Evolution in Heterogeneous Environments: Between Soft and Hard Selection

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abstract: Since their first formulations about half a century ago, the soft and hard selection models have become classical frameworks to study selection in subdivided populations. These models differ in the timing of density regulation and represent two extreme types of selection: density- and frequency-dependent selection (soft) and density- and frequency-independent selection (hard). Yet only few attempts have been made so far to model intermediate scenarios. Here, we design a model where migration may happen twice during the life cycle: before density regulation with probability d_J (juvenile migration) and after density regulation with probability d_A (adult migration). In the first step, we analyze the conditions for the coexistence of two specialists. We find that coexistence is possible under a large range of selection types, even when environmental heterogeneity is low. Then, we investigate the different possible outcomes obtained through gradual evolution. We show that polymorphism is more likely to evolve when the trade-off is weak, environmental heterogeneity is high, migration is low, and in particular when juvenile migration is low relative to adult migration, because the timing of migration affects the magnitude of frequency-dependent selection relative to gene flow. This model may provide a more general theoretical framework to experimentally study evolution in heterogeneous environments.

Keywords: heterogeneous environment, subdivided population, soft selection, hard selection, gradual evolution, coexistence.

Introduction

Soft and hard selection are two classical ways of modeling selection in subdivided populations (Christiansen 1975; Wallace 1975), and they have been the subject of numerous studies (for a review, see Ravigné et al. 2009). The terms soft and hard selection were originally coined by Wallace (1968) and were borrowed from international money exchange (referring to soft and hard currencies). Christian-

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sen (1975) then used these terms to label two alternative mechanisms of local deme size regulations in subdivided populations. Christiansen's (1975) definition has now become classical, and we choose it in this article. Levene's (1953) and Dempster's (1955) models (or models derived from them) are classically used to illustrate the concepts of soft and hard selection, respectively, even though these models were designed before the terms were actually coined.

In both types of models, the environment contains two or more kinds of habitats. The whole population that lives there is divided into subpopulations. In both models, the individuals spend part of their lifetime in a patch, isolated from the individuals in other subpopulations, and part of their lifetime mixed with all the individuals of the whole population. They undergo selection while in a patch, and selection is habitat dependent. Under soft selection, density regulation happens locally within a patch (see fig. 1A). Consequently, the contribution of a habitat to the next generation is fixed, and there is no relation between the output of a habitat and its genetic composition (Karlin and Campbell 1981; Wade 1985; Lenormand 2002). Under soft selection, selection is both frequency and density dependent (Wallace 1975). On the contrary, under hard selection, density regulation happens at the scale of the whole population, after global pooling (see fig. 1B). Consequently, the relative output of each habitat depends on its genetic composition; selection is both density and frequency independent (Wallace 1975). These two models, however, can been seen as two particular cases (Christiansen 1975). Still, only a few attempts have been made to model intermediate selection, either by designing a mixed model (de Meeus and Goudet 2000) or by modifying the order of events in the life cycle (Sasaki and de Jong 1999; Ravigné et al. 2004).

De Meeus and Goudet (2000) designed mixed models, where a meta-environment is divided into two subenvironments, one of them (in proportion x) under soft se-
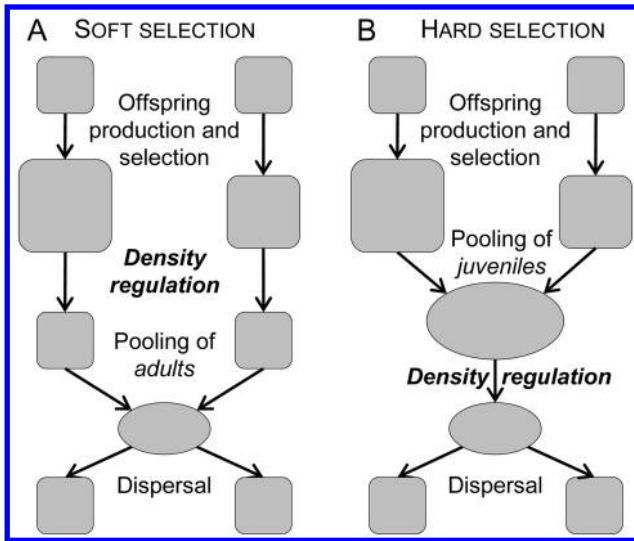
Figure 1: Life cycle under soft selection (*A*) and hard selection (*B*; adapted from Ravigné et al. 2004). In these figures, the two habitats have the same sizes ($q = 1/2$). The main difference between the two life cycles is the relative timing of selection, migration, and density regulation. Under soft selection (*A*), migration happens after density regulation, and we call it adult migration. On the contrary, migration happens between selection and density regulation under hard selection (*B*), and we call it juvenile migration. Since there is no habitat choice, Ravigné et al.'s (2004) model 3 (pooling-dispersal-regulation) and the hard selection model (pooling-regulation-dispersal) are equivalent.

lection, the other (in proportion $1 - x$) under hard selection. The meta-environment is either soft regulated (model 1) or hard regulated (model 2; for an illustration, see fig. 1 in de Meeus and Goudet 2000). When $x = 1$, the population is under pure soft selection; when $x = 0$, it is under pure hard selection; and $0 < x < 1$ corresponds to intermediate selection (de Meeus and Goudet 2000). Yet it might look quite artificial to model a life cycle where the type of selection (i.e., soft or hard) depends on the environment where an individual lands, the two environments containing the exact same types of habitats. In addition, the authors investigated only a limit case by choosing a linear trade-off (Kisdi 2001), which mitigates the generality of their study.

Sasaki and de Jong (1999) designed a complex life cycle, to which our model is closely related. In their model, the individuals can change habitats once during their lifetime. They undergo density regulation twice and are selected after habitat change. Hence, density regulation happens right after dispersal (while it is usually selection that happens after dispersal in classical hard and soft selection models). But in Sasaki and de Jong's (1999) model, the survivorship functions used for density regulation are

more complex than the simple scaling that is classically done in the hard and soft selection models. Finally, at the end of their lifetime, all individuals join the global pool of migrants (see figs. 1 and 2 in Sasaki and de Jong 1999). Hard and soft selection can be retrieved by manipulating the survivorship functions (Sasaki and de Jong 1999).

Similar to Sasaki and de Jong's (1999) model, density regulation happens between dispersal and selection in Ravigné et al.'s (2004) model 3 (see the right-hand panel of fig. 1 in Ravigné et al. 2004). Ravigné et al.'s (2004) model 3 shares common features with both the soft and hard selection models. As in soft selection, regulation remains local, but habitat output is variable as in hard selection (Ravigné et al. 2004). Nevertheless, when there is no habitat choice, which is the case we consider in this article, model 3 is equivalent to hard selection.

Our model is a quantitative intermediate between hard and soft selection. Similar to these classical models, we consider an environment with two habitats. Selection happens right after offspring production. During the whole life cycle, there are two stages of dispersal, one right before density regulation (which we call juvenile dispersal) and the other after density regulation (which we call adult dispersal). At each stage of dispersal, only a fraction of the population (d_J for juvenile dispersal and d_A for adult dispersal) is actually pooled, contrary to the model of Sasaki and de Jong (1999), where all individuals are eventually pooled (see fig. 2). We investigate how the intensity of migration and its timing in the life cycle influence the maintenance and the evolution of polymorphism in a subdivided population.

We first study our model in the absence of mutation (short-term evolution; Eshel et al. 1998; Kisdi and Geritz 1999) and derive the conditions for the coexistence of two specialists. We then allow for mutations and identify the diversity of outcomes through gradual evolution (long-term evolution). In particular, we focus on the conditions for the emergence of a stable polymorphism. To this end, we start by analyzing our model with a general trade-off for the particular case where the two habitats have the same size. Finally, we use numerical methods to study other conformations of the environment.

The Model

Life Cycle

We model a haploid, asexually reproducing population living in an environment containing two types of habitats, 1 and 2. The relative areas of habitats 1 and 2 are q and $1 - q$, respectively. We assume that both habitats host the same density of individuals, so that q and $1 - q$ are also the fractions of the total population living in habitats 1
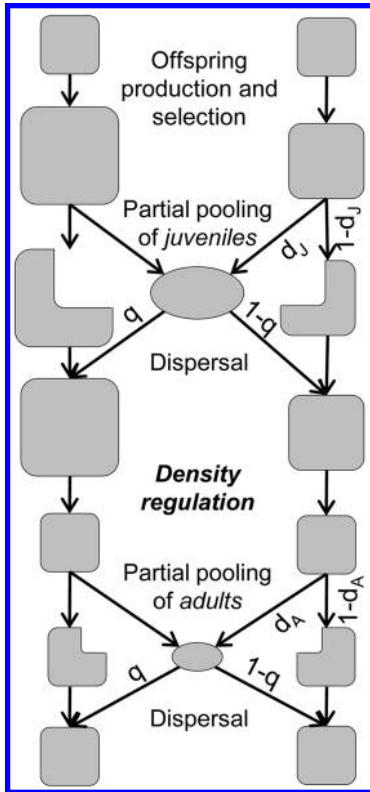
Figure 2: Life cycle in our model. There are two migration steps: before density regulation (juvenile migration, with probability d_J) and after density regulation (adult migration, with probability d_A). Soft selection (fig. 1*A*) is recovered by setting $d_J = 0$ and $d_A = 1$, and hard selection (fig. 1*B*) is recovered by setting $d_J = 1$ and $d_A = 0$. The latter case corresponds in fact to Ravigné et al.'s (2004) model 3 but is equivalent to hard selection (see legend of fig. 1).

and 2, respectively. This is equivalent to considering a metapopulation, where there are two patch types in proportions q and $1 - q$, with each patch hosting the same density of individuals. The generations are discrete and nonoverlapping. Our model is deterministic, and we assume that the subpopulations are large enough so that we can neglect drift. The parameters of the model are summarized in table 1.

The proportion of type j individuals at time t in habitat 1 is $p_{j,t}^{(1)}$. The total number of adult individuals is fixed and equal to N after regulation; at time t, there are $p_{j,t}^{(1)}qN$ type j individuals in habitat 1. The life cycle goes as follows (see fig. 2).

Offspring Production and Selection. In both habitats, the individuals produce B offspring ($B \gg 1$ so that the habitats are always saturated), which undergo viability selection. The survival of type j offspring depends on the genotype of the parents (j) and on the habitat where the offspring

is produced. After production and selection of offspring, the number of type j individuals in habitat 1 is

$$Bw_j^{(1)}p_{j,t}^{(1)}qN, \tag{1}$$

where B is the habitat- and genotype-independent fecundity and $w_j^{(1)}$ is the probability of survival of type j individuals in habitat 1.

Migration of Juveniles. After this, a fraction d_J of juveniles is pooled and redistributed in the two habitats; this corresponds to juvenile migration. The succession of pooling and redistribution is equivalent to the classical island migration model (Wright 1943). There is no habitat choice: if q is the relative area of habitat 1, then the pooled individuals have a probability q of landing in habitat 1. After pooling of a fraction d_J of juveniles and migration, the number of type j individuals in habitat 1 becomes

$$(1 - d_J)Bw_j^{(1)}p_{j,t}^{(1)}qN$$

$$+ qd_J[Bw_j^{(1)}p_{j,t}^{(1)}qN + Bw_j^{(2)}p_{j,t}^{(2)}(1 - q)N]. \tag{2}$$

The first term in equation (2) corresponds to the juveniles who do not migrate. The second term corresponds to the juveniles from both habitats who migrate and are pooled and then redistributed into the habitats, with a probability of landing in habitat i equal to the proportion of the environment consisting of habitat i. Note that there is no cost associated with movement.

Density Regulation. Density in the two habitats is then regulated: a constant density of individuals survive (and juveniles become adults). After density regulation, the frequency of type j individuals in habitat 1 is (after a bit of algebra)

$$\mathcal{P}_{j,t}^{(1)} = \frac{w_j^{(1)}p_{j,t}^{(1)} + d_J(1 - q)(w_j^{(2)}p_{j,t}^{(2)} - w_j^{(1)}p_{j,t}^{(1)})}{\bar{w}_t^{(1)}(1 - d_J) + d_J\bar{w}_t}, \tag{3}$$

where $\bar{w}_t^{(i)}$ is the mean survival in habitat i at time t,

$$\bar{w}_t^{(i)} = \sum_k w_k^{(i)}p_{k,t}^{(i)}, \tag{4}$$

Table 1: Parameters of the model

Parameter	Definition
d_J	Juvenile migration: probability of migrating before density regulation
d_A	Adult migration: probability of migrating after density regulation
μ	Probability of migrating at least once during the life cycle (see eq. [18])
q	Proportion of habitat 1
β	Shape of the power trade-off

and $\bar{w}_t$ is the global mean survival at time t (i.e., averaged over the two habitats),

$$\bar{w}_t = q\bar{w}_t^{(1)} + (1 - q)\bar{w}_t^{(2)}. \tag{5}$$

Replace q by $1 - q$ and superscript 1 by 2, and vice versa, to obtain $\mathcal{P}_{j,t}^{(2)}$, the postregulation frequency of type j individuals in habitat 2.

Adult Migration. Finally, a proportion d_A of adults is pooled and then redistributed; this corresponds to adult migration. After pooling and migration of adults, the frequency of type j individuals in habitat 1 is

$$p_{j,t+1}^{(1)} = [\mathcal{P}_{j,t}^{(1)} + d_A(1 - q)(\mathcal{P}_{j,t}^{(2)} - \mathcal{P}_{j,t}^{(1)})]. \tag{6}$$

The classical soft and hard selection models are particular cases of this general life cycle. Figure 3*A* illustrates the effect of the migration parameters d_J and d_A on the type of selection. When $d_J = 1$ and $d_A = 0$ (black circle in fig. 3*A*), the model is equivalent to Ravigné et al.'s (2004) model 3 (the equations describing the evolution of allele frequencies are the same). Because there is no habitat choice, it is also equivalent to the hard selection model (fig. 1*B*). A global pooling at the juvenile stage ($d_J = 1$) homogenizes the whole population, and posterior adult migration has no impact on the outcome; the black line therefore also refers to hard selection. The vertical dark gray line ($d_A = 0$, $d_J < 1$) corresponds to hard selection with philopatry or with partial pooling. When $d_J = 0$ and $d_A = 1$ (light gray circle in fig. 3*A*), the model is equivalent to the soft selection model (fig. 1*A*). If $d_J = 0$ and $d_A < 1$ (light gray line in fig. 3*A*), it is an extension of the soft selection model with partial pooling or, equivalently, with philopatry.

Beyond this link to previous models of selection in subdivided populations, it is important to note a crucial difference between juvenile and adult migration. Though both homogenize allele frequencies between habitats and thus counteract the effect of local selection (making the environmental grain finer), juvenile migration plays a particular role. The denominator of $\mathcal{P}_{j,t}^{(1)}$ in equation (3) shows how juvenile migration d_J influences the intensity of frequency dependence. If $d_J = 1$ (hard selection), the regulation is done relative to the whole population; fitness is measured relative to the global mean fitness, and selection is therefore frequency independent. When $d_J = 0$, however, the regulation is done relative to the local population only; selection is totally frequency dependent. For intermediate values of d_J ($0 < d_J < 1$), fitness is measured relative to a mix of local and global mean fitnesses; d_J tunes the intensity of frequency-dependent selection in the model. Adult migration, on the contrary, does not influence the intensity of frequency-dependent selection.
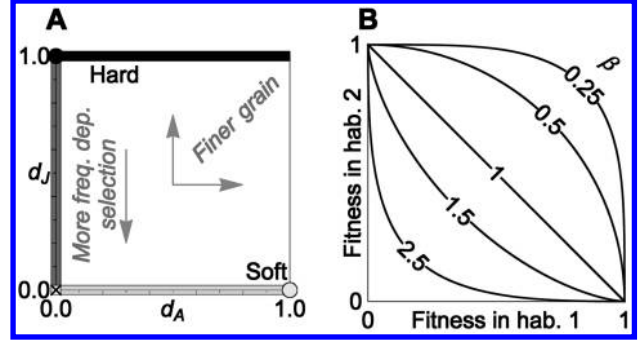
Figure 3: Types of selection and power trade-off. *A*, Types of selection, depending on adult (d_A) and juvenile (d_J) migration probabilities. The light gray circle is soft selection (fig. 1*A*), and the light gray line refers to soft selection with partial pooling or philopatry. The black circle is hard selection (fig. 1*B*), and the black line is also hard selection (because $d_J = 1$ homogenizes the two subpopulations before density regulation, and additional migration after will not change the outcome). The dark gray line is hard selection with partial pooling. Note that although both d_A and d_J homogenize allele frequency and make the environmental grain finer, only d_J affects the intensity of frequency-dependent selection (see eq. [3]). *B*, Power trade-off u_P for various values of the parameter β. The trade-off is weak when $\beta < 1$, strong when $\beta > 1$, and linear when $\beta = 1$. The corresponding fitness functions are given in equation (9).

Trade-Offs

General Trade-Off. We assume that fitness (i.e., survival) in both environments is under the control of an adaptation trait s. An individual j with trait s has a fitness $w_j^{(1)} = f_1(s)$ in habitat 1 and $w_j^{(2)} = f_2(s)$ in habitat 2. The fitnesses are scaled so that all values lie between 0 and 1. Pure specialists have a fitness of 1 in one habitat and 0 in the other. A function u links the fitnesses f_1 and f_2:

$$f_2(s) = u(f_1(s)). \tag{7}$$

The function u is decreasing and is called the trade-off function.

We further assume that the underlying fitness functions f_1 and f_2 in each habitat are symmetrical around one central trait value s_0. The strategy s_0 is an intermediate strategy, equidistant from the two optimal strategies. Because of symmetry, the two fitnesses are equal at s_0, and the slope of the trade-off is -1, which in mathematical terms means that (the prime denotes the derivative)

$$f_1(s_0) = f_2(s_0), \tag{8a}$$

$$u'(f_1(s_0)) = -1. \tag{8b}$$

If the trade-off function u is linear, since the fitnesses are between 0 and 1, we have $f_1(s_0) = f_2(s_0) = 1/2$. With a nonlinear trade-off, we say that the costs of the intermediate strategy s_0 are low if $f_1(s_0) > 1/2$ and are high

otherwise. The strength of the trade-off depends not only on this cost but also on the concavity of the trade-off curve at s_0 (which is $u''(f_1(s_0))$). We will show later that what matters for trade-off strength is the $f_1(s_0)u''(f_1(s_0))$ product (the lower the $f_1(s_0)u''(f_1(s_0))$ product, the weaker the trade-off).

We study the model with this general trade-off and then illustrate our results with a specific function (see fig. 3*B*), a power trade-off u_P (e.g., Egas et al. 2004; Spichtig and Kawecki 2004).

Power Trade-Off. For the power trade-off u_P, the fitness functions are

$$f_1(s) = s^\beta, \tag{9a}$$

$$f_2(s) = (1 - s)^\beta. \tag{9b}$$

The optimum value of the adaptation trait s is 1 in habitat 1 and 0 in habitat 2; the intermediate strategy is $s_0 = 1/2$. The parameter β determines the strength of the trade-off (see fig. 3*B*).

When $\beta > 1$, the cost of the intermediate strategy is high ($f_1(s_0) < 1/2$) and the trade-off curve is convex ($u_P''(f_1(s_0)) > 0$), which corresponds to a concave fitness set (in the sense of Levins [1962]); the trade-off is strong (Ravigné et al. 2009). When $\beta = 1$, the trade-off curve is linear ($u_P''(f_1(s_0)) = 0$) and $f_1(s_0) = 1/2$; this is a limit case. Finally, when $\beta < 1$, the cost of the intermediate strategy is low ($f_1(s_0) > 1/2$) and the trade-off curve is concave ($u_P''(f_1(s_0)) < 0$), which corresponds to a convex fitness set (in the sense of Levins [1962]); the trade-off is weak (Ravigné et al. 2009).

To allow for a comparison with Ravigné et al.'s (2009) results, we present an alternative power trade-off in appendix B and figure B1, with an additional parameter x_0, which is the minimum fitness. Note that the power trade-off presented in the main text is a particular case of that alternative power trade-off, with the minimum fitness x_0 set equal to 0.

Invasion Analysis

Suppose that we have a monomorphic resident population (r) with a trait x; can a mutant (m) with a trait y invade? The resident population is fixed, and the mutants are rare; after linearizing, we obtain the following initial dynamics for the mutant frequency:

$$\begin{pmatrix} p_{m,t+1}^{(1)} \\ p_{m,t+1}^{(2)} \end{pmatrix} = \mathbf{M} \begin{pmatrix} p_{m,t}^{(1)} \\ p_{m,t}^{(2)} \end{pmatrix}. \tag{10}$$

The value of the matrix $\mathbf{M}$ is given in appendix A. The dominant eigenvalue of $\mathbf{M}$, λ, is the initial growth rate of individuals with the mutant strategy. Its expression is quite

long, so we do not include it here. The mutant strategy has a positive probability of invasion when $\lambda > 1$ (Jagers 1975; Caswell 2001).

Results

Coexistence of Two Specialists

Here we focus on the case where the resident and the mutant are the two extreme specialists of habitats 1 and 2, respectively, so that

$$w_r^{(1)} = 1,$$

$$w_r^{(2)} = 0, \tag{11a}$$

$$w_m^{(1)} = 0,$$

$$w_m^{(2)} = 1. \tag{11b}$$

With these values, selective advantages are large, which favors polymorphism (Maynard Smith and Hoekstra 1980). We find that specialists of habitat 2 (resp. 1) invade a population of specialists of habitat 1 (resp. 2) when $\lambda_{2,1} > 1$ (resp. $\lambda_{1,2} > 1$), with

$$\lambda_{2,1} = \frac{1}{d_J}\left[\frac{d_A(1 - d_J)}{d_J(1 - q) - 1} + \frac{1}{q}\right] - 1. \tag{12}$$

The threshold value $\lambda_{1,2}$ is obtained by replacing q by $1 - q$ in equation (12).

The two specialists coexist when both $\lambda_{1,2}$ and $\lambda_{2,1}$ are above unity. The range of migration parameters for which coexistence is possible depends on the frequency of the two habitats. When $d_J = 0$, the threshold values $\lambda_{1,2}$ and $\lambda_{2,1}$ both tend to $+\infty$, which means that the two specialists always coexist (provided $0 < q < 1$).

When the environment is symmetrical ($q = 1/2$), the two specialists coexist, provided that juvenile migration is not equal to unity (see fig. 4*A*). This means that they coexist for all types of selection, except for pure hard selection ($d_J = 1$). The case $d_J = 1$ is the only case with purely frequency-independent selection in the model; this means that the coexistence of the two specialists requires a pinch of frequency dependence, as it is, for instance, the case for hard selection with philopatry ($d_J < 1$, $d_A = 0$).

When there is less habitat 1 than habitat 2 in the environment ($q < 0.5$), specialists of habitat 2 are favored. In this case, they can always invade a population of the other specialist ($\lambda_{2,1} > 1$). Specialists of habitat 1, however, can invade a population of the other specialist only when juvenile migration is below a threshold value that depends on adult migration: invasion is successful when
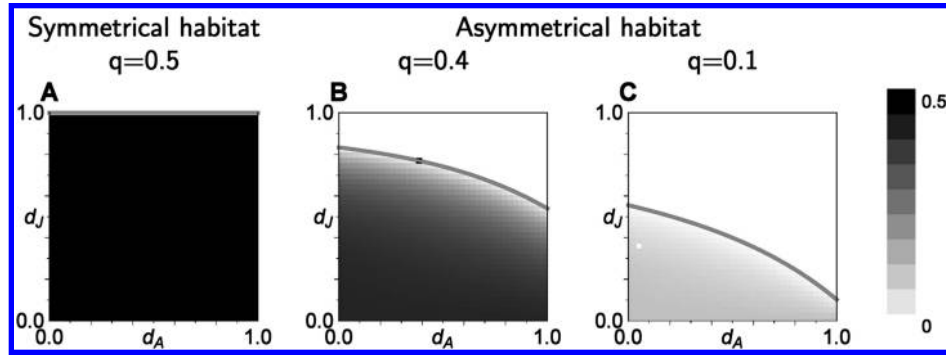
Figure 4: Analytical conditions for the maintenance of polymorphism, depending on the values of adult (d_A) and juvenile (d_J) migrations. The gray lines correspond to the threshold migration values given in equation (13). The different shading illustrates the overall proportion of the specialist of the rarer habitat, at equilibrium. There is no coexistence in the white areas above the gray lines. In A ($q = 0.5$), there is a protected polymorphism whenever $d_J \neq 1$ (i.e., any selection but hard selection sensu stricto). In B ($q = 0.4$) and C ($q = 0.1$), there is a protected polymorphism when d_J is below the threshold given in equation (13).

$$d_J <$$

$$\frac{d_A q + 2 - (d_A + q) - \{[d_A q + 2 - (d_A + q)]^2 - 8[1 - d_A(1 - q)](1 - q)q\}^{1/2}}{4q(1 - q)}.$$

$$\text{(13)}$$

This is thus also the condition for a protected polymorphism (because there is reciprocal invasion). See figure 4B and 4C for an illustration. When $q > 0.5$, replace q by $1 - q$ in equation (13) to obtain the condition for polymorphism.

In particular, we see that coexistence can be maintained even for very asymmetrical environments (q close to 0 or to 1), provided that juvenile migration is low enough compared with adult migration, if we have

$$d_J < 1 - \frac{1}{2 - d_A}. \qquad \text{(14)}$$

But note that in these very asymmetrical environments, the overall proportion of the specialist of the rare habitat is very low (see fig. 4C).

Gradual Evolution

We now study the gradual evolution of the adaptation trait s under different types of selection. To this end, we use the framework of adaptive dynamics (Geritz et al. 1998); we assume that mutations are rare and have a small phenotypic effect. We study the evolution of s in an initially monomorphic population.

A singular strategy x^* is a strategy at which the local fitness gradient cancels (Geritz et al. 1998):

$$\left.\frac{\partial \lambda}{\partial y}\right|_{y=x=x^*} = 0. \qquad \text{(15)}$$

When the two habitats have the same size, $q = (1 - q) = 1/2$, the intermediate strategy s_0 (as defined above) is a solution of equation (15). Here, s_0 can be called a generalist strategy. We first study analytically the stability of this solution and then find numerically other singular strategies and study their stabilities.

Note that in this section, we assume that some individuals migrate at least once in the life cycle; the adult and juvenile migrations are not together null, $(d_A, d_J) \neq (0, 0)$. When there is no migration at all, the two specialists are the only stable strategies, and they can coexist, provided that there are two habitats in the environment ($0 < q < 1$).

Stability of the Intermediate Strategy s_0 in a Symmetrical Environment

Convergence Stability

A singular strategy x^* is convergence stable (CS; i.e., attainable by gradual evolution) if (Christiansen 1991; Taylor 1996)

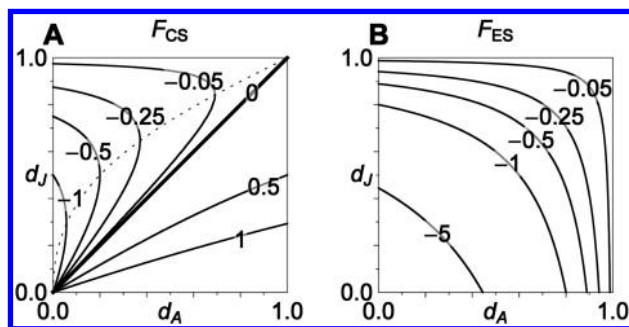$$\left[\frac{\partial^2 \lambda}{\partial x \partial y} + \frac{\partial^2 \lambda}{\partial y^2}\right]_{y=x=x^*} < 0. \qquad \text{(16)}$$

Condition (16) is fulfilled when

$$f_1(s_0)u''(f_1(s_0)) < F_{CS}, \qquad \text{(17a)}$$

$$F_{CS} = \frac{2(d_A - d_J)(1 - d_J)}{d_A + d_J - d_A d_J}. \qquad \text{(17b)}$$

The higher the F_{CS} and the weaker the trade-off, the easier it is to fulfill condition (17a). Figure 5A shows a

Figure 5: Critical values for convergence and evolutionary stability, depending on adult (d_A) and juvenile (d_J) migration probabilities. *A*, Isoclines of F_{CS}, the critical value for the convergence stability of the generalist strategy (see eq. [17]); the values of F_{CS} are written on the isoclines. The dotted line corresponds to $\tilde{d}_J$ (see eq. [20]), the value at which $\partial F_{CS}/\partial d_J$ changes signs. *B*, Isoclines of F_{ES}, the critical value for the evolutionary stability of the generalist strategy (see eq. [24]); the values of F_{ES} are written on the isoclines.

contour plot of the value of F_{CS}, depending on adult (d_A) and juvenile (d_J) migrations.

We define μ as the probability of migrating at least once during the life cycle:

$$\mu = 1 - (1 - d_A)(1 - d_J) = d_A + d_J - d_A d_J, \quad (18)$$

and we can rewrite F_{CS}:

$$F_{CS} = \frac{2(d_A - d_J)(1 - d_J)}{\mu}. \quad (19)$$

Note that μ, since it is a probability, lies between 0 and 1.

F_{CS} is positive when adult migration is greater than juvenile migration ($d_A > d_J$; bottom right triangle in fig. 5*A*) and negative otherwise. F_{CS} is an increasing function of adult migration d_A; in figure 5*A*, the values of F_{CS} increase from left to right. Therefore, increasing d_A makes s_0 convergence stable under a wider range of trade-off shapes (i.e., more CS). When adult migration takes place, the densities of the two habitats have already been regulated; adult migration induces changes in frequencies in the two habitats but does not change densities. Because it homogenizes allele frequencies between habitats, increasing adult migration makes the environmental grain finer; it is as if the two habitats were progressively replaced by two identical averaged habitats. A fine grain favors generalist strategies such as s_0, which explains why s_0 is more convergence stable when d_A increases.

The effect of juvenile migration on F_{CS} is nonmonotonic; F_{CS} is a decreasing function of d_J when $d_J < \tilde{d}_J$ and an increasing function of d_J otherwise. This threshold value

$\tilde{d}_J$ is given by the following equation and is plotted as a dotted line in figure 5*A*:

$$\tilde{d}_J = \frac{d_A - [(2 - d_A)d_A]^{1/2}}{d_A - 1}. \quad (20)$$

Why such a nonmonotonic effect of juvenile migration on the convergence stability of the generalist strategy s_0? Two opposite forces are at work. On the one hand, increasing d_J makes selection more frequency independent (see eq. [3]); this is detrimental to the generalist strategy, which is a suboptimal strategy in both habitats. This explains why evolution initially leads away from s_0 when d_J increases ($d_J < \tilde{d}_J$). On the other hand, increasing juvenile migration (similar to increasing adult migration) increases the mixing of the two habitats and makes the environmental grain finer; this favors generalist strategies such as s_0 and explains why s_0 is more convergence stable for high values of d_J ($d_J > \tilde{d}_J$).

These effects of adult and juvenile migration on F_{CS} also explain the high variation in F_{CS} values near the point $(d_A, d_J) = (0, 0)$ (or $\mu = 0$). As mentioned as a foreword, the generalist s_0 is never stable when both adult and juvenile migrations are null, because there is no migration at all between habitats. Let us start from $(d_A, d_J) = (0, 0)$ and assume that migration is added to the life cycle ($\mu > 0$). If adult migration is greater than juvenile migration, the frequency-dependent component of selection prevails, and $F_{CS} > 0$; s_0 is more likely to be convergence stable. On the contrary, if juvenile migration is higher than adult migration, the frequency-independent component of selection dominates, and $F_{CS} < 0$; that is, the generalist strategy s_0 is less likely to be convergence stable. However, it shall be noted that the high sensitivity of F_{CS} near the point $(d_A, d_J) = (0, 0)$ is a consequence of the assumption of mutations of infinitesimally small effect. In the neighborhood of the $(d_A, d_J) = (0, 0)$ point indeed, drawing pairwise invasibility plots would show that virtually any non–infinitesimally small mutation can invade and that the population will become polymorphic, evolving toward the two specialist strategies.

Power Trade-Off. With the power trade-off, equations (17) become

$$\beta < \frac{d_A + d_J - d_A d_J}{(2 - d_J)d_J}, \quad (21)$$

or, using μ,

$$\beta < \frac{\mu}{(2 - d_J)d_J}. \quad (22)$$

Under soft selection ($d_J = 0$, with or without philopatry), $s_0 = 1/2$ is always convergence stable (remember that d_J

and d_A are both between 0 and 1). Note that this is not always the case with the alternative power trade-off (see app. B). See the gray dashed lines in figure 6A and 6C for an illustration with particular trade-off strengths. In this figure, the generalist strategy s_0 is stable by convergence on the right-hand side of the gray dashed lines.

Evolutionary Stability

A singular strategy x^* cannot be invaded by any other strategy (i.e., is evolutionarily stable [ES]) if (Geritz et al. 1998)

$$\left. \frac{\partial^2 \lambda}{\partial y^2} \right|_{y=x=x^*} < 0. \tag{23}$$

With a general trade-off, condition (23) is fulfilled for the generalist strategy s_0 when

$$f_1(s_0) u''(f_1(s_0)) < F_{ES}, \tag{24a}$$

$$F_{ES} = -\frac{4(1 - d_A)(1 - d_J)}{d_A + d_J - d_A d_J} = -\frac{4(1 - \mu)}{\mu}. \tag{24b}$$

The higher the F_{ES} and the weaker the trade-off, the easier it is to fulfill condition (24a). Figure 5B shows a contour plot of the value of F_{ES}, depending on adult (d_A) and juvenile (d_J) migrations. We see that F_{ES} is always negative. A necessary but insufficient condition for the evolutionary stability of s_0 is therefore a concave trade-off curve at s_0, which corresponds to $u''(f_1(s_0)) < 0$. If the trade-off curve is convex at s_0, the intermediate strategy s_0 can never be ES, whatever the intensity of migration.

The condition for evolutionary stability is easier to fulfill when μ, the chance of migrating at least once, increases (F_{ES} is an increasing function of μ). Contrary to the condition for convergence stability, here adult and juvenile migrations have symmetrical effects (i.e., you can interchange d_A and d_J in eq. [24b]). What matters for evolutionary stability is thus not when during the life cycle dispersal happens (i.e., before or after density regulation) but the overall chance of migrating μ.

Note also that here evolutionary stability implies convergence stability, because $F_{ES} < F_{CS}$. There are therefore never Garden of Eden configurations, where an uninvadable strategy cannot be reached by gradual evolution (Hofbauer and Sigmund 1990). There are, however, trade-off shapes such that $F_{ES} < f_1(s_0)u''(f_1(s_0)) < F_{CS}$, that is, where the generalist strategy s_0 is attainable by gradual evolution but not ES. For such trade-off shapes, branching happens
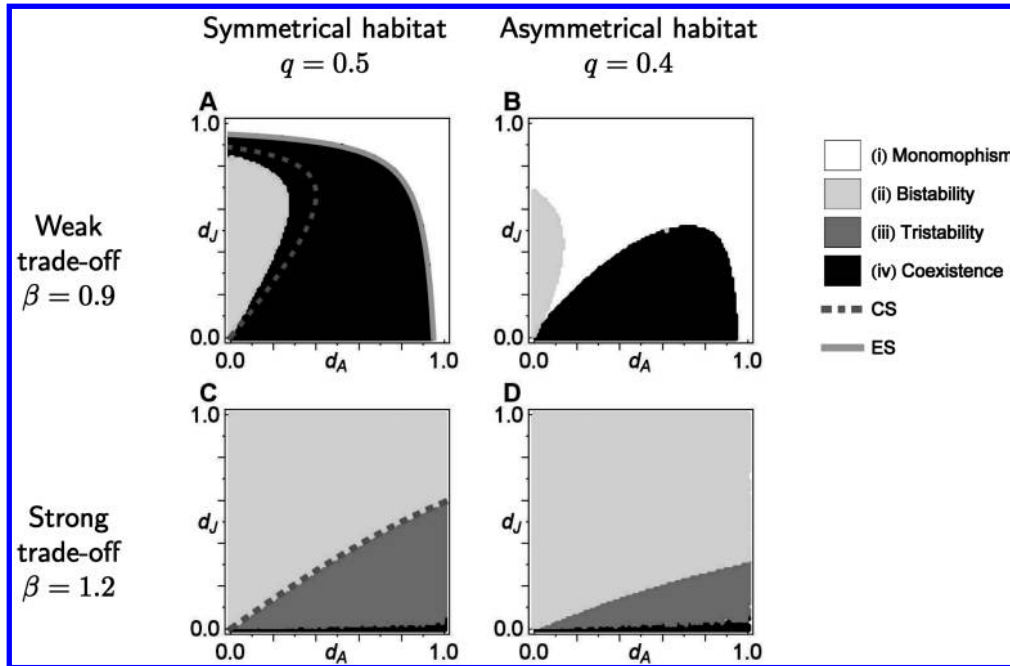
Figure 6: Evolutionary outcome of the model under the power trade-off for various environmental configurations (q, proportion of habitat A) and trade-off strengths (β), depending on the values of adult (d_A) and juvenile (d_J) migration probabilities. *White*, monomorphic outcome. *Black*, polymorphism. *Light gray*, bistability (end up monomorphic). *Dark gray*, tristability (end up either monomorphic or polymorphic). *Dashed line*, analytical condition for stability by convergence of the generalist strategy s_0 (see eq. [21]). *Solid line*, analytical condition for evolutionary stability of the generalist strategy s_0 (see eq. [25]).

and the population ends up polymorphic (Geritz et al. 1998).

Power Trade-Off. With a power trade-off, condition (24) becomes

$$\beta < \frac{d_A + d_J - d_A d_J}{2 - d_A - d_J + d_A d_J},$$ (25)

or, using μ,

$$\beta < \frac{\mu}{2 - \mu}.$$ (26)

As mentioned for a general trade-off, juvenile and adult migration have symmetrical effects, and the generalist strategy s_0 is never ES when the trade-off is too strong. The threshold $\mu/(2 - \mu)$ is between 0 and 1, and therefore s_0 is never ES when $\beta > 1$ (strong trade-off). See the gray solid line in figure 6A for an illustration. The generalist strategy s_0 is ES on the right-hand side of the gray solid line in figure 6A, where global migration is higher. The strategy s_0 is never ES in figure 6C because of the strong trade-off ($\beta > 1$).

Other Singular Strategies in a Symmetrical Environment

The values and stabilities of strategies other than the generalist strategy s_0 are investigated numerically. We use the particular case of the power trade-off and study two trade-off strengths: a weak trade-off ($\beta = 0.9$) and a strong trade-off ($\beta = 1.2$).

For a given trade-off (β), for each couple (d_A, d_J) of migration values, we solve equation (15) numerically to find singular strategies; we count them and study their stabilities. From this we deduce the evolutionary outcome, which is plotted as a point in figure 6. The values and stabilities of these singular strategies are plotted in figure C1.

In our description of the results, we focus on whether evolution leads to a polymorphic outcome. We identify four types of outcomes (see fig. 6): (1) monomorphism (white), (2) bistability (light gray), (3) tristability (dark gray), and (4) coexistence (black). Types 2 and 3 correspond to outcomes that depend on the initial conditions. For bistability (2), the outcome is always monomorphic (one or the other specialist). For tristability (3), the outcome is either monomorphic (one or the other specialist) or polymorphic. See figures C2E (bistability) and C3C (tristability) for illustrations.

Evolution with a Weak Trade-Off. With a weak trade-off (fig. 6A), there are singular strategies other than the pure generalist strategy s_0 only on the parameter domain where

s_0 is a repellor (i.e., left of the gray dashed line in fig. 6A). These other singular strategies are either evolutionarily stable strategies (ESSs) or branching points (see fig. C1A).

They are ESSs and correspond to specialist strategies for low values of d_A; in this case, the evolutionary outcome is a bistability between two specialists (light gray shading in fig. 6A). This means that for those parameters, there are two possible evolutionary outcomes, and which one is attained depends on the initial conditions. But both possible outcomes are monomorphic.

The other singular strategies can also be branching points; there, the outcome is a polymorphic state (black shading in fig. 6A). This means that the parameter domain where polymorphism evolves is greater than what can be deduced from the stability of s_0 only.

Evolution with a Strong Trade-Off. With a strong trade-off (fig. 6C), there are other singular strategies than s_0 in the parameter domain where s_0 is a branching point (i.e., for low values of d_J; bottom of the gray dashed line in fig. 6C). These additional singular strategies are repellors; this means that there are tristabilities (i.e., three possible outcomes) for these parameter values (dark gray shading in fig. 6C). Depending on the starting value of the adaptation trait s, the outcome can be one specialist only, the other specialist only, or the coexistence of two specialists.

When $d_J = 0$, the additional singular strategies are the two specialists (which have a fitness of 1 in one habitat and 0 in the other); the outcome is therefore unique and polymorphic (black shading in fig. 6C). When d_J is higher (above the gray dashed line in fig. 6C), the three singular strategies merge into the generalist strategy, which is a repellor. For this parameter domain, the outcome is never polymorphic and is either one or the other specialist (light gray shading in fig. 6C).

Asymmetrical Environment ($q \neq 1/2$)

Evolution with a Weak Trade-Off

With a weak trade-off (see fig. 6B), evolution leads to a polymorphic outcome when juvenile migration d_J is low and adult migration d_A is not too close to 1 (black shading in fig. 6B). Otherwise, the outcome is always monomorphic. For a wide range of parameters, the evolved strain is the specialist of the most frequent habitat (see fig. C1B).

For low values of adult migration d_A, bistabilities appear (light gray shading in fig. 6B); one or the other specialist evolves, depending on the initial value of the trait. The population can adapt to the least frequent habitat.

Evolution with a Strong Trade-Off

With a strong trade-off, the results are qualitatively similar to the ones obtained with $q = 1/2$ (cf. fig. 6C, 6D). The outcome is polymorphic (black shading in fig. 6D) when juvenile migration is null. For low values of juvenile migration ($d_J > 0$), there are tristabilities (dark gray shading in fig. 6D), where the outcome depends on the initial conditions but can be polymorphic. Finally, for higher values of juvenile migration, there are bistabilities (light gray shading in fig. 6D), and the outcome is always monomorphic.

Discussion

In this article, we investigate how the intensity and the timing of migration in a life cycle influence the maintenance and the evolution of polymorphism. In our model, the environment is divided into two habitats in proportions q and $1 - q$. We model a population of haploid asexually reproducing individuals. During their life cycle, the individuals can migrate twice: with a probability d_J before density regulation (which we call juvenile migration) and with a probability d_A right after density regulation (which we call adult migration). Particular combinations of d_A and d_J correspond to the classical soft and hard selection models (see fig. 3), but our model allows us to explore intermediate scenarios as well. Crucially, we show that many results—and, in particular, the maintenance of polymorphism—are explained by the effect of juvenile migration on the intensity of frequency-dependent selection.

We first study the conditions for the maintenance of a polymorphism between the two extreme specialist strategies. We find that when the environment is symmetrical ($q = 1/2$), polymorphism is maintained under any type of selection, provided selection is not totally frequency independent ($d_J = 1$, or hard selection; see fig. 4A). When the environment is asymmetrical ($q \neq 1/2$), there is a protected polymorphism when adult migration is below a threshold, which depends on juvenile migration and on q (see eq. [13]). We recover the classical result that a polymorphism is never possible under hard selection sensu stricto ($d_J = 1$) and that it is always possible under soft selection, even with philopatry ($d_J = 0$; Karlin and Campbell 1981). Of course, when $q = 0$ or $q = 1$, there is only one habitat in the environment, and there is therefore no polymorphism, no matter the type of selection.

We then focus on the conditions for the emergence of polymorphism through gradual evolution (which we expect to be more restrictive). We first study analytically the stability of the intermediate strategy in the special case where the two habitats have the same size ($q = 1/2$), and

we complete our analysis with numerical resolutions to find the other singular strategies (see fig. 6). We find that evolution leads to the intermediate strategy s_0 (which is a generalist strategy) only under a weak trade-off and for high adult and/or juvenile migration (or, equivalently, for a high chance of migrating at least once, μ). Polymorphism can be evolutionarily attainable under both a weak and a strong trade-off. Under a weak trade-off, evolution leads to polymorphism under a quite wide range of migration parameters: the probability of migrating at least once, μ, shall not be too high, and adult migration d_A shall not be too low. Under a strong trade-off, polymorphism is attained only when there is no juvenile migration ($d_J = 0$, soft selection with philopatry) or for a restricted set of initial conditions when juvenile migration is low. Interestingly, when branching happens, we see that evolution leads to the two extreme specialists (see figs. C2, C3).

All in all, it is easier to obtain a polymorphic outcome when the trade-off is weak, when juvenile migration d_J is low relative to adult migration d_A (i.e., frequency-dependent selection is high relative to gene flow; this corresponds to the bottom right triangle in fig. 3A), and when the habitats are of equivalent sizes (q close to 1/2). The outcome is always monomorphic when juvenile migration d_J is close to 1, because selection is more and more frequency independent but also because high migration values correspond to a finer environmental grain, to a single homogenized habitat instead of two (top left-hand corner in fig. 3A). Outside of these well-defined parameter domains, the outcome depends on the relative intensity of juvenile and adult migration and on the trade-off strength. The distinction between adult migration and juvenile migration has already been made by Karlin and Kenett (1977) in a model of evolution in a heterogeneous environment. But these terms refer to different mechanisms than in our model. In Karlin and Kenett's (1977) model, the individuals are distributed in separate demes, where selection happens, and then they mate and reproduce in mating areas. There are two stages of migration during the life cycle: adults migrate from demes to mating areas; after mating and reproduction, juveniles migrate from the mating areas to the deme sites. But in Karlin and Kenett's (1977) model, the relative contribution of each deme to the total mating pool is fixed. Therefore, their model corresponds to a form of soft selection (Ravigné et al. 2004). In our model, the distinction between juvenile and adult migration relies on whether migration occurs before or after density regulation.

Our model relies on the assumption that the habitats are saturated, always at carrying capacity. Previous models on adaptation in subdivided populations have considered more realistic population dynamics (see, e.g., Brown and Pavlovic 1992; Meszena et al. 1997; Ronce and Kirkpatrick

2001; Parvinen and Egas 2004), but these models correspond to soft selection because of independent density regulation in the two patches (Meszena et al. 1997). Still, it would be interesting to investigate the behavior of our model with unsaturated habitats, using more realistic forms of density dependence (for an inventory, see Henle et al. 2004).

In our model, the migration parameters are fixed quantities. What would happen if both juvenile and adult migration could evolve? The evolution of dispersal is known to be influenced by a multiplicity of factors (Ronce 2007) and, in particular, by the spatial heterogeneity of the environment. Balkau and Feldman's (1973) model of dispersal evolution (which corresponds to soft selection with philopatry) shows that increased dispersal is always counterselected. Similarly, Hastings (1983) shows that spatial variation alone cannot select for dispersal. Additional features, such as temporal variation (Gillespie 1981) or drift (Billiard and Lenormand 2005), would be required in our model to select for dispersal. Still, our model would provide an interesting framework to study at which step of the life cycle dispersal is more likely to be favored. In addition, we focused in this article on deterministic processes. Rice and Papadopoulos (2009) have shown that when migration influences local deme sizes, an increase in the variance in migration rates reduces the impact of immigration on any particular deme, relative to selection. How stochasticity in deme sizes and migration rates influences the conclusions of our study remains to be investigated.

Finally, a number of studies of experimental evolution have confirmed that heterogeneity may promote diversity (reviewed in Kassen 2002). Still, few studies have investigated the implications of soft versus hard selection on the maintenance or the evolution of diversity. To our knowledge, there is only one published experiment where the authors tried to test the predictions of the hard and soft selection models (Bell 1997). Bell (1997) selected green algae (*Chlamydomonas reinhardtii*) for about 50 generations, under different selection regimes. There was global pooling at each generation; for hard selection, a fixed volume was taken from each culture; for soft selection, a fixed amount of cells was taken. Hence, the experimenter directly controlled density regulation. In Bell's (1997) experiment, there were eight habitats, which differed by the presence or absence of three different macronutrients. Bell (1997) did not observe a reduction in genetic variance in the hard selection regime (Kassen 2002), potentially because of the large number of different habitats. It would be worth doing the experiment again with a simpler setting, with two qualitatively different habitats. For the sake of simplicity, our model contains restrictive assumptions (e.g., the habitats are saturated, and there is no stochasticity); still, we believe that it provides a useful framework for testing the evolutionary implications of the timing and intensities of migrations in heterogeneous environments.

Acknowledgments

APPENDIX A

Mutant Initial Dynamics

We linearize the model near the equilibrium with the resident strain only, where $(p_{r,t}^{(1)}\ p_{r,t}^{(2)}) = (1\ 1)$. We obtain the following initial dynamics for the mutant frequency:

$$\begin{pmatrix} p_{m,t+1}^{(1)} \\ p_{m,t+1}^{(2)} \end{pmatrix} = \mathbf{M} \begin{pmatrix} p_{m,t}^{(1)} \\ p_{m,t}^{(2)} \end{pmatrix}, \tag{A1}$$

where

$$\mathbf{M} = (M_{i,j})_{i,j \in \{1,2\}}, \tag{A1}$$

$$M_{1,1} = \frac{[1 - d_J(1 - q)]w_m^{(1)}}{[1 - d_J(1 - q)]w_r^{(1)} + d_J(1 - q)w_r^{(2)}}[1 - d_A(1 - q)] + d_A(1 - q)\frac{d_J q w_m^{(1)}}{(1 - d_J q)w_r^{(2)} + d_J q w_r^{(1)}}, \tag{A2a}$$

$$M_{1,2} = \frac{d_J(1 - q)w_m^{(2)}}{[1 - d_J(1 - q)]w_r^{(1)} + d_J(1 - q)w_r^{(2)}}[1 - d_A(1 - q)] + d_A(1 - q)\frac{(1 - d_J q)w_m^{(2)}}{(1 - d_J q)w_r^{(2)} + d_J q w_r^{(1)}}, \tag{A2b}$$

$$M_{2,1} = \frac{d_J q w_m^{(1)}}{(1 - d_J q)w_r^{(2)} + d_J q w_r^{(1)}}(1 - d_A q) + d_A q\frac{[1 - d_J(1 - q)]w_m^{(1)}}{[1 - d_J(1 - q)]w_r^{(1)} + d_J(1 - q)w_r^{(2)}}, \tag{A2c}$$

$$M_{2,2} = \frac{(1 - d_J q)w_m^{(2)}}{(1 - d_J q)w_r^{(2)} + d_J q w_r^{(1)}}(1 - d_A q) + d_A q\frac{d_J(1 - q)w_m^{(2)}}{[1 - d_J(1 - q)]w_r^{(1)} + d_J(1 - q)w_r^{(2)}}. \tag{A2d}$$

APPENDIX B

Alternative Power Trade-Off

The alternate power trade-off is derived from the following fitness functions (Ravigné et al. 2009):

$$f_1(s) = (1 - x_0)s^\beta + x_0, \tag{B1a}$$

$$f_2(s) = (1 - x_0)(1 - s)^\beta + x_0. \tag{B1b}$$

The parameter x_0 ($0 \leq x_0 \leq 1$) determines the minimum value of fitness in one habitat. See figure B1 for an illustration of this alternative power trade-off.

Singular Strategy

Because it satisfies equation (15), $s_0 = 1/2$ is a singular strategy.

Convergence Stability

Power Trade-Off. The condition for convergence stability is presented in the main text for the limit case where $x_0 = 0$. It is more complicated when $x_0 > 0$ (see below for the definitions of $\tilde{d}_A$ and $\tilde{x}_0$). When $\beta < 1$ (weak trade-off),

$$\text{if } d_A > \tilde{d}_A, \; s_0 \text{ is always CS,} \tag{B2a}$$

$$\text{if } d_A < \tilde{d}_A, \; s_0 \text{ is CS if } x_0 > \tilde{x}_0. \tag{B2b}$$

When $\beta > 1$ (strong trade-off),

$$\text{if } d_A > \tilde{d}_A, \; s_0 \text{ is CS if } x_0 < \tilde{x}_0, \tag{B3a}$$

$$\text{if } d_A < \tilde{d}_A, \; s_0 \text{ is never CS,} \tag{B3b}$$

with $\tilde{d}_A$ (resp. $\tilde{x}_0$), the critical values for convergence stability of adult migration d_A (resp. minimum fitness x_0), defined as

$$\tilde{d}_A = -\frac{d_J}{1 - d_J}[1 - (2 - d_J)\beta], \tag{B4a}$$

$$\tilde{x}_0 = \left[1 - \frac{2^\beta(d_A + d_J - d_A d_J)(1 - \beta)}{d_A + d_J - d_A d_J - (2 - d_J)d_J\beta}\right]^{-1}. \tag{B4b}$$

When the trade-off is weak ($\beta < 1$), increasing the minimum value of fitness (x_0) has a stabilizing effect; it increases the parameter domain where the strategy s_0 is convergence stable (CS). On the contrary, when the trade-off is strong ($\beta > 1$), increasing x_0 reduces the parameter domain where s_0 is CS. See the lines in figure 5 for an illustration.

Under soft selection ($d_J = 0$), when $x_0 > 0$, the generalist strategy s_0 is not convergence stable if the trade-off is very strong (which is consistent with the findings of Ravigné et al. [2009]).

Evolutionary Stability

Again, the condition for convergence stability is more complicated when $x_0 > 0$ (see below for the definition of $\hat{d}_A$). When $\beta < 1$ (weak trade-off), s_0 is ES if $d_A > \hat{d}_A$; when $\beta > 1$ (strong trade-off), s_0 is never ES, with $\hat{d}_A$, the critical value of adult dispersal d_A for evolutionary stability, defined as

$$\hat{d}_A = \frac{2^\beta d_J x_0(\beta - 1) - (1 - x_0)[d_J(1 + \beta) - 2\beta]}{-(1 - d_J)[2^\beta x_0(\beta - 1) - (1 - x_0)(1 + \beta)]}. \tag{B5}$$

Here, under a weak trade-off ($\beta < 1$), increasing x_0 increases the parameter domain where s_0 is ES. When the trade-off is strong, s_0 is not ES, no matter the value of x_0.
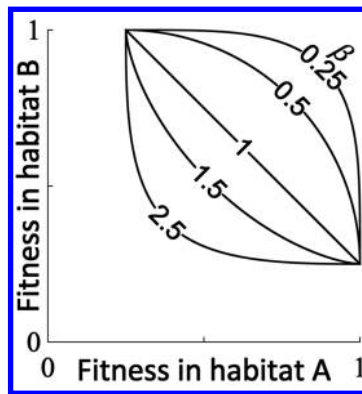
Figure B1: Alternative power trade-off used by Ravigné et al. (2009). The minimum fitness is $x_0 = 0.25$, and the trade-off is plotted for various values of β, which are written on the lines.

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