

# ON THE EVOLUTION OF MIGRATION IN HETEROGENEOUS ENVIRONMENTS

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Received October 21, 2013

Accepted February 17, 2014

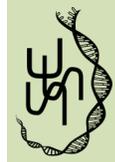
Populations often experience variable conditions, both in time and space. Here we develop a novel theoretical framework to study the evolution of migration under the influence of spatially and temporally variable selection and genetic drift. First, we examine when polymorphism is maintained at a locus under heterogeneous selection, as a function of the pattern of spatial heterogeneity and the migration rate. In a second step, we study how levels of migration evolve under the joint action of kin competition and local adaptation at a polymorphic locus. This analysis reveals the existence of evolutionary bistability, whereby a low or a high migration rate may evolve depending on the initial conditions. Last, we relax several assumptions regarding selection heterogeneity commonly made in previous studies and explore the consequences of more complex spatial and temporal patterns of variability in selection on the evolution of migration. We found that small modifications in the pattern of environmental heterogeneity may have dramatic effects on the evolution of migration. This work highlights the importance of considering more general scenarios of environmental heterogeneity when studying the evolution of life-history traits in ecologically complex settings.

**KEY WORDS:** Dispersal, kin competition, metapopulation, spatial heterogeneity, stochasticity, temporal change.

Migration is a key life-history trait that affects both the demography and evolution of species (Clobert et al. 2001). It can affect the maintenance of diversity (Levene 1953; Gavrilets 2003) but also the spatial distribution of this diversity, and in particular patterns of local adaptation (Gandon 2002; Lenormand 2002). There is ample evidence that migration propensity is heritable and may thus evolve rapidly under selection (Roff and Fairbairn 2001; Haag et al. 2005; Ronce 2007; Cheptou et al. 2008). But selection acting on dispersal in natural populations is particularly complex. Multiple evolutionary forces have been shown to select for higher migration rates like the ability to recolonize empty sites (Comins et al. 1980), the avoidance of kin competition (Hamilton and May 1977; Frank 1986; Taylor 1988; Gandon and Michalakis 1999), the avoidance of inbreeding depression (Roze and Rousset 2005, 2009). Yet, several forces may act in the opposite direction and select against migration. The development of specific dispersal structures may impose a direct fitness cost on this trait (Roff and Gelinas 2003). Moreover, the migration event and the settling

in a new environment are risky and may impose an additional cost. Interestingly, the performance in a novel habitat is governed by the level of local adaptation, which in turn depends on the population structure at loci involved in adaptation to the local environments. Thus, a theoretical understanding of the effect of local adaptation on the evolution of migration requires a multilocus model in which one locus governs migration (modifier locus of migration) and another governs the level of adaptation to the environment (locus under direct selection). Those models show that in a spatially heterogeneous environment, adaptation to local environmental conditions generates a fitness cost to migrants, which selects against dispersal (Balkau and Feldman 1973).

In realistic ecological scenarios multiple evolutionary forces are likely to interact. This raises a theoretical challenge because the models trying to combine these different forces are difficult to handle (Clobert et al. 2001; Ronce 2007). Previous attempts to study the evolution of migration under more ecologically complex scenarios often rely on a set of very restrictive assumptions. For



example, we previously analyzed a two-locus model to study the evolution of migration when selection can vary both in space and in time (Blanquart and Gandon 2011). We showed that some form of temporal variability can favor higher rates of migration because gene flow is a way to increase the speed of adaptation to a variable environment. Analytical tractability in this model was reached at the cost of assuming (i) periodical fluctuations, (ii) a specific pattern of spatial variation in selection, (iii) large population sizes so that the effect of genetic drift can be neglected. Similarly, Drown et al. (2013) analyze a two-locus model with host–parasite interaction, showing that coevolutionary fluctuations select for migration, but also neglecting the impact of genetic drift. Billiard and Lenormand (2005) analyzed another two-locus model with spatially heterogeneous environment and considered the effect of finite population size on the evolution of migration. They showed that relatedness generated by genetic drift can counteract the cost induced by local adaptation and may favor the evolution toward intermediate levels of migration. This model achieved analytical tractability by assuming (i) two patches, (ii) a specific pattern of variation in selection, (iii) no temporal variability in the environment. The robustness of these results remains to be investigated in a broader range of ecological scenarios. In particular, spatial variability in selection should be associated with spatial variability in population density, because both follow from spatial variability in some biotic or abiotic factors of the environment (parasitism, temperature, humidity . . .). Variability in density is known to select against migration (Hastings 1983; Holt 1985) and could reinforce the impact of local adaptation on the evolution of migration. Besides, the interaction between local adaptation and genetic drift when selection varies in time has never been investigated.

In the present study, we attempt to study the evolution of migration in a broad range of ecological scenarios, and unify disparate results. Extending the method developed for multilocus models (Kirkpatrick et al. 2002; Roze and Rousset 2008), we analyze the evolution of a spatially structured population at several loci using joint spatial moments of the allele frequencies and the linkage disequilibrium. First, we analyze the maintenance of polymorphism on a selected locus in a spatially variable environment. Second, we characterize the spatial patterns of adaptation under the joint action of selection, genetic drift, and migration. Third, we analyze the evolution of migration under the action of spatially variable selection and genetic drift. Fourth, we allow for temporal variability of selection and analyze its impact on the evolution of migration.

## The Model

### LIFE CYCLE

We consider a metapopulation with a large number of demes. Each deme is filled with a finite number  $N$  of haploid individuals. Each individual's genome is described as two genes on a single

chromosome. The first diallelic locus (alleles  $a$  or  $A$ ) is under spatially (and temporally) variable selection. The second diallelic locus (alleles  $m$  or  $M$ ) controls the propensity to migrate. There are thus four different genotypes,  $am$ ,  $aM$ ,  $Am$ , and  $AM$ . The life cycle is as follows:

### Sex and recombination

Individuals encounter at random and recombine with rate  $\phi$ .

### Reproduction and selection

Individuals produce a large number of juveniles given by  $f(1 + s_{i,A})$  and  $f(1 + s_{i,a})$  for individuals bearing alleles  $A$  and  $a$ , respectively, in population  $i$ . The parameter  $f$  refers to the baseline number of offspring, whereas  $s_{i,A}$  and  $s_{i,a}$  refer to the selection coefficients acting on the two alleles. Note that these coefficients vary with space but they may also vary in time (see section “Dynamics of the linked modifier of migration”). After reproductions all adults die.

### Migration

Juveniles migrate to a randomly chosen deme in the metapopulation (“island model” of migration with no isolation by distance). The migration rates of individuals carrying the  $m$  and  $M$  alleles are  $m$  and  $m + \Delta m$ , respectively (to avoid confusion, in the following “ $m$ ” will always refer to the migration rate, not to the low-migration allele). Note that migration and/or carrying the  $M$  allele may be associated with direct fitness costs (see section “Dynamics of the linked modifier of migration”).

### Population regulation

Regulation occurs just after migration. In other words, we assume that good quality habitat producing a higher number of offspring will contribute more to the pool of migrants (i.e., “hard selection” model). We discuss later on how alternative life cycles (i.e., “soft selection” in which regulation occurs before migration) could modify our results. Regulation consists in the random sampling of  $N$  juveniles who survive and contribute to the next adult generation. This random sampling induces random changes in genotype frequencies (i.e., genetic drift).

## ANALYSIS

We combine the equations describing the different steps of the life cycle to get the exact changes of genotype frequencies over a life cycle in one deme  $i$  (Appendix S1). It is more convenient to describe our system in terms of local allele frequencies  $p_{i,A}$  and  $p_{i,M}$  and linkage disequilibria  $d_i$  instead of genotypic frequencies. We thus obtain exact recursion equations for these changes through one step of the life cycle in each deme. Note that because of the random sampling during population regulation these three quantities are random variables.

A complete description of our system would require following these frequencies and disequilibrium in each deme. Instead, we describe the metapopulation in terms of the spatial averages and spatial moments of selection ( $s_{i,a}$  and  $s_{i,A}$ ) and of the variables ( $p_{i,A}$ ,  $p_{i,M}$ , and  $d_i$ ; see also Roze and Rousset 2008). Because there are infinitely many such moments, we will use a moment closure approximation (Appendix S2). To this end, we assume that selection and genetic drift are small (specifically,  $s_{i,a}$ ,  $s_{i,A}$  are of the order of a small dummy variable  $\epsilon$  and  $1/N$  is of the order of  $\epsilon^2$ , see Appendix S2) and that the effect of the modifier of migration is also small ( $\Delta m$  is of order  $\epsilon$ ). Under these assumptions, a  $n$ th order moment is of order  $\epsilon^n$ . Consequently, to approximate the dynamics of the system to the order  $n$  we need to follow the averages and moments up to the  $n$ th order moment. In the present study, the evolutionary forces affecting the modifier are of order  $\epsilon^3$ , and therefore we will follow the dynamics of all moments up to the third order. We use the recursion equations for the variables ( $p_{i,A}$ ,  $p_{i,M}$ , and  $d_i$ ) to derive recursion equations for all the relevant moments.

In this study, we assume that the number of demes is sufficiently large so that stochasticity occurring at the level of the metapopulation can be neglected. Specifically, we assume that the number of demes is large enough that the realized spatial average of a variable is very close to the expected value of the spatial average (e.g.,  $E[P_A] \approx \langle P_A \rangle$ , where  $\langle \rangle$  stands for the average over the random variables and  $E[\ ]$  stands for the spatial average). In the following, the capital letters  $S_A/S_a$ ,  $P_A$ ,  $P_M$ , and  $D$  stand for the variables describing the spatial distributions and not for the actual values of these variables. The spatial averages of these variables are called  $s_A/s_a$ ,  $p_A/p_a$ ,  $p_M$ , and  $d$  for simplicity.

Finally, we end up with a system of recursion equations for the three average variables  $p_A$ ,  $p_M$ , and  $d$  and for the spatial moments. To the third order, the recursion equations for the moments are a system of linear equations. Because migration is assumed to be large relative to other forces acting on the dynamic variable, we use a separation of time scale argument (Kirkpatrick et al. 2002; Whitlock and Gomulkiewicz 2005) based on the idea that spatial moments evolve much faster than the metapopulation average values of the variables. When selection is variable in space but not in time, we solve the recursion equation of the spatial moments to obtain equilibrium values of these moments. When selection is also variable in time, spatial moments may not reach an equilibrium point but keep varying with time. Yet, in both cases it is possible to plug the values of these spatial moments into the recursion equations for  $p_A$ ,  $p_M$ , and  $d$  to follow the evolution of these mean variables in the metapopulation. In the following, we show that analysis of the dynamics of  $p_A$  can be used to study the conditions for the maintenance of polymorphism in the metapopulation. In a second step, we analyze the dynamics of  $p_M$  to study the evolution of migration under a range of ecological scenarios.

## Results

### DYNAMICS AT THE SELECTED LOCUS

For the sake of simplicity, we focus on the situation in which selection does not change in time but varies in space. We first examine the conditions for the maintenance of polymorphism at this locus. Then we study the spatial distribution of this polymorphism and quantify the effects of selection, migration, and genetic drift on local adaptation and spatial differentiation at this locus.

### MAINTENANCE OF POLYMORPHISM

We derived a recursion equation for the average allele frequency  $p_A$  in the metapopulation and find equilibrium values for  $p_A$ . Assuming without loss of generality that  $s_A \geq s_a$  ( $s_A$  and  $s_a$  refer to the spatial averages of the selection coefficients), we found the condition for the existence of a stable interior equilibrium (Appendix S3). Explicit solutions for the general case exist but are lengthy and do not lend themselves easily to interpretation. For the sake of simplicity, we focus on a more restrictive set of assumptions where  $V[S_a] = V[S_A] = V_S$ , where  $V_S$  measures the spatial variance of selection. Furthermore, we define  $\rho$  as the spatial correlation between selection coefficients acting on the alleles  $a$  and  $A$ , that is,  $\text{Cov}[S_a, S_A] = \rho V_S$ . The correlation  $\rho$  lies in the interval  $[-1, 1]$ . In the special case where  $s_{i,a} = s_{i,A} + \delta_s$  in all demes, both genotypes perform similarly in the same environment and  $\rho = 1$ . At the other extreme, when  $s_{i,a} = -s_{i,A} + \delta_s$  in all demes, there is a strong trade-off between these genotypes and  $\rho = -1$ . Lastly, we assume without loss of generality that  $s_a = 0$  (fecundity  $f$  can always be rescaled so that this condition is fulfilled) and rename  $s_A = \delta_s$ . We find the polymorphic equilibrium is stable if and only if:

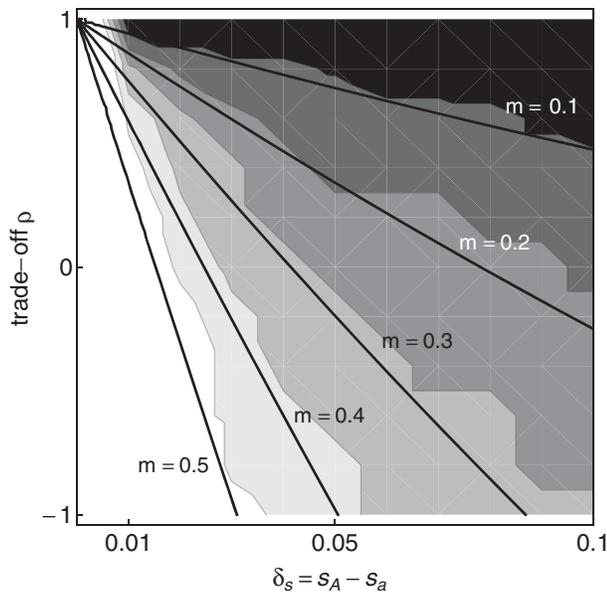
$$V_S(1 - \rho) > \frac{m(1 - \delta_s)\delta_s}{(2 - m)(1 - m)}. \quad (1)$$

The above condition reveals that polymorphism is most easily maintained when the average difference in performance  $s_A - s_a$  is small, when the spatial variance of selection  $V_S$  is large, and when the trade-off in performance of genotypes  $\rho$  is negative.

Equation (1) can be rearranged to show that polymorphism is maintained when migration is below the threshold value:

$$m < \frac{1}{2} \left( 3 + \frac{(1 - \delta_s)\delta_s}{(1 - \rho)V_S} - \sqrt{\frac{(1 - \rho)^2 V_S^2 + 6(1 - \rho)V_S(1 - \delta_s)\delta_s + (1 - \delta_s)^2 \delta_s^2}{(1 - \rho)^2 V_S^2}} \right). \quad (2)$$

Equation (2) is illustrated in Figure 1, where we show the critical migration rate below which polymorphism is maintained as a function of  $\rho$  and  $\delta_s$ . Simulations show that this critical migration rate is well captured by equation (2) (see details of simulations in Appendix S5).



**Figure 1.** The maximal migration rate that allows maintenance of polymorphism at the selected locus, as a function of the difference in fecundities  $\delta_s = s_A - s_a$  and the spatial correlation  $\rho$  between the fecundity of alleles  $a$  and  $A$ . Above this migration rate, polymorphism is lost. Shaded areas are the result of simulations; lines are the analytical criterion given by equation (2) of the main text. Simulations were conducted for a normal distribution of fecundities with  $V_S = 0.01$ . The metapopulation has 100 demes with  $N = 1000$  individuals per deme. We ran 10 replicate runs for each set of parameters.

The main biological insights given by equations (1) and (2) agree with previous literature (e.g., Gavrillets and Gibson 2002, and many others). We extend previous results by considering multiple populations, a general pattern of spatial variability in selection, and by demonstrating that genetic drift happening locally (within each deme) has a negligible effect on the maintenance of polymorphism. More precisely, in our approximation, the maintenance of polymorphism does not depend on local population size  $N$  because we consider a large number of demes with no stochasticity at the level of the metapopulation. In practice, whenever the number of demes is finite, the eventual fate of an allele is to fix or to get extinct. With a finite number of demes, more precisely, the system will first rapidly converge to the state our analysis predicts in this section; then, on a slower time scale, stochastic effects will eventually cause fixation of one allele in the whole metapopulation (Yeaman and Otto 2011).

## MEASURES OF POPULATION DIFFERENTIATION

There is a natural link between the spatial moments we use to describe the metapopulation and two measures of population differentiation that are often measured by experimentalists.

The first is  $F_{ST}^{sel}$ , the spatial differentiation at a selected locus. In the context of our study, we define  $F_{ST}^{sel}$  as  $V[P_A]/(p_A(1 - p_A))$ , where  $V[P_A]$  is the spatial variance of allele frequency at the selected locus and  $p_A(1 - p_A)$  is the total variance. Thus  $F_{ST}^{sel}$  quantifies the fraction of the variance at the selected locus explained by the metapopulation structure. We find  $F_{ST}^{sel}$  is (Appendix S4):

$$F_{ST}^{sel} = \frac{1}{(2 - m)mN} + p_A(1 - p_A) \frac{(1 - m)^2}{m^2} 2V_S(1 - \rho). \quad (3)$$

In this equation, the first term is the differentiation caused by genetic drift. A neutral locus would precisely exhibit this level of differentiation (i.e.,  $F_{ST}^{neut} = \frac{1}{(2 - m)mN}$ ; see Roze and Rousset 2008). The second term is always positive and is the differentiation caused by heterogeneous selection. In other words, differentiation at the selected locus increases when selection varies a lot in space (large spatial variance  $V_S$  and strongly negative trade-off:  $\rho = -1$ ) and when gene flow among populations is limited.

The second measure is local adaptation, a measure that is obtained using transplant experiments and is defined as the difference between the mean fitness (i.e., mean fecundity) populations achieve in sympatry and the mean fitness they achieve in allopatry (Kawecki and Ebert 2004; Blanquart et al. 2012, 2013, see section “Local adaptation” in Appendix S4). In our model, under weak selection, we found local adaptation is given by

$$\lambda = 2p_A(1 - p_A) \frac{1 - m}{m} V_S(1 - \rho), \quad (4)$$

which is always positive. It is striking that the extra differentiation at a selected locus is proportional to local adaptation:

$$F_{ST}^{sel} = \frac{1}{(2 - m)mN} + \frac{1 - m}{m} \lambda. \quad (5)$$

Thus, joint measures of  $F_{ST}^{neut}$ ,  $F_{ST}^{sel}$ , and  $\lambda$  would allow direct calculations of  $m$ ,  $N$ , and  $V_S(1 - \rho)$  under the assumptions of our model.

The above equation confirms that the genotypic composition in each deme matches local selection under the action of divergent selection. This pattern of local adaptation should limit the evolution of dispersal (because, on average, dispersal leads to worst environments). Finite population size, however, also leads to the buildup of genetic differentiation. This process, on the contrary, promotes the evolution of dispersal (because it allows avoiding competition among related individuals). In the next section, we investigate how these conflicting forces emerge and how their interaction drives the evolution of migration.

## DYNAMICS OF THE LINKED MODIFIER OF MIGRATION

As mentioned above, to follow the dynamics of the modifier of migration we need to describe the system at the order  $\varepsilon^3$ . At

this order there are 43 spatial moments to compute on top of the three equations for the average variables. To characterize the evolutionary dynamics at the modifier locus, it is useful to write the change in frequency at the modifier locus in the following way:

$$p'_M = p_M + s_M p_M (1 - p_M), \quad (6)$$

where  $s_M$  measures the selection gradient at the modifier locus. To go further in the analysis of this selection gradient, we will examine a series of scenarios. In a first step we consider the scenario where  $s_{i,a} = -s_{i,A}$  in each deme, such that  $\delta_s = 0$ ,  $V[S_a] = V[S_A] = V_S$ , and  $\rho = -1$ . This scenario imposes balanced selection on both genotypes and a strong trade-off between them, which favors maintenance of polymorphism. Second, we relax the assumption that  $\rho = -1$  to consider the influence of the ecological trade-off on the evolution of migration. Third, we relax the assumption that selection is perfectly balanced by considering  $\delta_s > 0$  (one allele is, on average, fitter than the other in the whole metapopulation). Lastly, we extend the model to account for various shapes of temporal variability in selection.

### SCENARIO 1: PERFECT TRADE-OFF, SELECTION IS BALANCED

In this scenario, it is assumed that  $\delta_s = 0$  and  $\rho = -1$ . Such scenario corresponds, for example, to a metapopulation where in half of the demes  $W_a = 0.9$  and  $W_A = 1.1$ , and in the other half of the demes  $W_a = 1.1$  and  $W_A = 0.9$ . It can be readily shown using the analysis above that the average allele frequency converges to  $p_A \rightarrow 1/2$ , which is a stable equilibrium. The average modifier frequency in the metapopulation evolves as (Appendix S3):

$$p'_M = p_M + \underbrace{2(1 - \phi)\text{Cov}[S_A, D]}_{\text{local adaptation effect}} + \underbrace{\Delta m(1 - m)V[P_M]}_{\text{kin selection effect}}. \quad (7)$$

The first term represents indirect selection on the modifier due to local adaptation. The second term is always positive and represents the automatic advantage to migration due to population structure at the  $M$  locus (often interpreted in terms of kin selection). Indeed, when genetic differentiation at the  $M$  locus is strong, philopatry leads to competition among related individuals. Hence, dispersal may be viewed as an altruistic act because it provides a way to avoid competition among kin (Hamilton and May 1977; Taylor 1988). The two relevant spatial moments for the dynamics of the modifier of migration equilibrate at the following levels:

$$\begin{aligned} \text{Cov}[S_A, D]^* &\approx -\frac{1}{2} \frac{\Delta m p_M (1 - p_M) V_S}{m(1 - (1 - \phi)(1 - m))} \\ V[P_M]^* &\approx \frac{p_M(1 - p_M)}{(2 - m)mN}. \end{aligned} \quad (8)$$

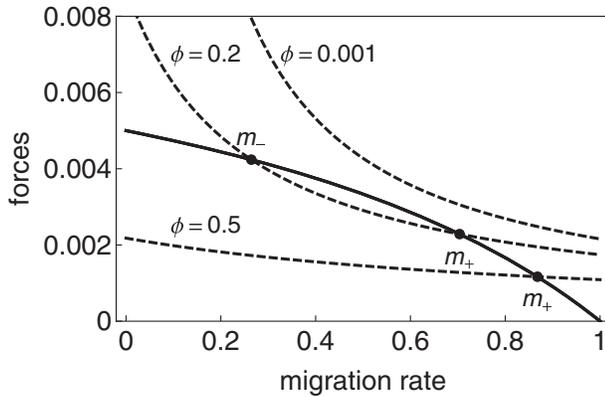
The covariance between local selection and the linkage disequilibrium is negative. This emerges from the fact that maladapted individuals tend to be associated with the  $M$  allele (the one that induces higher migration) at the modifier locus (Balkau and Feldman 1973). In demes where  $A$  is favored,  $a$  are preferentially associated with  $M$  that creates a negative linkage disequilibrium; on the contrary in demes where  $a$  is favored,  $A$  is associated with  $M$  that generates a positive linkage disequilibrium. The second equation shows that to this order the spatial structure at the modifier locus is generated by genetic drift only. This is because the linkage between both loci is too small for the structure at the second locus to be affected by selection at the first locus.

Plugging the equilibrium expressions (8) into equation (7), we obtain the selection gradient on the modifier  $s_M$  (Appendix S3):

$$s_M = \frac{\Delta m}{m} \left( -\frac{(1 - \phi)}{m(1 - \phi) + \phi} V_S + \frac{1 - m}{(2 - m)N} \right). \quad (9)$$

The conflicting impacts of genetic drift and environmental heterogeneity appear in the selection gradient. Note that extra terms may be incorporated into equation (9) to account for the cost of migration. A direct cost (fecundity cost paid by all individuals with allele  $M$ ) would require the extra term  $-c_{dir}$ , whereas an indirect cost (cost paid by all migrant individuals regardless of their genotype) would require the extra term  $-\Delta m c_{ind}$ . When there is no spatial variance of selection (i.e.,  $V_S = 0$ ) local adaptation vanishes (eq. 4) and evolution results simply from the balance between these extra costs of dispersal and the avoidance of kin competition. In this case, as expected, we can use (9) to recover the classical results of earlier kin selection models of dispersal evolution (Taylor 1988).

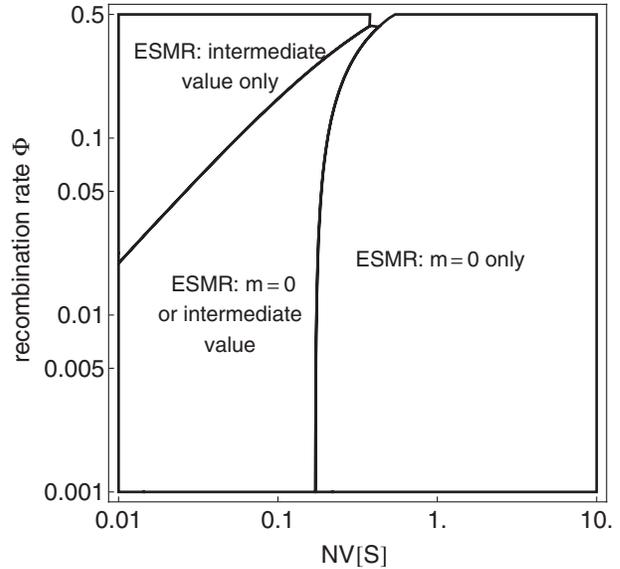
Under the assumption that the migration rate evolves by successive invasions of mutants of small effects, what rate of migration will evolve? We solved for the value of migration that cancels the selection gradient (9) and found explicit solutions for two roots  $m_-$  and  $m_+$  (see section ‘‘Scenario 1: perfect negative trade-off and selection is balanced’’ in Appendix S3). We examined the stability of these equilibria and identified three evolutionary outcomes. Specifically, the evolutionary outcome depends on  $NV_S$ , which quantifies the balance between local adaptation and kin selection (the bigger  $NV_S$  is, the stronger local adaptation is relative to kin selection), and on the level of recombination (see section ‘‘Scenario 1: perfect negative trade-off and selection is balanced’’ in Appendix S3). In Figure 2, we compare the impact of local adaptation and genetic drift on the gradient of selection of the modifier of migration. For low values of  $NV_S$ , kin selection overwhelms the effect of local adaptation and migration evolves to a high level  $m = m_+$ . Conversely, for high values of  $NV_S$ , local adaptation predominates and  $m = 0$  is the only evolutionarily



**Figure 2.** Quantities proportional to the absolute value of direct selection due to drift ( $\frac{1-m}{(2-m)N}$  plain line, see eq. 9 and indirect selection due to local adaptation ( $\frac{(1-\phi)}{m(1-\phi)+\phi}V_S$  dashed lines) on the modifier of migration, as a function of the migration rate. Indirect selection is shown for three values of recombination. Migration tends to evolve to higher rates when selection due to drift (plain line) is above indirect selection. For a low value of recombination, only  $m = 0$  is stable. For an intermediate value, both  $m = 0$  and  $m = m_+$  are stable and the outcome depends on the initial migration rate relative to  $m_-$ . For a high value of recombination, only  $m = m_+$  is stable. Parameter values are  $NV_S = 0.218$ .

stable migration rate (ESMR). For intermediate values of  $NV_S$ , there is evolutionary bistability: the ES MR is 0 if the initial migration rate is small, and it is  $m_+$  if the initial migration rate is high. This bistability occurs in a wider range of conditions when recombination is smaller (Figs. 3 and 4). Bistability emerges because of the nonlinear effects of migration on the evolutionary forces generated by local adaptation and genetic drift (Fig. 2).

To check the above analysis, we simulated the evolution of the metapopulation with selection, migration, and genetic drift and investigated the evolution of the migration rate (details in Appendix S5). Our simulation results confirmed our analytical predictions and revealed interesting evolutionary dynamics. In particular, when there is evolutionary bistability, the population may jump between the different equilibria because of the



**Figure 3.** The outcome of a modifier of migration in the space of parameters defined by  $NV_S$  and the recombination rate  $\phi$ , in the simplest scenario (scenario 1). The lines are the analytical boundaries described in section “Dynamics of the linked modifier of migration” (see also section “Scenario 1: perfect negative trade-off and selection is balanced” in Appendix S3).

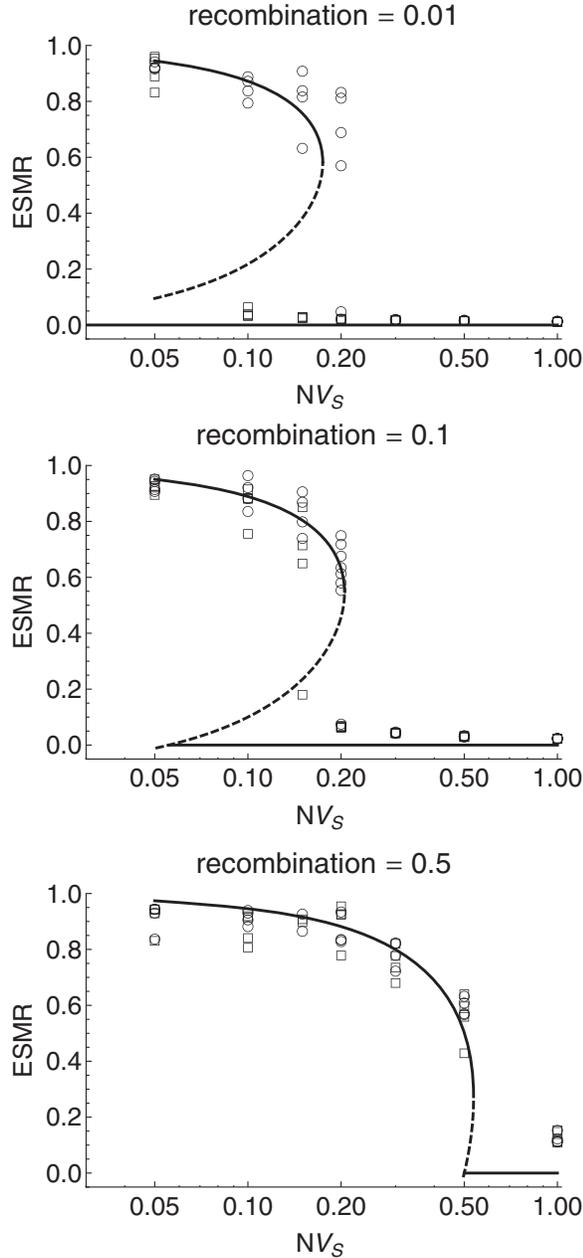
**SCENARIO 2: IMPERFECT TRADE-OFF, SELECTION IS BALANCED**

As in scenario 1, we assume that  $V[S_a] = V[S_A] = V_S$  and that selection is perfectly balanced at the level of the metapopulation ( $\delta_s = 0$ , i.e.,  $s_A = s_a = 0$ ). Here, however, we examine the effect of the correlation between the performance of one genotype and the other across environments ( $\rho \neq -1$ ). For example, a metapopulation where  $W_a$  and  $W_A$  are drawn independently in the same distribution in each deme would result in  $s_A = s_a = 0$  and  $\rho = 0$ . In this scenario 2, it can be readily shown using the analysis above that the average allele frequency converges to  $p_A \rightarrow 1/2$ , which is a stable equilibrium. The average modifier frequency in the metapopulation evolves as (see section “Scenario 2: imperfect trade-off and selection is balanced” in Appendix S3):

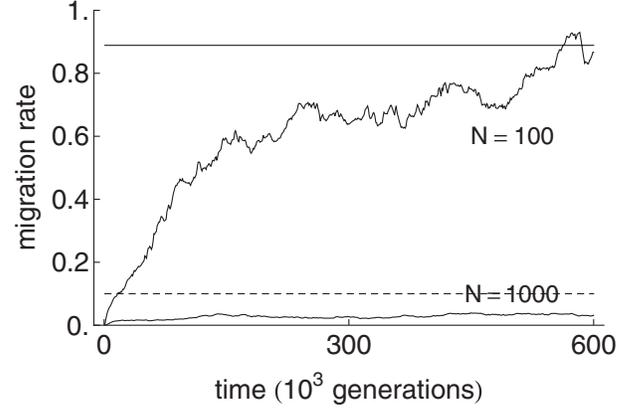
$$\begin{aligned}
 p'_M = & p_M + \underbrace{(1 - \phi)(\text{Cov}[S_A, D] - \text{Cov}[S_a, D])}_{\text{local adaptation effect}} + \underbrace{(1 - m)\Delta m V[P_M]}_{\text{kin selection effect}} \\
 & + \underbrace{(\Delta m + m(2 - m - \Delta m))((1 - p_A)\text{Cov}[S_a, P_M] + p_A\text{Cov}[S_A, P_M]) + \Delta m(1 - m)\frac{1}{2}p_M(1 - p_M)V_S(1 + \rho)}_{\text{habitat heterogeneity effect}} \quad (10)
 \end{aligned}$$

stochasticity of the evolutionary process. In those cases, the evolutionary outcome depends on the initial condition as well as the amount of genetic drift. Each evolutionary equilibrium is much more stable when the local population size is larger (Fig. 5).

We are familiar now with the first two terms, which represent indirect selection on the modifier due to local adaptation and direct selection due to kin competition, respectively. The first term (local adaptation) has a slightly more complicated form than



**Figure 4.** The evolutionarily stable migration rate (ESMR) as a function of  $NV_S$  for three recombination rates, in scenario 1. Plain lines represent the analytical prediction given by the selection gradient ( $m = m_+$  and  $m = 0$ , eq. 9, section “Scenario 1: perfect negative trade-off and selection is balanced” in Appendix S3). The dashed line is the barrier ( $m = m_-$ ) when the equilibrium is bistable. Open symbols are the result of simulations starting from low migration (squares) or high migration (circles). Each point is the average migration rate in one simulation, averaged over 100 time points taken every 1000 generations from generations  $5 \times 10^5$  to  $6 \times 10^5$ . All these simulations were run with 100 demes and  $N = 100$  individuals per deme (Appendix S5).



**Figure 5.** The evolution of the migration rate through time, when  $N = 100$  (top curve) and when  $N = 1000$  (bottom curve). In both cases, the recombination rate is  $\phi = 0.1$  and the balance between heterogeneous selection and kin competition is characterized by  $NV_S = 0.1$ . For these parameters, a bistable outcome is predicted. The low ESMR is 0, the high ESMR is shown as a plain line, and the barrier separating these outcomes is shown as a dashed line.

in equation (7), because in equation (7) (scenario 1), we used the simplification  $\text{Cov}[S_a, D] = -\text{Cov}[S_A, D]$ , a relationship that no longer applies in scenario 2. In scenario 2, interestingly, a third term emerges (compare eqs. 10 and 7). This term represents the impact of differences in habitat quality on the evolution of the modifier. Interestingly, this term did not appear previously before because of the perfect symmetry between  $s_{i,a}$  and  $s_{i,A}$ , which ensured there were no differences in habitat quality. In the present scenario, however, some demes are better than others on average and this affects the evolution of the modifier. This demographic phenomenon appears in our population genetics model because demes with higher quality habitats contribute more to the next generation (hard selection). We found equilibrium expressions for the relevant spatial moments and plugged them into equation (10), and using (8) we obtain an approximation of the selection gradient on the modifier  $s_M$  (see section “Scenario 2: imperfect trade-off and selection is balanced” in Appendix S3):

$$s_M = \frac{\Delta m}{m} \left( -\frac{(1-\rho)(1-\phi)}{2(m(1-\phi)+\phi)} V_S + \frac{(1-m)}{(2-m)N} - \frac{m}{2}(1+\rho)V_S \right). \quad (11)$$

Again, the selection gradient  $s_M$  may be plugged into equation (8) to describe the evolution of the modifier. The final term in (11) reveals that differences in habitat quality emerging when the trade-off is imperfect ( $\rho > -1$ ) selects against migration. This relates to classical studies showing migration is selected against in a spatially heterogeneous, temporally constant habitat (Hastings 1983; Holt 1985). This effect is generated because there

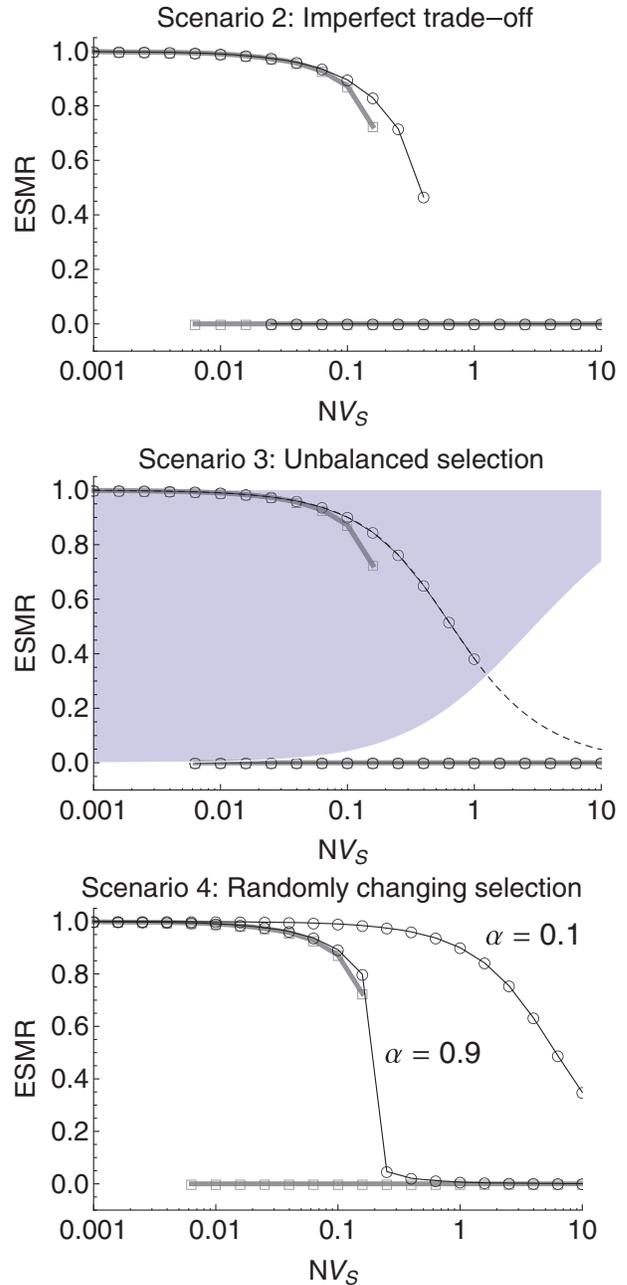
are more individuals in high-quality demes after reproduction, which makes migration not advantageous on average. Interestingly, an imperfect trade-off also means lower local adaptation (eq. 4), which lowers the force selecting against migration (first term in eq. 11). Because these two effects are antagonistic, it is not immediately obvious how an imperfect trade-off affects the evolutionary outcome. Numerical simulations using the selection gradient (11), however, show that a major effect of increasing  $\rho$  is to stabilize the evolution toward the higher evolutionary equilibrium (Fig. 6).

**SCENARIO 3: PERFECT TRADE-OFF, SELECTION IS NOT BALANCED**

Here we investigate a scenario in which the trade-off is perfect ( $\rho = -1$ ) but where allele  $A$  is better than allele  $a$  at the scale of the metapopulation ( $\delta_s > 0$ ). Such scenario corresponds, for example, to a metapopulation where in half of the demes  $W_a = 0.9$  and  $W_A = 1.2$ , and in the other half of the demes  $W_a = 1.1$  and  $W_A = 1$  (in which case  $\delta_s = 0.1$ , allele  $A$  is better on average). In this scenario 3, the equilibrium frequency of the allele  $A$  in the metapopulation (i.e.,  $p_A^*$ ) converges to a value greater than  $1/2$ . As in previous scenarios, an equation for the evolution of the modifier as a function of the spatial moments (analogous to eqs. (7) and (10) above) can be derived. Plugging in the equilibrium expressions for the moments, we found the selection gradient on the modifier is (see section “Scenario 3: perfect trade-off and asymmetric selection” in Appendix S3):

$$s_M = \frac{\Delta m}{m} \left( -\frac{4p_A^*(1-p_A^*)(1-\phi)}{m(1-\phi)+\phi} V_S + \frac{1-m}{(2-m)N} - mV_S(1-2p_A^*)^2 \right), \tag{12}$$

where  $p_A^* \approx \frac{2(2-m)(1-m)V_S+m\delta_s}{4(2-m)(1-m)V_S+m\delta_s^2}$ . Unbalanced selection only acts through its effect on  $p_A^*$ , the equilibrium frequency of  $A$  in the metapopulation. At this migration-selection equilibrium, some demes (those where  $A$  is fitter) are of higher quality on average. As in scenario 2, this heterogeneity in habitat quality selects against migration. But, unbalanced selection reduces local adaptation (see eq. 4), which indirectly selects for higher migration. These two effects counteract each other, but numerical simulations using the gradient (12) show that the effect of  $\delta_s$  on the reduction of local adaptation overwhelms the effect on habitat quality. Consequently, the range of parameters under which the evolutionary bistability is maintained and a high level of migration can evolve is greater when  $\delta_s > 0$  (Fig. 6). Another important effect of unbalanced selection is to reduce the possibility to maintain polymorphism on the selected locus. As soon as the migration rate exceeds the threshold value expressed in equation (2), the polymorphism cannot be maintained and local adaptation vanishes. In this case the first term in (12) disappears and migration evolves toward



**Figure 6.** The ESMR as a function of  $NV_S$  for the recombination rate  $\phi = 0.01$  in three more complex scenarios of environmental variability (scenarios 2, 3, and 4) is compared with the ESMR found in the simpler scenario 1. The ESMR is found by numerical solution of the selection gradients. The ESMR for scenario 1 is shown with gray squares and gray lines, whereas the ESMR for alternative scenarios are shown with black circles and black lines. Top panel: scenario 2, where the trade-off is imperfect ( $\rho = 0.5$ ). Middle panel: scenario 3, where selection is not balanced at the scale of the metapopulation ( $\delta_s = 0.1$ ). The zone in which polymorphism is lost is shown in gray. The theoretical ESMR when polymorphism is lost is shown in dashed line (eq. 13). Bottom panel: scenario 4, where the environment changes in a random autocorrelated fashion with autocorrelation parameter  $\alpha = 0.9$  (left curve) and  $0.1$  (right curve).

an intermediate value given by the balance between kin competition and spatial heterogeneity in habitat quality (see section “Scenario 3: perfect trade-off and asymmetric selection” in Appendix S3):

$$m^* = \frac{2}{1 + 2NV_S + \sqrt{1 + 4N^2V_S^2}}. \quad (13)$$

This expression illustrates again that the evolution of migration is governed by the product  $NV_S$ .

#### SCENARIO 4: CHANGING ENVIRONMENTS

In a previous study, we showed that local adaptation may select for high levels of migration when the environment is changing periodically (Blanquart and Gandon 2011). The present framework extends this analysis and yields the selection gradient on the modifier of migration for any shape of environmental change, in the simplified scenario where  $V[S_a] = V[S_A] = V_S$ ,  $\rho = -1$ , and  $\delta_s = 0$ . In section “Scenario 4: changing selective pressure” in Appendix S3, we show that the (temporally variable) covariance between the local selection coefficient and linkage disequilibrium equilibrates to:

$$\text{Cov}[S_{A,t}, D_t] \approx -2\Delta m p_A(1 - p_A)p_M(1 - p_M) \left[ \sum_{\tau=1}^{\infty} [(1 - \phi)(1 - m)]^{\tau-1} \left( \sum_{j=0}^{\infty} (1 - m)^j \text{Cov}[S_{A,t-\tau-j}, S_{A,t}] \right) \right]. \quad (14)$$

More explicit scenarios of environmental change can be considered after plugging in the appropriate expression  $\text{Cov}[S_{A,t-\tau-j}, S_{A,t}]$  and simplifying the sums. In contrast to what happens in a constant environment (see eq. 7), the above covariance is not always negative in a changing environment. In particular if the environment changes periodically, the above covariance can be positive for some intermediate values of migration, which selects for higher migration rates (Blanquart and Gandon 2011). In fact, simplifying expression (14) for the special case of a sine wave function, plugging the resulting covariance in equation (7) and neglecting the term corresponding to genetic drift (second term in eq. 7) gives a selection gradient proportional to that found in Blanquart and Gandon (2011). However, some other scenarios of temporal change in the environment will not favor the evolution of higher migration rates. For example, consider the case in which selection fluctuates in a random autocorrelated way, such that selection from one time step to the next follows an autoregressive model  $s_{i,A,t+1} = \alpha s_{i,A,t} + (1 - \alpha)\beta$ , where  $\beta$  is drawn in a random distribution. This scenario results in a temporal autocovariance  $\text{Cov}[S_{A,t-\tau-j}, S_{A,t}] \sim e^{-\alpha(\tau+j)}$ , where  $\alpha$  quantifies the level of temporal correlation. Because these covariances are all positive, the covariance between local selective pressure and the linkage disequilibrium will be positive as well, and as a consequence this

type of temporal variation will select against migration (Levin et al. 1984).

Because the population structure at the modifier locus is unaffected by the selection pressure at the nearby locus, equation (14) can be used with the equation for the evolution of the modifier (eq. 7) to find the selection gradient under spatiotemporal variation and genetic drift in any scenario of changing environment. The selection gradient obtained in this way may be solved numerically to find the ESMR. This numerical solution reveals that a random autocorrelated change in the environment radically changes the evolutionary outcome for migration (Fig. 6). In particular, the evolutionary bistability vanishes as soon as the temporal autocorrelation is below a threshold that depends on recombination. The loss of bistability is due to the effect of temporal variability on local adaptation and yields a single ESMR even with very strong levels of temporal autocorrelation (the bistability disappears when  $\alpha < 0.84$ , see Supporting Information). In general temporal fluctuations cause a reduction in local adaptation (but periodic fluctuations can have the opposite effects, Blanquart and Gandon 2011), which allows evolution of a higher migration rate, especially in a weakly correlated environment (Fig. 6).

### Discussion

Here we study the evolution of migration in ecologically complex situations and show how kin competition as well as spatial and temporal variability of the environment interact to shape the evolution of migration. We use a multilocus framework to model the evolution of a modifier of migration partially linked to a locus under selection. We predict how migration evolves under direct selection due to kin competition and indirect selection due to selection at a nearby locus. Our framework allows relaxing common assumptions regarding environmental variability, and in particular to investigate how the strength of the trade-off, the difference in average fitness of the genotypes, and temporal variability of selection affect the evolution of migration.

#### MAINTENANCE OF POLYMORPHISM AND LOCAL ADAPTATION

We first describe the dynamics of adaptation at the selected locus and show that the excess of spatial structure caused by spatially heterogeneous selection relative to drift alone (i.e.,  $F_{ST}^{sel} - F_{ST}^{neut}$ ) is proportional to local adaptation, which links naturally these two commonly used measures of population differentiation. Ideally, this relationship could be used to infer the migration rate, local population size, and heterogeneity in selection, using local adaptation and  $F_{ST}^{neut} - F_{ST}^{sel}$  data. It would be interesting to test this idea using studies that connect molecular variation to patterns of variation in fitness (e.g., Fournier-Level et al. 2011). We also derive a new condition for the maintenance of

polymorphism in a heterogeneous environment with general scenarios of spatial heterogeneity in selection. We show that polymorphism is most easily maintained when spatial variation in selection is large, average fitness differences between alleles are small, the trade-off in the performance of the two alleles across environments is strong, and when migration is low. These results are in line with those of many previous studies that use a variety of approaches to study adaptation in heterogeneous environments (Pollack 1966; Nagylaki 1980; Tachida and Iizuka 1991; Gavrillets and Gibson 2002; Whitlock and Gomulkiewicz 2005; Yeaman and Otto 2011). Our framework is based on the assumption that there are a large number of demes, which allows neglecting stochasticity at the level of the whole metapopulation. Incorporating such stochastic effects is expected to reduce the range of parameters under which polymorphism is maintained (Yeaman and Otto 2011) and would be an interesting extension of this model.

## EVOLUTION OF MIGRATION

Next we investigate the evolution of the modifier of migration and reveal several novel results regarding the evolution of dispersal in heterogeneous environments. First, we fully analyze a simple and symmetrical ecological scenario, showing that the evolutionary outcome mainly depends on the value of  $NV_S$ , the product of local population size and the spatial variance in selection (which quantifies the strength of local adaptation vs. the strength of drift), relative to the recombination rate, which determines how strongly local adaptation impacts the modifier locus. Specifically, at low  $NV_S$ , a high dispersal rate evolves, whereas at high  $NV_S$ , a low dispersal rate evolves. At intermediate  $NV_S$ , we observe a bistable outcome in which either a low or a high migration may evolve depending on initial conditions. In a second step, we relax the assumptions regarding environmental heterogeneity. Under more general scenarios, heterogeneous environments result in heterogeneous selective pressures, but also heterogeneous habitat quality and population density (in our setting, differences in density emerge just before migration because we consider a “hard selection” model, such that the contributions to the next generation differ across demes). As a consequence, local adaptation is generally weaker than in the simple and symmetrical scenario, which yields selection for higher migration levels. Predictions from the symmetrical scenario (scenario 1) may be qualitatively altered when one allele is favored over the other at the scale of the metapopulation. In this case polymorphism may be lost and migration evolves to an intermediate, stable value under the balance between kin selection and variability in habitat quality. Predictions are also qualitatively altered when the selection coefficient fluctuates randomly. In this case local adaptation is weaker, the bistability disappears, and an intermediate value of migration evolves. These results demonstrate that relaxing common

assumptions regarding environmental variability may radically alter evolutionary predictions on dispersal evolution.

Another important result of this study regards the limitations of the ESS concept in the presence of genetic drift. Indeed, with genetic drift, the migration rate does not remain exactly at its equilibrium value, but wanders around it because of the random fixation of deleterious alleles. Interestingly, this phenomenon (drift load) may modify the endpoint of evolution in the presence of evolutionary bistability. Indeed, the population may cross the boundary between the basins of attraction and remain in the high migration zone, while a deterministic analysis would have predicted it to be stuck at a zero migration rate (see Fig. 5). The new framework proposed by Lehmann (2012) to describe the quasiequilibrium distribution of phenotypic variation resulting from the balance between selection and drift may be extremely valuable to study more quantitatively such situations.

The present analysis relies on a very specific life cycle in which all populations are regulated to a constant level at the end of each generation, and after migration (hard selection). Alternatively, one could imagine that populations are regulated before migration, in which case individuals compete within deme but not between demes (soft selection). Soft selection would have two consequences: first, it would facilitate the maintenance of polymorphism (Christiansen 1975), which should reinforce local adaptation and thus select against migration. However, under soft selection the demographic effects would disappear, which would favor more migration. It is not clear how these two effects average out. It is important to note, however, that our results are qualitatively similar to the ones obtained with soft selection models (Billiard and Lenormand 2005; Blanquart and Gandon 2011). Yet, some effects, like the demographic effect revealed with scenarios 2 and 3 appear only under the hard selection regime. More generally, and beyond the dichotomy between hard and soft selection (Débarre and Gandon 2011), it is important to take explicitly into account the details of the life cycle to evaluate correctly the selection acting on modifiers of migration.

Billiard and Lenormand (2005) obtained very similar results using a different approach. One minor difference between their results and ours is that they found that the lower equilibrium of the ESMR is small but higher than zero, while we found that strict philopatry is evolutionary stable. Our simulations indeed suggest the existence of a positive low ESMR, which is not captured by our high-migration approximation. Second, they suggest that local adaptation at the selected locus amplifies population structure at the modifier locus when both loci are tightly linked, leading to the evolution of high dispersal rates when recombination is small. We found no evidence of such effect in our analysis and in our simulations. To investigate further whether this discrepancy was due to differences in the assumptions of their model, we

used our individual based simulations to analyze a case with two populations only and a soft selection life cycle. Although we used the same set of parameters as in their Figure 3, we did not observe the evolution of high dispersal rates when recombination was small. We found that low dispersal rates evolve when local population size is high enough ( $N \geq 100$ ), as predicted by our analysis. Interestingly, we found that small local population sizes reinforce the bistability, because when the initial dispersal rate is high polymorphism at the selected locus does not persist very long (even with a relatively large mutation rate  $\mu = 10^{-4}$ ), leading to the evolution of high dispersal rate under the action of kin competition alone. This observation confirms the importance of determining the conditions for the maintenance of polymorphism at the selected locus before deriving evolutionary predictions for the evolution of dispersal.

Our theoretical predictions could be useful in several natural and experimental settings. For example, the metapopulation concept has been extensively used to understand the demographic and evolutionary dynamics of Glanville fritillary butterfly, which lives in a fragmented landscape with hundreds of relatively independent patches of suitable habitat (Hanski 1998). Interestingly, the gene coding for the phosphoglucose isomerase (Pgi) is associated with variation in the propensity to disperse (Haag et al. 2005). Moreover, Pgi has pleiotropic consequences on several fitness components. In particular, the growth rate of small patches positively correlated with the frequency of high-dispersal genotype, and conversely the growth rate of large patches positively correlated with the frequency of the low-dispersal genotypes, suggesting that variation in Pgi is associated with local adaptation to patch size (Hanski and Saccheri 2006). In this example the local adaptation locus may be closely linked with the dispersal modifier. More generally, the ability to disperse is associated with multiple life-history traits (dispersal syndromes), so it is likely that loci controlling the propensity to disperse also control local adaptation to some environmental factor. Finally, other promising perspectives to test predictions on the evolution of migration are offered by some new experimental systems using microbes (e.g., bacterial strains differing in their ability to disperse used in Taylor and Buckling 2010).

To conclude, the novel framework we develop in this study, based on the description of a metapopulation using spatial moments and a moment closure approximation, allows deriving relatively simple analytical results for models with spatial structure, multilocus genetics, complex spatial and temporal environmental variability, and genetic drift. This framework is very close to that developed by Roze and Rousset (2008) except that we consider heterogeneous environments. Beyond the specific question of the evolution of migration, this framework may be used to address many other questions on life-history evolution and adaptation in heterogeneous environments.

## ACKNOWLEDGMENTS

We thank I. Olivieri, O. Ronce, D. Roze, S. Billiard, and F. Rousset for very stimulating discussions on this project, A. Agrawal and two anonymous reviewers for helpful suggestions, and G. Boaglio for his help with the individual-based simulations. Our work was funded by the Centre National de la Recherche Scientifique (CNRS), the grant 07 JCJC 0128 EPICE and European Research Council Starting Grant 243054 EVOLEPID to SG, and by a PhD fellowship of French Ministère de la Recherche to FB.

## DATA ARCHIVING

The doi for our data is 10.5061/dryad.k257g.

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Associate Editor: A. Agrawal

### Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

- Appendix S1.** Evolution of the variables in one deme through the life cycle.
- Appendix S2.** Scaling up to the metapopulation.
- Appendix S3.** Dynamics of the metapopulation.
- Appendix S4.** Measuring differentiation in populations.
- Appendix S5.** Details of evolutionary simulations.