Migration load in plants: role of pollen and seed dispersal in heterogeneous landscapes

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Introduction

Local adaptation is a well-studied phenomenon resulting from the action of spatially heterogeneous selection and characterized by a higher fitness of individuals in their native environment compared with immigrants (Kawecki & Ebert, 2004). Patterns of local adaptation have been particularly documented in plants, where genetic differentiation recurrently evolves in response to, for example, climatic gradients (Etterson & Shaw, 2001; Rehfeldt et al., 2002; Etterson, 2004a,b; Savolainen et al., 2004; Goldringer et al., 2006) or spatially heterogeneous edaphic conditions (e.g. adaptation to soil contamination by heavy metals, McNeilly, 1968; Antonovics & Bradshaw, 1970; MacNair, 1987; Jimenez-Ambriz et al., 2007). The evolution of local adaptation can sometimes be considered as a step toward speciation, in particular when it involves shifts in phenology as documented in Mimulus guttatus on mine tailings (McNeilly & Antonovics, 1968; Antonovics, 2006; Hall & Willis, 2006). Local adaptation can also be of crucial importance for conservation practices, because of the potentially harmful consequences of releasing maladapted individuals (Keller et al., 2000; for a review, see McKay et al., 2005).

Gene flow is generally thought to oppose the effect of divergent natural selection, and to increase the genetic load that depresses mean fitness in heterogeneous environments (Lenormand, 2002). There are, however, several dimensions to such migration load, which interact in a complex manner. First, gene flow may prevent adaptive divergence, measured by the difference in mean phenotype, of populations experiencing different selection pressures (for theoretical predictions in the case of polygenic traits, see García-Ramos & Kirkpatrick, 1997; Tufto, 2000; Hendry et al., 2001; for empirical evidence see, e.g. Hendry & Taylor, 2004). Second, gene flow may affect the evolution of genotypic variance within local populations (for theoretical predictions in the case of polygenic traits see in particular Goldstein & Holsinger, 1992; Phillips, 1996; Lythgoe, 1997; Barton, 1999; Tufto, 2000; for empirical evidence see Yeaman & Jarvis, 2006). Large genotypic variance for a phenotypic trait depresses mean fitness when selection on this trait is stabilizing.

Abstract

Evolution of local adaptation depends critically on the level of gene flow, which, in plants, can be due to either pollen or seed dispersal. Using analytical predictions and individual-centred simulations, we investigate the specific influence of seed and pollen dispersal on local adaptation in plant populations growing in patchy heterogeneous landscapes. We study the evolution of a polygenic trait subject to stabilizing selection within populations, but divergent selection between populations. Deviations from linkage equilibrium and Hardy–Weinberg equilibrium make different contributions to genotypic variance depending on the dispersal mode. Local genotypic variance, differentiation between populations and genetic load vary with the rate of gene flow but are similar for seed and pollen dispersal, unless the landscape is very heterogeneous. In this case, genetic load is higher in the case of pollen dispersal, which appears to be due to differences in the distribution of genotypic values before selection.

Keywords:
dispersal; local adaptation; metapopulation; pollen; quantitative genetics; seed.

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within local populations (Barton, 1986). Genotypic variance is, however, also the necessary fuel for adaptation by natural selection. Increased genotypic variance within populations may in turn facilitate adaptive divergence between them (e.g. Hendry et al., 2001). The interactions between different components of the genetic load are especially complex in the case of polygenic characters as the evolution of the mean phenotype and the genotypic variance may in part be independent (e.g. see Spichtig & Kawecki, 2004). The net effect of gene flow on genotypic load can thus be ambiguous. For instance, the prediction that gene flow limits species range (Kirkpatrick & Barton, 1997) does not hold when the effect of gene flow on genotypic variance is taken into account (Barton, 2001). Migration might replenish genetic variation eroded by drift and improve local adaptation in peripheral populations as predicted by recent simulation studies (see, e.g. Holt et al., 2003; Alleaume-Benharira et al., 2006). Higher migration rate also promotes local adaptation to antagonistic partners engaged in a coevolutionary arms race (for theoretical prediction see Gandon et al., 1996; for empirical evidence see Morgan et al., 2005).

The relative contributions of seeds and pollen to gene flow can vary greatly among species (for a review, see Ouborg et al., 1999). Estimates of pollen to seed flow ratio can, for instance, range from 1.8 in Eucalyptus nitens (Moran, 1992) to 500 in Quercus petraea (Petit et al., 1993) and vary also within species depending on the spatial scale considered (as in Silene alba, McCauley, 1997). For allogamous species, estimates of the ratio of pollen to seed flow are generally considered as high, both within and between populations (Latta, 2006, but see Bacles et al., 2006). Few theoretical models exploring the effect of gene flow on genotypic load and local adaptation explicitly deal with pollen and seed dispersal (Nagylaki, 1997; Hu & Li, 2001, 2002; Hu, 2005). The number of gene copies carried by a migrating seed is twice that carried by a migrating pollen grain. When allelic frequencies are heterogeneous through space, migration of zygotes through seeds results in local heterozygote deficiency, whereas migration of male gametes only, through pollen, generates, in contrast, a local excess of heterozygotes. When selection is spatially heterogeneous, immigrant genes are counter-selected in individuals combining resident and immigrant alleles with pollen dispersal, whereas selection acts more often on individuals carrying either two immigrant alleles or two resident alleles with seed dispersal. As a consequence, the response of migration load to these two modes of gene flow could be quite different. Considering a phenotypic trait under the control of a major locus, Hu & Li (2001) predicted that seed dispersal and pollen dispersal differently affect the shape of clines in genotypic variance along a sharp environmental transition. How such results generalize to polygenic traits in patchy landscapes is, however, unclear.

Here, we explore theoretically the specific consequences of gene flow through seed and pollen for the evolution of genetic load in a self-compatible plant inhabiting a patchy heterogeneous landscape, such as the heavy metal tolerant plant Thlaspi caerulescens growing in a network of polluted and nonpolluted sites (Jimenez-Ambriz et al., 2007). We consider the evolution of a single quantitative character with polygenic variation, which is subject to both stabilizing selection within local populations and disruptive selection across populations in different habitats. We explore the consequences of gene flow for: (i) the maintenance of genetic variability within populations; (ii) the evolution of genetic divergence between populations in different environments; and (iii) the genetic load depressing the mean fitness within local populations, which integrates the effect of the former two parameters. Individual-based simulations are used to explore the evolution of within-population genotypic variance with seed and pollen dispersal. We derive analytical predictions for the divergence between populations and the genetic load assuming that the genotypic variance is known and the distribution of genotypic values is Gaussian within populations, following Tufto (2000) and Hendry et al. (2001). Our analytical model takes drift, selection and migration of both seed and pollen into account. We compare these predictions with the individual-based simulations and investigate how seed and pollen dispersal affect departures from the assumptions of the analytical model.

Methods

General assumptions

Even though we conceive our model to be quite general, we find it useful to illustrate its relevance with some real case study. In southern France, the heavy metal tolerant plant T. caerulescens grows in a network of contaminated former mining sites and noncontaminated sites, only a few kilometres away from each other (Escarré et al., 2000). Comparison of divergence for quantitative traits and molecular markers suggests strong divergent selection on several life-history traits in contaminated vs. noncontaminated sites, but weak stabilizing selection within each habitat type (Jimenez-Ambriz et al., 2007). Gene flow between populations is weak but reveals no preferential exchanges between populations of the same habitat type (Dubois et al., 2003; Jimenez-Ambriz et al., 2007). The species is insect pollinated, self-compatible and seeds are dispersed ballistically at a short distance.

In our model, we consider a patchy population of a self-compatible hermaphroditic annual plant with no seed bank. There are $n$ discrete patches of plants, each of size $N$. Migration of both seeds and pollen occurs between patches following an island model of migration. No selfing occurs prior to pollen dispersal. We consider
the effect of stabilizing selection on a single quantitative character. The landscape is heterogeneous, with different patches of habitat characterized by different optimal values for the phenotypic trait. Generations are discrete and nonoverlapping. The order of the events in the life cycle is: (1) selection acting via juvenile survival; (2) density regulation to a constant number of adults \( N \) in each population; (3) gametogenesis, pollen dispersal and syngamy; and (4) seed dispersal. We assume that survival probability in stage (1) is a function of genotype (see below) and that a very large number of seeds and pollen grains are produced at stages (3) and (4). A proportion \( m_p \) of pollen grains present after dispersal in a given local population originates from the \( n - 1 \) other populations. Similarly, \( m_e \) is the seed migration rate. Mating occurs randomly after pollen dispersal and by considering a self-compatible species, we allow for random selfing to occur.

The genotypic value \( G \) of an individual for the quantitative character is determined by its diploid genotype at \( l \) loci. We assume that allelic effects on the quantitative character are additive, both within each locus (codominance) and across loci (no epistasis), i.e.,

\[
G = \sum_{i=1}^{l} (X_i^{o} + X_i^{p}),
\]

where \( X_i^{o} (X_i^{p}) \) is the allelic value inherited through the ovule (pollen grain) at locus \( i \). The phenotype \( Z \) of an individual is given by the sum of its genotypic value \( G \) and a random environmental effect distributed normally with mean 0 and variance \( \sigma^2_e \). The survival probability of an individual with phenotype \( Z \) in population \( i \) is described by the Gaussian function:

\[
W_i(Z) = \exp \left( -\frac{(Z - \theta_{i})^2}{2\omega} \right)
\]

with \( \theta_{i} \) the optimal value of the quantitative character in population \( i \) and \( 1/\omega \) the intensity of stabilizing selection (here assumed to be the same in all populations). The expected survival probability of an individual with genotypic value \( G \) is

\[
\bar{W}_i(G) = \int \frac{1}{\sqrt{2\pi\sigma_e}} \exp \left( -\frac{(z - G)^2}{2\sigma_e^2} \right) W_i(z) dz,
\]

which is also:

\[
\bar{W}_i(G) = \frac{\omega}{\sigma_e^2} \exp \left( -\frac{(G - \theta_{i})^2}{2\sigma_e^2} \right), \quad \text{with} \quad \sigma^2_s = \sigma^2_e + \omega \quad (1)
\]

We define \( \bar{G}_i \), as the mean genotypic value in population \( i \), \( \bar{G} \) the mean genotypic value in the metapopulation, \( V_{i}^{\mu} \) is the variance of genotypic values in population \( i \), \( V_s \) is the mean within-population variance of the metapopulation, \( V_i^{\mu} \) is the variance of mean genotypic values among populations in the metapopulation. Similarly, \( \bar{W}_i \) is the mean fitness in population \( i \) and \( \bar{W} \) the mean fitness at the scale of the metapopulation. These are random variables, which fluctuate through time because of drift. We are interested in the expected values of these random variables. We follow the expected mean genotypic variance within populations \( \sigma^2_s \), the expected variance in genotypic values between populations \( \sigma^2_t \) and the expected mean genetic load \( \lambda \) in the metapopulation:

\[
\sigma^2_s = E[V_{i}^{\mu}] = E \left[ \sum_{j=1}^{n} \frac{V_{i}^{\mu}}{n} \right] \quad (2)
\]

\[
\sigma^2_t = E[V_{i}^{\mu}] = E \left[ \sum_{i=1}^{n} \frac{(G_i - \bar{G})^2}{n} \right] \quad (3)
\]

\[
\lambda = 1 - E[\bar{W}] = 1 - E \left[ \sum_{i=1}^{n} \frac{\bar{W}_i}{n} \right] \quad (4)
\]

Our measure of load describes how the mean fitness at the scale of the metapopulation deviates from its maximal value of 1. Without loss of generality, we can recalculate the phenotype so that:

\[
E[\bar{G}] = E \left[ \sum_{i=1}^{n} \frac{G_i}{n} \right] = 0 \quad (5)
\]

To better understand the effect of pollen and seed migration on the evolution of the genotypic variance, we further decompose the variance of genotypic values in different terms (see, e.g. Bulmer, 1989 for a similar decomposition). Using the expression for genotypic value \( G \), the expected within-population genotypic variance is:

\[
\sigma^2_s = \frac{1}{n} \sum_{i=1}^{n} E_i [(G - \bar{G}_i)^2] \quad (6)
\]

where \( E_i \) denotes the expectation in population \( i \). This sum can be rearranged as:

\[
\sigma^2_s = \sigma^2_s + \delta_1 + \delta_2 \quad (7)
\]

with

\[
\sigma^2_s = \frac{1}{n} \sum_{j=1}^{n} \sum_{k=1}^{l} E_i [(X_i^{p})^2] + E_i [(X_i^{o})^2] - 2E_i [\bar{X}_k]^2 \quad (8)
\]

where

\[
\bar{X}_k = \frac{X_i^{p} + X_i^{o}}{2},
\]

\[
\delta_1 = \frac{2}{n} \sum_{i=1}^{n} \sum_{j=1}^{l} \left( E_i [(X_i^{p})^2] + E_i [(X_i^{o})^2] - 2E_i [\bar{X}_k] E_i [\bar{X}_i] \right),
\]

and
\[ \delta_2 = \frac{1}{2} \sum_{n=1}^{N} \sum_{i=1}^{n} \sum_{k=1}^{l} \left( E_i[X_i^2 X_k^2] - E_i[X_i] E_i[X_k] \right). \] (10)

The term \( \sigma_g^2 \) is the expected genic variance at Hardy–Weinberg equilibrium (HWE) and linkage equilibrium, \( \delta_1 \) is the part of the variance contributed by gametic linkage disequilibrium at HWE and \( \delta_2 \) is the part of the variance due to deviations of genotypic frequencies with respect to HWE. Note that \( \delta_1 \) and \( \delta_2 \) are covariance terms and can be negative. Expressions in eqns 8–10 are slightly different from that in Bulmer (1989) to take into account potentially different allelic frequencies in male and female gametes. In particular, with pollen dispersal in heterogeneous environments, \( \delta_2 \) is nonzero even if reproduction is panmictic because of the different allelic frequencies in pollen and ovules.

**Analytical model**

We assume that genotypic values are distributed normally after seed migration and before selection. This is unlikely to hold if both migration and selection are strong. Comparison of the present predictions to simulations will allow measuring the effect of non-Gaussian distribution of phenotypes. We further assume that, before selection, the within-population genotypic variance \( V_g \) varies little around its expected value and does not vary much across populations, so that \( V_g \approx \sigma_g^2 \). Finally, we assume that all loci recombine freely (no physical linkage). Equations for changes of: (i) the mean phenotype \( \tilde{G}_i \) in each local population; (ii) the expected genotypic variance \( \sigma_g^2 \) within populations; and (iii) the genotypic variance between populations \( \sigma_g^2 \) through the life cycle, are given in Appendix S1 (see Supplementary Material). Solving for the equilibrium value of \( \sigma_g^2 \), however, requires computing the effect of selection, drift and migration on complex components of the genotypic variance (see eqns A12–A14 and 7–10), which is out of the scope of the present paper. Instead, we will consider the value of \( \sigma_g^2 \) as a parameter and derive predictions for the divergence between populations \( \sigma_g^2 \) and the mean genetic load \( \lambda \) when the within-population genotypic variance is known (as in Hendry et al., 2001, or Garcia-Ramos & Kirkpatrick, 1997). Evolution of the mean variance in genotypic values within populations \( \sigma_g^2 \) and its components (eqns 7–10) will be studied through simulations.

**Simulations**

In line with the analytical model, we ran individual-centred simulations. Throughout, we use a value of \( \sigma_g^2 \), so that all phenotypic measures are standardized by the environmental standard deviation. We simulate highly or slightly fragmented metapopulations: \( n = 32 \) and \( N = 25 \) or \( n = 4 \) and \( N = 200 \), respectively, so that the metapopulation total size is constant and equal to 800 adults despite different degrees of fragmentation. We do not investigate cases where the local population size is very large. For the sake of simplicity, we assume that there are only two types of habitat with optimal phenotypes \( \theta_1 \) and \( \theta_2 \), respectively (e.g. polluted vs. non-polluted), and an equal number of patches of each type. Note that such symmetry facilitates the maintenance of genetic diversity. Habitat heterogeneity is measured by \( \Delta \theta = \theta_1 - \theta_2 \). We study three levels of landscape heterogeneity corresponding to homogeneous, moderately heterogeneous and highly heterogeneous landscapes with \( \Delta \theta \) values of 0, 1 and 3 respectively. When both seeds and pollen disperse, preliminary simulations showed that results were always intermediate between those obtained for pure pollen grains and pure seed dispersal. To illustrate the effect of the dispersal mode, we therefore show simulation results for these two extreme cases only (pure pollen dispersal \( m_s = 0 \) and pure seed dispersal \( m_p = 0 \)).

In most of the simulations presented here, we assume that the trait value is determined by 10 freely recombining loci. Simulations were also run for two, five and 30 loci with little qualitative or quantitative differences (results not shown). To illustrate the effect of physical linkage, we also present results with 10 linked loci, with a recombination probability of 0.01 between adjacent loci. The number of alleles segregating simultaneously at each locus is not limited. Mutation creates a new allele with an allelic effect obtained as the sum of the parental allelic effect and a normally distributed deviation with mean 0 and variance \( \sigma^2 \). Mutations occur independently at each locus on each gamete with probability \( \mu \). According to estimates from mutation–accumulation studies (e.g. Shaw et al., 2002), we used two values for the diploid genomic mutation rate \( (U = 2l\mu = 10^{-2} \text{ or } 10^{-1}) \), which represents the expectation for the number of new mutations of a diploid zygote. We standardized values of \( \sigma^2 \) so the total variance introduced by mutation \( \sigma_m^2 = U\sigma^2 \) is constant and \( \sigma_m^2 = 10^{-2} \sigma^2 \) as suggested by the literature (see, e.g. Bürger et al., 1989). Thus, we simulate either rare mutations with large effects on the phenotype, or more frequent mutations with smaller effects. We use a rather high intensity of selection, \( \omega = 1 \) (which is, however, compatible with some empirical estimations, see discussion in Johnson & Barton, 2005). Ovule production is Poisson distributed with expectation \( F = 12 \) per individual. All ovules are fertilized and \( F \) is sufficiently large to ensure that the number of surviving juveniles in the simulations is always greater than the carrying capacity and that the number of adult plants per patch is constant.

We used the batch method for Markov chains (Hastings, 1970) to obtain estimates and confidence intervals for variables of interest (see complete description in Appendix S2). We checked the validity of our simulation programme by comparing its results with analytical predictions and previously published simulation results. We ran simulations with a single isolated population and verified that, when using the same parameter values as in Bürger et al. (1989), the estimated variance in our simulations was in...
close agreement with that observed in their simulations (see their Table 1). We also compared estimates of the within-population genotypic variance with predictions of the ‘Stochastic house-of-card approximation’ (SHOC, Bürger et al., 1989). The estimated genotypic variance in our simulations was, in general, close to the SHOC approximation. Yet, when both population size and mutation rate were large \( (N = 200, \ U \geq 10^{-1}) \) and the number of loci was not very large \( (l < 50) \), the estimated genotypic variance was overestimated by the SHOC approximation. We also ran simulations with a neutral quantitative character and compared the mean local genotypic variance at equilibrium, the variance in genotypic values between populations and the time to reach this equilibrium to analytical approximations derived by Lande (1992), and to more exact analytical results derived in the case of pollen and seed dispersal. We obtained a very good agreement between our simulation results and the analytical predictions in the neutral case (data not shown).

### Results

#### Divergence between populations when the genotypic variance is known

**Analytical predictions**

Let us first assume that the within-population genotypic variance at equilibrium \( (\hat{\sigma}_g^2) \) is known. Then, solving eqn A19 and recursions (eqns A4–A18, Appendix S1) shows that the expected value of the mean genotypic value in population \( i \) at equilibrium is:

\[
\hat{E}[\hat{G}_i] = \hat{\theta}(1 - \hat{m}_i) \frac{\hat{\sigma}_g^2}{\hat{m}_i \hat{\sigma}_i^2 + \hat{\sigma}_g^2},
\]

where

\[
\hat{m}_i = \hat{m} + \frac{\hat{m}_p}{2} (1 - \hat{m}_i), \quad \hat{m}_p = \frac{n}{n - 1} m_p \quad \text{and} \quad \hat{m}_s = \frac{n}{n - 1} m_s.
\]

The term \( \hat{m}_i \) in eqn 12 can be interpreted as the net migration rate, which takes into account gene copies introduced by immigrant seeds and those introduced by immigrant pollen having fertilized nondispersed seeds. The migration rate of pollen must be twice that of seeds to achieve the same level of gene flow. Pollen and seed dispersal rates are furthermore rescaled as functions of the number of demes (see eqn 12). Equation (11) leads to the same prediction about divergence in mean phenotype as eqn 8 in Hendry et al. (2001). In particular, the expected mean phenotype in population \( i \) depends on the net migration rate, but not on how pollen and seeds contribute to such migration rate. The mean phenotype is closer to the local optimum if the net migration rate is low, the intensity of selection high \( (\hat{\sigma}_i^2) \) smaller) and the within-population genotypic variance high.

By substituting into eqn A6 and solving recursions (eqns A5–A18, Appendix S1), we obtain the between-population variance at equilibrium as a function of the within-population genotypic variance. Differentiation between populations for quantitative traits is classically measured through statistics such as \( Q_{ST} \) (e.g. Bonnin et al., 1996), which are functions of the ratio of between- and within-population variances \( \hat{\sigma}_b^2/\hat{\sigma}_g^2 \). The expression for \( Q_{ST} \) also depends on \( F_{ST} \) (Bonnin et al., 1996, Appendix), which itself depends on the selfing rate and dispersal rates (Rousset, 2004, p. 132). Here, we simply compute \( \hat{\sigma}_b^2/\hat{\sigma}_g^2 \) as a standardized measure of between-population differentiation:

\[
\frac{\sigma_b^2}{\sigma_g^2} = \frac{(n - 1)(1 - \tilde{m}_i)^2}{n N \tilde{m}_i (2 - \tilde{m}_i)} \quad \text{when} \quad \sigma_g^2 \to +\infty, \quad (14)
\]

Equation (13) predicts that differentiation between populations increases with increasing variance in optimal phenotypes \( \sum_{i=1}^{n} \theta_i^2/n \) and decreasing patch size \( N \) (see also Fig. 1). Differentiation is predicted to depend only on the net migration rate, independent of the allocation between seed and pollen dispersal. It declines with increasing migration. Increasing the genotypic variance within populations \( \hat{\sigma}_g^2 \) has nonmonotone effects on the differentiation between populations. When the migration rate is very low, differentiation decreases with increasing genotypic variance within populations (see Fig. 1). Conversely, differentiation increases with increasing genotypic variance within populations when the migration rate is large (Fig. 1). When selection is weak \( (\sigma_i^2 \) is very large), we can verify that differentiation between populations tends towards that expected under neutrality of the phenotypic trait, i.e.

\[
\frac{\hat{\sigma}_b^2}{\hat{\sigma}_g^2} \to \frac{(n - 1)(1 - \tilde{m}_i)^2}{n N \tilde{m}_i (2 - \tilde{m}_i)} \quad \text{when} \quad \sigma_g^2 \to +\infty, \quad (14)
\]

which is consistent with earlier results (Rousset, 2004, equation 8.16).

In the presence of disruptive selection between populations \( \sum_{i=1}^{n} \theta_i^2/n \neq 0 \) but stabilizing selection within populations \( (\sigma_i^2 \) small), differentiation between populations for selected traits as predicted by eqn 13 is larger than for neutral traits (eqn 14) when the migration rate is large. When the migration rate is low, however, differentiation between populations for selected traits may be lower than that expected under neutrality of the trait, despite the divergent selection.

**Comparison with simulations**

To check on the accuracy of our predictions, we used the estimated genotypic variance measured in the simulations \( \hat{\sigma}_g^2 \) to compute the differentiation between populations using eqn 13 and compared these predictions to the estimated differentiation between populations from the simulations. Our aim here is not to assess, through simulations, the validity of the predicted relationship between \( \hat{\sigma}_b^2/\hat{\sigma}_g^2 \) and \( \hat{\sigma}_g^2 \) for all values of the latter
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Fig. 1 Between-population differentiation measured by the ratio of between- to within-population genotypic variance $\hat{r}_y^2/\hat{r}_g^2$ as a function of mean within-population genotypic variance $\hat{r}_g^2$ in different landscapes. Lines are analytical predictions from eqn 13, for different values of the net migration rate. Open (filled) symbols correspond to simulation results with pure pollen (seed) dispersal, for two values of the genomic mutation rate ($U = 10^{-2}, 10^{-3}$) and five values of the net migration rate; crosses and continuous lines: $\hat{m}_t = 0$; squares and dotted lines: $\hat{m}_t = 10^{-1}(n/(n-1))$; circles and short-dashed lines: $\hat{m}_t = 10^{-2}n/(n-1)$; triangles and dot-dashed lines: $\hat{m}_t = 10^{-1}n/(n-1)$; diamonds and long-dashed lines: $\hat{m}_t = 2 \times 10^{-1}n/(n-1)$. Left panels (a,c,e) show moderately fragmented landscapes of $n = 4$ populations of $N = 200$ individuals. Right panels (b,d,f) show highly fragmented landscapes of $n = 32$ populations of $N = 25$ individuals. Habitat heterogeneity increases from top to bottom: (a,b) $\Delta \theta = 0$, (c,d) $\Delta \theta = 1$, (e,f) $\Delta \theta = 3$. Free recombination between loci. Confidence intervals are smaller than size of symbols. Confidence intervals on the x-axis range from $10^{-4}$ to $9 \times 10^{-3}$. Some simulation points are missing (20 over 120 parameters sets) due to lack of convergence to a stable equilibrium (see Appendix S2). Missing points correspond to the following parameter sets: ($N = 25$, $n = 32$, $\hat{m}_t = 10^{-3} \times 32/31$, for all values of the seed dispersal rate, mutation rate and habitat heterogeneity) ($N = 200$, $\hat{m}_t = 10^{-1} \times 4/3$, $U = 10^{-1}$, for all values of the seed dispersal rate and habitat heterogeneity) ($N = 200$, $\hat{m}_t = 10^{-3} \times 4/3$, $U = 10^{-2}$, $\Delta \theta = 3$ only for pure pollen dispersal) ($N = 200$, $\hat{m}_t = 10^{-2} \times 4/3$, $U = 10^{-1}$, $\Delta \theta = 3$ only for pure seed dispersal).
parameter. In particular, only a limited range of values for $$$r^2_g$$ are biologically relevant for a given landscape structure and genetic architecture. Instead, we compare the deviation between analytical predictions and simulation results for a discrete number of parameter sets. This comparison helps us to evaluate the effect of deviations from a Gaussian distribution of genotypic values. Figure 1 shows that eqn 13 performs best when habitat heterogeneity is moderate and local population size is large. A very good quantitative agreement is then found for both pure pollen dispersal and pure seed dispersal. In general, eqn 13, however, underestimates differentiation between populations when migration is large, especially when habitat heterogeneity is large (Fig. 1). Whereas between-population differentiation observed in the simulations is very similar for pure pollen and pure seed dispersal when habitat heterogeneity is moderate, observed differentiation is higher with seed dispersal in strongly heterogeneous landscapes. It appears that seed dispersal causes stronger departures from model predictions in strongly heterogeneous landscapes than pollen dispersal does. Quantitative differences between the two modes of dispersal remain, however, small.

### Genetic load when the genotypic variance is known

#### Analytical predictions

Using eqn 11 and assuming that the mean phenotype in population $$i$$ varies little around its expected value, the expected mean fitness in population $$i$$ can be approximated by:

$$E[W_i] \approx \frac{\exp \left( -\frac{1}{2} \left( \frac{\sigma^2_i}{r^2_s + \sigma^2_g} \right) \right)}{\sqrt{2\pi (\sigma^2_s + \sigma^2_g)}}.$$

(15)

Note that such approximation should be less accurate when local population size is small and the mean phenotype fluctuates widely around its expected value because of drift. Equation (15) predicts that, for a given within-population genotypic variance $$\sigma^2_g$$, the local genetic load depends only on the net migration rate $$\tilde{m}_t$$ and not on how pollen and seed dispersal contribute to total gene flow. In particular, eqn 15 predicts that the genetic load always increases with increasing net migration rate $$\tilde{m}_t$$ when the genotype variance is held constant (see also Fig. 2). Equation (15) also suggests that the genetic load decreases with increasing genotypic variance when such variance is low, but increases again

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**Fig. 2** Mean genetic load as a function of mean within-population genotypic variance $$\sigma^2_g$$ in different landscapes. Lines are analytical predictions from eqn 15, for different values of the net migration rate. Open (filled) dots correspond to simulation results with pure pollen (seed) dispersal for two values of the mutation rate ($$U = 10^{-2}, 10^{-1}$$) and five values of the migration rate (same values of the migration rate and associated symbols as in Fig. 1). Left panels (a,c,e) show moderately fragmented landscapes of $$n = 4$$ populations of $$N = 200$$ individuals. Right panels (b,d,f) show highly fragmented landscapes of $$n = 32$$ populations of $$N = 25$$ individuals. Habitat heterogeneity increases from top to bottom: (a,b) $$\Delta \theta = 0$$, (c,d) $$\Delta \theta = 1$$, (e,f) $$\Delta \theta = 3$$ Free recombination between loci. Confidence intervals are smaller than size of symbols. Confidence intervals on the x-axis range from $$10^{-4}$$ to $$9 \times 10^{-1}$$. Missing data points are as in Fig. 1.
with higher level of variance as illustrated in Fig. 2. Such nonmonotone patterns of variation of the genetic load with increasing genotypic variance are predicted for intermediate dispersal rates in heterogeneous landscapes. The genetic load is predicted to increase with increasing habitat heterogeneity.

**Comparison with simulations**

As previously with between-population differentiation, Fig. 2 shows that eqn 15 performs best when habitat heterogeneity is moderate and local population size is large. Genetic load observed in the simulations is in particular very similar for pure pollen and pure seed dispersal when habitat heterogeneity is moderate. Genetic load in small isolated populations is underestimated by eqn 15. Deviations from analytical predictions are, however, small in moderately heterogeneous landscapes even for small populations. When habitat heterogeneity is large, for both small and large local population size, eqn 15 greatly overestimates the genetic load and more strikingly so in the case of pure seed dispersal than for pure pollen dispersal (Fig. 2). In the range of parameters used in the simulations, genetic variance evolves to levels such that genetic load always increases with the local genetic variance (Fig. 2). Even with unrealistically low mutation rates (results not shown), intermediate migration rates in heterogeneous landscapes help maintain relatively large amounts of within-population variance in our model, so that situations predicted by eqn 15, where genetic load decreases when genetic variance increases were never observed.

The observed distribution of phenotypic values within a population before selection (Fig. 3) strongly deviates from a Gaussian distribution, for both pure seed and pollen dispersal when habitat heterogeneity is high. In particular with pure seed dispersal in strongly heterogeneous landscapes, the distribution of phenotypes is characterized by a fat tail, corresponding to immigrants from a different habitat, which are clearly distinct from the local resident population.

Figure 4 compares the mean genetic load at the scale of the metapopulation for pure pollen and pure seed dispersal as a function of habitat heterogeneity. As habitat heterogeneity increases, the genetic load caused by pollen migration is always higher than with pure seed dispersal. Contrary to our analytical prediction, above some level of heterogeneity, the genetic load eventually decreases as habitat heterogeneity increases in the case of seed dispersal while it reaches a plateau for pollen dispersal.

**Effect of pollen and seed dispersal on the genotypic variance**

**Analytical predictions**

Our analytical model does not allow us to solve for the within-population genotypic variance at equilibrium. Equations A11–A18, Appendix S1, however, give some
insights about the effect of pollen and seed dispersal on the evolution of the within-population genotypic variance. Consider the case of pure pollen dispersal \((\bar{m}_p = 0)\). Then eqn A18 reads:

\[
\sigma_g^2(4) = \frac{\sigma_0^2(2)}{2} - \frac{\rho^2}{2} + \frac{\sigma_\tau^2(2)}{2} + \frac{\bar{m}_t}{1 - \bar{m}_t} \sigma_y,
\]

where \(\sigma_g^2(2)\) and \(\sigma_g^2(4)\) are the within-population genotypic variance, respectively, in adults before dispersal and in juveniles after dispersal, \(\sigma_\tau^2\) is the between-population genotypic variance at equilibrium as given by eqn 13, and \(\sigma_\tau^2(2) - \rho^2\) is a complex term which varies with the genic variance and deviations from HWE in adults after selection (see eqn A13). Conversely, with pure seed dispersal \((\bar{m}_p = 0)\), eqn A18 becomes:

\[
\sigma_g^2(4) = \frac{\sigma_0^2(2)}{2} - \frac{\rho^2}{2} + \frac{\sigma_\tau^2(2)}{2} + \frac{\bar{m}_t(2 - \bar{m}_t)}{(1 - \bar{m}_t)} \sigma.
\]

Seed dispersal is therefore predicted to introduce more genotypic variance within populations than pollen dispersal for the same net migration rate. This is because a large part of the total genotypic variance is contained within hybrid individuals, rather than between individuals, after pollen dispersal and syngamy.

Equations (16–17) further suggest that the variance due to migration does not increase monotonically with dispersal, as \(\sigma_g^2\) itself decreases with increasing migration (see previous section about divergence between populations). Yet, fully understanding how pollen and seed dispersal affect the evolution of the genotypic variance requires describing their effects on each of the different components of the genotypic variance (in particular computing the term \(\sigma_0^2(2) - \rho^2\)), which our analytical model does not explore. We therefore resort to simulations to investigate this question.

Simulations results

Figure 5 compares the within-population genotypic variance and its components \((\sigma_0^2, \delta_1\) and \(\delta_2\)) as a function of landscape heterogeneity \(\Delta \theta\), in the cases of pure pollen or pure seed dispersal. In the case of pure pollen dispersal, the amount of genic variance \(\sigma_0^2\) represents the major component of genotypic variance (Fig. 5) and increases regularly with landscape heterogeneity. The two other components are negative and comparatively weak in magnitude. The component of variance due to deviations from panmixia \(\delta_2\) decreases as habitat heterogeneity increases (Fig. 5). With pure seed dispersal, we observe a different pattern. Genic variance \(\sigma_0^2\) is always smaller with pure seed dispersal than with pure pollen dispersal. It is maximal for intermediate habitat heterogeneity. Contrary to the case of pollen dispersal, in highly heterogeneous landscapes, the other components of variance \((\delta_1\) and \(\delta_2\)) are positive and grow large as habitat heterogeneity increases (Fig. 5).

Therefore, in moderately heterogeneous landscapes, higher total genotypic variance with pollen dispersal results from a higher genic variance. On the contrary, in highly heterogeneous landscapes, seed dispersal generates strong positive linkage disequilibrium and heterozygote deficiency, inflating the genotypic variance above that expected with pollen dispersal. Note that, even though the components of genotypic variance are widely different between the two dispersal modes, their combined effects lead to very similar level of total variance. For both modes of dispersal, total genotypic variance increases with landscape heterogeneity.

![Fig. 5 Within-population genotypic variance and its components as a function of landscape heterogeneity and dispersal mode in a highly fragmented landscape of 32 populations of 25 individuals. Open (filled) symbols correspond to pure pollen (pure seed) dispersal. (a) Total within-population genotypic variance \((\sigma_g^2)\), (b) mean genic variance at HWE \((\sigma_0^2)\), (c) mean part of the genotypic variance contributed by gametic linkage disequilibrium at HWE \((\delta_1)\), (d) mean part of the variance due to deviations of genotypic frequencies with respect to HWE \((\delta_2)\). See eqns 7–10 for definitions. Genomic mutation rate \(U = 0.01\). Free recombination between loci. Net migration rate \(\bar{m}_t = 0.1 \times 32/31\). Confidence intervals are smaller than plotting symbols.](image)
Increasing the migration rate has the same qualitative effect on within-population genotypic variance with pure seed dispersal and pure pollen dispersal (results not shown). In homogeneous landscapes, low migration rates raise the genotypic variance much above that expected in isolated populations (Fig. 6a). Yet, a critical threshold in migration is soon reached, such that genotypic variance decreases with higher migration rate and converges again towards levels expected in isolated populations (Fig. 6). As habitat heterogeneity increases, migration increases the within-population genotypic variance more strongly and the critical migration threshold, above which the genotypic variance starts to decrease, is much higher (Fig. 6). The evolution of the genic variance \( \sigma_n^2 \) as a function of the migration rate follows identical patterns and contributes the major part of the genotypic variance (Fig. 6). The component of variance due to gametic linkage disequilibrium \( \delta_1 \) contributes little to the total genotypic variance: it is negative in isolated populations, reaches a minimum for low migration rates and becomes positive only in highly heterogeneous landscapes with high rates of seed dispersal (Fig. 6). The contribution of deviations from HWE genotypic frequencies \( \delta_2 \) to the total genotypic variance increases with seed migration rate in highly heterogeneous landscapes (Fig. 6d).

**Effect of physical linkage on genetic load and genotypic variance**

We also investigated the effects of physical linkage between loci involved in local adaptation, using simulations. The effect of physical linkage on the genetic load and genotypic variance depends on the mutation rate and is noticeable only when habitat heterogeneity is not too high (see Fig. 7). Physical linkage affects the evolution of genotypic variance and genetic load, but similarly for seed and pollen dispersal and conclusions about differences between the two modes of dispersal are unaffected (results not shown). When the mutation rate is high, both the genetic load and genotypic variance are higher when the loci are freely recombining than when they are physically linked. The reverse is true when the mutation rate is low. Figure 7 shows that this pattern is due to the fact that: (i) linkage increases the genic variance \( \sigma_n^2 \), but decreases the component of genotypic variance due to gametic linkage disequilibrium \( \delta_1 \) (linkage disequilibrium, which is negative, increases in
absolute value); (ii) the proportional contribution of \( \delta_1 \) to the total genotypic variance is higher when the mutation rate is higher. Therefore, the negative effect of linkage on the evolution of the genotypic variance dominates when the mutation rate is high, and smaller within-population genotypic variance then causes less genetic load.

**Discussion**

Using analytical predictions and individual-centred simulations, we studied the impact of dispersal on the within-population genotypic variance, population differentiation and mean genetic load and investigated how the dispersal mode (through seeds or pollen grains) or the level of landscape heterogeneity affect the results.

**Effect of seed vs. pollen dispersal on genetic load and between-population differentiation**

Our analytical model predicts that, for a given net migration rate, the dispersal mode should affect neither the mean genetic load nor the differentiation between populations, provided that similar levels of within-population genotypic variance evolve for various rates of pollen and seed dispersal. For one locus, previous models have also found that spatial changes in allelic frequencies in plant populations under selection could be described as in animal models when pollen and seed dispersal parameters are aggregated in some appropriate combination (Nagylaki, 1997; Hu & Li, 2001). Our simulations confirm in part such predictions, as the effect of the dispersal mode on either the within-population variance, the between-population differentiation or the genetic load, was very small for most of the range of parameters explored. In highly heterogeneous landscapes, however, the genetic load was greater and the differentiation between populations was smaller with pollen dispersal than with seed dispersal. Selection thus better opposes the effect of gene flow when seeds disperse rather than pollen. This increased efficacy of selection is not simply due to differences in genotypic variance, as our analytical model based on a Gaussian distribution of phenotypes largely underestimates the difference in genetic load between seed and pollen dispersal (Fig. 4). Instead, differences in distribution of genotypic values before selection could be involved. This is reminiscent of results obtained by Ronce & Kirkpatrick (2001), who found that the deleterious effects of dispersal on maladaptation depended on the
relative order of migration and recombination affecting the distribution of genotypic values before selection. In highly heterogeneous landscapes, individuals originating from migrant seeds from the wrong habitat indeed represent a separate class of phenotypes (Fig. 3). For extreme values of habitat heterogeneity, most immigrants may be so distant from the local optimum that they are eliminated immediately after migration. Under the assumptions of our simulations, the genetic load is then expected to converge toward the immigration rate from the wrong habitat, i.e. to $m_t/2$, in the case of pure seed dispersal (Fig. 4). In the case of pollen dispersal, badly adapted immigrant alleles are counter-selected only as heterozygotes together with locally fit alleles. At values of landscape heterogeneity for which most immigrant seeds fail to recruit, many of the heterozygous individuals derived from immigrant pollen survive, which introduces maladapted genes within local populations and increases the genetic load. Effective migration rate is thus higher with pollen than with seed dispersal. The second consequence of pollen dispersal is that twice the number of selective deaths is necessary to eliminate maladapted alleles from the population just after migration than with seed dispersal. With pollen dispersal, the limit value of the genetic load when habitat heterogeneity increases is thus twice that expected with seed dispersal. Consequences for the joint evolution of seed and pollen dispersal (see Ravigné et al., 2006) in presence of local adaptation loci (see Billiard & Lenormand, 2005) deserve further exploration. Our model does not consider selling in excess that expected under random mating in a self-compatible species. Higher selling rate would decrease the amount of gene flow achieved by pollen dispersal. Higher homozygosity due to inbred mating might also result in the distribution of genotypic values deviating more strongly from a Gaussian distribution in heterogeneous landscapes. We can therefore conjecture that increasing the selling rate would have comparable qualitative effects on genetic load and genetic variance as increasing the contribution of seeds migration to gene flow.

**Effect of seed vs. pollen dispersal on genotypic variance**

The overall effect of the dispersal mode on within-population genotypic variance is relatively small in the range of parameters explored in this study. Dispersal mode has, however, strong opposite effects on different components of the genotypic variance. Genic variance is higher in the case of pollen dispersal compared with seed dispersal because of the higher effective immigration rate with pollen in heterogeneous landscapes and the more efficient removal of maladapted alleles with seed dispersal (see above). Conversely, heterozygote deficiency generated by seed dispersal inflates the genotypic variance considerably in heterogeneous landscapes. Greater differentiation between populations with seed dispersal also results in greater contribution of gametic disequilibrium to genotypic variance. Whereas only weak contributions to genotypic variance arise from gametic linkage disequilibrium ($\delta_1$) and deviation of genotypic frequencies from HWE ($\delta_2$) in the case of pure pollen dispersal, $\delta_1 + \delta_2$ can reach up to 80% of the total variance in very heterogeneous landscapes for pure seed dispersal. Such components of variance appear to be quickly converted in genic variance with pollen dispersal. These different effects of the dispersal mode on different components of the genotypic variance, however, largely compensate each other, leading to values of local genotypic variance very similar for pure seed or pure pollen dispersal. The robustness of this surprising outcome of our simulations remains to be confirmed by further analytical studies. Hu & Li (2001) showed that, for a trait under the control of a major locus, the ratio of pollen to seed dispersal affected the shape and position of clines in additive and dominance variance along some sharp environmental transition, as well as spatial pattern in deviation of genotypic frequencies with respect to HWE. The mechanisms underlying the specific effects of pollen and seed dispersal were not discussed explicitly. Our model considers only additive effects of alleles on the phenotype expression. Effects of seed and pollen dispersal on the expression of genotypic variance might be different in the presence of dominance interactions between alleles.

**Effect of habitat heterogeneity**

The global influence of the level of habitat heterogeneity on genetic load or within-population genotypic variance was much higher than the effect of the dispersal mode. Local genotypic variance increases with landscape heterogeneity in our simulations, in agreement with Yeaman & Jarvis’ (2006) experimental work on populations of lodgepole pine. We also showed, both analytically and with our simulation model, that an increase in habitat heterogeneity always led to higher levels of population differentiation. This contrasts with predictions of theoretical models taking into account feedback between population dynamics and local adaptation, which have shown that beyond some critical level of habitat heterogeneity, differentiation between populations collapsed (Kirkpatrick & Barton, 1997; Ronce & Kirkpatrick, 2001; Holt et al., 2003). Strong assumptions about symmetry in our simulations prevent us to witness phenomena of gene swamping from a particular habitat type. We found that the genetic load can increase and then decrease with increasing habitat heterogeneity, as observed with seed dispersal. Genetic load decreases in highly heterogeneous landscapes when selection against migrants is so strong that maladapted alleles do not introgress into the local population, which is not predicted by analytical models based on a Gaussian distribution of phenotypic values.
Effect of migration on differentiation between populations

In agreement with other studies (see, e.g. Hendry et al., 2001 for theoretical predictions, and Hendry & Taylor, 2004 for empirical results), we found a negative relationship between the level of gene flow and differentiation between populations. Differentiation in our model results from both genetic drift and divergent selection in different habitats. It is opposed by gene flow and stabilizing selection within habitats. Interestingly, our model predicts that differentiation between populations for a selected character could then be larger or smaller than for a neutral character depending on the migration rate, a result also observed in simulations by Le Corre & Kremer (2003). The implications of these findings for inferences about divergent selection based on $Q_{ST}$–$F_{ST}$ comparisons (e.g. Porcher et al., 2006, for more references see Latta, 2006) deserve further exploration.

Effect of migration on the maintenance of genetic variation within populations

Whereas stabilizing selection tends to reduce variability within populations, levels of quantitative variation found in natural populations are usually high (for a general review see Johnson & Barton, 2005). A putative mechanism for the maintenance of variation invokes the effect of gene flow between genetically differentiated populations. Using a model of stabilizing selection, Phillips (1996) showed that migration can serve as a source of variation in the same way as mutation does, even in a homogeneous environment. This is due to genetic redundancy and local drift, which maintain different genotypes with similar phenotypes in different localities (see Goldstein & Holsinger, 1992). Mixing then increases the local genotypic variance but, as no strong evolutionary force opposes the homogenizing effect of migration, a critical migration rate is soon reached so that differentiation between populations vanishes (see also Lythgoe, 1997).

In homogeneous landscapes, we indeed showed that within-population genotypic variance reaches a maximum for very low dispersal rates, in good agreement with these previous results. In heterogeneous landscapes, however, selection opposes the effect of gene flow on differentiation more strongly. The critical migration threshold increases dramatically with habitat heterogeneity, which is in agreement with results obtained by Tufto (2000) (see his Fig. 2b). Note, however, that demographical asymmetries in heterogeneous landscapes could much decrease such critical migration rate. Our simulations showed that genotypic variance before selection could be multiplied by a factor of 30 due to the effect of migration in highly heterogeneous landscapes. This suggests that migration could be a major force maintaining high levels of genotypic variance despite stabilizing selection, as suggested by the data collected by Yeaman & Jarvis (2006).

Effect of migration on the genetic load

The overall influence of migration on the genetic load is difficult to predict a priori. Ignoring the effect of migration on genotypic variance, our analytical model predicts that the genetic load increases with increasing dispersal. We also found that increasing gene flow has nonmonotone effects on the level of within-population genotypic variance, which, in turn, has a nonmonotone effect on the genetic load. Overall, simulations suggest that the genetic load generally increases with increasing dispersal rates. Genetic load was sometimes observed to decline with increasing migration in homogeneous landscapes, but it was largely explained by the decrease in genotypic variance when migration was above a critical threshold. In heterogeneous landscapes, we observed no instance when increasing migration improved the mean fitness in small populations, as found in species margins by previous simulation studies (Holt et al., 2003; Alleaume-Benharira et al., 2006). This suggests that demographic asymmetries included in the latter studies, but not in the present model, are critical to the observation of such rescue effects of dispersal. Finally, genetic load has no demographic consequences under the assumptions of our model. An important perspective of this work would be to incorporate feedbacks between population dynamics and genetics to predict the effect of seed and pollen migration for the persistence of populations in heterogeneous landscapes.

Effect of physical linkage between loci

We investigated whether physical linkage can alter the general results obtained for unlinked loci. We show that linkage does not affect the general conclusions concerning the influence of the dispersal mode. For limited habitat heterogeneity, it, however, influences the level of within-population genotypic variance and hence the genetic load. This effect is due to contrasting effects of linkage on different components of the genotypic variance, leading to an increase or a decrease in the local variance depending on the relative contribution of linkage disequilibrium to total within-population genotypic variance. This phenomenon deserves more detailed investigations.

Implications for analytical models

Analytical predictions about the effect of gene flow on the evolution of genotypic variance for polygenic characters under stabilizing selection are difficult to obtain and generally rely on strong assumptions (see Barton, 1999). Two extreme models are often considered. The infinitesimal model assumes that the local
genic variance at linkage equilibrium is constant and that most changes in genotypic variance are due to changes in linkage disequilibrium (for applications in the case of dispersal in heterogeneous landscapes see, e.g. Barton, 1999; Tufto, 2000). Conversely, some other models neglect the contribution of linkage disequilibrium to the genotypic variance altogether (see also Barton, 1999). In the range of parameters explored in our simulations, the latter approach appears more appropriate as genic variance contributed to a large part of the total genotypic variance and responded strongly to habitat heterogeneity, dispersal intensity and mode of dispersal. Gametic linkage disequilibrium, however, makes significant contribution to genotypic variance in highly heterogeneous landscapes with seed dispersal. Finally, our model also suggests that deviation of genotypic frequencies from HWE in the case of pollen and seed dispersal could significantly alter the evolution of the genotypic variance, which is little studied by available analytical approaches (see, however, Hu & Li, 2001).

In agreement with Tufto (2000), we showed that, except for high levels of landscape heterogeneity and dispersal intensity, a model assuming a Gaussian distribution of genotypic values before selection produces reasonably accurate predictions for the mean genetic load and between populations differentiation when the local variance is known. In highly heterogeneous landscapes, violation of this assumption has more important consequences: analytical models based on the Gaussian assumption largely overestimate the genetic load and underestimate differentiation between populations.

**Implications for empirical studies**

Altogether, we showed that the dispersal mode has a rather small influence on local adaptation, unless the landscape is very heterogeneous. It means that, in general, species with different dispersal modes are unlikely to show consistent strong differences in migration load. In the rare endangered *Centaurea corymbosa* and *Brassica insularis*, gene flow among extant populations is extremely rare (Hurtrez-Bousses, 1996; Fréville et al., 2001; Wilson & Rannala, 2003) and there is evidence that loss of genetic diversity in some populations may compromise their persistence (Glémí et al., 2005). Human-mediated gene flow might be considered as a management practice to improve the long-term viability of such species. In the absence of evidence for strong disruptive selection among populations (Petit et al., 2001), our model suggests that the choice of transferring pollen or seeds should depend on other considerations than their putative effects on local adaptation.

Situations with strongly divergent selection between sites and relatively large gene flow are more favourable to observing large differences in migration load depending on dispersal mode. In this case, gene flow mediated by pollen is expected to be more harmful than seed flow, with regard to local adaptation. Our model then predicts that anemophilous plants with pollen dispersal over large spatial scales (like many tree species) might suffer from higher migration load than plants with reduced pollen dispersal but higher seed dispersal (e.g. autogamous plants). Some introgressions between cultivated plants and their wild relatives present a combination of high gene flow and strongly divergent selection on domestication traits (Ellstrand, 2003). Gene flow from cultivated rice *Oryza sativa* has, for instance, been shown to result in decreased fitness in wild endemic rice populations of *Oryza rufipogon* (Ellstrand, 2003). Gene flow between cultivated and wild species is, in general, mediated by pollen flow, as crop species have been selected for reduced seed dispersal during domestication. Our model predicts that pollen flow from abundant crops may cause more genetic pollution than if seeds escape from cultivated fields, even if seeds and pollen disperse at the same distance. Plant communities found on heavily contaminated soils are also candidate case studies with strong divergent selection and potentially large gene flow. Most species in such communities are indeed also found on normal soils, sometimes at a short distance from contaminated sites (Escarre et al., 2000), and have developed ecotypes specialized on contrasting edaphic conditions, as documented, for instance, in *T. caerulescens* (Jimenez-Ambriz et al., 2007). Studying the distribution of dispersal syndromes in such communities, as well as contrasting the pattern of differentiation for traits under divergent selection to the differentiation for nuclear and cytoplasmic neutral molecular markers (using *Q*\_S\_T vs. *F*\_S\_T comparisons, for instance) may help to assess the relative importance of pollen and seed migration in constraining local adaptation. Finally, our model predicts that restoration of genetic diversity through artificial gene flow in endangered species showing strong patterns of local adaptation is more likely to succeed if pollen flow is increased, rather than seed migration, due to the more difficult introgression in the latter case and to the faster breakage of linkage disequilibrium between locally mal-adapted alleles and beneficial migrant alleles in the former (Papa et al., 2005).

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Supplementary material

The following supplementary material is available for this article:

Appendix S1 Changes in mean phenotype and intra- and inter-population variance through the life cycle.

Appendix S2 Method for the analysis of simulation results.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/abs/10.1111/j.1420-9101.2007.01442.x

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