

The effects of migration and drift on local adaptation to a heterogeneous environment

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Abstract

Local adaptation experiments are widely used to quantify the levels of adaptation within a heterogeneous environment. However, theoretical studies generally focus on the probability of fixation of alleles or the mean fitness of populations, rather than *local adaptation* as it is commonly measured experimentally or in field studies. Here, we develop mathematical models and use them to generate analytical predictions for the level of local adaptation as a function of selection, migration and genetic drift. First, we contrast *mean fitness* and *local adaptation* measures and show that the latter can be expressed in a simple and general way as a function of the spatial covariance between population mean phenotype and local environmental conditions. Second, we develop several approximations of a population genetics model to show that the system exhibits different behaviours depending on the rate of migration. The main insights are the following: with intermediate migration, both genetic drift and migration decrease local adaptation; with low migration, drift decreases local adaptation but migration speeds up adaptation; with high migration, genetic drift has no effect on local adaptation. Third, we extend this analysis to cases where the trait under selection is continuous using classical quantitative genetics theory. Finally, we discuss these results in the light of recent experimental work on local adaptation.

Introduction

Populations often experience spatial heterogeneity in their environment. Adaptation to such heterogeneous environments can lead to corresponding patterns of population genetic structure. To what extent populations specialize to their local environment is a key question in evolutionary biology, because it determines, for example, the cost of migration (Balkau & Feldman, 1973), or how likely speciation will be (Gavrilets, 2003). Various methods can be used to quantify the adaptation of populations to their local environment. For example, correlations between ecologically relevant environmental variables (e.g. temperature, precipitation) and phenotypic or genotypic traits suggest that the traits have evolved as

an adaptation to the local environments (Fumagalli *et al.*, 2011; Hancock *et al.*, 2011). Another method to assess the impact of selection on patterns of adaptation compares the levels of spatial variation in quantitative traits with those for neutral loci ($Q_{ST}-F_{ST}$ comparison, McKay & Latta, 2002).

The most common method used to assess adaptation to heterogeneous environment, however, is the local adaptation experiment. Such experiments are generally conducted by measuring the fitness of populations when transplanted to other locations. More precisely, *local adaptation* quantifies the specialization of populations to their local environment by measuring the difference between performance of populations in their local environment and their performance within other environments (Kawecki & Ebert, 2004). Local adaptation is relatively easy to measure, and as a result, a large number of studies have estimated local adaptation and identified factors that shape its magnitude. Recent meta-analyses of these studies reveal that local adaptation is

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widespread; for example, Hereford (2009) compiled 777 estimates of local adaptation coming from 74 studies and showed that on average, fitness of native populations was 45% greater than that of foreign populations. Leimu & Fischer (2008) gathered data on local adaptation in plants from 35 studies and showed that local plants performed better than foreign plants in 71.0% of the cases.

Despite the widespread evidence for local adaptation, few experimental studies have successfully identified the factors determining the level of local adaptation. Hereford (2009) showed that in general, a greater 'environmental distance' (i.e. a greater heterogeneity in selection) leads to higher levels of local adaptation. Gene flow is expected to reduce the level of local adaptation (Storfer *et al.*, 1999; see Lenormand, 2002 for a review). Last, Leimu & Fischer (2008) showed that larger population sizes produce higher levels of local adaptation, but the reasons for this are not clear because population sizes have multiple and complex effects on the process of adaptation. One of the effects that is most often referred to is genetic drift, which reduces standing additive genetic variation in populations (Willi *et al.*, 2007) and slows the spread and fixation of beneficial mutations (Robertson, 1960).

A vast amount of theoretical work has been devoted to understanding how drift, gene flow and heterogeneous selection interact to shape adaptation in metapopulations. Many studies seek to find the probability of fixation of a mutant allele in a heterogeneous environment (Nagylaki, 1980; Gavrilets & Gibson, 2002; Whitlock & Gomulkiewicz, 2005). These studies are concerned with the rate of adaptation (of the whole metapopulation) in a heterogeneous vs. homogeneous environment and do not discuss the implications of these results for the emergence of local adaptation. Other studies address the probability of invasion of a locally beneficial allele in a sink (Holt & Gomulkiewicz, 1997; Gomulkiewicz *et al.*, 1999; Kawecki, 2000, 2008). These studies rely on specific scenarios and highlight demographic effects, for example the fact that migration allows the population to persist outside of its niche, but can also decrease absolute fitnesses of genotypes if there is negative density dependence. All the above-mentioned studies deal with simple genetic determinism of the trait. Examples of work dealing with more complex genetic determinism include Hendry *et al.* (2001) for the effects of migration and heterogeneous selection on 'adaptive divergence', and Alleaume-Benharira *et al.* (2006) and Lopez *et al.* (2008) for the effects of drift, migration and heterogeneous selection on population's mean fitness.

From an experimental perspective, however, classical measures of adaptation (i.e. probability of fixation, mean population fitness) are often less accessible than other measures, such as trait-environment correlations, Q_{ST} - F_{ST} comparisons or local adaptation. But in general,

few theoretical studies have specifically tested how these experimental measures are affected by divergent selection, migration and drift (see Martin *et al.*, 2008 and Whitlock & Guillaume, 2009 for the Q_{ST} - F_{ST} comparison; Nuismer *et al.*, 2010 for the trait-environment correlation in the context of host-parasite interactions). Specifically, to our knowledge, no theoretical study has investigated the emerging pattern of *local adaptation* under drift-migration-selection dynamic. As a consequence, the above studies offer little guidance for understanding how evolutionary processes shape local adaptation in experimental or wild populations (but see Gandon & Nuismer (2009) in the context of host-parasite interactions). Moreover, the link between local adaptation and other measures of adaptation remains unclear.

In this study, we develop a model that shows in a very general way what *local adaptation*, as it is generally measured in empirical studies, actually quantifies, and show how this measure differs from *mean fitness*. In order to better understand the evolutionary forces that shape local adaptation, we subsequently use specific models of evolution that integrate drift, migration and spatially variable selection to derive analytical expressions for the level of local adaptation. These expressions allow us to predict how local adaptation changes as a function of population size, migration and the heterogeneity of selection.

Disentangling local adaptation and mean fitness

In order to make clear the distinction between *local adaptation* and *mean fitness*, we first propose a general model that does not formalize the evolutionary process but just the spatial pattern of adaptation. This model describes a metapopulation living in a heterogeneous environment. Each deme is characterized by its environment x (the environment of deme i is denoted x_i), and each individual is described by its phenotype z . The phenotype of the k th individual of deme i is denoted z_{ik} , and the mean phenotype in deme i is \bar{z}_i . The fitness of the k th individual of deme i transplanted in deme j is assumed to be a function of deme j 's environment x_j and the individual's trait z_{ik} :

$$w_{i,j,k} = f(x_j, z_{ik}). \quad (1)$$

(the fitness of an individual in its own deme is therefore $w_{i,i,k} = f(x_i, z_{ik})$).

We approximate this fitness function locally as a quadratic function with a Taylor series (see details in Appendix A, online; note that the expressions below are actually exact in many simple models). This allows us to derive the following expression for the mean fitness of the metapopulation:

$$\begin{aligned}
 E[\bar{W}] = & f(E[X], E[\bar{Z}]) + \underbrace{\frac{V[X] \partial^2 f}{2 \partial x^2} \Big|_{(E[X], E[\bar{Z}]}}_{\text{environmental load}} \\
 & + \underbrace{\frac{E[\|Z_i\|] \partial^2 f}{2 \partial z^2} \Big|_{(E[X], E[\bar{Z}]}}_{\text{local variance load}} + \underbrace{\frac{V[\bar{Z}] \partial^2 f}{2 \partial z^2} \Big|_{(E[X], E[\bar{Z}]}}_{\text{spatial variance load}} \\
 & + \underbrace{\text{Cov}[X, \bar{Z}] \frac{\partial^2 f}{\partial x \partial z} \Big|_{(E[X], E[\bar{Z}]}}_{\text{adaptation to the environment}} \quad (2)
 \end{aligned}$$

where the operators E[], V[] and Cov[] refer to the spatial average, variance and covariance, respectively, and the operator $\| \cdot \|$ is the variance across all individuals in a deme. X and Z̄ are the variables taking the values xi and z̄i, respectively, in deme i. Zi is the variable describing population i and takes the value zik for individual k.

Equation (2) decomposes mean fitness in a heterogeneous environment into several components. The mean fitness of the metapopulation first depends on the fitness that an individual with the average trait E[Z̄] would have in the average environment E[X], which is the first term in (2). But mean fitness also depends on the details of the heterogeneity of the environment and of the mean trait. This is described by the four last terms in (2). In all these terms, the properties of the fitness function are described by its second-order derivatives, evaluated at the point (E[X], E[Z̄]).

If fitness is reduced in more extreme environments (i.e. if the fitness function is concave, $\partial^2 f / \partial x^2 |_{(E[X], E[\bar{Z}])} < 0$), then the mean fitness of the metapopulation will be all the more reduced when the environment is highly variable (i.e. that V[X] is big). This is described by the second term, ‘environmental load’. Of course, the effect will be the opposite if fitness is higher in more extreme environments (convex fitness function). An analogous effect holds for the relationship between the trait and fitness. If extreme traits have a lower fitness ($\partial^2 f / \partial z^2 |_{(E[X], E[\bar{Z}])} < 0$), then a greater variance in the trait will tend to decrease the mean fitness of the metapopulation. This phenomenon happens at the scale of the deme (‘local variance load’ that depends on the within-deme variance) and at the scale of the metapopulation (‘spatial load’ that depends on the between-deme variance). Again, we refer to these terms as ‘loads’ because people often consider concave fitness functions, but if extreme traits have a higher fitness, these terms will tend to enhance mean fitness.

The fifth and last term corresponds to the adaptation of populations to their local environment and requires that fitness depends on the matching between the environment and the trait (i.e. $\partial^2 f / \partial x \partial z |_{(E[X], E[\bar{Z}])} \neq 0$). The derivative $\partial^2 f / \partial x \partial z |_{(E[X], E[\bar{Z}])}$ represents how a change in the environment changes the selection gradient $\frac{\partial f}{\partial z}$ and can therefore be thought of as the trait–environment

interaction for fitness. We now show that this last term quantifies local adaptation.

Several approaches have been used to quantify local adaptation in empirical studies, but most rely on some form of reciprocal translocation experiment where mean fitness is estimated for individuals transplanted among a set of natural or experimental populations. It has recently been argued that a ‘local vs. foreign’ design should be used over a ‘home vs. away’ design (Kawecki & Ebert, 2004). However, because the expectation of both of these measures is identical (Morgan *et al.*, 2005), we simply focus on this expectation as our measure of local adaptation. More specifically, we calculate local adaptation as the difference between mean fitness in sympatry and the *global* mean fitness of the metapopulation, not the mean fitness *in allopatry*. These two definitions are always linked by the simple relationship $\Delta_{\text{sympatric vs. global}} = \frac{n}{n-1} \Delta_{\text{sympatric vs. allopatric}}$ where n is the number of demes (Morgan *et al.*, 2005; Nuismer & Gandon, 2008). It can be shown, using the model for fitness described above, that the experimental measure of local adaptation is the last term in eqn (2) (see derivation in Appendix A):

$$\Delta = \text{Cov}[X, \bar{Z}] \frac{\partial^2 f}{\partial x \partial z} \Big|_{(E[X], E[\bar{Z}])} \quad (3)$$

This result reveals that local adaptation has the appealing property of directly quantifying the extent to which population mean phenotypes match local environmental conditions (Nuismer & Gandon, 2008). Note that local adaptation can be thought of as an extension for many demes of Hendry *et al.*’s (2001) measure of population divergence, which is defined as the difference between the mean traits in two populations experiencing different selection regimes. Actually, when there are two patches only, local adaptation is proportional to population divergence (F. Débarre, O. Ronce and S. Gandon, unpublished result). However, divergence may be measured only in situations where the ecologically relevant trait for a metapopulation is clearly identified. In contrast, local adaptation Δ is easily measured experimentally as the difference between the performance of populations in their local environment and their performance when transplanted to other habitats. Local adaptation measures, interestingly, quantify how the underlying ecologically relevant trait matches the local environment, without requiring prior knowledge and measurement of the trait or the environment.

Equation (2) reveals that to understand the impact of migration and drift on mean fitness, we first need to understand their effects on (i) local standing genetic variance, E[||Zi||], (ii) the spatial variance in mean phenotypes, V[Z̄], and (iii) local adaptation Cov[X, Z̄] $\partial^2 f / \partial x \partial z |_{(E[X], E[\bar{Z}])}$. In contrast, to understand the evolution of *local adaptation*, we must ‘simply’ study how natural selection, gene flow and genetic drift interact to

mould the covariance between phenotype and environment in (3). To do so, we now apply the above framework to two models of adaptation. The first is a population genetic model where a single locus is under spatially variable selection and the fitness function is linear. We analyse this model and provide several approximations for local adaptation, which describe different regions of the parameter space with different behaviours of the system. The second is a quantitative genetics model where a continuous trait is under stabilizing selection with spatially varying optimum. For this more complicated model, we do a less complete analysis and find an expression for local adaptation under the classical quantitative genetics assumption that the additive genetic variance is a known and constant parameter.

Models of adaptation

A population genetics model

Local adaptation and mean fitness in the population genetics model

We assume that the individuals are haploid and that a single diallelic locus determines adaptation. The phenotypes of the individuals carrying the *a* or the *A* alleles are $z = 0$ and $z = 1$, respectively. The mean phenotype in deme *i*, denoted \bar{z}_i , is thus equal to the frequency of the *A* allele. The fitness of the *k*th individual of deme *i* transplanted into deme *j* is given by $w_{i,j,k} = f(s_j, z_{ik}) = 1 + (2z_{ik} - 1)s_j/2$. Here, s_j is a selection coefficient that varies across space (s_j may be negative) and represents the environment. Hence, the fitness function defines a genetic trade-off between levels of adaptation in different habitats.

If we define *S* as the variable taking the value s_i in deme *i*, applying eqn (2) yields the mean fitness of the metapopulation:

$$E[\bar{W}] = 1 - \frac{1}{2} \underbrace{(2E[S]E[\bar{Z}] - E[S])}_{f(E[X],E[Z])} + \underbrace{\text{Cov}[S, \bar{Z}]}_{\text{adaptation to the environment}}, \tag{4a}$$

where local adaptation is as follows:

$$\Delta = \text{Cov}[S, \bar{Z}]. \tag{4b}$$

First, note that the loads identified in (2) (the second, third and fourth terms in (2)) do not appear in (4a) because the fitness function is linear. Migration does not affect $E[\bar{Z}]$, the average phenotype in the metapopulation, and if we assume there is a large number of demes, drift will not affect it either. Hence in this case, the only way drift and migration act on mean fitness is through their effects on local adaptation.

In order to better understand how drift, gene flow and selection interact to shape this covariance, we now specify the life cycle: in each deme, *N* adults produce a

large number of gametes according to their fitness, then the population is regulated to conserve *N* juveniles (random drift), and a proportion *m* of juveniles eventually move between demes. In the sections below, we derive several approximations for local adaptation under a drift–migration–selection balance.

The diffusion approximation

Here, we use the classical diffusion approximation (e.g. Crow & Kimura, 1970; Rice, 2004) to determine the probability distribution of allele frequency in a single deme, which we then use to find local adaptation. This approximation relies on the assumption that changes in allele frequency from one generation to the next are small, and works best when selection and migration are weak, and local population sizes are large. Selection and migration, on average, change the mean phenotype in each deme, whereas drift does not change the mean phenotype but creates a sampling variance around it. The distribution of the population mean phenotype in one deme at time *t* is given by $\psi[\bar{z}_i, t]$, which evolves following the Kolmogorov forward equation:

$$\frac{\partial \psi[\bar{z}_i, t]}{\partial t} = - \frac{\partial}{\partial \bar{z}_i} [\psi[\bar{z}_i, t]M[\bar{z}_i]] + \frac{1}{2} \frac{\partial^2}{\partial \bar{z}_i^2} [\psi[\bar{z}_i, t]v[\bar{z}_i]] \tag{5}$$

where $M[\bar{z}_i]$ is the directional change of the phenotype in deme *i* due to selection and migration and $v[\bar{z}_i]$ is the variance in the phenotype due to drift. The equilibrium distribution of the mean phenotype can be solved using (5) to give

$$\psi^* = \frac{C}{v} e^{\int \frac{2M}{v} d\bar{z}_i} \tag{6}$$

where *C* is an integration constant. In a model with selection, drift and migration, the functions *M* and *v* are given by

$$M[\bar{z}_i] = \underbrace{m(\bar{z}' - \bar{z}_i)}_{\text{migration}} + (1 - m) \underbrace{G_i S_i}_{\text{selection}} \tag{7}$$

$$v[\bar{z}_i] = \underbrace{\frac{G_i'}{N}}_{\text{drift}}$$

where \bar{z}' is the average trait in the pool of migrant individuals (which, in the island model, is the average trait in the metapopulation after selection), *m* is the migration rate, G_i is the additive genetic variance in deme *i*, S_i is the selection gradient in deme *i*, and *N* is the population size. The ' denotes a variable measured after selection. Note that eqn (7) can be applied to any fitness function and any genetic determinism with the appropriate G_i and S_i . In our model, we have, assuming weak selection, $S_i = s_i$, $G_i = \bar{z}_i(1 - \bar{z}_i)$ and $G_i' = \bar{z}'_i(1 - \bar{z}'_i) \approx \bar{z}_i(1 - \bar{z}_i)$ (\bar{z}'_i is the allele frequency in deme *i* after selection). Plugging these *M* and *v* into eqn (6), we find the following equilibrium distribution:

$$\psi^*[\bar{z}_i] = Ce^{2N(1-m)\bar{z}_i s_i} (1 - \bar{z}_i)^{2N(1-\bar{z}')m-1} \bar{z}_i^{2N\bar{z}'m-1} \quad (8)$$

where C is a constant such that $\int \psi^*[\bar{z}_i] d\bar{z}_i = 1$. This classical distribution was first derived by Wright (1942) and will allow us to find the level of local adaptation in the metapopulation. Equation (4b) shows that to calculate local adaptation, we need to know how the expected allele frequency in each deme, $\langle \bar{z}_i \rangle$, covaries with local selective pressures s_i . Direct calculations using (8) show that this expected allele frequency is given by

$$\begin{aligned} \langle \bar{z}_i \rangle &= \int_0^1 \bar{z}_i \psi^*[\bar{z}_i] d\bar{z}_i \\ &= \bar{z}' \frac{\mathcal{M}[1 + 2N\bar{z}'m, 1 + 2Nm, 2N(1-m)s_i]}{\mathcal{M}[2N\bar{z}'m, 2Nm, 2N(1-m)s_i]} \end{aligned} \quad (9)$$

where $M[a, b, x]$ is the confluent hypergeometric function and is given by $M[a, b, x] = \sum_{n=0}^{\infty} \frac{(a)_n x^n}{(b)_n n!}$ where $(y)_n = y(y+1)\dots(y+n-1)$. There are several issues with eqn (9). First, it depends on \bar{z}' , the allele frequency in the pool of migrants, which is, under the island model, the average allele frequency in the metapopulation. A numerical solution for \bar{z}' can be found, given a spatial distribution of the coefficients of selection $\phi[s_i]$, by solving $\bar{z}' = \int \phi[s_i] \langle \bar{z}_i \rangle ds_i$ ($\langle \bar{z}_i \rangle = \bar{z}' \frac{\mathcal{M}[1+2N\bar{z}'m, 1+2Nm, 2N(1-m)s_i]}{\mathcal{M}[2N\bar{z}'m, 2Nm, 2N(1-m)s_i]}$ is a function of \bar{z}'). But determining analytically the equilibrium value of \bar{z}' is more difficult. No analytical result exists for this problem in general, even in a deterministic model (see Nagylaki & Lou, 2008 for a review of the deterministic case, and Yeaman & Otto, 2011 for conditions for the maintenance of polymorphism with drift in a two-patch model).

The second issue with (9) is that it depends in a complicated way on local selection s_i . Rewriting the covariance of eqn (4b) in terms of the spatial distribution of selection yields

$$\Delta = \text{Cov}[S, \bar{Z}] = \int \phi[s_i] s_i \langle \bar{z}_i \rangle ds_i - \int \phi[s_i] \langle \bar{z}_i \rangle ds_i \int \phi[s_i] s_i ds_i \quad (10)$$

Therefore, in general, local adaptation depends on all the moments of the spatial distribution of s_i including the variance, skew and higher-order moments of $\phi[s_i]$. The integrals in (10) can be numerically calculated for an arbitrary spatial distribution of selection coefficients, which readily gives predictions for local adaptation under the drift–migration–selection equilibrium. An analytical prediction for local adaptation can also be found under the assumption that there are only two types of habitats ($s_i = \pm s_{\max}$), but it is sufficiently complicated that it provides little insight. Therefore, to extend our analysis, we provide below different approximations for $\langle \bar{z}_i \rangle$ under various assumptions regarding the relative strength of selection, migration and drift. This yields several expressions for local adaptation that may be used under very different ecological scenarios.

Selection is weak relative to drift

First, (9) may be approximated as a Taylor series expansion around $Ns_i \approx 0$, which yields the following value of local adaptation:

$$\Delta \approx \frac{2N(1-\bar{z}')\bar{z}'(1-m)V[S]}{1+2Nm} \quad (11)$$

Equation (11) shows that local adaptation is a decreasing function of migration and an increasing function of population size. But the use of eqn (11) will be limited because little local adaptation is expected when Ns_i is small.

Selection is strong relative to drift and migration ('deterministic approximation')

Another approximation for $\langle \bar{z}_i \rangle$ may be obtained by assuming that each deme is nearly fixed for the locally favoured allele, which requires that selection be strong relative to migration and drift (this approximation is used in the context of inbreeding depression in Bataillon & Kirkpatrick, 2000; Glémin *et al.*, 2003). Practically, the term corresponding to selection in the M of eqn (7) is linearized in $s_i(1-\bar{z}_i)$ in demes where $s_i > 0$ and $s_i \bar{z}_i$ if $s_i < 0$. The distribution (9) can then be approximated by a beta distribution, and the expected value of the trait is $\langle \bar{z}_i \rangle = 1 - \frac{m(1-\bar{z}')}{m+(1-m)s_i}$ if $s_i > 0$ and $\langle \bar{z}_i \rangle = \frac{m\bar{z}'}{m-(1-m)s_i}$ if $s_i < 0$. Applying eqn (10) for a case where $s_i = \pm s_{\max}$ yields (Appendix B)

$$\Delta = \text{Cov}[S, \bar{Z}] = \frac{s_{\max}^2}{2} \frac{1-m}{m+(1-m)s_{\max}} \quad (12)$$

In this regime, population size has no effect on local adaptation, and in the following, we thus refer to the above expression as the 'deterministic approximation'. Note that the approximation for $\langle \bar{z}_i \rangle$ is sufficiently simple for easily interpretable expression for local adaptation to be derived under various other spatial distributions of selection (see Appendix B for a derivation with a Gaussian distribution of s_i , Fig. S1).

High migration

We now examine the case where the rate of migration is high relative to selection and drift. In such situations, allele frequencies in each deme are very near the average allele frequency \bar{z}' . Actually, in this region of parameter space, the metapopulation almost behaves as a single panmictic population, and if one allele is favoured over the other at the scale of the metapopulation, it will eventually fix in the metapopulation and local adaptation will vanish (Nagylaki & Lou, 2008). Therefore, for this analysis, we focus on the case where selection is perfectly balanced in the metapopulation.

With high migration, the distribution of allele frequencies within each deme given by (8) is concentrated around the average allele frequency of the migrants \bar{z}' . This assumption allows us to derive the following approximation for local adaptation (Appendix C):

$$\Delta = \bar{z}'(1 - \bar{z}')V[s] \frac{1 - m}{m}. \quad (13)$$

Note that eqn (11) can be approximated when Nm is large (such that $1 + 2Nm \approx 2Nm$) as $\Delta \approx \bar{z}'(1 - \bar{z}')V[s] \frac{1 - m}{m}$, which is identical to eqn (13). Interestingly, when the rate of migration is high, drift does not affect the local adaptation. This is because migration is so frequent, it maintains genetic variance regardless of drift. But when selection is not perfectly balanced in the metapopulation, the favoured allele may eventually fix if drift and/or migration are too strong, so in this situation the intensity of drift will indeed affect the equilibrium value of local adaptation (Yeaman & Otto, 2011). Local adaptation will develop initially, as the favoured allele sweeps through the metapopulation at different speeds in the different habitats, but it will decrease to vanishing levels as the allele reaches fixation in all the populations (Fig. S3, Appendix C; details of the simulations are given below).

Low migration

When the number of migrants is small ($Nm \ll 1$), each deme is generally fixed for one of the alleles. Therefore, the equilibrium distribution (8) may be approximated by two peaks at $\bar{z}_i = 0$ and $\bar{z}_i = 1$. This kind of description of the system is akin to Sella & Hirsh's (2005) method to study the selection–drift–mutation balance. In practice, we call $p_{i,t}$ the probability that deme i is fixed for the allele 1 at time t . For a single deme, transition from one state to the other occurs when a migrant of the unfixed genotype comes into the deme and spreads to fixation. We describe this dynamic with the probabilities of transition from allele 1 to allele 0 (respectively from 0 to 1) in deme i $\pi_{i,1 \rightarrow 0}$ (respectively $\pi_{i,0 \rightarrow 1}$). The π s combine the probability of a migrant coming into a deme Nm with the probability that it invades the deme and gets fixed:

$$\begin{aligned} \pi_{i,1 \rightarrow 0} &= \bar{z}'Nm \frac{1 - e^{2s_i}}{1 - e^{2Ns_i}} \\ \pi_{i,0 \rightarrow 1} &= (1 - \bar{z}')Nm \frac{1 - e^{-2s_i}}{1 - e^{-2Ns_i}} \end{aligned} \quad (14)$$

where $\bar{z}'Nm$ and $(1 - \bar{z}')Nm$ are the probabilities that a migrant of the unfixed genotype comes into a deme, and $\frac{1 - e^{2s_i}}{1 - e^{2Ns_i}}$ and $\frac{1 - e^{-2s_i}}{1 - e^{-2Ns_i}}$ are the probabilities that the alleles 0 and 1, respectively, invade the deme. At equilibrium, the probability that deme i is fixed for allele 1 is given by the balance between the transition probabilities: the probability that the deme is fixed for 1, which also is the expected allele frequency, is $p_i^* = \langle \bar{z}_i \rangle = \frac{\pi_{i,0 \rightarrow 1}}{\pi_{i,1 \rightarrow 0} + \pi_{i,0 \rightarrow 1}}$. In the general case, the average allele frequency in the metapopulation can be found numerically, given the spatial distribution of the selection coefficient, by solving $\bar{z}' = \int \phi[s_i] \langle \bar{z}_i \rangle ds_i$. Then, local adaptation can be calculated using eqn (10) of the main text.

For example, in the two-habitat case where $s_i = \pm s_{\max}$, $\bar{z} = 1/2$ by symmetry. It follows from the expected allele frequency above that local adaptation at equilibrium is as follows:

$$\Delta^* = \frac{s_{\max} \pi_{(+),0 \rightarrow 1} - \pi_{(+),1 \rightarrow 0}}{2 \pi_{(+),1 \rightarrow 0} + \pi_{(+),0 \rightarrow 1}} \quad (15)$$

where $\pi_{(+),0 \rightarrow 1}$ and $\pi_{(+),1 \rightarrow 0}$ are the probability of transitions given by (14) with $s_i = \pm s_{\max}$. Actually, under these assumptions, the system's dynamic is controlled by a linear recurrence equation, so it is possible to follow the full dynamic of local adaptation and not only its equilibrium value (Appendix D):

$$\Delta_t = \Delta^* + (\Delta_0 - \Delta^*)(1 - \pi_{(+),1 \rightarrow 0} - \pi_{(+),0 \rightarrow 1})^t \quad (16)$$

where Δ_0 is the initial level of local adaptation. This analysis allows a better understanding of the processes going on in the low-migration regime. Quite strikingly, (15) reveals that the rate of migration does not influence local adaptation [m cancels in the numerator and the denominator of (15)]. However, the rate of migration does influence the rate of approach to the equilibrium value of local adaptation (eqn 16). This is because migration is sufficiently small that its only role is to make the demes shift from one state to another, but does not significantly reduce adaptation. In this regime, if we start from a situation where each deme is initially polymorphic, in a first step local adaptation quickly converges to a low value Δ_0 where one allele or the other is fixed in each deme. But then migration progressively increases local adaptation (Fig. 3; details of the simulations are given below). This equilibrium value Δ^* is reduced by drift but not by migration, because migration is assumed to be too low to maintain maladapted genes for very long. Approach to equilibrium can be quite slow if migration is low. Because of these transient dynamics, if the environment changes through time, it is possible that greater rates of migration will enhance local adaptation.

Individual-based simulations

In summary, we have identified different approximations for the level of local adaptation reached at a drift–migration–selection equilibrium. To check the accuracy of these approximations, we performed individual-based numerical simulations of the population genetics model. In the simulations, the metapopulation consists of 100 demes inhabited by N individuals. Generations are discrete and nonoverlapping. In all simulations, mutation is implemented as a symmetric two-allele model with a per locus mutation rate of $\mu = 10^{-5}$. The life cycle is identical to the analytical model: adults produce N juveniles and die. Each juvenile then migrates with probability m to a randomly chosen deme (no isolation by distance), and populations experience viability selection within demes (soft selection) depending on their genotype and the deme they live in: in half of the demes,

the viability of A and a individuals is 1 and 0.9, respectively, whereas in the other half of the demes, the viabilities are 0.9 and 1 (this is equivalent to $s_i = \pm 0.1$; thus, maximum local adaptation is 0.05). Local adaptation is calculated as the difference between the fitness of populations in sympatry with their fitness in allopatry, just as in classical local adaptation experiments. For example, a local adaptation value of 0.05 indicates that a population's fitness is on average 0.05 higher in sympatry than in allopatry. For each parameter set, we ran simulations until equilibrium was reached, and to reduce the impact of temporal fluctuations caused by drift, we recorded the temporal average of local adaptation for ten points taken at regular intervals in the final 10% of generations. Because drift sometimes causes large variation in the value of local adaptation across replicates, we replicated this procedure until the standard error across replicates was smaller than a hundredth of the maximum achievable local adaptation.

In summary, the main findings of section 'A population genetics model' are confirmed. The most general approach, which combines (9) with (10), works quite well in the range of parameters tested, except when the rate of migration is high and population size is small (because for these parameters, the change of allele frequency from one generation to the next may be strong). In our simulations, we did not address parameter combinations such that Ns_i is small because we feel this case has little biological relevance (in these cases, local adaptation will be extremely small), so we do not check the validity of approximation (11). Interestingly, the deterministic approximation (12) accurately predicts local adaptation for population sizes as low as $N = 20$, indicating that drift has – in general – little effect on local adaptation. For high rates of migration, eqn (13) is the most accurate and population size has no effect on local adaptation. For low rates of migration, eqn (15) – which neglects transient polymorphism in the demes – accurately describes the effect of population size on local adaptation (upper graph on Fig. 1a), and also the plateau of Fig. 1b at low migration (see Fig. S4 for the accuracy of each approximation as a function of population size and migration rate).

In order to further explore the importance of spatial distributions of the selection coefficients, we conducted additional numerical investigations. We first compared the two-habitat case (Fig. 1) with a case where environments are normally distributed. Simulations show that the shape of the distribution of the selection coefficients does not greatly affect local adaptation (Fig. S1). Second, we investigated the case where one allele is favoured over the other at the scale of the metapopulation. In this case, our numerical results demonstrate that local adaptation is reduced relative to the symmetric scenario, and can even vanish if polymorphism is lost (Fig. S2; this happens in particular for high migration–high genetic

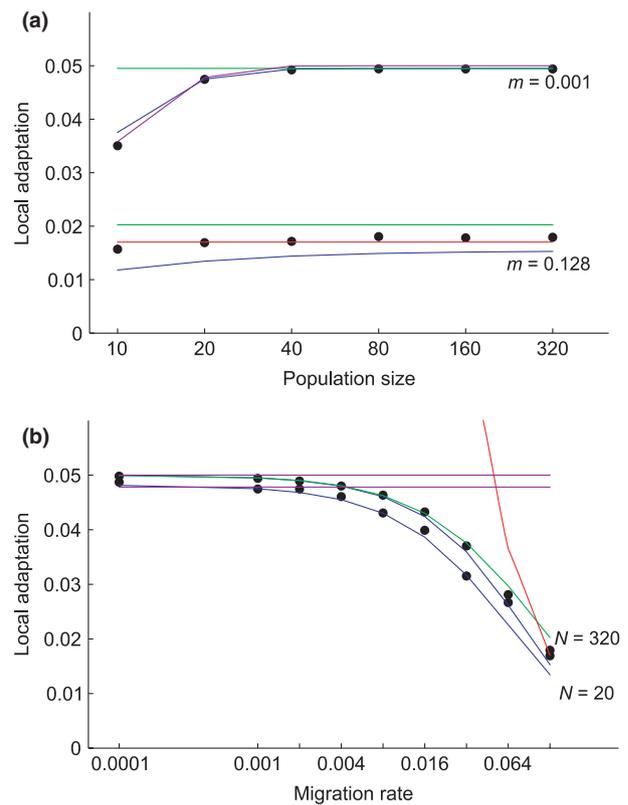


Fig. 1 (a) The influence of population size on local adaptation. Two migration rates are presented (upper and lower curves for $m = 0.001$ and $m = 0.128$, respectively). The results of simulations are shown (points), together with expressions for local adaptation given by the general formula (9–10) (blue line), the deterministic approximation (12) (green line), the high migration approximation (13) (red line) and the low migration approximation (15) (purple line). (b) The influence of migration on local adaptation for two population sizes, $N = 10$ (lower curves) and $N = 320$ (upper curves). Results of simulations are shown together with expressions for local adaptation given by the general formula (9–10) (blue line), the deterministic approximation (12) (green line), the high migration approximation (13) (red line) and the low migration approximation (15) (purple line).

drift). It is noteworthy that in both cases, numerical integration of (10) with (9) accurately predicts local adaptation, except when migration or drift is strong. The deterministic approximation also works well, except in the asymmetric scenario when polymorphism is greatly reduced (Appendix D, Fig. S1, S2). Third, because local adaptation is most likely to be found in cases where selection is strong (Hanski *et al.*, 2011; Hereford & Winn, 2008; Hereford, 2009), we simulated cases of strong selection. We found that in these cases, drift and migration have no influence on local adaptation, because these processes will have negligible effects compared to selection (data not shown).

Local adaptation in a quantitative genetics model

Many local adaptation experiments focus on continuous quantitative traits. In such cases, it is more appropriate to use a quantitative genetics formalism. Here, we introduce such a quantitative genetic model and study how drift and gene flow influence local adaptation.

We assume that the fitness of the *k*th individual of deme *i* is given by $w_{i,j,k} = f(\theta_j, z_{ik}) = e^{-\gamma(z_{ik}-\theta_j)^2}$ where γ is the spatially homogenous strength of stabilizing selection and θ_j is the trait optimum in deme *j* and represents the spatially variable local environment. Equations (6) and (7) can still be used with appropriate S_i and G_i : with this new fitness function, plus the additional assumptions that the additive genetic variance is fixed and selection is weak, $S_i = 2\gamma(\theta_i - \bar{z}_i)$ and $G_i = G$ (Lande, 1976).

For the quantitative genetic model, the equilibrium mean trait distribution is then given by

$$\psi^*[\bar{z}_i] = C' e^{\frac{2\gamma\bar{z}_i(-m\bar{z}_i+2m\bar{z}'-2G\bar{z}_i\gamma(1-m)+4G(1-m)\gamma\theta_i)}{G}} \quad (17)$$

where C' is a constant such that $\int \psi^*[\bar{z}_i]d\bar{z}_i = 1$. Mean fitness is given by

$$E[\bar{W}] = \underbrace{1 - \gamma(E[\bar{Z}]^2 + E[\theta]^2 - 2E[\bar{Z}]E[\theta])}_{f(E[X],E[Z])} \underbrace{-\gamma V[\theta]}_{\text{environmental load}} \underbrace{-\gamma E[\bar{Z}_i]}_{\text{local variance load}} \underbrace{-\gamma V[Z]}_{\text{spatial variance load}} + \underbrace{2\gamma \text{Cov}[\theta, \bar{Z}]}_{\text{adaptation to the environment}} \quad (18a)$$

Because the fitness function is more complex than the one used in section ‘A population genetics model’, migration and drift may now affect mean fitness not only through their effects on local adaptation, but also through their effects on the local variance load and the spatial variance load. The effects of these processes on mean fitness are therefore potentially complex. Local adaptation is given by

$$\Delta = 2\gamma \text{Cov}[\theta, \bar{Z}]. \quad (18b)$$

Assuming an island model of migration, the expression for local adaptation can be found by using (17) and showing that at equilibrium, the mean phenotype of the entire metapopulation converges to the mean of the optima (i.e. $\bar{z}' = E[\theta]$), which yields

$$\Delta = 2\gamma \text{Cov}[\theta, \bar{Z}] = 2\gamma E \left[\theta_i \int_{-\infty}^{+\infty} \bar{z}_i \psi^*[\bar{z}_i] d\bar{z}_i \right] = \frac{4\gamma^2 G V[\theta] (1-m)}{m + 2\gamma G (1-m)}. \quad (19)$$

Equation (19) reveals that local adaptation increases with the spatial heterogeneity of selection, $V[\theta]$, with the additive genetic variance G and with the strength of selection γ , but decreases with migration. This expression is similar to the one obtained by Hendry *et al.* (2001) in their study of adaptive divergence under selection–

migration balance, except that they calculate divergence (the difference between the mean traits in two demes) instead of local adaptation (the difference in fitness between sympatric and allopatric transplants). In contrast to Hendry *et al.*'s (2001) study, moreover, in our model, we included genetic drift, so it is noteworthy that population size does not directly impact local adaptation in (19). But genetic drift may, of course, affect local adaptation indirectly through its effects on the genetic variance G . Indeed, in contrast with the population genetics model where the additive genetic variance is given by $\bar{z}'_i(1 - \bar{z}'_i)$, and evolves as the allele frequencies change, in the quantitative genetics model, the variance is a constant G (Burger & Lande, 1994). The value of G will be determined by the interplay between selection, migration, drift and mutation; analysing these effects is a fascinating but extremely difficult problem well beyond the scope of the present paper (see Burger & Lande, 1994; Barton, 1999 for related models).

Individual-based simulations

To evaluate the accuracy of expression (19) for the quantitative genetics model, we performed individual-

based simulations where each individual's phenotype was determined by 10 haploid diallelic loci (recombination rate $r = 0.1$) with additive effects. In these simulations, the genetic variance is determined by the underlying dynamics of the genotypic frequencies and is not a fixed parameter. Results are shown in Fig. 2. The additive genetic variance G , which appears in (19) but for which we have no analytical prediction, is calculated from the results of the simulations. Although in general (19) accurately predicts local adaptation, sometimes it is an underestimate. This is probably due to the fact that because of migration, the distribution of phenotypes within each deme is skewed, which enhances the response to selection and improves adaptive divergence (Yeaman & Guillaume, 2009). This effect is not captured by the quantitative genetics analysis that neglects the skew and higher-order moments of the distribution. Otherwise, results are mostly similar to the population genetics model. Migration reduces local adaptation. Drift decreases local adaptation because it reduces the additive genetic variance by a factor $(1 - \frac{1}{N})$ in each generation (e.g. Lande, 1992), and thus lowers the equilibrium value of the genetic variance. Note that high migration or low population sizes drastically reduce the levels of genetic variance and hence local adaptation via gene swamping or genetic drift.

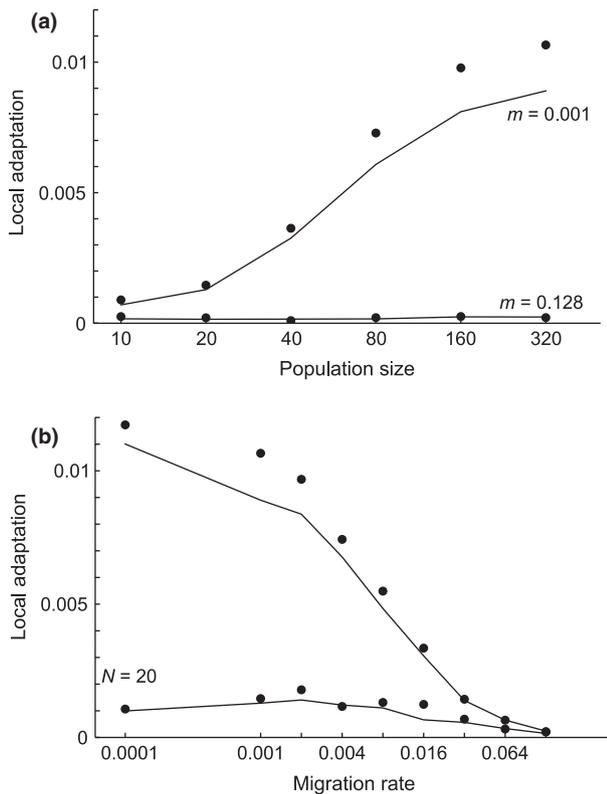


Fig. 2 (a) The expression for local adaptation as a function of population size in the quantitative genetics model, as given by (19) (plain lines), together with the results of simulations (points). The additive genetic variance G that appears in (19) is calculated from the results of the simulations. In this model, however, an individual's trait is coded with 10 diallelic loci with additive effect. For reproduction, individuals mate at random and two adjacent loci recombine with a rate $r = 0.1$. Populations experience stabilizing selection according to the fitness function $f(\theta_i, z_{ik}) = e^{-\gamma(z_{ik} - \theta_i)^2}$, where θ_i is the optimum randomly drawn in each deme from a uniform distribution $U(0,1)$, and the strength of stabilizing selection is $\gamma = 0.1$. For $m = 0.001$ (upper curve), local adaptation increases with population size. For $m = 0.128$ (lower curve), population size has no effect on average local adaptation. (b) The expression for local adaptation in the quantitative genetics model given by (19) (plain lines) together with the results of simulations (points), as a function of the migration rate for $N = 20$ (upper panel) and $N = 320$ (lower panel).

Discussion

In this study, we chose to focus on *local adaptation* because this quantity is commonly used to measure the patterns of adaptation in the wild or in experimental populations but few, if any, theoretical predictions are available under simple models of adaptation. Most existing theory derives expressions for mean fitness, which depends not only on local adaptation, but also on the 'local variance' load and the 'spatial variance' load,

all terms that are probably affected in complex ways by migration, selection and drift (eqn 2). For this reason, previous studies jointly examining these factors relied almost exclusively on simulations (e.g. Alleaume-Benharira *et al.* (2006)). By focusing only on the simpler quantity generally measured by empiricists – local adaptation – we show that local adaptation is proportional to the covariance between population mean phenotype and the variable describing the heterogeneous environment. This simplification allows the development of analytical predictions for how this covariance evolves as a function of gene flow, selection and drift.

Formalizing the links between local adaptation and other measures of adaptation and explicitly focusing on the former also allowed us to reveal new insights into the emergence of spatial patterns resulting from the action of multiple evolutionary forces acting on populations. One of our main results is that genetic drift affects local adaptation only through its effect on the genetic variance. Previous work argued that because drift generates differentiation between populations, it could directly alter the pattern of local adaptation (Kawecki & Ebert, 2004). This is not the case: although drift causes population mean phenotypes to deviate from their local optima, this does not affect the local adaptation on average (it only affects mean fitness through the spatial load). Ultimately, this property emerges because local adaptation is proportional to the covariance between the environment and the trait (eqn 3). Other measures of adaptive divergence may be directly affected by drift. For example, a spatial correlation between trait and environment would be affected by genetic drift, because such a correlation depends on the spatial variance of the trait, which is itself increased by drift (Nuismer *et al.*, 2010).

The present study also derives approximate analytical expressions for local adaptation under a drift–migration–selection balance in a heterogeneous environment. In particular, we developed four expressions for local adaptation in the population genetics model. The first (eqns 9–10) is quite general, but gives little analytical insight because it can be solved only numerically. We also derived three simpler approximations for local adaptation. The deterministic eqn (12) works well when drift and migration are not too strong relative to selection ($1/N \ll s_i$, $m \ll s_i$). In practice, it accurately predicts local adaptation for population sizes as low as $N = 20$, indicating that the effect of drift on local adaptation is moderate. The high and low migration approximations (eqns 13 and 15) perform well when $Nm \gg 1$ and $Nm \ll 1$, respectively (Fig. S4). We showed that drift reduces local adaptation indirectly by eroding genetic variance and that migration reduces local adaptation. For the quantitative genetics model, we also analytically demonstrated the negative impact of migration on local adaptation (eqn 19), and simulations showed that drift has a stronger impact

than in the population genetics model (Fig. 2). Our results suggest that the strong effect of population size on local adaptation reported in the meta-analysis of Leimu & Fischer (2008) is probably due to reductions in levels of local additive genetic variation due to genetic drift affecting polygenic traits. Second, the effects of migration are more complex than has been previously acknowledged. When migration is high, it cancels the effect of drift by replenishing genetic variance. Therefore, the negative impact of drift on local adaptation is strongest when migration, which restores genetic variation, is weak. Another important result is that although low rates of gene flow do not affect the equilibrium value of local adaptation, they can influence the rate at which local adaptation increases when genetic variation is limiting. Specifically, if the response to local selection is limited by an absence of favourable mutations, the rate at which local adaptation increases will be proportional to migration because migration plays the role of mutation in such conditions (Fig. 3). Of course, this effect will be of less importance if the response to local selection is not constrained by a lack of genetic variation as would be the case if, for example, mutation rates and local population sizes are large (in particular, if the mutation rate is of the order of or greater than $1/N$). Although none of these results is surprising in the light of existing theory studying how drift and gene flow interact to shape the mean fitness, they do formally demonstrate for the first time that predictions made for mean fitness carry over for local adaptation as measured in empirical studies.

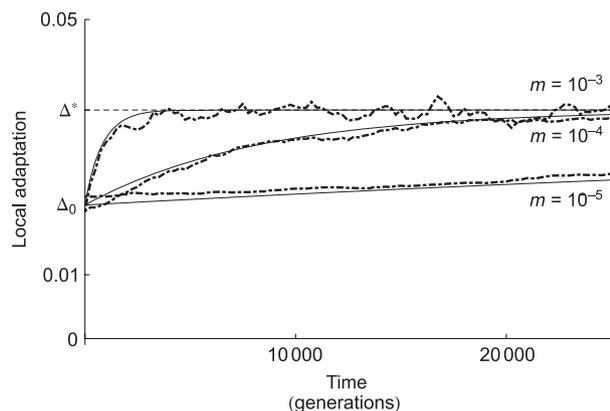


Fig. 3 represents local adaptation as a function of time for three values of migration ($m = 10^{-5}$, 10^{-4} , 10^{-3} from bottom to top). $s_i = \pm 0.1$, $N = 10$. The dot-dashed lines show the average local adaptation obtained with 20 runs of simulations, and the thin lines are the analytical result given by eqn (16). At the beginning, local adaptation quickly converges to the value Δ_0 predicted by the solution for no migration (eqn D-14), and then, the influx of migrants brings the metapopulation to the local adaptation Δ^* predicted by (15), according to the dynamic given by (16).

The fact that gene flow can have beneficial effects on the rate of adaptation when beneficial mutations are limiting suggests that gene flow may enhance local adaptation transiently following a change in the environment. A beneficial effect of migration on local adaptation has already been identified in cases where the environment changes (Gandon *et al.*, 1996; Gandon, 2002; Blanquart & Gandon, 2011), but the effect we illuminate in the present study is different because it involves the loss of variation due to genetic drift. We analytically demonstrated this effect in the low migration limit (eqn 16). But more generally, migration might transiently enhance local adaptation whenever local genetic variation is low. For example, if the metapopulation is initially monomorphic and a mutation appears that confers a selective advantage in some of the demes, but not in others, migration will help the mutation spread in the metapopulation. Therefore, local adaptation initially increases quicker if migration is higher (Fig. S3). But the equilibrium value of local adaptation is of course smaller if migration is higher. Such phenomena might explain why several meta-analyses investigating the effect of migration on local adaptation in host–parasite systems have found contrasted effects of migration on local adaptation (Van Zandt & Mopper, 1998; Greischar & Koskella, 2007; Hoeksema & Forde, 2008). In experimental evolution, Venail *et al.* (2008) showed similar effects of migration in a bacterial metacommunity in which each patch corresponded to a different carbon source. They started from a clonal metapopulation and let it evolve with different rates of migration between patches. They found that the functional diversity of the metapopulation is maximal for an intermediate migration rate. Functional diversity reflects adaptive differentiation and can be thought of as a measure of local adaptation. The mechanism behind this effect is probably that mutants spread more rapidly in the metapopulation with higher migration, as in Fig. S3. The role of migration in spreading beneficial mutations in metapopulations has also been observed in experimental populations of viruses, although not in the context of a heterogeneous environment (Miralles *et al.*, 1999). We hope that our work will guide and inspire future evolution experiments aimed at understanding how fundamental processes such as migration and drift influence the transient as well as the equilibrium adaptive divergence of populations.

Although our model has provided several insights into the forces moulding local adaptation, it has also identified areas ripe for further investigation. First, our study assumed symmetric migration, but relaxing this assumption could have interesting consequences. For example, Gomulkiewicz *et al.* (1999) briefly investigated the effects of drift and migration on local adaptation in a situation nearly identical to our ‘low migration’ approximation (eqn 14). In their model

though, migration was flowing unidirectionally from the source to the sink. Whereas we found that migration had no effect on the equilibrium level of local adaptation in this regime, they find that asymmetric migration increases the establishment rate of the good allele in the sink, which favours local adaptation. Second, we assumed that selection was balanced at the level of the metapopulation. It is not clear how local adaptation will be affected if one allele is favoured over the other at the scale of the metapopulation. As an extreme example, if selection is too asymmetric, the favoured allele will fix in the metapopulation, in which case local adaptation will vanish. However, the conditions in which polymorphism is lost in a metapopulation under heterogeneous selection, drift and migration have not been derived so far to our knowledge (see Yeaman & Otto, 2011 for the two-patch case). This is why we focused on a situation where polymorphism is always maintained (balanced selection and many demes), and then address the question of how much local adaptation is present. This approach is supported by studies documenting many polymorphic loci for local adaptation in the wild (Fournier-Level *et al.*, 2011). Third, when the ecologically relevant trait is determined by many loci, understanding in greater depth the evolution of local adaptation requires knowledge of the additive genetic variance under a drift–migration–selection equilibrium. This is a particularly challenging problem as the influx of migrants may cause local phenotypic distributions to deviate strongly from assumptions of normality that are key to closing statistical moments. Some analytical work has been carried out to understand the influence of migration on the response to selection (Yeaman & Guillaume, 2009), but to our knowledge, no analytical results exist on the genetic variance at a drift–migration–selection equilibrium (see Arnold *et al.*, 2008 for simulations). Finally, we assumed that population sizes were identical and fixed within all demes. Although integrating explicit demography into models such as ours is beyond the scope of this analysis, doing so may yield novel insights generated by the interplay between migration, demography and adaptation (Ronce & Kirkpatrick, 2001; Hanski, *et al.* 2011).

The present study is, at least to our knowledge, the first to derive analytical results for local adaptation under simple assumptions including heterogeneous selection, migration and drift. Although there is considerable scope for developing more general theoretical results, our study is an attempt to better link theoretical and empirical work and thus improve our overall understanding of adaptation in heterogeneous environments. We hope that this approach will stimulate further work using experimental evolution to test our quantitative predictions in simple scenarios of adaptation under a selection–migration–drift balance.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Appendix A General expressions for local adaptation.

Appendix B Local adaptation in the deterministic limit

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Figure S1 Local adaptation as a function of population size (upper panel) and the migration rate (middle panel for $N = 20$, lower panel for $N = 320$), for two types of spatial heterogeneity in selection.

Figure S2 Local adaptation as a function of population size (upper panel) and the migration rate (middle panel for $N = 20$, lower panel for $N = 320$) when selection is symmetric ($s_i = \pm 0.1$ as in Fig. 1) and when selection is asymmetric ($s_i = -0.05$ in half of the patches, $s_i = 0.15$ in the other half of the patches).

Figure S3 The temporal dynamic of local adaptation in cases where selection is asymmetric ($s_i = -0.05$ in half of the patches and $s_i = 0.15$ in the other half of the patches),

for three migration rates ($m = 0.001$, $m = 0.008$ and $m = 0.128$).

Figure S4 Summary of the four main approximations for local adaptation.

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Figure S1

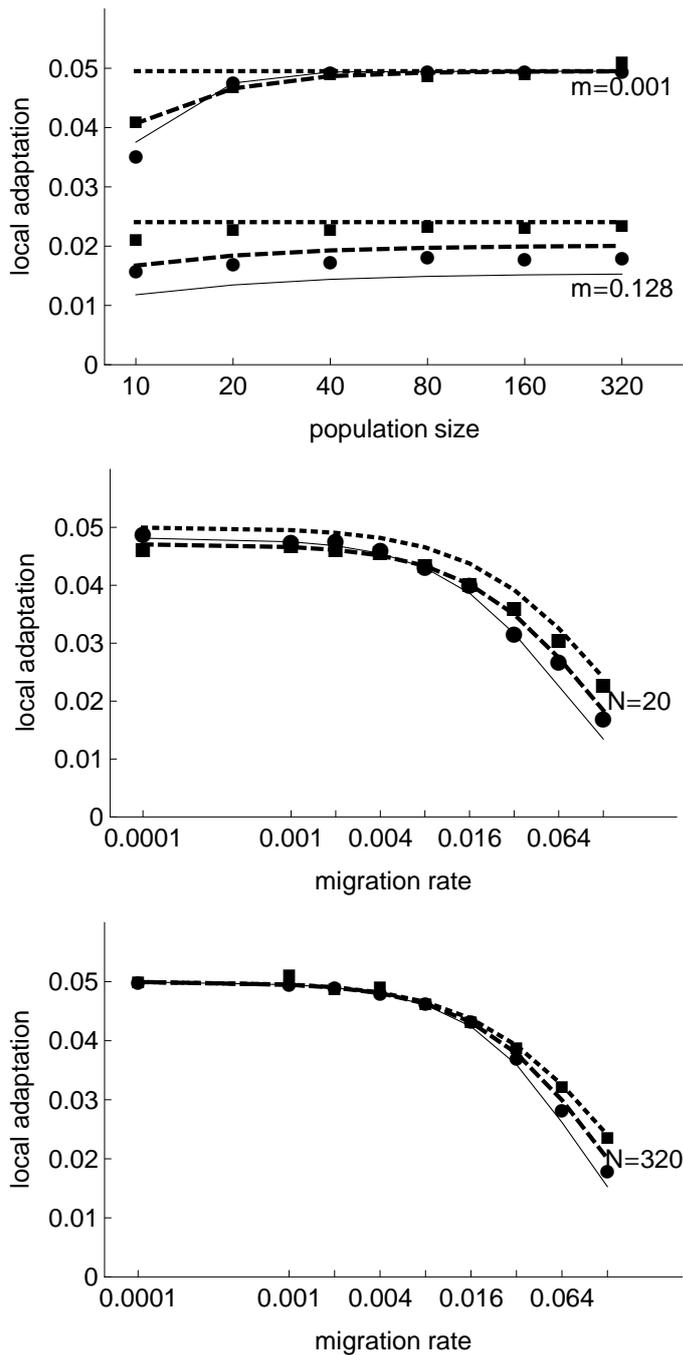


Figure S1: local adaptation as a function of population size (upper panel) and the migration rate (middle for $N = 20$, lower panel for $N = 320$), for two types of spatial heterogeneity in selection. Points are the results of simulations conducted as described in the main text: dots are the results when there are two habitats ($s_i = \pm 0.1$), as in fig.1, and squares are the results when the s_i are drawn in a normal distribution with mean 0 and standard deviation $0.1\sqrt{\pi/2}$, such that the average selection coefficient is 0.1. Plain lines are the results of numerical integration of (10) using (9) for the two habitats scenario. Dashed lines are the results of numerical integration of (10) using (9) for the normal distribution scenario. Dotted lines are the results of the deterministic approximation (equation B2) for the normal distribution scenario. Results are most of the time quantitatively similar for both scenarios. Numerical integration and the deterministic approximation predict well the value of local adaptation except when population size is small and the migration rate high.

Figure S2

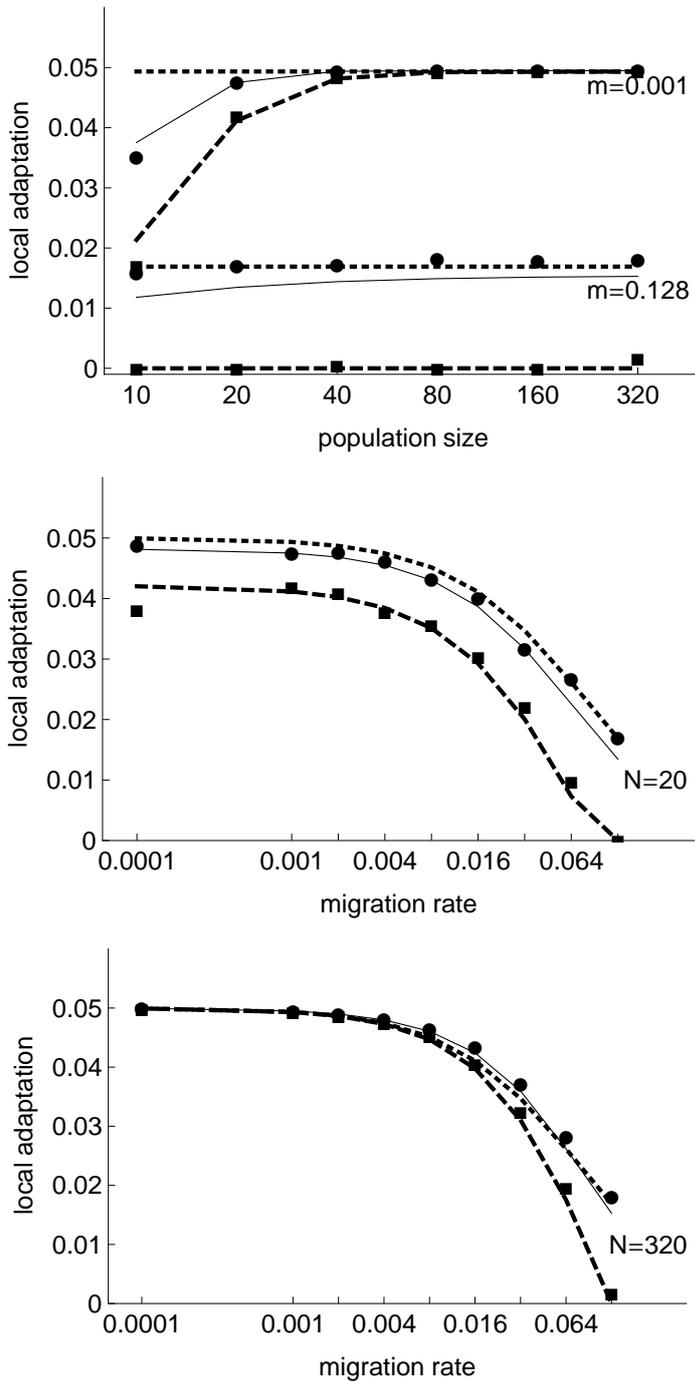


Figure S2: local adaptation as a function of population size (upper panel) and the migration rate (middle for $N = 20$, lower panel for $N = 320$) when selection is symmetric ($s_i = \pm 0.1$ as in fig. 1) and when selection is asymmetric ($s_i = -0.05$ in half of the patches, $s_i = 0.15$ in the other half of the patches). Dots and squares are the results of simulations, conducted as described in the main text, for the symmetric and asymmetric scenarios respectively. Plain and dashed lines are the results of numerical integration of (10) using (9) for the symmetric and the asymmetric scenario respectively. Dotted lines are the results of the deterministic approximation (equation B-3) for the asymmetric scenario. Asymmetric selection consistently results in lower local adaptation; this effect is particularly important for high migration and low population sizes, where polymorphism in the metapopulation is greatly reduced or even lost. Numerical integration predicts well the value of local adaptation. In contrast, the deterministic approximation does not capture the great reduction in local adaptation when migration is high.

Figure S3

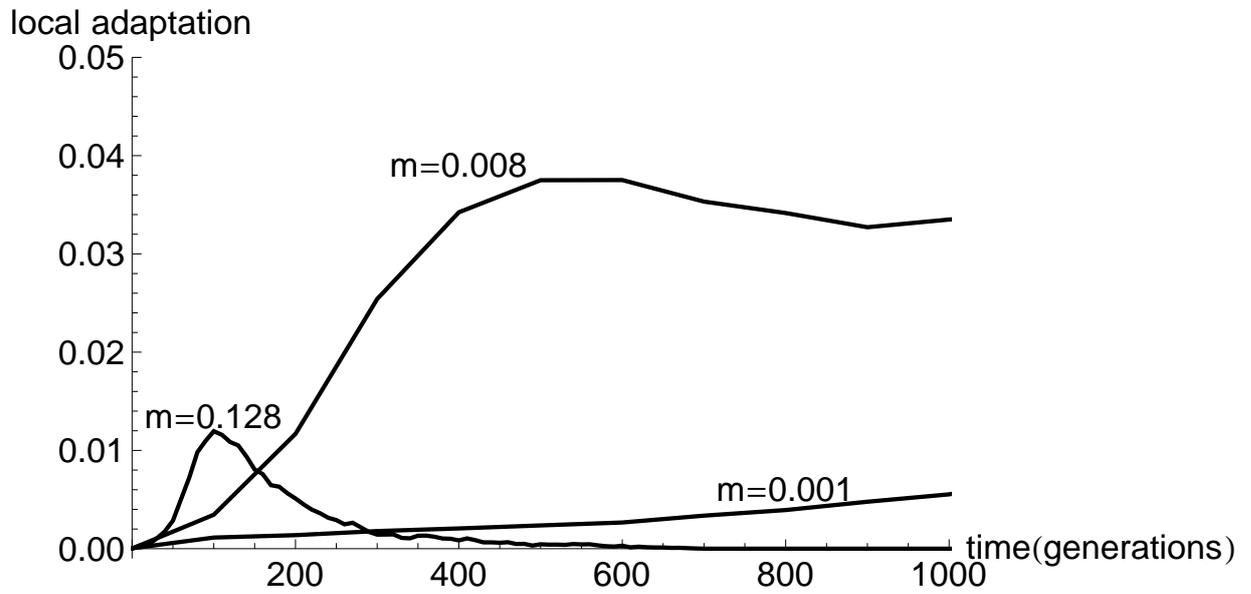


Figure S3: temporal dynamic of local adaptation in cases where selection is asymmetric ($s_i = -0.05$ in half of the patches, $s_i = 0.15$ in the other half of the patches), for three migration rates ($m = 0.001$, $m = 0.008$, $m = 0.128$). We assumed the favored allele initially appears as a single mutant in the metapopulation. The results are the average of 20 runs of simulations where this mutation is not initially lost and manages to spread in the metapopulation. The favored allele spreads through the metapopulation all the more quickly than migration is high. However the equilibrium value of local adaptation is higher with lower migration. When migration is strong ($m = 0.128$), the favored allele eventually fixes in the metapopulation, so local adaptation reaches a maximum value and finally goes down and vanishes.

Figure S4

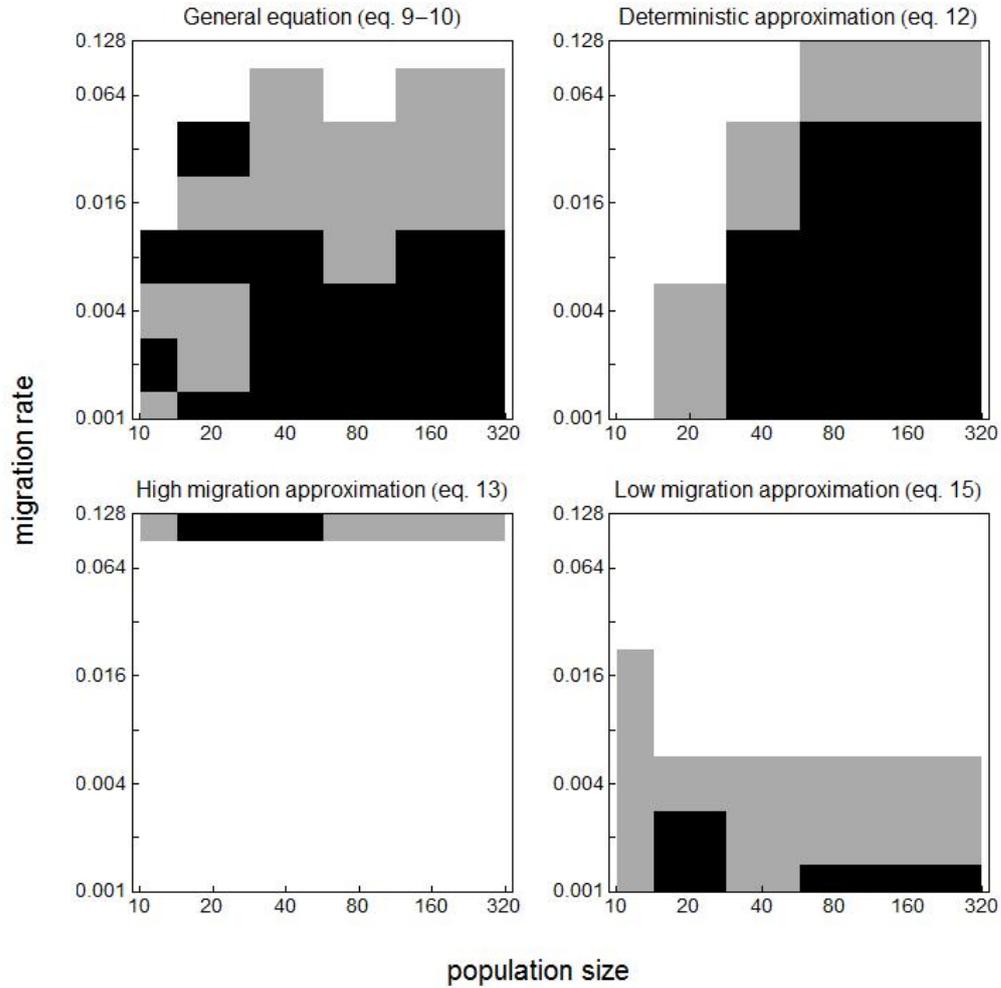


Figure S4: the four main approximations for local adaptation. For each approximation, we show, as a function of the migration rate and population size, when true local adaptation is predicted with a precision of 2.5×10^{-3} and 5×10^{-4} in grey and black respectively (remind that maximal local adaptation is 0.05). The general formula (eq. 9 - 10) works well in a wide range of parameters, except when population size is low and/or the migration rate is large. However, in most of the range the three simpler approximations (12), (13) and (15) are sufficient to accurately predict local adaptation. The deterministic approximation performs well for population sizes as low as 20. Last, the low and high migration approximations are accurate in their range of validity, i.e. when $Nm \ll 1$ and $Nm \gg 1$ respectively.

Appendix A: General expressions for local adaptation

We assume that each individual is described by its phenotype z . The phenotype of the k^{th} individual of deme i is denoted z_{ik} . We also assume that each deme is characterized by its environment x , the environment of deme j being denoted x_j . The fitness of the k^{th} individual of deme i transplanted in deme j is assumed to be a function of deme j 's environment and the individual's trait z_{ik} :

$w_{i,j,k} = f(x_j, z_{ik})$	(A1)
------------------------------	------

Assuming the environmental heterogeneity and the phenotypes' spatial heterogeneity are both weak, and that there is little variance in phenotype within populations, the fitness function can be well approximated by a Taylor expansion around $(E[X], E[\bar{Z}])$, the average environment and the average value of population mean phenotype in the metapopulation ($E[\cdot]$ is the average over all the demes of the metapopulation):

$w_{i,j,k} \approx f(E[X], E[\bar{Z}]) + (x_j - E[X]) \left. \frac{\partial f}{\partial x} \right _{(E[X], E[\bar{Z}])} + (z_{ik} - E[\bar{Z}]) \left. \frac{\partial f}{\partial z} \right _{(E[X], E[\bar{Z}])}$ $+ \frac{(x_j - E[X])^2}{2} \left. \frac{\partial^2 f}{\partial x^2} \right _{(E[X], E[\bar{Z}])} + \frac{(z_{ik} - E[\bar{Z}])^2}{2} \left. \frac{\partial^2 f}{\partial z^2} \right _{(E[X], E[\bar{Z}])}$ $+ (x_j - E[X])(z_{ik} - E[\bar{Z}]) \left. \frac{\partial^2 f}{\partial x \partial z} \right _{(E[X], E[\bar{Z}])}$	(A2)
--	------

Note that (A2) is actually exact for many simple models. The next step is to partition the difference between individual k 's phenotype z_{ik} and the average phenotype in the metapopulation $E[\bar{Z}]$ as the difference between z_{ik} and deme i 's mean phenotype \bar{z}_i plus the difference between \bar{z}_i and $E[\bar{Z}]$:

$ \begin{aligned} w_{i,j,k} \approx & f(E[X], E[\bar{Z}]) + (x_j - E[X]) \frac{\partial f}{\partial x} \Big _{(E[X], E[\bar{Z}])} + (z_{ik} - \bar{z}_i) \frac{\partial f}{\partial z} \Big _{(E[X], E[\bar{Z}])} \\ & + (\bar{z}_i - E[\bar{Z}]) \frac{\partial f}{\partial z} \Big _{(E[X], E[\bar{Z}])} + \frac{(x_j - E[X])^2}{2} \frac{\partial^2 f}{\partial x^2} \Big _{(E[X], E[\bar{Z}])} \\ & + \frac{(z_{ik} - \bar{z}_i)^2}{2} \frac{\partial^2 f}{\partial z^2} \Big _{(E[X], E[\bar{Z}])} + \frac{(\bar{z}_i - E[\bar{Z}])^2}{2} \frac{\partial^2 f}{\partial z^2} \Big _{(E[X], E[\bar{Z}])} \\ & + (z_{ik} - \bar{z}_i)(\bar{z}_i - E[\bar{Z}]) \frac{\partial^2 f}{\partial z^2} + (x_j - E[X])(z_{ik} - \bar{z}_i) \frac{\partial^2 f}{\partial x \partial z} \Big _{(E[X], E[\bar{Z}])} \\ & + (x_j - E[X])(\bar{z}_i - E[\bar{Z}]) \frac{\partial^2 f}{\partial x \partial z} \Big _{(E[X], E[\bar{Z}])} \end{aligned} $	(A3)
--	------

We average $w_{i,j,k}$ over all the individuals of the population to find $\bar{W}_{i \rightarrow j}$, the fitness of population i transplanted in deme j :

$ \begin{aligned} \bar{W}_{i \rightarrow j} = & f(E[X], E[\bar{Z}]) + (x_j - E[X]) \frac{\partial f}{\partial x} \Big _{(E[X], E[\bar{Z}])} + (\bar{z}_i - E[\bar{Z}]) \frac{\partial f}{\partial z} \Big _{(E[X], E[\bar{Z}])} + \\ & \frac{(x_j - E[X])^2}{2} \frac{\partial^2 f}{\partial x^2} \Big _{(E[X], E[\bar{Z}])} + \frac{[Z_i]}{2} \frac{\partial^2 f}{\partial z^2} \Big _{(E[X], E[\bar{Z}])} + \frac{(\bar{z}_i - E[\bar{Z}])^2}{2} \frac{\partial^2 f}{\partial z^2} \Big _{(E[X], E[\bar{Z}])} + (x_j - E[X])(\bar{z}_i - \\ & E[\bar{Z}]) \frac{\partial^2 f}{\partial x \partial z} \Big _{(E[X], E[\bar{Z}])} \end{aligned} $	(A4)
---	------

where $[Z_i]$ is the within-population variance, so $[Z_i]$ is the phenotypic variance in deme i .

The mean fitness of the metapopulation, W_{home} , is:

$ \begin{aligned} W_{home} &= E_i[\bar{W}_{i \rightarrow i}] \\ &= f(E[X], E[\bar{Z}]) + \frac{V[X]}{2} \frac{\partial^2 f}{\partial x^2} \Big _{(E[X], E[\bar{Z}])} + \frac{E[[Z_i]]}{2} \frac{\partial^2 f}{\partial z^2} \Big _{(E[X], E[\bar{Z}])} \\ &\quad + \frac{V[\bar{Z}]}{2} \frac{\partial^2 f}{\partial z^2} \Big _{(E[X], E[\bar{Z}])} + \text{Cov}[X, \bar{Z}] \frac{\partial^2 f}{\partial x \partial z} \Big _{(E[X], E[\bar{Z}])} \end{aligned} $	(A5)
---	------

where $V[X]$ is the spatial variance of variable X in the metapopulation and $\text{Cov}[X, \bar{Z}]$ is the spatial covariance between X and \bar{Z} . To calculate local adaptation, we define the mean fitness “global” as the expected mean fitness of a population transferred to another deme at random:

$ \begin{aligned} W_{global} &= E_{i,j}[\bar{W}_{i \rightarrow j}] \\ &= f(E[X], E[\bar{Z}]) + \frac{V[X]}{2} \frac{\partial^2 f}{\partial x^2} \Big _{(E[X], E[\bar{Z}])} + \frac{E[[Z_i]]}{2} \frac{\partial^2 f}{\partial z^2} \Big _{(E[X], E[\bar{Z}])} \\ &\quad + \frac{V[\bar{Z}]}{2} \frac{\partial^2 f}{\partial z^2} \Big _{(E[X], E[\bar{Z}])} \end{aligned} $	(A6)
--	------

Hence, local adaptation, which is given by W_{home} minus W_{global} , is:

$ \Delta = \text{Cov}[X, \bar{Z}] \frac{\partial^2 f}{\partial x \partial z} \Big _{(E[X], E[\bar{Z}])} $	(A7)
---	------

Appendix B: local adaptation in the deterministic limit

Another approximation for $\langle \bar{z}_i \rangle$ may be obtained by assuming that each deme is nearly fixed for the allele that is favored locally, which requires that selection be strong relative to migration and drift (Bataillon and Kirkpatrick 2000). Practically, the term corresponding to selection in the M of equation (7) is approximated by $s_i(1 - \bar{z}_i)$ if $s_i > 0$ and $s_i\bar{z}_i$ if $s_i < 0$. It follows that the migration – drift – selection probability distribution (8) can be approximated by a beta distribution with parameters $\alpha = 2N(\bar{z}'m + (1 - m)s_i)$ and $\beta = 2N(1 - \bar{z}')$ when $s_i > 0$. The expected value of the trait is therefore $\langle \bar{z}_i \rangle = \frac{\alpha}{\alpha + \beta} = 1 - \frac{m(1 - \bar{z}')}{m + (1 - m)s_i}$.

Symmetrically, when $s_i < 0$, the parameters of the beta distribution are $\alpha = 2N\bar{z}'m$ and $\beta = 2N(m(1 - \bar{z}') - (1 - m)s_i)$, and the expected value of the trait is $\langle \bar{z}_i \rangle = \frac{m\bar{z}'}{m - (1 - m)s_i}$. The last step is to use equation (10) of the main text to find the equilibrium value of local adaptation. For example, if half of the demes have $s_i = s_{max}$ and the other half $s_i = -s_{max}$, local adaptation is:

$\Delta = \text{Cov}[S, \bar{Z}] = \frac{s_{max}^2}{2} \frac{1 - m}{m + (1 - m)s_{max}}$	(B1)
--	------

This approximation implies that drift has no effect on local adaptation.

With the deterministic approximation, it is possible to derive analytical expressions for local adaptation for a scenario where selection is distributed as a gaussian (fig. S1) and a scenario where selection is asymmetric.

For the first case we assume s_i is drawn in a normal distribution with mean 0 and variance σ^2 , and find, using the expected value of the trait $\langle \bar{z}_i \rangle$ and equation (10), that local adaptation is:

$\Delta = \text{Cov}[S, \bar{Z}] = \frac{\sigma}{\sqrt{2\pi}} - \frac{m}{2(1-m)} + m^2 e^{-\frac{m^2}{2(1-m)^2\sigma^2}} \frac{\pi \operatorname{erfi}\left[\frac{m}{\sqrt{2}\sigma(1-m)}\right] - \operatorname{Ei}\left[\frac{m^2}{2(1-m)^2\sigma^2}\right]}{2(1-m)^2\sqrt{2\pi}\sigma}$	(B2)
--	------

where $\operatorname{erfi}[\]$ is the imaginary error function and $\operatorname{Ei}[\]$ is the exponential integral function.

Although the third term in (B2) is complicated, it is of order m^2 so it may be neglected when migration is weak.

For the asymmetric case, we assume $s_i = -s_1$ in half of the demes and $s_i = +s_2$ in the other half. We find that in this case the average trait in the metapopulation is

$$\bar{z}' = \frac{(m(1-s_1)+s_1)s_2}{2(1-m)s_1s_2+m(s_1+s_2)}$$

Using equation (10) and the expressions for $\langle \bar{z}_i \rangle$ we find local

adaptation is:

$\Delta = \text{Cov}[S, \bar{Z}] = \frac{(1-m)s_1s_2(s_1+s_2)}{4(1-m)s_1s_2+2m(s_1+s_2)}$	(B3)
---	------

The deterministic approximations (B2) and (B3) work well when drift is not too strong (fig. S1, S2). However expression (B3) does not capture the effects of a great reduction in polymorphism when migration and/or drift are strong. Indeed, the deterministic approximation rests on the assumption that the favored allele is nearly fixed in each deme; therefore in this approximation \bar{z}' cannot be very far from 1/2. This assumption is violated when the allele favored at the scale of the metapopulation is close to fixation.

Appendix C: local adaptation assuming migration is strong relative to selection and drift

It is possible to find yet another expression for local adaptation by assuming that migration is strong relative to selection and drift. The change in the frequency of A allele in deme i from one generation to the next, assuming weak selection and an island model of migration, is:

$\bar{z}_{i,t+1} = \underbrace{(1-m)(\bar{z}_{i,t} + s_i \bar{z}_{i,t}(1 - \bar{z}_{i,t}))}_{\text{philopatry}} + \underbrace{m \bar{z}'}_{\text{migration}} + \underbrace{\xi_i}_{\text{drift}}$	(C1)
---	------

Where \bar{z}' is the frequency of the allele A in the metapopulation, after selection; ξ_i is a random variable with average 0, variance $\frac{\bar{z}_{i,t}(1-\bar{z}_{i,t})}{N}$ and skew $\frac{\bar{z}_{i,t}(1-2\bar{z}_{i,t})}{N^2}$ which represents the effect of drift on the allelic frequency. In this section we make the crucial assumption that migration is strong relative to selection and drift; in this case (C1) shows that the difference between the mean allele frequency in each population and the average allele frequency in the metapopulation $\bar{z}_i - \bar{z}'$ will quickly be small. Taking the expectation of (C1) over the random variable describing genetic drift yields, if the variance of the distribution $\psi[\bar{z}_i]$ is small:

$\langle \bar{z}_{i,t+1} \rangle \approx (1-m)(\langle \bar{z}_{i,t} \rangle + s_i \langle \bar{z}_{i,t} \rangle (1 - \langle \bar{z}_{i,t} \rangle)) + m \bar{z}'$	(C2)
---	------

A simple equilibrium value for $\langle \bar{z}_{i,t} \rangle$ can be found assuming $\langle \bar{z}_{i,t} \rangle - \bar{z}'$ is small, by expanding (C2) as a first order Taylor series of $\langle \bar{z}_{i,t} \rangle$ around \bar{z}' :

$\langle \bar{z}_i \rangle \approx \frac{1-m}{m} \bar{z}' (1 - \bar{z}') s_i$	(C3)
---	------

Using equation (10) of the main text, it follows that local adaptation at equilibrium is:

$\Delta = \bar{z}'(1 - \bar{z}')V[S] \frac{1 - m}{m}$	(C4)
---	------

Interestingly, expression (C4) is very close to the expression obtained with the diffusion approximation assuming that selection is weak (equation (11)).

We assumed that the average allele frequency in the pool of migrants is a known constant \bar{z}' , which is true in the special case where selection is perfectly balanced in the metapopulation.

However, in general in this regime, it can be shown (by averaging (C2) over the metapopulation) that the average allele frequency evolves, to the first order, as:

$\bar{z}_{t+1} = \bar{z}_t + s\bar{z}_t(1 - \bar{z}_t)$	(C5)
---	------

where s is the spatial average of the local selection coefficients s_i . The metapopulation, in the large migration limit, behaves as a single panmictic population (Nagylaki and Lou 2008).

When selection is perfectly balanced in the metapopulation ($s = 0$), \bar{z}' shall be replaced by $1/2$. But if this is not the case, polymorphism will be lost and local adaptation will eventually be 0. If selection is asymmetric, local adaptation changes as the favored allele sweeps to fixation (fig. S3). In an attempt to describe analytically the dynamic of local adaptation as an allele sweeps to fixation in the metapopulation, we approximated the dynamic of the favored allele in the metapopulation as $\bar{z}_t = \frac{\bar{z}_0 e^{st}}{1 + (e^{st} - 1)\bar{z}_0}$ (which is the solution of (C5) approximated as a differential equation), then plugged this equation into (C4) to obtain local adaptation.

However this approximation is not very accurate for at least two reasons. First the equation

$\bar{z}_t = \frac{\bar{z}_0 e^{st}}{1 + (e^{st} - 1)\bar{z}_0}$ does not accurately describe the dynamic of the favored allele; in particular,

when \bar{z}_t is close to 0 or 1, drift plays an important role in the dynamic. Second, this

approximation implies that $\langle \bar{z}_i \rangle$ evolves on a faster time scale than \bar{z}_t , which is not the case in this scenario.

Appendix D: Dynamic of local adaptation when $Nm \ll 1$

Dynamic of local adaptation

Here we detail the case when migration is rare (N is small and $Nm \ll 1$). In this regime, each deme will be most of the time fixed for one of the alleles. We therefore approximate the equilibrium distribution (8) by two peaks at $\bar{z}_i = 0$ and $\bar{z}_i = 1$. Actually, under these assumptions it is possible to follow the full dynamic of local adaptation and not only its equilibrium value. We call $p_{i,t}$ the probability that deme i is fixed for the allele 1 at time t .

We have:

$p_{i,t+1} = (1 - \pi_{i,1 \rightarrow 0})p_{i,t} + \pi_{i,0 \rightarrow 1}(1 - p_{i,t})$	(D1)
---	------

where $\pi_{i,1 \rightarrow 0}$ is the probability of transition from allele 1 to allele 0 in deme i . Equation (D1)

implies that we neglect the time during which an allele spread and goes to fixation in a deme.

The π s combine the probability of a migrant coming into a deme Nm with the probability that it invades the deme and gets fixed:

$\pi_{i,1 \rightarrow 0} = \bar{z}'Nm \frac{1 - e^{2s_i}}{1 - e^{2Ns_i}}$	(D2)
$\pi_{i,0 \rightarrow 1} = (1 - \bar{z}')Nm \frac{1 - e^{-2s_i}}{1 - e^{-2Ns_i}}$	

Where $\bar{z}'Nm$ and $(1 - \bar{z}')Nm$ are the probabilities that a migrant of the unfixed genotype

comes into a deme, $\frac{1 - e^{2s_i}}{1 - e^{2Ns_i}}$ and $\frac{1 - e^{-2s_i}}{1 - e^{-2Ns_i}}$ are the probabilities that the allele 0 and 1

respectively invade the deme.

(D1) is a linear recursion and can be easily solved. It can be rewritten as:

$p_{i,t+1} = (1 - \pi_{i,1 \rightarrow 0} - \pi_{i,0 \rightarrow 1})p_{i,t} + \pi_{i,0 \rightarrow 1}$	(D3)
--	------

At any time t , the probability that deme i is fixed for the good allele will be:

$p_{i,t} = \sum_{j=0}^{t-1} \pi_{i,0 \rightarrow 1} (1 - \pi_{i,1 \rightarrow 0} - \pi_{i,0 \rightarrow 1})^j + (1 - \pi_{i,1 \rightarrow 0} - \pi_{i,0 \rightarrow 1})^t p_{i,0}$ $p_{i,t} = \pi_{i,0 \rightarrow 1} \frac{1 - (1 - \pi_{i,1 \rightarrow 0} - \pi_{i,0 \rightarrow 1})^t}{\pi_{i,1 \rightarrow 0} + \pi_{i,0 \rightarrow 1}} + (1 - \pi_{i,1 \rightarrow 0} - \pi_{i,0 \rightarrow 1})^t p_{i,0}$	(D4)
--	------

At equilibrium, the probability that deme i is fixed for allele i is given by the balance between the transition probabilities:

$p_i^* = \frac{\pi_{i,0 \rightarrow 1}}{\pi_{i,1 \rightarrow 0} + \pi_{i,0 \rightarrow 1}}$	(D5)
---	------

The probability distribution of allele frequency in deme i (equation (8)) can therefore be

approximated by two peaks at $\bar{z}_i = 0$ and $\bar{z}_i = 1$, with weights $\frac{\pi_{i,1 \rightarrow 0}}{\pi_{i,1 \rightarrow 0} + \pi_{i,0 \rightarrow 1}}$ and

$\frac{\pi_{i,0 \rightarrow 1}}{\pi_{i,1 \rightarrow 0} + \pi_{i,0 \rightarrow 1}}$ respectively. As a consequence the expected allele frequency in deme i at any time

point is simply given by $p_{i,t}$. As in the general case (see main text), the average allele

frequency in the metapopulation can be found numerically, given the spatial distribution of

the selection coefficient, by solving $\bar{z}' = \int \phi[s_i] \langle \bar{z}_i \rangle ds_i$. Then local adaptation can be

calculated using equation (10) of the main text.

For example, if there are two habitats ($s_i = \pm s_{max}$), $\bar{z} = 1/2$ by symmetry and equation (10)

of the main text becomes:

$\Delta = \text{Cov}[S, \bar{Z}] = \frac{1}{2} s_{max} \langle \bar{z}_i \rangle_{(+)} - \frac{1}{2} s_{max} \langle \bar{z}_i \rangle_{(-)} = s_{max} \left(\langle \bar{z}_i \rangle_{(+)} - \frac{1}{2} \right)$	(D6)
--	------

where $\langle \bar{z}_i \rangle_{(+)}$ and $\langle \bar{z}_i \rangle_{(-)}$ denote the expected allele frequency in the two habitats. Using (D4) which gives the full temporal dynamic of $\langle \bar{z}_i \rangle_{(+)}$, local adaptation can be shown to evolve following:

$\begin{aligned} \Delta_t &= s_{max} \left(\langle \bar{z}_i \rangle_{(+)} - \frac{1}{2} \right) \\ &= s_{max} \left(\pi_{(+),0 \rightarrow 1} \frac{1 - (1 - \pi_{(+),1 \rightarrow 0} - \pi_{(+),0 \rightarrow 1})^t}{\pi_{(+),1 \rightarrow 0} + \pi_{(+),0 \rightarrow 1}} \right. \\ &\quad \left. + (1 - \pi_{(+),1 \rightarrow 0} - \pi_{(+),0 \rightarrow 1})^t p_{(+),0} - \frac{1}{2} \right) \\ \Delta_t &= \left(\frac{s_{max}}{2} \frac{\pi_{(+),0 \rightarrow 1} - \pi_{(+),1 \rightarrow 0}}{\pi_{(+),1 \rightarrow 0} + \pi_{(+),0 \rightarrow 1}} \right. \\ &\quad \left. + s_{max} (1 - \pi_{(+),1 \rightarrow 0} - \pi_{(+),0 \rightarrow 1})^t \left(p_{(+),0} - \frac{\pi_{(+),0 \rightarrow 1}}{\pi_{(+),1 \rightarrow 0} + \pi_{(+),0 \rightarrow 1}} \right) \right) \end{aligned}$	(D7)
--	------

Where $\pi_{(+),0 \rightarrow 1}$ and $\pi_{(+),1 \rightarrow 0}$ are the probability of transitions given by (D2) when $s_i = +s_{max}$. The above equation makes clear that local adaptation at equilibrium is

$\Delta^* = \frac{s_{max}}{2} \frac{\pi_{(+),0 \rightarrow 1} - \pi_{(+),1 \rightarrow 0}}{\pi_{(+),1 \rightarrow 0} + \pi_{(+),0 \rightarrow 1}}$	(D8)
--	------

What's more, equation (D7) can be rewritten as

$\Delta_t = \Delta^* + (\Delta_0 - \Delta^*) (1 - \pi_{(+),1 \rightarrow 0} - \pi_{(+),0 \rightarrow 1})^t$	(D9)
---	------

The distance to equilibrium $\Delta_t - \Delta^*$ decays exponentially, and the rate of this decay is quicker if the rates of transition π are higher.

Initial value of local adaptation

In the regime where a migrant rarely comes in each deme ($Nm \ll 1$), one of the two alleles initially very quickly spread to fixation before any migrant enters the deme. The probability of fixation in deme i given that the initial allele frequency is $\bar{z}_{i,0}$ can be found using the Kolmogorov forward equation (Rice 2004), and is given by:

$u(\bar{z}_{i,0}) = \frac{\int_0^{\bar{z}_{i,0}} e^{\int \frac{M}{v} dz_i}}{\int_0^1 e^{\int \frac{M}{v} dz_i}}$	(D10)
--	-------

Under a drift-selection balance, equation (D10) becomes:

$u(\bar{z}_{i,0}) = \frac{1 - e^{-2Ns_i\bar{z}_{i,0}}}{1 - e^{-2Ns_i}}$	(D11)
---	-------

which is a classical result (Kimura 1962). Local adaptation is thus initially:

$\Delta_0 = \text{Cov}[S, \bar{Z}] = E_i[s_i u(\bar{z}_{i,0})] - E_i[s_i] E_i[u(\bar{z}_{i,0})]$	(D12)
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where $E_i[\]$ denotes the average over space, which accounts for averaging across the spatial distribution of selection $\phi[s_i]$ and across the initial allele frequencies in the metapopulation $\rho(\bar{z}_{i,0})$. In the simpler case where $s_i = \pm s_{max}$, (D12) simplifies in:

$\Delta_0 = s_{max} \left(E_i \left[\frac{1 - e^{-2Ns_{max}\bar{z}_{i,0}}}{1 - e^{-2Ns_{max}}} \right] - \frac{1}{2} \right)$	(D13)
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(D13) reveals that local adaptation is proportional to the difference between the average probability of fixation of the good allele $E_i \left[\frac{1-e^{-2Ns_{max}\bar{z}_{i,0}}}{1-e^{-2Ns_{max}}} \right]$ and $1/2$. To find an explicit expression for local adaptation, one last needs to integrate (D13) over the distribution of the initial allele frequencies. For example, if the initial allele frequencies $\bar{z}_{i,0}$ are uniformly distributed, (D13) becomes:

$\Delta_0 = \frac{Ns_{max} \text{Coth}[Ns_{max}] - 1}{2N}$	(D14)
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Expressions (D12)-(D14) predict the value of local adaptation to which the metapopulation very quickly converges when migration is low. We use them to predict Δ_0 in fig. 3. These equations are also adequate, however, to describe the equilibrium local adaptation when migration is null. (D14) is an increasing function of N : when migration is null, increasing population size will always increase local adaptation because it decreases the chance of fixation of the bad allele; when N is big, local adaptation tends to $s_{max}/2$ which corresponds to the maximum local adaptation that the metapopulation can achieve (when all demes are fixed for the right allele).