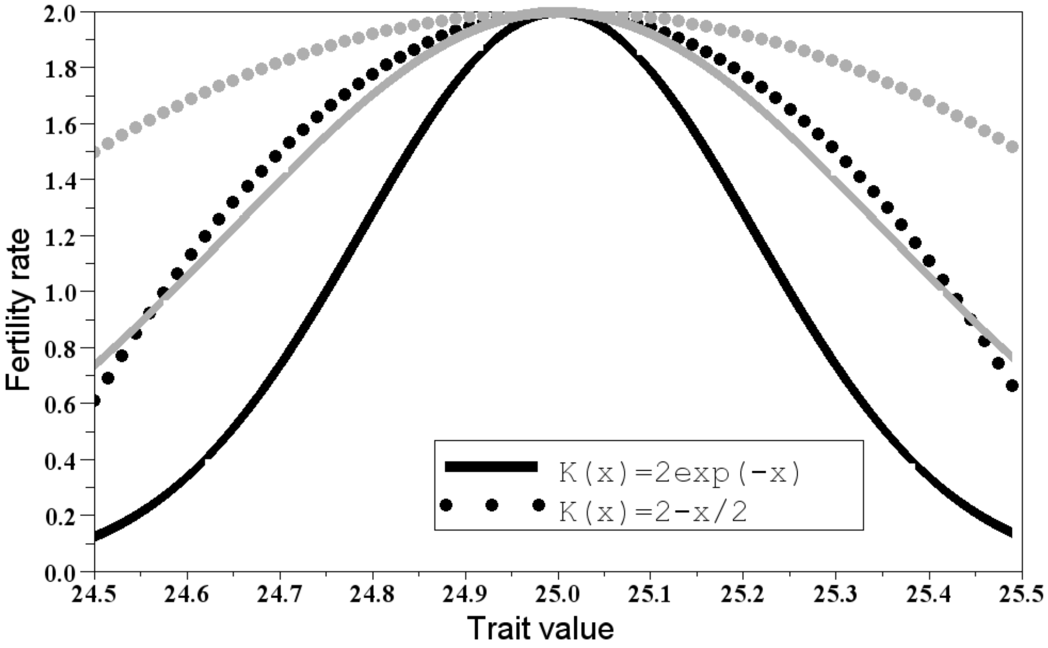


Figure A.1: Fertility rate for two different functions K depending on the trait value of the individual. $\sigma = 0.3$ for the black line and $\sigma = 0.5$ for the gray line. Environment value of the patch is 25.

A.2 On fitness and survival

The exact meaning of fitness for structured and evolving population can be a difficult question (cf. Metz et al. 1992). However, here, given that there are only two populations and a relatively low number of parameters, we use the following heuristics: when a mutant appears in the population, since the resident population is large, at the first order, the dynamics of the mutant population are close to linear. If we write the differential equation regarding the size of the mutant population z in a resident population (x, y), we can approximate it by the solution of

$$\begin{aligned} \dot{n}_1^z &= (b_1(z) - N_1(x,y))n_1^z + m(n_2^z - n_1^z) \\ \dot{n}_2^z &= (b_2(z) - N_2(x,y))n_2^z + m(n_1^z - n_2^z) \end{aligned} \tag{17}$$

i.e

$$\dot{n}^z = \Xi(z; x, y)n^z, \tag{18}$$

where $\Xi(z; x, y)$ is a 2×2 square matrix. There are solutions of Equation (17) that stay in $\mathbb{R}_+ - \{0, 0\}$ if and only if the greatest eigenvalue of Ξ is positive. This is what we call fitness and we can compute it explicitly

$$\begin{aligned} f(z;x,y) = \frac{1}{2}\Big(& b_1(z) + b_2(z) - [N_1(x,y) + N_2(x,y)] - 2m \\ & + \sqrt{4m^2 + (b_1(z) - b_2(z) - N_1(x,y) + N_2(x,y))^2}\Big) \end{aligned} \tag{19}$$

Because of the large population size, the competition between mutants is negligible in front of the competition pressure induced by the resident population. Then the birth and death process that the mutant population undergoes when it appears in the resident population can also be approximated by a linear birth and death process (i.e a two type branching process). Therefore we are now interested on the survival probabilities for a two-patch birth-death-migration linear process.

Lets $(Z_t^1, Z_t^2)_{t\geq 0}$ be such a process with *per capita* rates on patch i being respectively b_i, d_i and m. Write $g_i(n)$ the probability of survival of the process starting with a population of n individuals on patch i (i.e $Z_0^i = n, Z_0^{3-i} = 0$). Note that because the process is linear, and therefore branching, we have:

$$g_i(n) = g_i(1)^n. \tag{20}$$

Starting from one individual on patch 1, the total jump rate of the process is $b_1 + d_1 + m$. Then the probability of survival of the process starting from one individual on patch 1 is, conditioning on the first jump:

$$\begin{aligned} & g_1(1) = \mathbb{P}(\text{The first jump is a birth})g_1(2) + \mathbb{P}(\text{The first jump is a migration})g_2(1) \\ & g_1(1) = \frac{b_1}{b_1 + d_1 + m}(g_1(1))^2 + \frac{m}{b_1 + d_1 + m}g_2(1) \text{ i.e.} \\ & b_1 g_1(1)^2 - (b_1 + d_1 + m)g_1(1) + m g_2(1) = 0 \end{aligned} \tag{21}$$

Similar computation for a population starting from one individual on patch 2 allows us to conclude that $(g_1(1), g_2(1))$ is a solution in $[0,1]^2$ of the system

$$\begin{cases} b_1 g_1(1)^2 - (b_1 + d_1 + m)g_1(1) + m g_2(1) & = 0 \\ b_2 g_2(1)^2 - (b_2 + d_2 + m)g_2(1) + m g_1(1) & = 0. \end{cases} \tag{22}$$

Now, we define $g_i(z;x,y)$ as the survival probability of a mutant with trait value z arising in patch i with resident population of trait values x and y. Resident population sizes are computed according to (3). Taking $b_i = b_i(z)$ and $d_i = n_{i,x}(x,y) + n_{i,y}(x,y)$, we have $g_i(1) = g_i(z;x,y)$. With some algebric work on Equation (22), one can show that it implies that $g_1(z;x,y)$ is a root in $[0,1]$ of the following polynomial

$$P(X) = a_3 X^3 + a_2 X^2 + a_1 X + a_0 \tag{23}$$

with

$$\begin{aligned} & a_3 = b_1(z)^2 b_2(z) \\ & a_2 = 2b_1(z)b_2(z)(m + N_1(x,y) - b_1(z)) \\ & a_1 = b_2(z)(b_1(z) - N_1(x,y))^2 + m[b_1(m + N_2(x,y) - b_2(z))] \\ & \quad + m b_2[(m + N_1(x,y) - b_1(z)) + (N_1(x,y) - b_1(z))] \\ & a_0 = [(b_1(z) - N_1(x,y))(b_2(z) - N_2(x,y)) - m(b_1(z) + b_2(z) - N_1(x,y) - N_2(x,y))]\, m. \end{aligned} \tag{24}$$

$g_2(z;x,y)$ is a solution of a similar equation with the roles of x and y exchanged. Derivatives of these probabilities for Equation (4) can be computed explicitly using the fact that $g_i(x;x,y) = g_i(y;x,y) = 0$. Indeed, writing for the following lines $n_{1,x}(x,y) = n_1$ and $n_{2,x}(x,y) = n_2$

$$\begin{aligned}
\frac{d}{dz}P(g_1(z;x,y))|_{(x,x,y)} = 0 \Longleftrightarrow\ & g_1(x;x,y)\left[\frac{d}{dz}a_3 g_1(x;x,y)^2 + \frac{d}{dz}a_2 g_1(x;x,y) + \frac{d}{dz}a_1\right] \\
&+ \left[3a_3\frac{d}{dz}g_1(x;x,y)g_1(x;x,y) + 2a_2\frac{d}{dz}g_1(x;x,y)\right]g_1(x;x,y) \\
&+ \frac{d}{dz}(a_0)|_{(x,x,y)} + a_1(x;x,y)\frac{d}{dz}g_1(x;x,y) = 0 \\
\Longleftrightarrow\ & \frac{d}{dz}(a_0)|_{(x,x,y)} + a_1(x;x,y)\frac{d}{dz}g_1(x;x,y) = 0 \\
\Longleftrightarrow\ & \frac{d}{dz}g_1(x;x,y) = -\frac{1}{a_1(x;x,y)}\frac{d}{dz}(a_0)|_{(x,x,y)}.
\end{aligned} \tag{25}$$

But

$$\begin{aligned}
a_1(x;x,y) &= b_2(x)m^2(1-\frac{n_2}{n_1})^2 + m^2 b_1(x)(\frac{n_1}{n_2}) + m^2 b_2(x)(2\frac{n_2}{n_1} - 1) \\
&= m^2\left[b_2(x)(\frac{n_2}{n_1})^2 + b_1(x)\frac{n_1}{n_2}\right] \\
&= m^2\left[\frac{b_1(x)(n_1)^3 + b_2(x)(n_2)^3}{(n_1)^2 n_2}\right]
\end{aligned} \tag{26}$$

and

$$\begin{aligned}
\frac{d}{dz}a_0|_{(x;x,y)} &= m\left[b_1'(x)m(1-\frac{n_1}{n_2}) + b_2'(x)m(1-\frac{n_2}{n_1}) - m(b_1'(x)+b_2'(x))\right] \\
&= -m^2\left[\frac{b_1'(x)(n_1)^2 + b_2'(x)(n_2)^2}{n_1 n_2}\right].
\end{aligned} \tag{27}$$

So

$$\frac{d}{dz}g_1(x;x,y) = \partial_1 g_1(x;x,y) = n_1\frac{b_1'(x)(n_1)^2 + b_2'(x)(n_2)^2}{b_1(x)(n_1)^3 + b_2(x)(n_2)^3}. \tag{28}$$

And so the first component of (4) yields

$$\dot{x} = \frac{b_1(x)(n_{1,x}(x,y))^2 + b_2(x)(n_{2,x}(x,y))^2}{b_1(x)(n_{1,x}(x,y))^3 + b_2(x)(n_{2,x}(x,y))^3}p[b_1'(x)(n_{1,x}(x,y))^2 + b_2'(x)(n_{2,x}(x,y))^2] \tag{29}$$

and by symmetry

$$\dot{y} = \frac{b_1(y)(n_{1,y}(x,y))^2 + b_2(y)(n_{2,y}(x,y))^2}{b_1(y)(n_{1,y}(x,y))^3 + b_2(y)(n_{2,y}(x,y))^3}p[b_1'(y)(n_{1,y}(x,y))^2 + b_2'(y)(n_{2,y}(x,y))^2] \tag{30}$$

Now note that $\frac{b_1(x)(n_{1,x}(x,y))^2 + b_2(x)(n_{2,x}(x,y))^2}{b_1(x)(n_{1,x}(x,y))^3 + b_2(x)(n_{2,x}(x,y))^3}$ is strictly positive, provided the resident population are non-zero. Hence

$$\begin{aligned}
&\frac{b_1(x)(n_{1,x}(x,y))^2 + b_2(x)(n_{2,x}(x,y))^2}{b_1(x)(n_{1,x}(x,y))^3 + b_2(x)(n_{2,x}(x,y))^3}p[b_1'(x)(n_{1,x}(x,y))^2 + b_2'(x)(n_{2,x}(x,y))^2] = 0 \\
&\Leftrightarrow b_1'(x)(n_{1,x}(x,y))^2 + b_2'(x)(n_{2,x}(x,y))^2 = 0
\end{aligned} \tag{31}$$

In order to find equilibria of Equation (4), we can therefore find those of the simplified canonical equation (5):

$$\begin{cases} \dot{x} & = h_1(x,y) = b_1'(x)(n_{1,x}(x,y))^2 + b_2'(x)(n_{2,x}(x,y))^2 \\ \dot{y} & = h_2(x,y) = b_1'(y)(n_{1,y}(x,y))^2 + b_2'(y)(n_{2,y}(x,y))^2 \end{cases} \tag{5}$$

Regarding the stability of equilibria of both equations, they are equivalent if

$$\frac{b_1(x)(n_{1,x}(x,y))^2 + b_2(x)(n_{2,x}(x,y))^2}{b_1(x)(n_{1,x}(x,y))^3 + b_2(x)(n_{2,x}(x,y))^3} = \frac{b_1(y)(n_{1,y}(x,y))^2 + b_2(y)(n_{2,y}(x,y))^2}{b_1(y)(n_{1,y}(x,y))^3 + b_2(y)(n_{2,y}(x,y))^3}. \tag{32}$$

But this condition is always satisfied when $y = \bar{x}$ (see Appendix A.4). Therefore, for the purpose of our study, we can study the simplified equation (5).

A.3 There is no equilibria outside $[E_1, E_2]^2$

Indeed, if say $x < E_1$ then

$$b_1'(x) = \frac{2}{\sigma^2}(x - E_1)K'\left[\left(\frac{(x-E_1)}{\sigma}\right)^2\right]. \tag{33}$$

Since K is decreasing, $K'(z) < 0$ for all z and therefore $b_1'(x) > 0$. For similar reasons ($x < E_1 < E_2$), $b_2'(x) > 0$. Thus $b_1'(x)n_{1,x}^2(x,y) + b_2'(x)n_{2,x}^2(x,y) > 0$.

A.4 Population sizes

When both trait values in the population are equal to x^*, Equation (3) becomes much simpler. In that case $b_1(x^*) = b_2(x^*) := b$ and thus summing (3a) and (3c) together as well as summing (3b) and (3d) together yields

$$\begin{cases} bN_1(x^*,x^*) - N_1(x^*,x^*)^2 + m(N_2(x^*,x^*) - N_1(x^*,x^*)) & = 0 \\ bN_2(x^*,x^*) - N_2(x^*,x^*)^2 + m(N_1(x^*,x^*) - N_2(x^*,x^*)) & = 0. \end{cases} \tag{34}$$

Hence $N_1(x^*,x^*) = N_2(x^*,x^*) = b$. Reinjecting this in (3) yields

$$m(n_1(x^*,x^*) - n_2(x^*,x^*)) = 0$$

and therefore $n_1(x^*,x^*) = n_2(x^*,x^*)$.

If $x \neq x^*$ and the resident population has trait values x and $\bar{x}$, we can explicitly compute the population sizes, which will be useful next.

We look for a solution to (3) so that $n_{1,x}(x,\bar{x}) = n_{2,\bar{x}}(x,\bar{x})$ and $n_{2,x}(x,\bar{x}) = n_{1,\bar{x}}(x,\bar{x})$ because of (6). Hence $N_1(x,\bar{x}) = N_2(x,\bar{x}) = N$. We define X as $\frac{n_{1,x}}{N} = \frac{n_{2,\bar{x}}}{N}$. Summing (3a) and (3b) yields:

$$\begin{aligned} (b_1(x) - N)XN + (b_2(x) - N)(1-X)N + m(N_2 - N1) = 0 \\ \iff X = \frac{N - b_2(x)}{b_1(x) - b_2(x)}. \end{aligned} \tag{35}$$

Remember that $N_1 = N_2 = N$, using this in (3a) and dividing by N yields:

$$\begin{aligned}
&(b_1(x) - N)\frac{N - b_2(x)}{b_1(x) - b_2(x)} + m(\frac{N - b_1(x)}{b_2(x) - b_1(x)} - \frac{N - b_2(x)}{b_1(x) - b_2(x)}) = 0 \\
\iff &\frac{1}{b_1 - b_2}\left[N^2 - (b_1 + b_2 - 2m)N + b_1 b_2 - m(b_1 + b_2)\right] = 0 \\
\iff &N = \frac{1}{2}\left[b_1(x) + b_1(\bar{x}) - 2m + \sqrt{4m^2 + (b_1(x) - b_1(\bar{x}))^2}\right]
\end{aligned} \tag{36}$$

and

$$\begin{aligned}
n_{1,x} = n_{2,\bar{x}} &= \frac{1}{2}\left(1 + \frac{\sqrt{4m^2 + (b_1(x) - b_2(x))^2} - 2m}{b_1 - b_2}\right)N \\
n_{2,x} = n_{1,\bar{x}} &= \frac{1}{2}\left(1 + \frac{\sqrt{4m^2 + (b_1(x) - b_2(x))^2} - 2m}{b_2 - b_1}\right)N.
\end{aligned} \tag{37}$$

A.5 Proof of existence of a symmetrical equilibrium if Condition (12) is satisfied

It is a simple argument of continuity. Note that because of (6),

$$\dot{x}(x, \bar{x}) = 0 \iff \dot{y}(x, \bar{x}) = 0.$$

Recall the functions $h_1(x, y)$ and $h_2(x, y)$ from Equation (5). The previous equations enable us to study only the roots of, say, $x \mapsto h_1(x, \bar{x})$.

At $x = E_1$, $h_1(E_1, E_2) = b_2'(E_1)(n_{2,E_1}(E_1, E_2))^2 > 0$.

Now, if

$$\frac{d}{dx}[h_1(x, \bar{x})]_{|(x^*, x^*)} > 0$$

since $h_1(x^*, x^*) = 0$ (see Section 3.2) then for x sufficiently close to x^*, a simple argument of continuity for real functions ensures that $h_1(x, \bar{x}) < 0$.

Therefore, there exists an $x \in]E_1, x^*[$ such that $h_1(x, \bar{x}) = 0$. At the point (x^*, x^*), we deduce from (1), (36) and (37) that

$$\begin{aligned}
&b_1(x^*) = b_2(x^*),\ N(x^*, x^*) = b_1(x^*),\ n_{i,x^*} = \frac{1}{2}b_1(x^*) \text{ and} \\
&b_1'(x^*) = -b_2'(x^*) \text{ and } b_1''(x^*) = b_2''(x^*).
\end{aligned} \tag{38}$$

Moreover

$$\begin{aligned}
\frac{d}{dx}h_1(x, \bar{x}) &= b_1''(x)(n_1(x, \bar{x}))^2 + b_2''(x)(n_2(x, \bar{x}))^2 \\
&+ 2\left[b_1'(x)n_1(x, \bar{x})\frac{d}{dx}n_1(x, \bar{x}) + b_2'(x)n_2(x, \bar{x})\frac{d}{dx}n_2(x, \bar{x})\right].
\end{aligned} \tag{39}$$

(36) and (37) yield

$$\begin{aligned}\frac{d}{dx}n_1(x,\bar{x}) = (\frac{d}{dx}N(x,\bar{x}))&\left(1+\frac{\sqrt{4m^2+(b_1(x)-b_2(x))^2}-2m}{b_1-b_2}\right)\\ &+N(x,\bar{x})\frac{d}{dx}\left(1+\frac{\sqrt{4m^2+(b_1(x)-b_2(x))^2}-2m}{b_1-b_2}\right).\end{aligned}$$

But if $x = x^*$,

$$\frac{d}{dx}N(x,\bar{x}) = \frac{1}{2}\left(b_1'(x)+b_2'(x)+\frac{(b_1'(x)-b_2'(x))(b_1(x)-b_2(x))}{\sqrt{4m^2+(b_1(x)-b_2(x))^2}}\right) = 0.$$

Then:

$$\begin{aligned}\frac{d}{dx}\left(1+\frac{\sqrt{4m^2+(b_1(x)-b_2(x))^2}-2m}{b_1(x)-b_2(x)}\right) = &\frac{(b_1'(x)-b_2'(x))}{\sqrt{4m^2+(b_1(x)-b_2(x))^2}}\\ &-\frac{(\sqrt{4m^2+(b_1(x)-b_2(x))^2}-2m)(b_1'(x)-b_2'(x))}{(b_1(x)-b_2(x))^2}.\end{aligned}$$

By expanding around x^* the second term of the right hand side, we find that

$$\begin{aligned}\frac{d}{dx}\left(1+\frac{\sqrt{4m^2+(b_1(x)-b_2(x))^2}-2m}{b_1(x)-b_2(x)}\right)_{(x^*,x^*)} &= (b_1'(x^*)-b_2'(x^*))(\frac{1}{2m}-\frac{1}{4m})\\ &= -\frac{b_2'(x^*)}{2m}\end{aligned} \tag{40}$$

Finally, noting that $N(x^*) = b_2(x^*)$, and incorporating (40) in Equation (39) yields

$$\begin{aligned}\frac{d}{dx}h_1(x,\bar{x}) &= \frac{1}{2}b_2''(x^*)(b_2(x^*,x^*))^2\\ &+2\left(b_1'(x^*)\frac{b_1(x^*)}{2}(-\frac{b_2'(x^*)}{2m})+b_2'(x^*)\frac{b_2(x^*)}{2}(-\frac{b_1'(x^*)}{2m})\right)\\ &= \frac{1}{2}(b_2(x^*,x^*))^2\left[b_2''(x^*)+\frac{(b_2'(x^*)^2)}{m}\right].\end{aligned} \tag{41}$$

A.6 On stability

NB: For readability purposes, we will denote by $(n_1(x,y), n_2(x,y), n_3(x,y), n_4(x,y))$ *the vector* $(n_{1,x}(x,y), n_{2,x}(x,y), n_{1,y}(x,y), n_{2,y}(x,y))$*. Moreover when no confusion is possible, we will simply write* n_i *for* $n_i(x,y)$*.*

First, let us show that:

If $(x,\bar{x})$ *is an equilibrium then it is stable if and only if* $\frac{d}{dx}[h_1(x,\bar{x})] < 0$

We have to calculate the derivatives of the populations sizes: for all (x,y), differentiating (3) with respect to the first variable, we find

$$C(x,y)\begin{pmatrix}\partial_1 n_1(x,y)\\ \partial_1 n_2(x,y)\\ \partial_1 n_3(x,y)\\ \partial_1 n_4(x,y)\end{pmatrix} = \begin{pmatrix}-b_1'(x)n_1(x,y)\\ -b_2'(x)n_2(x,y)\\ 0\\ 0\end{pmatrix} \tag{42}$$

with

$$C(x,y) = \begin{pmatrix} b_1(x) - n_{1,x} - N_1 - m & m & -n_{1,x} & 0 \\ m & b_2(x) - n_{2,x} - N_2 - m & 0 & -n_{2,x} \\ -n_{1,y} & 0 & b_1(y) - N_1 - n_{1,y} - m & m \\ 0 & -n_{2,y} & m & b_2(y) - N_2 - n_{2,y} - m \end{pmatrix} \tag{43}$$

$C(x,y)$ is invertible because it is the Jacobian of System (3) at the point $(n_{1,x}, n_{2,x}(x,y), n_{1,y}(x,y), n_{2,y}(x,y))$, which is a stable equilibrium of the system (and its eigenvalues all have a negative real part). It is well known that the matrix $C^{-1} = (c_{ij})_{i,j\in\{1,2,3,4\}}$ can be computed using the comatrix of C. Hence the reader can easily convince himself that C^{-1} keeps some "symmetry properties" of $C(x,\bar{x})$ such as $c_{11} = c_{44}$ or $c_{13} = c_{42}$

This, (6) and (42) allow us to assert that

$$\begin{cases} \partial_1 n_1(x,\bar{x}) & = -\partial_2 n_4(x,\bar{x}) \\ \partial_1 n_2(x,\bar{x}) & = -\partial_2 n_3(x,\bar{x}) \\ \partial_1 n_3(x,\bar{x}) & = -\partial_2 n_2(x,\bar{x}) \\ \partial_1 n_4(x,\bar{x}) & = -\partial_2 n_1(x,\bar{x}) \end{cases} \tag{44}$$

Now taking the expression of $h_i(x,y)$ from (5), differentiating it with respect to the right variable, and then using (44) and differentiating (6) yields:

$$\partial_1 h_1(x,\bar{x}) = \partial_2 h_2(x,\bar{x}) \text{ and } \\ \partial_2 h_1(x,\bar{x}) = \partial_1 h_2(x,\bar{x}) \tag{45}$$

And since we have

$$B(x) = DF_{(x,\bar{x})} = \begin{pmatrix} \partial_1 h_1(x,\bar{x}) & \partial_1 h_2(x,\bar{x}) \\ \partial_2 h_1(x,\bar{x}) & \partial_2 h_2(x,\bar{x}) \end{pmatrix}, \tag{46}$$

we can deduce that B is a symmetrical matrix, therefore its eigenvalues are real. Having two negative eigenvalues is hence equivalent to $\left[\ tr(B(x)) < 0 \text{ and } \det(B(x)) > 0\right]$. We now prove our claim:

Necessary condition: If $\frac{d}{dx}[h_1(x,\bar{x})] > 0$ i.e.

$$\partial_1 h_1(x,\bar{x}) - \partial_2 h_1(x,\bar{x}) > 0, \tag{47}$$

then either

$$\partial_1 h_1(x,\bar{x}) + \partial_2 h_1(x,\bar{x}) > 0 \tag{48}$$

and in this case, $tr(B(x)) > 0$ so $(x,\bar{x})$ is unstable (since at least one eigenvalue is nonnegative), or

$$\partial_1 h_1(x,\bar{x}) + \partial_2 h_1(x,\bar{x}) < 0 \tag{49}$$

and then $det(B(x)) < 0$ so both eigenvalues have opposite signs.

Sufficient condition: It suffices to show that

$$\text{if } (x,\bar{x}) \text{ is an equilibrium, then } \partial_2 h_1(x,\bar{x}) = 0 \tag{50}$$

Indeed our hypothesis would then yield $\partial_1 h_1(x,\bar{x}) < 0$ which would allow us to conclude. Let us then prove (50). Differentiating h_1 with respect to the second variable yields:

$$\frac{1}{2}\partial_2 h_1(x,\bar{x}) = b_1'(x)n_1(x,\bar{x})\partial_2 n_1(x,\bar{x}) + b_2'(x)n_2(x,\bar{x})\partial_2 n_2(x,\bar{x}). \tag{51}$$

By(42):

$$\begin{aligned} \partial_2 n_1(x,\bar{x}) &= -b_1'(\bar{x})n_3c_{13} - b_2'(\bar{x})n_4c_{14} \\ \partial_2 n_2(x,\bar{x}) &= -b_1'(\bar{x})n_3c_{23} - b_2'(\bar{x})n_4c_{24}. \end{aligned} \tag{52}$$

We compute

$$\begin{aligned} c_{13} &= \frac{1}{\det(C)}\begin{vmatrix} m & -n1 & 0 \\ b_2-2n_2-n_1-m & 0 & -n2 \\ -n1 & m & b_1-2n_1-n_2-m \end{vmatrix} \\ &= \frac{1}{\det(C)}[m^2n_2 + n_1(b_1-2n_1-n_2)(b_2-2n_2-n_1) - n_1^2n_2] \end{aligned} \tag{53}$$

where $(n_1,n_2,n_3,n_4) = ((n_{1,x}(x,\bar{x}), n_{2,x}(x,\bar{x}), n_{1,\bar{x}}(x,\bar{x}), n_{2,\bar{x}}(x,\bar{x}))$ satisfy (3), so finally

$$\begin{aligned} c_{13} &= \frac{1}{\det(C)}(m^2n_2 + n_1(m\frac{n_2}{n_1}+n_1)(m\frac{n_1}{n_2}+n_2) - n_1^2n_2) \\ &= \frac{1}{\det(C)}\left(m^2n_2 + n_1\left[m(\frac{n_2^2}{n_1}+\frac{n_1^2}{n_2}) + m^2\right]\right) \end{aligned} \tag{54}$$

For the same reasons:

$$\begin{aligned} c_{24} &= \frac{1}{\det(C)}\begin{vmatrix} b_1-2n_1-n_2-m & -n_1 & 0 \\ m & 0 & -n2 \\ -n_2 & b_2-2n_2-n_1-m & m \end{vmatrix} \\ &= \frac{1}{\det(C)}(m^2n_1 + n_2(m\frac{n_2}{n_1}+n_1)(m\frac{n_1}{n_2}+n_2) - n_1n_2^2) \\ &= \frac{1}{\det(C)}\left(m^2n_1 + n_2\left[m(\frac{n_2^2}{n_1}+\frac{n_1^2}{n_2}) + m^2\right]\right) \end{aligned} \tag{55}$$

and

$$\begin{aligned} c_{14} &= m(n_1+n_2)\left(m\frac{n_1}{n_2}+n_2\right) \\ c_{23} &= m(n_1+n_2)\left(m\frac{n_2}{n_1}+n_1\right). \end{aligned} \tag{56}$$

Using (6),(54), (55), (56) we obtain:

$$\begin{aligned}\frac{\det(C)}{2}\partial_2 h_1(x,\bar{x}) &= b_1'(x)b_2'(x)n_1n_2\left(2m^2(n_1+n_2)+m(n_1+n_2)\left[\frac{n_2^2}{n_1}+\frac{n_1^2}{n_2}\right]\right)\\ &\quad + (b_1'(x))^2n_1^2\left(m\frac{n_1}{n_2}+n_2\right)+(b_2'(x))^2n_2^2\left(m\frac{n_2}{n_1}+n_1\right).\end{aligned} \tag{57}$$

But $(x,\bar{x})$ is an equilibrium, and so

$$b_1'^2n_1^2+b_2'^2n_2^2=0.$$

Hence

$$\begin{aligned}b_1'b_2'n_1n_2 &= -(b_2')^2\frac{n_2^3}{n_1}\\ &= -(b_1')^2\frac{n_1^3}{n_2}\end{aligned} \tag{58}$$

Incorporating this result in (57) yields

$$\partial_2 h_1(x,\bar{x})=0. \tag{59}$$

A.7 Uniqueness of the equilibrium

To prove the uniqueness of the equilibrium, we need to make an assumption on the form of the fertility rate. We want it to be regular enough for us to determine the sign of some quantities. If $x\mapsto K(X)$ satisfies one of the following conditions:

1. $\exists\lambda,\mu\in\mathbb{R},\forall x\in[E_1,E_2],K(X)=\lambda\exp(-\mu X)$, or
2. $x\mapsto b_1'(x)b_2'(x)$ and $x\mapsto\frac{b_1'(x)}{b_2'(x)}$ are respectively non-increasing and convex on the interval $]E_1,x^*[$,

then if there is an $x\in]E_1,x^*[$ so that $(x,\bar{x})$ is a stable equilibrium of (5), it is unique and Condition (12) is satisfied (cf Appendix A.7).

The general condition of point 2, although fairly technical, contains for example every function K so that $\exists\lambda,\mu\in\mathbb{R},\ k\in\mathbb{N}^*,\ \forall x\in[E_1,E_2],K(X)=\lambda-\mu X^k$. Hence we have already a large class of functions at our disposal, but we exclude functions with too fast or non-monotonous decay away from 0.

Now, note that if $x\neq E_2$ then

$$h_1(x,\bar{x})=0\iff n_2=\sqrt{\frac{-b_1'(x)}{b_2'(x)}}n_{1,x}(x,\bar{x}).$$

Putting this in (3) yields

$$h_1(x,\bar{x})=0\iff\begin{cases}n_{1,x}(x,\bar{x})\big(b_1(x)+m\sqrt{\frac{-b_1'(x)}{b_2'(x)}}\big) & =n_{1,x}(x,\bar{x})\big(n_{1,x}(x,\bar{x})+n_{1,\bar{x}}(x,\bar{x})+m\big)\\ n_{2,x}(x,\bar{x})\big(b_2(x)+m\sqrt{\frac{-b_2'(x)}{b_1'(x)}}\big) & =n_{2,x}(x,\bar{x})\big(n_{2,x}(x,\bar{x})+n_{2,\bar{x}}(x,\bar{x})+m\big)\end{cases}. \tag{60}$$

But as for our proof of Section 3.3, $n_{1,x}(x,\bar{x})$ and $n_{2,x}(x,\bar{x})$ are both different from 0. Moreover by a symmetry argument, we know that(see Appendix A.4) $n_{1,x}(x,\bar{x}) = n_{2,\bar{x}}(x,\bar{x})$ and $n_{2,x}(x,\bar{x}) = n_{1,\bar{x}}(x,\bar{x})$. Hence, simplifying then summing in (60) implies that $h_1(x,\bar{x}) = 0 \Rightarrow w(x) = 0$ where

$$w(x) = b_1(x) - b_2(x) + m\left(\sqrt{\frac{-b_1'(x)}{b_2'(x)}} - \sqrt{\frac{-b_2'(x)}{b_1'(x)}}\right). \tag{61}$$

Finding equilibria of (5) is now a matter of finding the roots of this function. We show that when Condition (12) is violated, $w(x) = 0$ has only one solution (for $x = x^*$) and so (5) has only one equilibrium, (x^*, x^*), which is stable. When Condition (12) is satisfied, w has 3 solutions being x^*, some $x_0 < x^*$ and $\bar{x_0}$ and so (5) has two equilibria, with only $(x_0, \bar{x_0})$ being stable.

It suffices to show that $w(x)$ has at most one solution on the interval $]E_1, x^*[$ when Condition (12) is satisfied and none otherwise. Since

$$w(x) \xrightarrow[x \to E_1]{} -\infty$$

and $w(x^*) = 0$, if there is $x_0 \in]E_1, x^*[$ so that $w(x_0) = 0$, there is by Rolle theorem, a $x_1 \in]x_0, x^*[$ such as $w'(0) = 0$.

But

$$w'(x) = (b_1'(x) - b_2'(x))\left(1 - \frac{m}{2}\frac{(b_1'(x)b_2''(x) - b_1''(x)b_2'(x))}{b_1'(x)b_2'(x)\sqrt{-b_1'(x)b_2'(x)}}\right) \tag{62}$$

i.e since $x \neq x^*$

$$w'(x) = 0 \Longleftrightarrow (-b_1'(x)b_2'(x))^{3/2} - \frac{m}{2}(b_1'(x)b_2''(x) - b_1''(x)b_2'(x)) = 0 \tag{63}$$

which can be rewritten, in the purpose of using Hypothesis 2 of the proposition, as:

$$\begin{aligned} w'(x) = 0 &\Longleftrightarrow (-b_1'b_2')\left((-b_1'b_2')^{1/2} - \frac{m}{2}(\frac{b_1''}{b_1'} - \frac{b_2''}{b_2'})\right) = 0 \\ &\Longleftrightarrow \tilde{w}(x) := (-b_1'b_2')^{1/2} - \frac{m}{2}\left[\log\left(\frac{-b_1'}{b_2'}\right)\right]' = 0. \end{aligned} \tag{64}$$

The function $\tilde{w}$ is non-decreasing thanks to Hypothesis 2. Indeed, for every function f, if f is concave then $\log(f)$ is concave.

Moreover, $\tilde{w}$ tends to $-\infty$ on E_1. So $\tilde{w}(x) = 0$ has no solution if $\tilde{w}(x^*) < 0$ and a unique solution in $]E_1, x^*[$ if $\tilde{w}(x^*) > 0$. But $\tilde{w}(x^*) > 0$ is equivalent to Condition (12), yielding the desired result.

The case where $K(X)$ is an exponential function is straightforward computation.

A.8 Explicit solution in the linear case

As explained above, finding the equilibrias of (5) requires us to find the roots of

$$w(x) = b_1(x) - b_2(x) + m\left(\sqrt{\frac{-b_1'(x)}{b_2'(x)}} - \sqrt{\frac{-b_2'(x)}{b_1'(x)}}\right). \tag{65}$$

Using the explicit form of b_i yields:

$$\begin{aligned} w(x) &= \frac{1}{\sigma^2}[(x-E_2)^2-(x-E_1)^2]+m\left(\sqrt{\frac{x-E_1}{E_2-x}}-\sqrt{\frac{E_2-x}{x-E_1}}\right) \\ &= (E_1+E_2-2x)\left[\frac{E_2-E_1}{\sigma^2}-\frac{m}{\sqrt{(x-E_1)(E_2-x)}}\right] \end{aligned} \tag{66}$$

i.e if $x < x^*$,

$$\begin{aligned} w(x)=0 &\iff \frac{(E_2-E_1)^2}{\sigma^4}\left[(x-E_1)(E_2-x)-\frac{m^2\sigma^4}{(E_1-E_2)^2}\right]=0 \\ &\iff \frac{(E_2-E_1)^2}{\sigma^4}\left[-x^2+(E_2+E_1)x-E_1E_2-\frac{m^2\sigma^4}{(E_1-E_2)^2}\right]=0. \end{aligned} \tag{67}$$

The second degree equation of the last line has the discriminant

$$\Delta=(E_1-E_2)^2\left[1-\left(\frac{2m}{A}\right)^2\right]. \tag{68}$$

It is positive when $A > 2m$. Then the roots of (67) are

$$\begin{cases} x_l &= \frac{E_1+E_2}{2}-\sqrt{\Delta} \\ x_r &= \frac{E_1+E_2}{2}+\sqrt{\Delta} \end{cases} \tag{69}$$

i.e:

$$\begin{aligned} x_l &= x^*-\frac{(E_2-E_1)}{2}\sqrt{1-\frac{4m^2}{A^2}} \\ x_r = \bar{x}_l &= x^*+\frac{(E_2-E_1)}{2}\sqrt{1-\frac{4m^2}{A^2}}. \end{aligned} \tag{70}$$

If $A < 2m$, (67) has no roots, and if $A = 2m$, $x_l = x_r = x^*$

A.9 Stability of the generalist equilibrium when the migration rate is not constant

As shown in Sections A.6 and A.7, the stability of the generalist equilibrium when m is a constant function depends only on the sign of the derivative of the function $w(x) = h_1(x, \bar{x})$ at the point x^*. For similar reasons, this is still the case when m varies, i.e. (x^*, x^*) is a stable equilibrium if and only if the function

$$\tilde{w}(x)=b_1'(x)(n_{1,x}(x,\bar{x}))^2+b_2'(x)(n_{2,x}(x,\bar{x}))^2+m'(x)(n_{2,x}(x,\bar{x})-n_{1,x}(x,\bar{x}))^2 \tag{71}$$

has a negative derivative at the point x^*. Computing this derivative yields

$$\begin{aligned} \tilde{w}'(x) =& b_1''(x)(n_{1,x}(x,\bar{x}))^2+b_2''(x)(n_{2,x}(x,\bar{x}))^2+m''(x)(n_{2,x}(x,\bar{x})-n_{1,x}(x,\bar{x}))^2 \\ & 2\left[b_1'(x)n_{1,x}(x,\bar{x})\frac{d}{dx}(n_{1,x}(x,\bar{x}))+b_2'(x)n_{2,x}(x,\bar{x})\frac{d}{dx}(n_{2,x}(x,\bar{x}))\right] \\ & +2m'(x)\left[n_{2,x}(x,\bar{x})-n_{1,x}(x,\bar{x})\right]\times\frac{d}{dx}\left[n_{2,x}(x,\bar{x})-n_{1,x}(x,\bar{x})\right]. \end{aligned} \tag{72}$$

But at the point (x^*, x^*), we know that (cf Appendix A.4) $n_{1,x^*}(x^*, x^*) = n_{2,x^*}(x^*, x^*)$. Hence $\tilde{w}'(x^*)$ only depends on $m(x^*)$ (and on function K of course), showing that the stability of the monomorphic equilibria does not depend on the shape of $m(X)$. In particular, it does not depend on $m(X)$ being constant.

B Online Appendix: Additional numerical analysis

B.1 Semelparous lifecycles

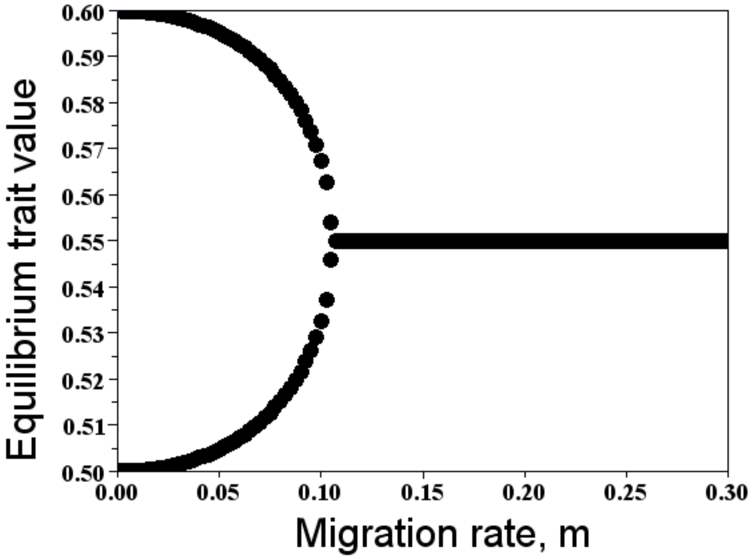


Figure B.1: Stable equilibria versus migration probability for a population with semelparous lifecycle. Other parameters $K(X) = 4 - X$, $\sigma = 0.1$, $\alpha = 0.01$

We changed the microscopic model to fit a semelparous life cycle, by assuming that individuals migrate only at birth with probability m (other mechanisms unchanged).

In a similar way as in Appendix A.2, we derive the new simplified canonical equation

$$\begin{cases} \dot{x} = & b_1'(x)b_1(x)(1-m)n_{1,x}^2(x,y) + b_2'(x)b_2(x)(1-m)n_{2,x}^2(x,y) \\ & +mn_{1,x}(x,y)n_{2,x}(x,y)(b_1'(x)b_2(x) + b_2'(x)b_1(x)) \\ \dot{y} = & b_1'(y)b_1(y)(1-m)n_{1,y}^2(x,y) + b_2'(y)b_2(y)(1-m)n_{2,y}^2(x,y) \\ & +mn_{1,y}(x,y)n_{2,y}(x,y)(b_1'(y)b_2(y) + b_2'(y)b_1(y)) \end{cases} \tag{73}$$

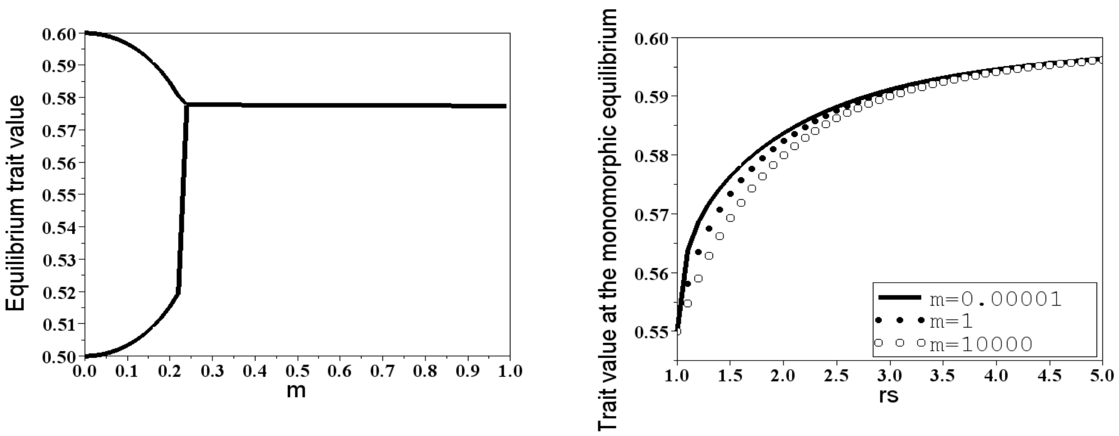
Computing the stable equilibria of (73) yields the same patterns as for iteroparous life cycles (numerical application presented on Fig. B.1). Computing the first coordinate of vector field at (E_1, E_2) yields

$$b_2'(E_1)n_{2,E_1}(E_1,E_2)\left[b_2(E_2)(1-m)n_{2,E_1}(E_1,E_2) + mb_1(E_1)n_{1,x}(x,y)\right]$$

which is strictly positive for the same reason as in Section A.3. Hence, even for population with semelparous lifecycles, there is no pure specialist equilibrium (unless $m = 0$).

B.2 Asymmetry of the selection parameter

Patch one has now selection parameter σ_1 and patch two, σ_2. Computing the strategies for this population yields the same patterns as for asymmetrical carrying capacities (see Figure B.2 (A)). As in Fig. 4, the strategies show a bias towards the more selective patch. Panel (B) shows how the bias of the monomorphic strategy increases with asymmetry rs.



(A) $\sigma_1 = 0.18$, $\sigma_2 = 0.1$

(B) $\sigma_2 = 0.06$, $\sigma_1 = \mathrm{rs}\sigma_2$

Figure B.2: Influence of an asymmetry in the selection parameters on specialization. Panel A shows how the pattern of equilibrium trait values is modified by asymmetry while Panel B shows how the value of the monomorphic equilibrium varies with asymmetry. Other parameters: $\alpha_1 = 0.01$, $K(X) = 4 - X$

B.3 Variable migration rate: The non-symmetrical case

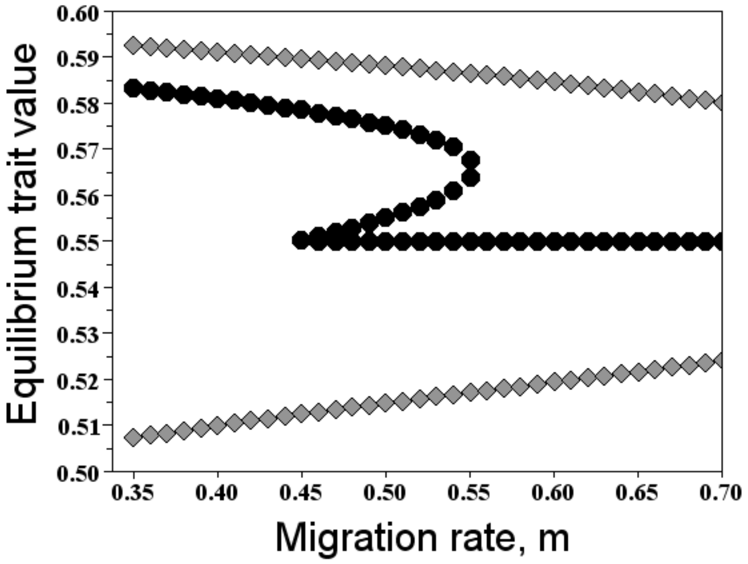


Figure B.3: Stable equilibria versus maximum migration rate. Black circles are monomorphic equilibria, gray diamonds are dimorphic equilibria. Other parameters $K(X) = exp(-X)$, $m(x) = m\exp(-50 * (x - \frac{4E_1+E_2}{3}))$, $\sigma = 0.1$, $\alpha = 0.01$, $E_1 = 0.5$, $E_2 = 0.6$

References

Adler, Raff, and Lauenroth. The effect of grazing on the spatial heterogeneity of vegetation. *Oecologia*, 128:465–479, 2001. ISSN 0029-8549. URL `http://dx.doi.org/10.1007/s004420100737`. 10.1007/s004420100737.

H. Adren and A. Delin. Habitat selection in the eurasian red squirrel, sciurus vulgaris, in relation to forest fragmentation. *Oikos*, 70:43–48, 1994.

JB Beltman and JAJ Metz. Speciation: more likely through a genetic or through a learned habitat preference? *Proceedings of the Royal Society B: Biological Sciences*, 272(1571):1455–1463, 2005.

C. Berticat, J. Bonnet, S. Duchon, P. Agnew, M. Weill, and V. Corbel. Costs and benefits of multiple resistance to insecticides for culex quinquefasciatus mosquitoes. *BMC evolutionary biology*, 8(1):104, 2008.

D.I. Bolnick, R. Svanbäck, J.A. Fordyce, L.H. Yang, J.M. Davis, C.D. Hulsey, and M.L. Forister. The ecology of individuals: incidence and implications of individual specialization. *The American Naturalist*, 161(1):1–28, 2003.

J.S. Brown and N.B. Pavlovic. Evolution in heterogeneous environments: effects of migration on habitat specialization. *Evolutionary Ecology*, 6(5):360–382, 1992.

N. Champagnat. A microscopic interpretation for adaptive dynamics trait substitution sequence models. *Stochastic processes and their applications*, 116(8):1127–1160, 2006.

N. Champagnat, S. Méléard, et al. Polymorphic evolution sequence and evolutionary branching. *Probability theory and related fields*, 151(1):45, 2011.

M.B. Davis, R.G. Shaw, and J.R. Etterson. Evolutionary responses to changing climate. *Ecology*, 86(7):1704–1714, 2005.

T. Day. Competition and the effect of spatial resource heterogeneity on evolutionary diversification. *American Naturalist*, 155(6):790–803, 2000.

F. Débarre and S. Gandon. Evolution of specialization in a spatially continuous environment. *Journal of Evolutionary Biology*, 23(5):1090–1099, 2010.

U. Dieckmann and R. Law. The dynamical theory of coevolution: a derivation from stochastic ecological processes. *Journal of Mathematical Biology*, 34(5):579–612, 1996.

L. Fahrig. Effects of habitat fragmentation on biodiversity. *Annual review of ecology, evolution, and systematics*, pages 487–515, 2003.

D.J. Futuyma and G. Moreno. The evolution of ecological specialization. *Annual Review of Ecology and Systematics*, 19:207–233, 1988.

M. Gyllenberg, K. Parvinen, and U. Dieckmann. Evolutionary suicide and evolution of dispersal in structured metapopulations. *Journal of Mathematical Biology*, 45(2): 79–105, 2002.

I. Hanski and D. Simberloff. The metapopulation approach, its history, conceptual domain, and application to conservation. *Metapopulation biology*, (1):5–26, 1997.

J. Hereford. A quantitative survey of local adaptation and fitness trade-offs. *The American Naturalist*, 173(5):579–588, 2009.

W.G. Hill. Understanding and using quantitative genetic variation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1537):73–85, 2010.

R.D. Holt. Adaptive evolution in source-sink environments: direct and indirect effects of density-dependence on niche evolution. *Oikos*, pages 182–192, 1996.

K. Johst, R. Brandl, and S. Eber. Metapopulation persistence in dynamic landscapes: the role of dispersal distance. *Oikos*, 98(2):263–270, 2002.

J. Konuma, N. Nagata, and T. Sota. Factors determining the direction of ecological specialization in snail-feeding carabid beetles. *Evolution*, 65(2):408–418, 2011.

R. Levins. *Evolution in changing environments: some theoretical explorations*, volume 2. Princeton Univ Pr, 1968.

J. Merilä. Evolution in response to climate change: In pursuit of the missing evidence. *BioEssays*, 2012.

G. Meszéna, I. Czibula, and S.A.H. Geritz. Adaptive dynamics in a 2-patch environment: a toy model for allopatric and parapatric speciation. *J. Biol. Syst*, 5(2):265–284, 1997.

JAJ Metz, RM Nisbet, and SAH Geritz. How should we define fitness for general ecological scenarios? *Trends in Ecology & Evolution*, 7(6):198–202, 1992.

J.A.J. Metz, S.A.H. Geritz, G. Meszéna, F.J.A. Jacobs, and JS Van Heerwaarden. Adaptive dynamics, a geometrical study of the consequences of nearly faithful reproduction. *Stochastic and spatial structures of dynamical systems*, 45:183–231, 1996.

D.W. Morris. Toward an ecological synthesis: a case for habitat selection. *Oecologia*, 136 (1):1–13, 2003.

D.W. Morris, D.E. Moore, S.O.M.B. Ale, and A. Dupuch. Forecasting ecological and evolutionary strategies to global change: an example from habitat selection by lemmings. *Global Change Biology*, 17(3):1266–1276, 2011.

M.B. Morrissey, C.A. Walling, A.J. Wilson, J.M. Pemberton, T.H. Clutton-Brock, and LE Kruuk. Genetic analysis of life-history constraint and evolution in a wild ungulate population. *The American naturalist*, 179(4):E97, 2012.

T. Nurmi and K. Parvinen. On the evolution of specialization with a mechanistic underpinning in structured metapopulations. *Theoretical population biology*, 73(2):222–243, 2008.

T. Nurmi and K. Parvinen. Joint evolution of specialization and dispersal in structured metapopulations. *Journal of Theoretical Biology*, 2011.

K. Parvinen and M. Egas. Dispersal and the evolution of specialisation in a two-habitat type metapopulation. *Theoretical population biology*, 66(3):233–248, 2004.

H.M. Pereira, P.W. Leadley, V. Proença, R. Alkemade, J.P.W. Scharlemann, J.F. Fernandez-Manjarrés, M.B. Araújo, P. Balvanera, R. Biggs, W.W.L. Cheung, et al. Scenarios for global biodiversity in the 21st century. *Science*, 330(6010):1496–1501, 2010.

T. Poisot, J.D. Bever, A. Nemri, P.H. Thrall, and M.E. Hochberg. A conceptual framework for the evolution of ecological specialisation. *Ecology letters*, 2011.

K.R. Räsänen, A. Laurila, and J. Merilä. Geographic variation in acid stress tolerance of the moor frog, rana arvalis. i. local adaptation. *Evolution*, 57(2):352–362, 2003.

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

O. Ronce. How does it feel to be like a rolling stone? ten questions about dispersal evolution. *Annu. Rev. Ecol. Evol. Syst.*, 38:231–253, 2007.

O. Ronce and M. Kirkpatrick. When sources become sinks: migrational meltdown in heterogeneous habitats. *Evolution*, 55(8):1520–1531, 2001.

C. Rueffler, T.J.M. Van Dooren, and J.A.J. Metz. The interplay between behavior and morphology in the evolutionary dynamics of resource specialization. *The American Naturalist*, 169(2):E34–E52, 2007.

E.W. Sanderson, M. Jaiteh, M.A. Levy, K.H. Redford, A.V. Wannebo, and G. Woolmer. The human footprint and the last of the wild. *BioScience*, 52(10):891–904, 2002.

J. Seixas. Assessing heterogeneity from remote sensing images: the case of desertification in southern portugal. *International Journal of Remote Sensing*, 21(13-14):2645–2663, 2000.

C.A. Stockwell, A.P. Hendry, and M.T. Kinnison. Contemporary evolution meets conservation biology. *Trends in Ecology & Evolution*, 18(2):94–101, 2003.

C. Teplitsky, NG Mouawad, J. Balbontin, F. De Lope, and AP Møller. Quantitative genetics of migration syndromes: a study of two barn swallow populations. *Journal of Evolutionary Biology*, 2011.

D.S. Wilson and J. Yoshimura. On the coexistence of specialists and generalists. *The American Naturalist*, 144(4):692–707, 1994.