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Evolution of Migration in a Periodically Changing Environment

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abstract: The ability to migrate can evolve in response to various forces. In particular, when selection is heterogeneous in space but constant in time, local adaptation induces a fitness cost on immigrants and selects against migration. The evolutionary outcome, however, is less clear when selection also varies temporally. Here, we present a two-locus model analyzing the effects of spatial and temporal variability in selection on the evolution of migration. The first locus is under temporally varying selection (various periodic functions are considered, but a general nonparametric framework is used), and the second locus is a modifier controlling migration ability. First, we study the dynamics of local adaptation and derive the migration rate that maximizes local adaptation as a function of the speed and geometry of the fluctuations in the environment. Second, we derive an analytical expression for the evolutionarily stable migration rate. When there is no cost of migration, we show that higher migration rates are favored when selection changes fast. When migration is costly, however, the evolutionarily stable migration rate is maximal for an intermediate speed of the variation of selection. This model may help in understanding the evolution of migration in a broad range of scenarios and, in particular, in host-parasite systems, where selection is thought to vary quickly in both space and time.

Keywords: migration, local adaptation, fluctuating selection, spatial heterogeneity, metapopulation.

Introduction

Migration has profound consequences on the demography and evolution of species. Migration influences the long-term persistence of populations (Roff 1974) and the coexistence of species (Comins et al. 1980). Migration also shapes the genetic structure of populations across space by increasing within-population diversity compared to between-population diversity (Wright 1969); for instance, this can impede local adaptation (Lenormand 2002) and influence the evolution of speciation (reviewed in Barton 2001).

The ability to disperse is typically variable and heritable (Roff and Fairbairn 2001). In plants, for example, seed size affects the propensity to disperse and is genetically variable (Roff 1992). In *Drosophila*, a trait such as locomotor activity, which is linked with migration behavior, has a high heritability (Connolly 1966). It has also been shown in a butterfly species that newly established populations present a higher frequency of a specific allele of a gene involved in metabolism (Haag et al. 2005); these populations also have a higher flight metabolic rate, which suggests that variation at this locus directly controls the propensity to disperse.

Various factors may affect the evolution of migration. On the one hand, dispersing away from one's natal patch is often risky and consequently often has costs. We distinguish between different costs of migration. First, higher migration ability may come with a fecundity cost if it requires, for instance, the development of specific dispersing structures. For example, in the sand cricket, the mass of flight muscles negatively correlates with fecundity (Roff and Gelinas 2003). Second, on migration, only a fraction of individuals may successfully settle in a new deme. This viability cost of migrants may occur, for instance, if dispersers are unlikely to land in a suitable environment because of habitat fragmentation (Cheptou et al. 2008) or because of local adaptation. On the other hand, several factors positively select for migration despite the above-mentioned costs: local extinction in metapopulation models (Comins et al. 1980; Gandon and Michalakis 1999), avoidance of kin competition (Hamilton and May 1977; Taylor 1988), and avoidance of inbreeding depression (Roze and Rousset 2005, 2009).

The recognition of the multiplicity of forces acting on the evolution of migration has been pointed out before (Clobert et al. 2001; Ronce 2007). However, the magnitude of these factors, their importance in the wild, and the interactions between them are not well understood. This

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is probably because of the increased level of complexity of models that try to combine these multiple factors. For example, a full understanding of the effect of local adaptation and of inbreeding depression on the evolution of migration requires a genetically explicit model allowing multilocus genetics. This is because other loci are responsible for the emergence of indirect benefits (avoidance of inbreeding depression) and costs (local adaptation) of migration. Very few studies, however, examine the evolution of migration in multilocus models (Balkau and Feldman 1973; Billiard and Lenormand 2005; Roze and Rousset 2005, 2009).

Another major source of complexity emerges from the attempt to combine the effects of both spatial and temporal variation in the environment. In the absence of temporal variation, gene flow erodes the level of local adaptation (Lenormand 2002), and this selects against migration (Balkau and Feldman 1973). When selection fluctuates in time, however, migration can increase the level of local adaptation (Gandon 2002). Besides, the combination of spatial and temporal variation may also select for migration because of bet hedging (Kuno 1981; Venable and Brown 1988). While spatial and temporal variations in the environment seem crucial for the evolution of migration, most studies rely on numerical explorations of these models (Venable and Brown 1988; McPeek and Holt 1992; Paradis 1998).

Gillespie's (1981) study is, to our knowledge, the only study examining the evolution of migration in a genetically explicit model where selection fluctuates in space and time. This model considers the fate of a modifier allele of migration on a locus partially linked with a second locus under selection. The fitnesses of each of the two alleles at the selected locus are assigned independently in each deme and in each generation. Hence, the fitnesses of each of these two alleles vary across demes and across time. Gillespie performed simulations of this system, showing that the temporal change of selection favors migration, while the spatial heterogeneity selects against migration. Thus, migration may evolve in a temporally changing environment, provided the spatial heterogeneity of selection is not too high. In this model, however, the link between the level of local adaptation and the evolution of migration remains unclear. This is partly because of Gillespie's underlying assumptions regarding the temporal change of selection. The fitnesses of each allele are drawn independently every generation, meaning that selection changes fast and there is no temporal autocorrelation in selection.

Here we analyze a multilocus model of migration evolution in a periodically fluctuating and spatially heterogeneous environment. We first derive a general expression for the level of local adaptation in a fluctuating environment as a function of migration. We model changing selection in a nonparametric way, using Fourier series, which allows us to study any periodically fluctuating selection pressure. We show that local adaptation is maximized for an intermediate level of migration. Then we study the evolution of migration and show that, in spite of local adaptation and other costs of migration, migration can evolve in a changing environment. We derive an analytical expression for the evolutionarily stable migration rate (ESMR) in a simple scenario of environmental change, and we show how the ESMR depends on the speed of environmental change and the level of recombination. This expression is shown to accurately describe the evolutionary outcome for other scenarios of environmental fluctuations.

The Model

We consider a metapopulation constituted by a large number of demes, in each of which live a large number of haploid individuals. We thus neglect the stochastic effects of drift on the evolution of migration through kin competition. Each individual's genome is described as two genes on a single chromosome. The first locus is under fluctuating selection. For instance, this gene can control the immune response to a parasite. Two alleles of the gene are present, a and A. A modifier gene is present on the second locus; it controls the ability of the individual to disperse. For instance, this gene can control the length of the wing on a fly or the size of a seed. This gene has two alleles, m and M; M is the allele with the higher probability to disperse. Because the individuals are haploid, there are four different genotypes: am, aM, Am, and AM. We can describe the system completely as four genotype frequencies. In the following, we describe the change of these frequencies through the different steps of the life cycle.

Selection

Selection for fecundity on locus 1 is changing in time. The alleles A and a undergo opposite selection. We let $s_i(t)$ equal the value of the selection coefficient on allele A at time t in deme i (the selection coefficient on allele a at time t is thus $-s_i(t)$). We assume that each individual produces a large number of progeny; this number also depends on the value of selection (well-adapted individuals produce more offspring).

Here we assume that the change of selection through time is any periodic function. Selection is also heterogeneous in space. The selection function captures the effect of temporally variable selection imposed by some abiotic or biotic factors in the environment. Locus 1 under selection may, for example, be involved in immune defense and has to evolve rapidly to track the changes in the parasites' genotypes. Adults who will be less affected by par-

asitism, that is, those who match more closely the selection pressure, will produce more offspring. On the modifier locus, we further assume that the M allele carries a cost c_f reducing fecundity (only the individuals carrying the M allele will pay this cost). After the production of a large number of juveniles, adults die, and the population in each deme is regulated before migration, as in soft selection (Christiansen 1975). After regulation and just before migration, all the demes are thus assumed to have the same number of juveniles.

Migration

We assume that migration follows the rule of an island model, with no isolation by distance. The juveniles migrate. Individuals bearing the m and M alleles have a probability μ_m and $\mu_M = \mu_m + \Delta\mu$ of migrating, respectively, with $\Delta\mu > 0$. Migrants settle in a randomly chosen deme. Only a fraction $1 - c_v$ of the migrants (where c_v is the viability cost of migration) will successfully settle in a new deme, because migrants do not always reach a favorable habitat, for example (Cheptou et al. 2008).

Sex and Recombination

After migration, the haploid individuals engage in sexual reproduction, and their chromosomes recombine with a probability ψ. These events do not change allele frequencies, but the linkage disequilibrium decays because of recombination.

Overview of the Analysis

We combine the equations describing the different steps of the life cycle to get the exact change of genotype frequencies over a life cycle (app. A in the online edition of the *American Naturalist*). To simplify the analysis, it is convenient to change the variables and describe our system in terms of $\delta_{iA}(t)$, the departure in deme i of the frequency of allele A from 1/2 (1/2 is the average frequency of A in the population); $\delta_{iM}(t)$, the departure in deme i of the frequency of allele M from the average frequency of M in the metapopulation p_M; and $D_i(t)$, the linkage disequilibrium between the two loci in deme i. The dynamic of local adaptation will be calculated from the dynamics of $\delta_{iA}(t)$, while the evolution of the frequency of the modifier in the metapopulation will simply be obtained from the dynamic of $\delta_{iM}(t)$ averaged over the metapopulation (over all demes i). In the following, we will drop the argument t for clarity.

For analytical tractability, we make the following assumptions: (i) selection on locus 1 is weak, (ii) the modifier of migration has a small effect, (iii) the fecundity and migrant viability costs are both weak, and (iv) the fluctuations of selection are assumed to be unsynchronized. See appendix A for details on the approximations and the equations describing the evolution of the system. We will test later the effects of violating these assumptions with simulations. The table of notations (table 1) shows all the variables and parameters we use.

We first study the effects of the geometry of fluctuations in selection and the effects of migration on the dynamics of local adaptation. Then, in a second step, we analyze the fate of a modifier allele increasing the level of migration. We derive an expression for the change in the frequency of M over the whole metapopulation, which yields the ESMR.

Results

Evolution of Local Adaptation

Over one generation, to the first order, the frequency of allele A at locus 1 changes as

$$\delta_{iA}(t+1) - \delta_{iA}(t) = \underbrace{-\mu_m \delta_{iA}(t)}_{\text{migration}} + \underbrace{(1-\mu_m)\frac{1}{2}s_i(t)}_{\text{selection}}. \quad (1)$$

The first term in the above equation expresses the fact that migration reduces spatial differentiation at the selected locus (i.e., reduces δ_{iA}). The second term refers to the action of natural selection and shows that genotype frequencies track the change of the environment. For the sake of generality, we use a Fourier series (i.e., a sum of simple oscillating functions) to characterize the fluctuation of selection (see app. B in the online edition of the *American Naturalist*):

$$s_i(t) = \sum_{k=1}^{\infty} f_i(k, t), \quad (2)$$

where

$$f_i(k, t) = s_k \sin(\beta_k t + \theta_k - \tau_i),$$

where $\beta_k = k(2\pi/T) = (2\pi/T_k)$ is the frequency of the kth component of the sum, τ_i is the phase difference of the selection function in deme i, and s_k and θ_k are parameters that depend on the intensity and shape of selection, respectively. The decomposition in a Fourier series allows us to consider any shape of fluctuating selection. We use equation (2) to solve the recurrence equation (1) (app. B), which yields

$$\delta_{iA}(t) = \sum_{k=1}^{\infty} g(k, t), \quad (3)$$

where $g(k, t) = \alpha_k \sin(\beta_k t + \theta_k - \tau_i - \sigma_{A,k})$. In other words, for each function f_i there is a corresponding func-

Table 1: Table of notations

Symbol	Definition
μ_M, μ_m	Migration rate of individuals with M and m allele, respectively
$\Delta\mu = \mu_M - \mu_m$	Effect of the modifier of migration
ψ	Recombination rate
$s_{\max}$	Amplitude of selection fluctuations (on locus 1)
β	Frequency of selection fluctuations (on locus 1)
$T = 2\pi/\beta$	Period of selection fluctuations (on locus 1)
c_f, c_v	Fecundity cost of migration and cost on the viability of migrants
s_{cost}	Direct selection on the M allele resulting from the costs c_f and c_v
τ_i	Phase shift of selection (on locus 1) in deme i
X_{ij}	Frequency of genotype j in deme i
$\delta_{iA}(t)$	Departure of the frequency of allele A in deme i from 1/2
$a_{\max}$, σ_A	Amplitude of the fluctuations of δ_{iA} and phase difference with selection
$\delta^S_{iA}(t)$	Departure of the frequency of allele A in deme i from 1/2 after selection
$a^S_{\max}$, σ^S_A	Amplitude and phase difference with selection of the fluctuations of δ^S_{iA}
$\overline{\Delta}$, $\overline{\Delta^S}$	Average local adaptation before and after selection
δ_{iM}	Departure of the frequency of allele M in deme i from p_M
p_A, p_M	Average frequency of A and M in the metapopulation
D_i	Linkage disequilibrium in deme i
$D_{\max}$, σ_D	Amplitude and phase difference with selection of the fluctuations of linkage disequilibrium
σ^*	Phase difference between the fluctuations of linkage disequilibrium at quasi-linkage equilibrium (QLE) and the linkage disequilibrium that does not assume QLE

tion $g(k, t)$ describing the fluctuation of allele frequency. This function fluctuates with an amplitude α_k,

$$\alpha_k = \frac{s_k(1-\mu_m)}{2\sqrt{2(1-\mu_m)[1-\cos(\beta_k)]+\mu_m^2}},$$

and follows the corresponding selection term with a lag $\sigma_{A,k}$:

$$\sigma_{A,k} = \pi + \xi\cos^{-1}\left\{\frac{1-\mu_m-\cos(\beta_k)}{\sqrt{2(1-\mu_m)[1-\cos(\beta_k)]+\mu_m^2}}\right\},$$

where $\xi = +1$ if $T_k = (2\pi/\beta_k) < 2$ and $\xi = -1$ if $T_k > 2$. The lags $\sigma_{A,k}$ measure how close the population follows the changing selective pressure and thus provide a measure of the level of adaptation to local environmental conditions. Under our assumptions (i.e., many demes under unsynchronized fluctuations in selection), the arithmetic mean fitness averaged over the metapopulation is the arithmetic mean fitness of one population averaged over one period of the fluctuation of selection, which is (using eq. [3])

$$\overline{W} = 1 + \frac{1}{T}\int_{t=0}^{T} 2s_i(t)\delta_{iA}(t)dt = 1 + \sum_{k=1}^{\infty} s_k\alpha_k\cos(\alpha_{A,k}). \quad (4)$$

We define local adaptation at the scale of a metapopulation as the difference between the mean fitness of populations in their native environment ("at home"), $\overline{W}$, and the mean fitness of populations when these populations are transplanted to another deme at random ("away"). Under the assumptions of our model, the latter is always equal to 1, which yields the following expression for average local adaptation:

$$\overline{\Delta} = \overline{W} - 1 = \sum_{k=1}^{\infty} s_k\alpha_k\cos(\sigma_{A,k}). \quad (5a)$$

Note that the alternate definition, where local adaptation is measured as the difference between the mean fitness of sympatric and allopatric individuals (local vs. foreign; Kawecki and Ebert 2004), yields the same average value of local adaptation (Gandon and Nuismer 2009). Local adaptation may also be calculated just before migration (i.e., just after selection). The allele frequency after selection, $\delta^S_{i,A}(t)$, is given by

$$\delta_{i,A}(t) + \frac{1}{2}s_i(t).$$

In appendix B, we show that the average level of local adaptation after selection is

$$\overline{\Delta^s} = \overline{\Delta} + \frac{1}{2}\sum_{k=1}^{\infty} s_k^2. \quad (5b)$$

Local adaptation is increased by selection and will always be positive after selection (see app. B). Another way to derive the expressions for local adaptation is to recall that local adaptation is the covariance between selection and allele frequency at the selected locus (Gandon and Nuismer 2009). It will be positive if, on average, the frequency of *A* is greater in demes where this allele is selected for. Hence, in a periodically changing environment, local adaptation depends on how closely the allele frequency follows the fluctuations of the environment. These fluctuations are described as a sum of multiple components (i.e., multiple harmonics; see eq. [2]). It is not easy to see how the dynamics of allele frequency (eq. [3]) will look and how much it will lag behind the fluctuations of selection. As a consequence, it is difficult to understand the effect of the shape of the fluctuation of selection on local adaptation (eq. [5]). We explore numerically the effects of various shapes of the fluctuations of selection, ranging from a simple sinusoidal function to other temporal variations (square wave, sawtooth wave; fig. 1). We find that whatever the geometry of the temporal change in selection, local adaptation is maximized for an intermediate rate of migration (approximately the same for the different shapes of selection). The magnitude of local adaptation, however, varies, depending on the shape of selection. In the sum that describes selection (eq. [2]), the first component is the slowest and has the highest amplitude. In other words, we expect the first component to be the biggest contributor to local adaptation, because it is the most important one (in amplitude) and the one that allele frequency will be able to track most easily. For the three selection functions we consider in figure 1, the square wave has the biggest first component, and hence the highest local adaptation, while the sawtooth wave has the smallest first component and the lowest local adaptation. We also find that the difference between the three functions is higher when we consider local adaptation after selection. This is because local adaptation after selection also depends on $(1/2)\sum_{k=1}^{\infty} s_k^2$ (eq. [5b]), which measures the variance over one period of the selection function. The square wave function has the highest variance, so local adaptation is greatly increased by selection, while the sawtooth wave function has the lowest variance and hence local adaptation is only weakly increased by selection. Interestingly, local adaptation before selection (i.e., after migration) can be negative if the migration rate is low, meaning that the populations do not track the fluctuations of selection close enough and, as a consequence, are maladapted. However, local adaptation after selection is always positive under our assumptions (fig. 1; see also app. B). As we will see in the following, this has important consequences for the evolution of migration rate.

Because the behavior of local adaptation as a function of migration is not qualitatively different for the various geometries of selection, in the remainder of the study we will focus on the sine wave function (the first function represented in fig. 1*A*), which is the simplest function that describes the fluctuation in selection:

$$s_i(t) = s_{\max} \sin(\beta t - \tau_i),$$

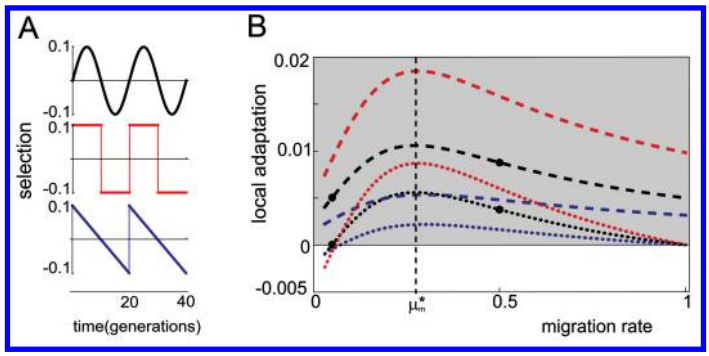

Figure 1: Local adaptation before and after selection for various geometries of the temporal change in selection. *A*, Three fluctuating functions of selection with $s_{max} = 0.1$ and $T = 20$ (*black*, sine wave; *red*, square wave; *blue*, sawtooth wave). *B*, Local adaptation before selection $\overline{\Delta}$ (*dotted lines*) and after selection $\overline{\Delta^s}$ (*dashed lines*) plotted as a function of the migration rate for the three fluctuating functions of selection (shown in *A*). Local adaptation is calculated from equation (5), with the first 100 terms of the Fourier series. The two measures of local adaptation (before and after selection) peak for the same migration rate (*dotted line*, μ_m^*; see eq. [6]). Although $\overline{\Delta^s}$ is always positive, $\overline{\Delta}$ can be negative when migration is low. The points show local adaptation for the two migration rates for which the dynamic of allele frequencies is shown in figure 2.

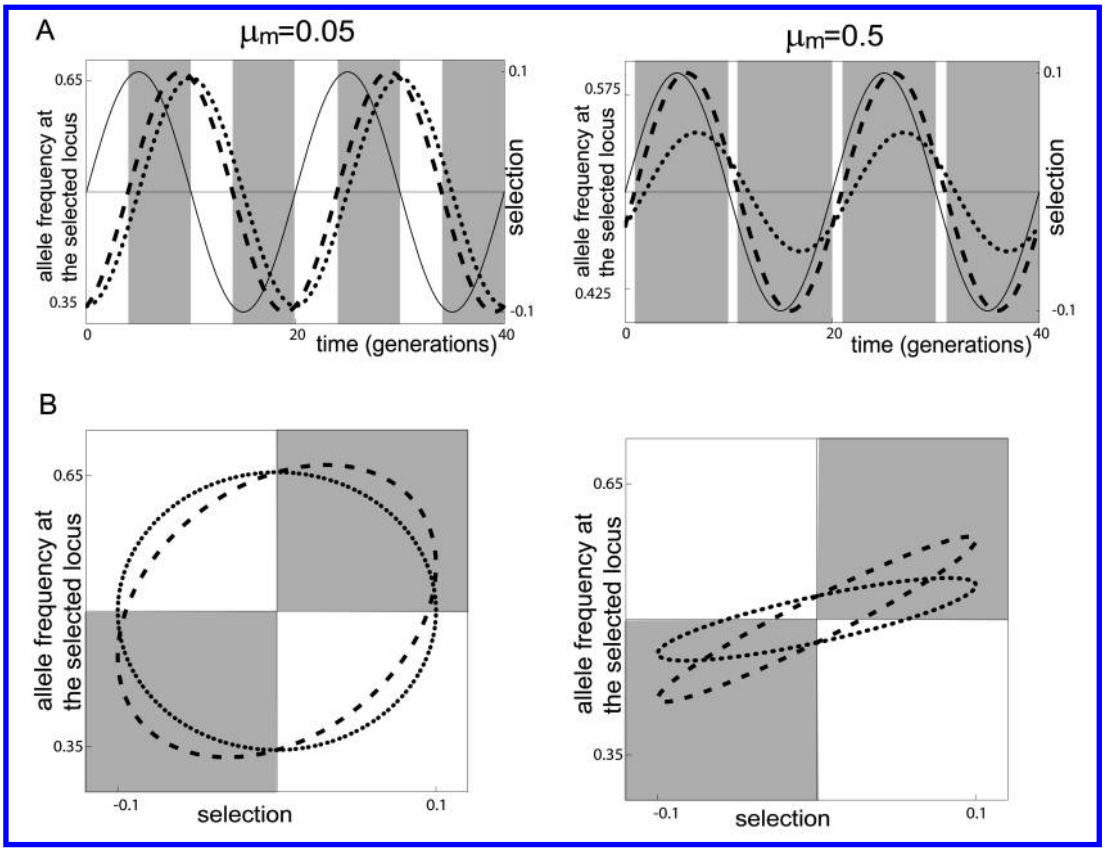

Figure 2: Higher migration rate decreases the lag between selection and allele frequency at the selected locus and decreases the amplitude of the oscillations in allele frequency. *Left column*, $\mu_m = 0.05$; *right column*, $\mu_m = 0.5$. *A*, Selection on the first locus is shown (*solid lines*) together with the allele frequency before (*dotted lines*) and after (*dashed lines*) selection. The allele frequency tracks selection with a lag σ_A and σ_A^S before and after selection, respectively. The period of time during which the population is locally adapted after selection is shown in gray ($\overline{\Delta^S} > 0$). *B*, Parametric plot showing the fluctuations of allele frequency as a function of selection for the same parameter values as above. The gray quadrants are the zones where local adaptation is positive. When migration is high, the population is more often locally adapted because δ_{iA} follows selection with a shorter lag. Note also that migration decreases the amplitude of the fluctuations of allele frequencies. In both cases, $s_{max} = 0.1$ and $T = 20$.

which yields (see app. B for the dynamics of allele frequency after selection)

$$\delta_{iA}(t) = \alpha_{max} \sin(\beta t - \tau_i - \sigma_A),$$

with

$$\alpha_{max} = \frac{s_{max}(1-\mu_m)}{2\sqrt{2(1-\mu_m)[1-\cos(\beta)] + \mu_m^2}},$$

$$\sigma_A = \pi + \xi \cos^{-1}\left\{\frac{1-\mu_m-\cos(\beta)}{\sqrt{2(1-\mu_m)[1-\cos(\beta)] + \mu_m^2}}\right\}.$$

Under this simpler scenario, the average level of local adaptation reduces to (see app. B for the level of local adaptation after selection)

$$\overline{\Delta} = s_{max}\alpha_{max}\cos(\beta\sigma_A).$$

In this simple case, it is possible to analyze the details of the effect of migration on local adaptation via its effect on the fluctuations of allele frequency at the selected locus. Figure 2 shows the dynamics of allele frequency at the selected locus and selection for two migration rates and helps to understand the effect of migration on local adaptation. Migration reduces both the amplitude of oscillations α_{max} and the lag σ_A (fig. 2; see also fig. D1 in the online edition of the *American Naturalist*), and these two effects explain the nonmonotonous effect of migration on local adaptation (fig. 1). When migration is very low, the lag with allele frequency is high ($\sigma_A > \pi/2$), which yields local maladaptation (i.e., $\overline{\Delta} < 0$). Higher levels of migration reduce the lag between allele frequency oscillations and selection, increasing local adaptation. When migration is very high, however, the amplitude of the oscillations of

allele frequency is very low, which leads to very low levels of local adaptation ($\lim_{\mu_m \to 0}(\overline{\Delta}) = 0$). As a consequence, local adaptation is maximized for an intermediate level of migration:

$$\begin{cases} \mu_m^* = 1 - \dfrac{1}{\cos(\beta)[1 - \sin(\beta)]} & \text{if } T = (2\pi/\beta) > 4 \\ \mu_m^* = 1 & \text{otherwise.} \end{cases} \tag{6}$$

The same level of migration maximizes local adaptation after selection.

Evolution of Migration

In the following, we focus on the fate of the migration modifier. The assumptions detailed above allow us to get a simple equation for its change in frequency. In one generation, in deme i, the frequency of modifier allele M changes as follows:

$$\begin{aligned} \delta_{iM}(t+1) - \delta_{iM}(t) = & \underbrace{-\mu_m \delta_{iM}(t)}_{\text{migration}} + (1-\mu_m) 2 s_i(t) D_i(t) \\ & + \mu_m \underbrace{2\overline{s_i(t) D_i(t)}}_{\text{indirect selection}} + p_M(1-p_M) s_{\text{cost}}. \end{aligned} \tag{7}$$

This equation presents some similarities with equation (1). Three forces act on the evolution of the modifier. First, as above (see eq. [1]), migration has a homogenizing effect and pushes the allele frequency toward the metapopulation mean. Second, selection also acts on the modifier. In equation (1), we saw that selection acted directly on locus 1. Here, selection operates indirectly, through the statistical associations between locus 1 and locus 2. These associations are represented by the linkage disequilibrium $D_i(t)$. Indirect selection in deme i is decomposed in a first term representing indirect selection in the philopatric individuals and another term representing indirect selection on the individuals who migrated into deme i (the bar denotes the average over the metapopulation). Last, both costs of migration impose a direct selection on the modifier and always decrease the frequency of allele M. These costs are referred to as s_{cost}, which is always negative and can be approximated as $s_{\text{cost}} = -(c_f + \Delta\mu c_v)$ (see the end of app. A).

Equation (7) represents the change in the frequency of the modifier in one deme; we now have to average equation (7) across all demes to see how the modifier evolves in the metapopulation. At this stage of the derivation, it is important to note that the population size of the demes is not exactly the same before and after migration. Indeed, because the genotypes do not migrate in the same proportion, the number of individuals does not remain constant in each deme (a deme with a frequency of M higher than the average will have a lower density after migration). However, under the assumptions of weak modifier and strong migration, population structure at the M locus is extremely weak, and therefore, the differences in the population size of each deme after migration are negligible (see app. A, "Change of Allele Frequencies and Linkage Disequilibrium"). Hence, in the following, we neglect these variations in densities in our average of the frequency of M at the scale of the metapopulation. This yields the following change in modifier frequency:

$$\delta_M(t+1) - \delta_M(t) = \underbrace{2\overline{s_i(t) D_i(t)}}_{\text{indirect selection}} + p_M(1-p_M) \underbrace{s_{\text{cost}}}_{\substack{\text{direct} \\ \text{selection}}}. \tag{8a}$$

Note that the first term in equation (7) cancels out in equation (8a) because migration has no effect on allele frequency at the scale of the metapopulation. Hence, equation (8a) shows that indirect selection on the modifier depends on the balance between direct and indirect selection. Indirect selection on the modifier depends on $\overline{s_i(t) D_i(t)} = \text{Cov}[s(t), D(t)]$, which is the spatial covariance between selection $s_i(t)$ and $D_i(t)$. Under the assumption that the metapopulation consists of many unsynchronized demes, this covariance across space is also equal to the covariance over time during one period of the fluctuation in selection, which yields

$$\delta_M(t+1) - \delta_M(t) = 2\frac{1}{T}\int_{t=0}^{T} \underbrace{s_i(t) D_i(t) dt}_{\text{indirect selection}} + p_M(1-p_M) \underbrace{s_{\text{cost}}}_{\substack{\text{direct} \\ \text{selection}}}. \tag{8b}$$

In order to determine the sign and strength of selection on the modifier, we need to find an expression for $s_i(t) D_i(t)$. We will now examine the dynamics of the linkage disequilibrium.

Dynamics of Linkage Disequilibrium and Evolutionarily Stable Migration Rate. Under our assumptions, the linkage disequilibrium is generated mainly by migration. The change in linkage disequilibrium over one generation is given by

$$D_i(t+1) = \underbrace{(1-\psi)}_{\text{recombination}} [\underbrace{(1-\mu_m) D_i(t)}_{\text{philopatry}} - \underbrace{\Delta\mu p_M(1-p_M)\delta_{iA}^S(t)}_{\text{migration and selection}}]. \tag{9}$$

Three forces act on the evolution of the linkage disequilibrium. First, the linkage disequilibrium decays because of recombination. Second, philopatry maintains the previous level of association between the two loci. Third, migration also generates a systematic bias on linkage disequilibrium if there is some spatial differentiation on the first locus. For instance, if $\delta_{i,A}^S$ is positive, there is more allele A on average in the focal deme i (recall that $\delta_{i,A}^S$ is the frequency of A taken after selection), and the linkage disequilibrium will decrease (eq. [9]). In this case, migration increases the frequency of both the M allele, because

it is overrepresented among migrants, and the *a* allele, because migration reduces spatial differentiation at the first locus. Consequently, migration will increase the frequency of *aM* genotypes in the focal deme, resulting in a reduction of the linkage disequilibrium. In a spatially heterogeneous but constant environment (Balkau and Feldman 1973), this process alone is expected to lead to negative association between the two loci (negative D_i). In general, the *M* allele is less often associated with the locally adapted allele than is the *m* allele. In other words, in constant environments, migrating individuals are expected to be less adapted to their local habitat than are philopatric ones. This is because migration counteracts the effect of local adaptation, and this is what selects against dispersal in a constant but spatially heterogeneous environment. In a temporally variable environment, linkage disequilibrium fluctuates through time according to equation (9). In the following, we use two different approaches to make explicit the dynamics of linkage disequilibrium and to predict which rate of migration will be selected for.

If linkage disequilibrium has a very fast dynamic compared to the selected allele frequency, we can use a quasi-linkage equilibrium (QLE) approximation. QLE approximation assumes that associations between loci are weak because they are broken down by recombination and that they converge to equilibrium values faster than the allele frequencies. We thus find $D_i^{\mathrm{QLE}}(t)$ by solving equation (9) for the equilibrium value (see app. C in the online edition of the *American Naturalist*):

$$D_i^{\mathrm{QLE}}(t) = -\frac{\Delta\mu(1-\psi)p_M(1-p_M)\delta_{iA}^S(t)}{\psi+(1-\psi)\mu_m}. \qquad (10a)$$

The linkage disequilibrium is equal to a negative constant times $\delta_{iA}^S(t)$. Therefore, being at QLE means that disequilibrium is in antiphase with the frequency of *A* after selection. Hence,

$$\mathrm{Cov}\,[s(t), D(t)] = -\frac{\Delta\mu(1-\psi)p_M(1-p_M)}{\psi+(1-\psi)\mu_m}\underbrace{\{\mathrm{Cov}\,[s(t), \delta_A^S(t)]\}}_{\overline{\Delta^S}}.$$

Remembering that $\mathrm{Cov}\,[s(t), D(t)]$ determines the fate of the modifier allele when there is no cost (see eq. [8b]), we conclude that with the QLE approximation, the fate of the modifier allele is totally determined by $\overline{\Delta^S}$, the level of local adaptation after selection. As pointed out above, local adaptation after selection and before individuals migrate is always positive (see fig. 1; app. B, C). Hence, under the QLE approximation, indirect selection on the modifier is always negative and migration is never selected for. The ESMR is always 0.

However, the picture gets more complicated if the linkage disequilibrium does not evolve faster than the allele frequency at the selected locus. In this case, the QLE approximation might not hold. This will occur in particular if selection changes quickly and/or recombination is low. If so, $\mathrm{Cov}\,[s(t), D(t)]$ does not depend directly on local adaptation. To calculate this, we need to solve the recurrence (eq. [8]). We find (app. C)

$$D_i(t) = D_{\max}\sin\,[\beta t - \tau_i - \underbrace{(\sigma_A^S+\pi)}_{\text{lag of } D_i \text{ at QLE}} - \underbrace{\sigma^*}_{\substack{\text{lag out}\\ \text{of QLE}}}], \qquad (10b)$$

where σ_A^S is the phase difference between selection and allele frequencies at the selected locus after selection and σ^* is the phase difference between the linkage disequilibrium at QLE and the linkage disequilibrium out of QLE (see fig. 3). In other words, σ^* is the delay in the dynamics of linkage disequilibrium caused by the quick change of allele frequency; $D_{\max}$, σ_A^S, and σ^* are given in appendixes B and C and are complicated functions of migration, recombination, and selection period.

We can rewrite equation (10b) as $D_i(t) = D_{\max}\sin\,(\beta t - \tau_i - \sigma_D)$, with $\sigma_D = \sigma_A^S + \pi + \sigma^*$ (fig. D2 in the online edition of the *American Naturalist*). The linkage disequilibrium lags behind selection as the result of two processes. First, there is a lag between selection and allele frequency after selection (eq. [2]). This lag is small because populations are always locally adapted just before migration. Second, there is a lag between allele frequency and the linkage disequilibrium. This lag is π at QLE, meaning that the linkage disequilibrium and the allele frequency are in antiphase ($\sigma_D^{\mathrm{QLE}} = \sigma_A^S + \pi$ because $\sigma^* = 0$). But when we make explicit the dynamic of the linkage disequilibrium, this lag turns out to be greater than π because $\sigma^* > 0$. We will see that this lag in the dynamics of the linkage disequilibrium is crucial in determining the fate of the modifier.

Figure 3 shows the dynamics of linkage disequilibrium as a function of time. The QLE value of the linkage disequilibrium (eq. [10a]) is in antiphase with the oscillations in the allele frequencies. In contrast, the linkage disequilibrium (eq. [10b]) is not in antiphase with δ_{iA}^S but lags behind the QLE value. While QLE assumes that linkage disequilibrium quickly reaches an equilibrium value, this second approach better takes into account the dynamics of creation and generation of the linkage disequilibrium. Figure D2 gives further details on how $D_{\max}$ and σ_D depend on ψ and T.

We now rewrite equation (8). In particular, the first term, $2(1/T)\int_0^T s_i(t)D_i(t)dt$, can be calculated, replacing $D_i(t)$ by $D_{\max}\sin\,(\beta t - \tau_i - \sigma_D)$, using equation (10b). Equation (8) becomes

$$\delta_M(t+1) - \delta_M(t) = s_{\max}D_{\max}\cos\,(\sigma_D) + p_M(1-p_M)s_{\mathrm{cost}}. \qquad (11)$$

This is the main result of our analysis. This equation shows

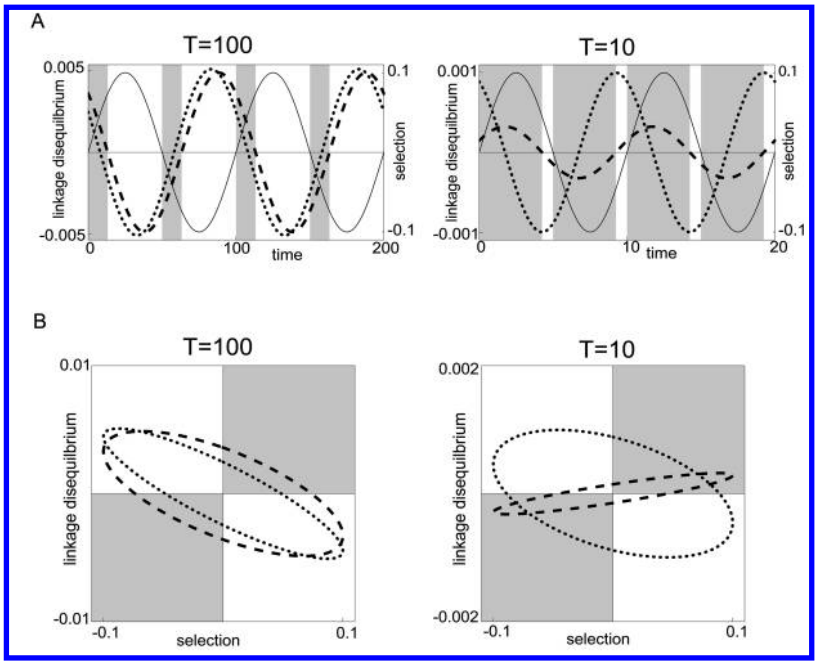

Figure 3: Dynamics of the linkage disequilibrium when the environment changes quickly (*right column*, $T = 10$) and when the environment changes slowly (*left column*, $T = 100$). *A*, Selection on the first locus is shown (*solid lines*) together with the linkage disequilibrium D_i at quasi-linkage equilibrium (QLE; *dotted lines*) and with no QLE (*dashed lines*) as a function of time. When $T = 100$, the dynamics of D_i^{QLE} and D_i are nearly identical. They are almost in antiphase with selection, meaning that the population is well adapted (δ_{iA} is in phase with selection). When $T = 10$, D_i lags behind D_i^{QLE}. The periods of time during which the modifier of migration is selected for ($\mathrm{Cov}[s(t), D(t)] > 0$) are shown in light gray (only for D_i [*dashed line*]). *B*, Parametric plot showing the fluctuations of linkage disequilibrium as a function of selection for the same parameter values as above. The gray quadrants show when the modifier of migration is selected for. The left column shows a case where the modifier does not increase in frequency over one period. In contrast, the right column shows a case where the modifier does increase in frequency over one period. Note that with the QLE assumption, the modifier is selected for during a shorter amount of time than without QLE. $\mu_m = 0.5$, $s_{\max} = 0.1$, $\psi = 0.1$, $\Delta\mu = 0.01$, $p_M = 0.5$.

that in the absence of costs of migration, selection on the modifier depends on the amplitude of the linkage disequilibrium $D_{\max}$ and on the phase difference between the disequilibrium and selection σ_D. The latter determines the sign of selection and can thus be used to find the ESMR. When the fluctuations of selection are not too fast (i.e., $T > 4$), we obtain

$$\mu_{\mathrm{ES}}^{*} = \frac{-2 + \psi + 2(1-\psi)\cos(\beta) + \sqrt{\psi^2 + 2(1-\psi)[1-\cos(2\beta)]}}{2(1-\psi)\cos(\beta)}. \tag{12}$$

Figure 4 shows the influence of the period of cycles and the recombination rate on the above values of ESMR. Higher levels of migration are selected for when the period of oscillations decreases (see fig. 4*A*). In particular, for rapid fluctuations of selection (i.e., $(4/3) < T < 4$), the actual ESMR is $\mu_{\mathrm{ES}}^{*} = 1$. Even faster fluctuations of selection (i.e., $T < (4/3)$) can actually select for low values of migration because these selection regimes can be expressed as slowly fluctuating functions of selection. In any case, these parameter values are probably not very relevant biologically. We thus choose to focus on larger values of T in the following. Note, in particular, that when the oscillations are extremely slow ($T \to \infty$), the ESMR is 0, as in the classical Balkau and Feldman (1973) model. Note also that when recombination increases, lower levels of migration are selected for (fig. 4*B*). This is because recombination decouples the link between the two loci and consequently decreases the lag between linkage disequilibrium and the fluctuations in selection, which decreases the selection for migration (see also Gillespie 1981; Billiard and Lenormand 2005). Last, when there is no recombination, the ESMR is the rate of migration that maximizes local adaptation (fig. 4*A*).

These results greatly contrast with the QLE analysis, where migration is never selected for. At QLE, we neglected the fact that the dynamics of linkage disequilibrium can also be delayed compared to the dynamics of allele frequency. In a quickly varying environment, the QLE as-

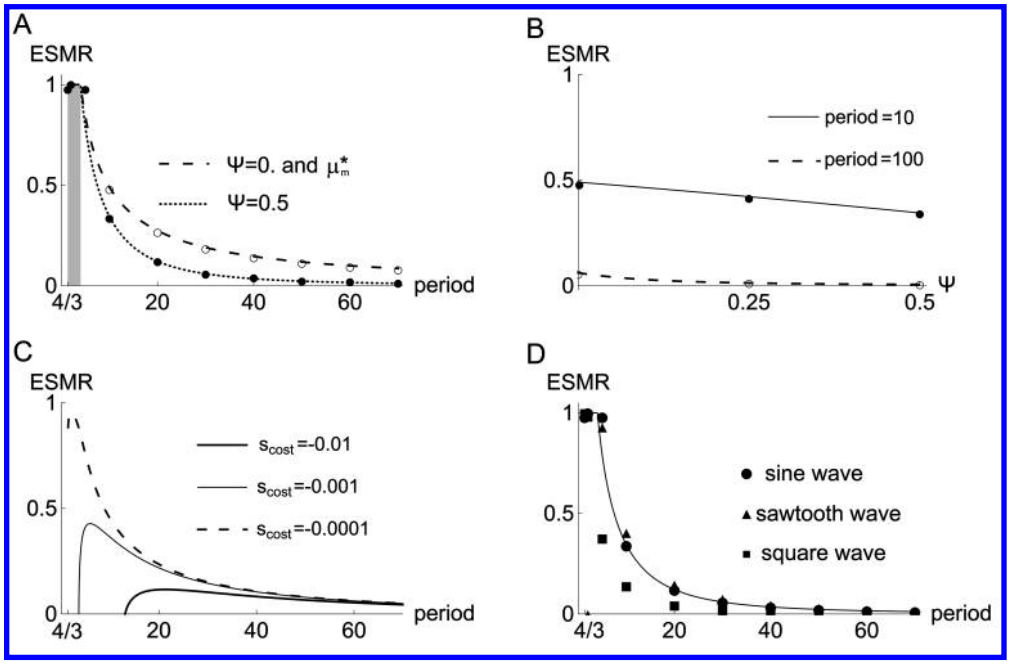

Figure 4: Evolutionarily stable migration rate (ESMR). *A*, ESMR as a function of the period of fluctuations with no costs for $\psi = 0$ (*dashed line*) and $\psi = 0.5$ (*dotted line*). The migration rate maximizing local adaptation (see eq. [6]) is equal to the ESMR for $\psi = 0$ and is thus also shown with the dashed line. The circles show the results of simulations for $\psi = 0$ (*open circles*) and $\psi = 0.5$ (*filled circles*). The gray zone shows when maximal migration is selected for. *B*, ESMR as a function of the recombination rate for $T = 10$ (*solid line, filled circles*) and $T = 100$ (*dashed line, open circles*). The circles show the result of simulations, while the line is the analytical result (eq. [12]). $s_{max} = 0.1$. *C*, ESMR as a function of the period of fluctuations for various costs of migration. The ESMR is obtained by numerical solving of $\delta_M(t+1) - \delta_M(t) = 0$ (see eq. [11]). As the cost increases, migration is not selected for any longer for quick environmental change. When migration is costly, an intermediate period of selection cycles maximizes the ESMR. $s_{max} = 0.5$, $\psi = 0.1$, $\Delta\mu = 0.01$, $p_M = 0.5$. *D*, ESMR for various geometries of selection fluctuations. The solid line is the analytical ESMR (eq. [12]). The circles, triangles, and squares show the results of simulations for a sine wave, a sawtooth wave, and a square wave, respectively. $s_{max} = 0.1$, $\psi = 0.5$, $\Delta\mu = 0.01$, $p_M = 0.5$.

sumption may not hold, and the lag between linkage disequilibrium and allele frequencies will be crucial in determining the sign of Cov $[s(t), D(t)]$. Thus, when the dynamics of the linkage disequilibrium is explicitly taken into account, migration can be selected for even if local adaptation is positive.

Influence of the Cost of Migration. It is worth noting that although the intensity of selection, s_{max}, influences the intensity of indirect selection on the modifier, it does not affect the ESMR value when there is no cost. Indeed, when there is no cost, the ESMR depends only on the sign of indirect selection. When migration is costly, however, the intensity of selection will influence the ESMR (see eq. [11]). We saw previously that the direct selection due to the costs can be approximated as $-(c_f + \Delta\mu c_v)$. Both the fecundity cost and the migrant viability cost influence the evolution of the modifier in a similar way, but the fecundity cost has a stronger effect because only the individuals bearing the modifier pay it, while the migrant viability cost is paid by all the migrants regardless of their genotype. Numerical solutions of ESMR when migration triggers a cost are shown in figure 4*C*. Of course, adding a cost of dispersal selects against migration and lowers the ESMR. More surprisingly, perhaps, the presence of this cost interacts with the effect of the speed of the change of the environment on the evolution of migration. In particular, the ESMR is maximized for intermediate fluctuation periods (fig. 4*C*). Equation (11) can help in understanding this effect (see also fig. D3 in the online edition of the *American Naturalist*). On the one hand, the value of D_{max} is a decreasing function of the speed of the fluctuations because disequilibrium needs some time to build up (fig. D3*B*). On the other hand, $\cos(\sigma_D)$ is high when selection oscillates fast because both σ_A^S and σ^* decrease when selection changes less frequently (fig. D3*C*). Hence, the first term in equation (11) is maximized for intermediate values of the speed of the fluctuations of the environment.

Simulations. The above analytic and numerical results rely

on a set of simplifying assumptions. We used numerical simulations of the exact equations describing the changes in our system over time to explore the potential effect of several of these assumptions. To do so, we iterate the recursions over 1,000 generations and record the change in the frequency of allele M (which migrates with probability $\mu_m + \Delta\mu$) from generation 100 to 1,000 for different values of μ_m. The ESMR is the value of migration for which the change in the frequency of M is null.

First, we explore the effect of the intensity of selection on the evolutionary outcome. We find that the match between our analytical results and numerical simulations is very good, even when selection on the first locus is strong (fig. D4 in the online edition of the *American Naturalist*).

Second, our analytical results (in particular, the integration of eq. [8]) crucially rely on the fact that there are many unsynchronized demes. We tested the influence of synchronization of selection with simulations. We considered the case where there are only two demes and computed the actual ESMR value for various phase differences between the two selective cycles. We find that, indeed, synchronization is important in determining the ESMR (fig. D5 in the online edition of the *American Naturalist*). Not surprisingly, the ESMR is maximized when the two demes are in antiphase. When the two demes are in antiphase, selection is highly heterogeneous, and this case is close to our assumptions. The actual ESMR is close to the one we predict with a large number of demes. As the two selective cycles get more synchronized, however, the ESMR gets lower.

Last, our analytical derivations are based on the assumption that selection is a simple sinusoidal function. We provide an expression for indirect selection on the modifier valid for any shape of fluctuating function of selection (app. C, "Linkage Disequilibrium and Selection on the Modifier for Other Selection Functions"). But as for local adaptation (eq. [5]), this general equation is not readily interpretable. We used numerical simulations to derive the ESMR when selection is a square wave and a sawtooth wave (fig. 4*D*). As for local adaptation, the geometry of the change of selection does not affect qualitatively the evolution of migration. The ESMR is a decreasing function of the recombination rate and of the speed of the fluctuations of selection. Hence, the analysis conducted with a simple sine function is sufficient to describe the main effects of fluctuating selection on the evolution of migration. Interestingly, we find that in comparison with the sine wave, the ESMR is lower for the square wave and higher for the sawtooth wave. This could be explained by the fact that the square wave and the sawtooth wave yield higher and lower, respectively, levels of local adaptation than does the sine wave. Predicting how the geometry of the temporal change in selection influences quantitatively the evolution of migration, however, would require further investigation.

Discussion

Spatial variation is known to be a force that counteracts the evolution of migration (Balkau and Feldman 1973; Hastings 1983). One reason behind this effect is that migration is a force that limits the ability of populations to adapt to local environmental conditions (Lenormand 2002). With temporal variation, however, migration can increase the level of local adaptation (see also Gandon 2002). Could this effect select for migration in temporally variable environments? The answer to this question is complicated by the fact that temporal variability may select for migration for different reasons. In particular, in a model with no evolution of local adaptation, temporal variability in habitat quality acting on the demography of populations could also select for migration. This has been shown regarding the effects of local extinctions (Comins et al. 1980; Gandon and Michalakis 1999) but also for weaker effects on demography (Cohen and Levin 1991). Migration evolves when habitat quality changes through time as a way to track the high-quality demes. In this context, migration can be seen as a bet-hedging strategy. Spatial and temporal variability in habitat quality and their effects on the evolution of migration have been widely studied. In contrast, to our knowledge, the soft-selection model (i.e., regulation of population size occurs before migration) of Gillespie (1981) is the only attempt to examine the effect of both spatial and temporal variability in selection on the evolution of migration. Gillespie's study shows that, indeed, temporal variability can select for migration. But most of these results rely on numerical simulations, and the link with local adaptation is not really discussed. Our model is an attempt to clarify this link and to derive analytical results on the evolution of migration in a fluctuating environment.

In a first step, we contrast two measures of local adaptation: one taken after migration and one taken before migration. In particular, we show that the former can be negative if selection changes too quickly, while the latter is always positive under our assumptions (fig. 1; app. B). We then show that under fluctuating selection, there exists a migration rate that maximizes local adaptation. In particular, we show that migration has a twofold effect on local adaptation. First, migration creates a load because of the increased genetic variance in the population (migration increases $\alpha_{\max}$). Second, migration allows a better tracking of environmental change (migration decreases σ_A). These two effects result in an intermediate level of migration that maximizes local adaptation. These two effects of migration are akin to the analysis of Lande and Shannon (1996),

who studied the adaptation of a population by tracking the change of an optimal phenotype in a quantitative genetic framework. An increase in genetic variability creates a genetic load but allows a better tracking of environmental change and decreases the evolutionary load.

The above analysis, however, does not help identify the evolutionary forces acting on migration. Thus, in a second step, we analyze the evolutionary dynamics on the modifier locus governing the probability of migration. We showed that under the classical QLE approximation, migration should never evolve, because local adaptation just before migration is always positive. However, the QLE approximation, because it assumes a quick change of linkage disequilibria, does not capture all the interesting features of adaptation in a changing environment. In fact, the QLE approximation works best when the environment changes slowly and recombination is high enough, as already pointed out in previous studies (Barton and Otto 2005). Therefore, QLE should not be used when one is interested in the delays in the dynamics of adaptation triggered by quickly changing selective pressure (see also Gandon and Otto 2007; M'Gonigle et al. 2009). When we explicitly look at the dynamics of the linkage disequilibrium, a certain level of migration can evolve. Interestingly, the level of migration that evolves (ESMR) is always lower than the one maximizing local adaptation. Migration evolves because the response of the linkage disequilibrium to the change in allele frequency is delayed, and higher migration rates may evolve even if local adaptation is positive. In general, we find that the delay in the dynamic of the linkage disequilibrium is bigger when selection changes faster, which selects for higher migration rates. Also, increasing the recombination rates decreases the ESMR.

If migration is costly, lower levels of migration evolve. The sign, but also the strength of indirect selection on the modifier, is important in determining the ESMR. In this case, the ESMR is maximal for an intermediate level of the speed of the fluctuation of the environment. In particular, it is unlikely that very high migration rates evolve as suggested by the no-cost curve in figure 4*A*, because indirect selection is quite weak when selection changes quickly. If migration imposes a fecundity cost, migration should rarely evolve, because very low fecundity costs on migration are sufficient to prevent any evolution of higher migration rates in the absence of other evolutionary forces.

Our model shares some similarities with models of the evolution of recombination (Gandon and Otto 2007) or the evolution of mutation rate (M'Gonigle et al. 2009). These models consider the evolution of a modifier loosely linked with a locus under fluctuating selection. In these two models, mutation and recombination play a role similar to migration in our model. Namely, they allow a better tracking of selection but create a load. All those traits help populations adapt to a changing environment by increasing the genetic variability on which selection can act. Mutation and recombination are sometimes considered a bet-hedging strategy, so migration in our model could be called bet hedging as well. However, the type of selection acting in the present model is different from what is classically called bet hedging in the context of the evolution of migration, because we consider a soft-selection model with no demography (population sizes are infinite).

The assumption that selection changes through time is crucial in our model. If selection is constant, migration never evolves. In the wild, selection on a number of traits is likely to change through time (Siepielski et al. 2009), for example, because of changing abiotic factors such as climate. In most of this study, we considered a very specific (sine wave) function for describing the change in selection. However, we derived general expressions that help to understand how the level of local adaptation and the ESMR are affected by the geometry of the temporal change in selection (figs. 2, 4*D*). Moreover, our qualitative results regarding the effect of migration on local adaptation and the ESMR are unaffected by the shape of selection. The sine wave function is thus a convenient tool for studying evolution in a periodically changing environment in a quite general way. Some work remains to be done to understand how local adaptation and migration evolve when the environment changes nonperiodically. For example, Lande and Shannon (1996) show that the total genetic load (equivalent to local adaptation in our model) is not the same in randomly changing environments as it is in periodically changing environments, indicating that the evolutionary outcome in our case may be different for a nonperiodic selection function.

Another crucial assumption is that the environment is highly heterogeneous and there is no isolation by distance. Thus, migrants are of any possible genotype. In contrast, if selection was correlated spatially among neighboring demes, migrants would probably be very similar to residents, and the positive effects of migration would vanish (fig. D5). The assumption we made will hold if selection is sufficiently spatially heterogeneous. Again, in the context of host-parasite interactions, selection has been shown to be highly heterogeneous in space (Burdon and Thrall 1999). Moreover, in host-parasite systems, drift, demographic processes, or varying selection intensity can maintain heterogeneity in space; even without these processes, the spatial dynamic of antagonistic interactions leads to patterns of high heterogeneity in space when there is isolation by distance (Gandon 2002; Sasaki et al. 2002) or even in a simple island model (Sasaki et al. 2002; Gavrilets et al. 2008).

Host-parasite systems often present a high temporal and spatial variability in selection (Burdon and Thrall 1999).

Moreover, evidence exists that migration can increase local adaptation (Morgan et al. 2005; Greischar and Koskella 2007) in host-parasite systems, which is a result analogous to equation (3). Our model can thus reflect interesting features of these systems. In this respect, it would be interesting to extend the model to account explicitly for coevolution between a host and a parasite. Coevolution would add a level of complication, as changes in migration rates would affect the spatial and temporal heterogeneity of selection. In addition, one could also let migration rates of the two interacting species coevolve (on the coevolution of recombination and mutation rates, see Gandon and Otto 2007 and M'Gonigle et al. 2009, respectively).

In this study, we highlight the importance of one force affecting the evolution of migration. But as pointed out in the "Introduction," many other forces act on migration. How do other forces interact with the temporal change of the environment to mold the rate of migration? In particular, another force will select for migration when habitat quality is temporally changing and acts on the demography of populations. It will also be interesting to relax the assumption of infinite population size. With drift, migration will be selected for as a way to avoid kin competition. Billiard and Lenormand (2005) showed that kin competition alone could counteract the effect of spatial heterogeneity and could also lead to interesting dynamics (i.e., evolutionary bistability). An exploration of these effects when there are some temporal variations of the environment remains to be carried out. In a broader perspective, we believe that the interaction between multiple factors needs to be considered to get a better theoretical understanding of the evolution of migration (Clobert et al. 2001; Ronce 2007) but also of other traits allowing populations to adapt in a changing world.

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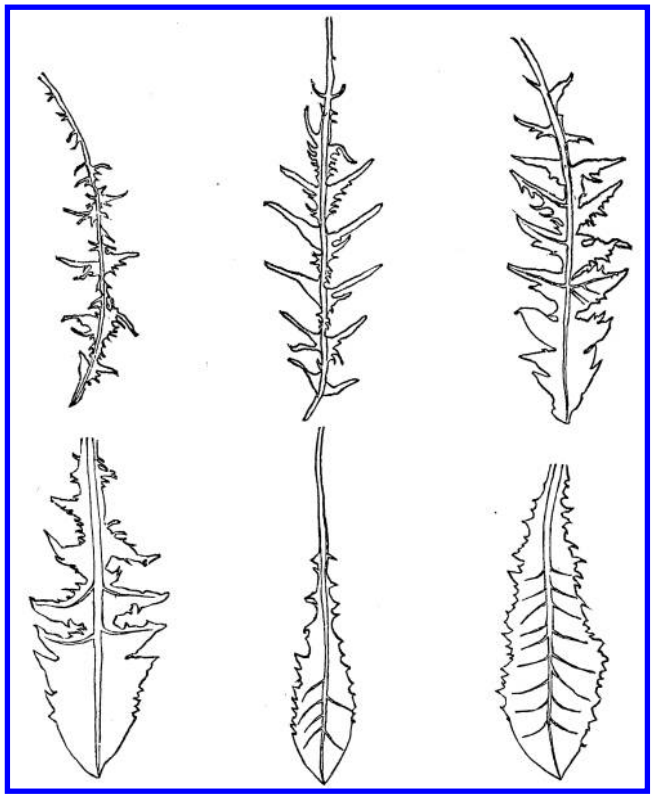

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