

# **Supplementary Information for “On the evolution of migration in heterogeneous environments”**

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# Supplementary Information A. Evolution of the variables in one deme through the life cycle

We will follow the frequencies of the 4 genotypes ( $X_{i,j}$  where  $j = am, Am, aM, AM$  stands for the frequencies of the corresponding genotypes in deme  $i$ ) in one deme over one generation.

## A1. Sex and reproduction

Sex:

Adults encounter at random within their local deme and reproduce. The genotype frequencies after sex and recombination (subscript “S”) are given by:

$$X_{i,am}^S = X_{i,am} - \psi d_i$$

$$X_{i,Am}^S = X_{i,Am} + \psi d_i$$

$$X_{i,aM}^S = X_{i,aM} + \psi d_i$$

$$X_{i,AM}^R = X_{i,AM} - \psi d_i$$

where  $d_i = X_{i,am}X_{i,AM} - X_{i,aM}X_{i,Am}$  is the linkage disequilibrium between the two loci in the deme  $i$ , and  $\psi$  is the recombination rate. These events do not change allele frequencies, but decay the linkage disequilibrium by a factor  $(1 - \psi)$ .

Selection:

Following sex, a number of juveniles is produced. The number of juveniles of each genotype after reproduction (superscript “R”) is given by:

$$N_{i,am}^R = f(1 + s_{a,i,t})X_{i,am}^R$$

where  $f$  is the baseline fecundity and  $s_{a,i,t}$  and  $s_{A,i,t}$  is the additional fecundity for loci  $a$  and  $A$  respectively, in deme  $i$  at time  $t$ .

## A2. Migration

Following reproduction, adults die and the juveniles migrate in a deme chosen at random (island model). The modifier locus determines the migration rate, such that the  $m$  and  $M$  genotypes migrate at rates  $m$  and  $m + \Delta m$  respectively. The numbers of genotypes in deme  $i$  after migration (superscript “M”) are thus:

$$N_{i,am}^M = (1 - m)N_{i,am}^R + m N_{am}^R$$

$$N_{i,Am}^M = (1 - m)N_{i,Am}^R + m N_{Am}^R$$

$$N_{i,aM}^M = (1 - m - \Delta m)N_{i,aM}^R + (m + \Delta m) N_{aM}^R$$

$$N_{i,AM}^M = (1 - m - \Delta m)N_{i,AM}^R + (m + \Delta m) N_{AM}^R$$

where the  $N_j^R$  are the average number of individuals per deme of genotype  $j$  in the metapopulation. Of course, the frequency of genotype  $j$  in deme  $i$  is then given by

$$X_{i,j}^M = \frac{N_{i,j}^M}{\sum_k N_{i,k}^M}$$

### A3. Population regulation

Following migration, the population is regulated within each deme to  $N$  individual. This event does not change genotype frequencies on average but it introduces a sampling variance (genetic drift). We model the change in genotype frequencies following regulation as:

$$X_{i,j}^D = X_{i,j}^M + \xi_{i,j}$$

$\xi_{i,j}$  is the random variable representing the deviation of the frequency of genotype  $j$  from  $X_{i,j}^M$  due to drift.  $X_{i,j}^D = N_{i,j}^D/N$  where  $N_{i,j}^D$  is the number of individuals with genotype  $j$  in deme  $i$  after drift, and is a random variable that follows a multinomial distribution with parameters  $(N, X_{i,am}^M, X_{i,aM}^M, X_{i,Am}^M, X_{i,AM}^M)$ .

### A4. Change of variables to allele frequencies and linkage

#### disequilibrium

We combine the equations above to obtain the change in genotype frequencies over one generation in any deme  $i$  (that is, the  $X_{i,j}^M$  as a function of the  $X_{i,j}$ ). Then we change the variables to express evolution of the system in terms of the two allele frequencies  $p_{i,A}$  and  $p_{i,M}$  and the linkage disequilibrium between the two loci  $d_i$ .

Solving this system in terms of the allele frequencies/linkage disequilibrium within each deme is difficult for two reasons. First, migration introduces a coupling between the dynamic in one deme and the dynamic of the whole metapopulation. Second, because of random drift, the dynamic in one deme is not deterministic. To overcome these issues, we choose to describe the system of terms of average properties in the metapopulation instead of local properties. We present the method in Supplementary Information B.

# Supplementary Information B. Scaling up to the metapopulation

## B1. Average properties of the metapopulation

Our system of equations is of the form

$$\begin{cases} p_{i,A,t+1} = f(p_{i,A,t}, p_{i,M,t}, d_{i,t}) \\ p_{i,M,t+1} = g(p_{i,A,t}, p_{i,M,t}, d_{i,t}) \\ d_{i,t+1} = h(p_{i,A,t}, p_{i,M,t}, d_{i,t}) \end{cases}$$

To simplify, we assume that all evolutionary forces (selection, drift) are weak relative to migration and that the modifier of migration also has a weak effect. Specifically, we assume that  $s_{a,i,t}$ ,  $s_{A,i,t}$  and  $\Delta m$  are of the order of a small dummy variable  $\epsilon$  and that  $1/N$  is of the order of  $\epsilon^2$  (since the variance of a multinomial distribution is of order  $\epsilon^2$ , the deviations  $\xi_{i,j}$  induced by drift are of order  $\epsilon$ ). Under these assumptions, the linkage  $d_{i,t}$  within each deme will also be of order  $\epsilon$  provided that recombination  $\psi$  is not too weak. Furthermore, because migration is stronger than all the forces generating spatial differentiation across demes, the allele frequencies will not be very different across demes ( $p_{i,A,t} - p_{A,t}$  and  $p_{i,M,t} - p_{M,t}$  are of order  $\epsilon$ , where  $p_{A,t}$  and  $p_{M,t}$  stand for the spatial average of the expected value of  $p_{i,A,t}$  and  $p_{i,M,t}$  respectively in the population). Finally, integrating these assumptions in the above equations yield a simplified set of equations:

$$\begin{cases} p_{i,A,t+1} = F(p_{i,A,t}, p_{i,M,t}, d_{i,t}) \\ p_{i,M,t+1} = G(p_{i,A,t}, p_{i,M,t}, d_{i,t}) \\ d_{i,t+1} = H(p_{i,A,t}, p_{i,M,t}, d_{i,t}) \end{cases}$$

where crucially, the recursions are now under the form of polynomial functions  $F$ ,  $G$  and  $H$ .

We will describe the metapopulation in terms of expected value of average variables and expected value of covariances between these variables. We thus need to average twice the above recursions, first over space and second over the random variable describing drift and over space. These averages are denoted  $E[\ ]$  and  $\langle \ \rangle$ , respectively. In addition, note that the spatial variance and covariance, that we will use later on, are denoted  $V[\ ]$  and  $\text{Cov}[\ ]$ , respectively.

The quantities we are interested in are the expected value of the average variables in the metapopulation,  $p_{A,t} = \langle E[P_{A,t}] \rangle$ ,  $p_{M,t} = \langle E[P_{M,t}] \rangle$ ,  $d_t = \langle E[D_t] \rangle$  where the upper case symbols  $P_{A,t}$ ,  $P_{M,t}$  and  $D_t$  stand for the variables taking value  $p_{i,A,t}$ , etc... in deme  $i$ . We will also calculate the spatial moments of the distribution of the variables, given for example by:

$$\langle \text{Cov}[P_{A,t}, P_{M,t}] \rangle = \langle E[(p_{i,A,t} - p_{A,t})(p_{i,M,t} - p_{M,t})] \rangle$$

Note that in the above expression, we use  $p_{A,t} = \langle E[P_{A,t}] \rangle$  while strictly speaking the covariance over space should be defined with respect to  $E[P_{A,t}]$  (the allele frequency averaged over space only). But we assume that the number of demes is big enough that the *realized* variable  $E[P_{A,t}]$  is not very different from its expected value  $\langle E[P_{A,t}] \rangle$ . In other words, we assume there are enough demes to neglect stochasticity at the level of the metapopulation. This assumption is key because it allows calculating first the expected value over the random variable within each deme, and in a second step averaging over space (see below). Last, we also need to compute the covariances between variables and the parameters  $s_{i,A,t}$  and  $s_{i,a,t}$  that determine the local fecundities of the two genotypes.

In general thus, we are looking for recursion equations for the expressions of the form:

$$E \left[ \langle (s_{i,A,t} - s_{A,t})^{i1} (s_{i,a,t} - s_{a,t})^{i2} (p_{i,A,t} - p_{A,t})^{i3} (p_{i,M,t} - p_{M,t})^{i4} (d_{i,t} - d_t)^{i5} \rangle \right]$$

where the order of the above moment is  $i1 + i2 + i3 + i4 + i5$ . Of course there is an infinity of such moments. Furthermore, the recursion equation for a moment of some order will involve moments of higher order. We thus have to close the moments.

## B2. Closing the moments

The assumption of weak selection, weak drift allows closing the moments. Indeed, in any moment the terms  $s_{i,A,t} - s_{A,t}$  and  $s_{i,a,t} - s_{a,t}$  are of order  $\epsilon$  because of weak selection, while the terms  $p_{i,A,t} - p_{A,t}$ ,  $p_{i,M,t} - p_{M,t}$  and  $d_{i,t} - d_t$  are also of order  $\epsilon$  because of weak spatial structure. Thus the general moment given above in part B1 is of order  $i1 + i2 + i3 + i4 + i5$ .

This remark provides a natural way to close the moments. For example, approximating the system up to order 2 in  $\epsilon$  involves calculating the moments up to order 2 and the higher order moments can be neglected.

## B3. Averaging across the random variable

The recursion equations for the moments involve calculating the average  $\langle \cdot \rangle$  over the random variables  $\xi_{i,j} = X_{i,j}^D - X_{i,j}^M$  where  $X_{i,j}^D = N_{i,j}^D/N$  where  $N_{i,j}^D$  is a random variable that follows a multinomial distribution with parameters  $(N, X_{i,am}^M, X_{i,aM}^M, X_{i,AM}^M, X_{i,AM}^M)$  (see Supplementary Information A3).

Typically, we will have to compute terms of the form

$$\begin{aligned} & \langle \xi_{i,am}^{j1} \xi_{i,aM}^{j2} \xi_{i,AM}^{j3} \xi_{i,AM}^{j4} \rangle \\ &= \left\langle \left( \frac{N_{i,am}^D}{N} - X_{i,am}^M \right)^{j1} \left( \frac{N_{i,aM}^D}{N} - X_{i,aM}^M \right)^{j2} \left( \frac{N_{i,AM}^D}{N} - X_{i,AM}^M \right)^{j3} \left( \frac{N_{i,AM}^D}{N} - X_{i,AM}^M \right)^{j4} \right\rangle \end{aligned}$$

This moment involves in turn a linear combinations of moments of  $N_{i,j}^D$  of order  $j_1 + j_2 + j_3 + j_4$  or less. These moments can be found using the moment-generating function of the multinomial distribution,  $\mathcal{M}_X(t_1, t_2, t_3, t_4) = (X_{i,am}^M e^{t_1} + X_{i,aM}^M e^{t_2} + X_{i,Am}^M e^{t_3} + X_{i,AM}^M e^{t_4})^N$ .

This is automatically computed in a Mathematica notebook available upon request.

### B3. Averaging across space

Once the expected value over the random variable corresponding to drift is computed, we need to average the result over space. This involves averages of terms of the form of  $s_{i,A,t}^{i_1} s_{i,a,t}^{i_2} p_{i,A,t}^{i_3} p_{i,M,t}^{i_4} d_{i,t}^{i_5}$ , which are spatial cumulants of the variables. These cumulants can be translated into a linear combination of averages and spatial moments of the variables. This is automatically computed in a Mathematica notebook available upon request.

### B4. Summary of the procedure

To summarize, describing the dynamic of the metapopulation involves four stages:

- Deriving recursions for the local variables and simplifying them in polynomial function using weak selection / weak drift / weak modifier / weak linkage / weak spatial structure.
- Choosing the order of the approximation and computing the three variables and all products of the form  $(s_{i,A,t} - s_{A,t})^{i_1} (s_{i,a,t} - s_{a,t})^{i_2} (p_{i,A,t} - p_{A,t})^{i_3} (p_{i,M,t} - p_{M,t})^{i_4} d_{i,t}^{i_5}$  with  $i_1 + i_2 + i_3 + i_4 + i_5 \leq \text{order}$  to form a new set of recursion equations.
- Averaging these recursions over the random variable describing drift using the moments of the multinomial distribution.
- Averaging over space using the formulas for transforming the cumulants into moments.

Following this procedure, we end up with a set of recursion equations with 3 equations for the averages and a number of equations for the spatial moments that describe the evolutionary dynamics of the metapopulation.

In general these equations may be complicated and non-linear. However, in our case two properties greatly simplify the analysis. First, it is possible to apply a separation of time-scale between the average variables and the moments. This involves assuming that all moments equilibrate much faster than the average variables because migration rate is assumed to be large relative to the other evolutionary forces acting on the spatial moments. As a consequence we can first solve the equilibrium values of the moments and then plug these equilibrium values into the dynamical equations for the averages  $p_{A,t}$ ,  $p_{M,t}$  and  $d_t$ . Moreover, to the third order the system of equations governing the evolution of spatial moments is linear, which makes it relatively easy to obtain explicit solutions in a number of scenarios (see below).

# Supplementary Information C. Dynamic of the metapopulation

## C1. Second order approximation

### C1.1. Equations for the moments

For simplicity we begin by deriving second order approximations in  $\epsilon$ . In this approximation we need to compute recursion equations for the 3 average variables  $p_A$ ,  $p_M$  and  $d$  and the 12 second order spatial moments. We apply the separation of time-scale argument and first analyze the equilibrium of the 12 second order spatial moments. This analysis reveals that to the second order, only 5 moments are non null. Thus the system of recursion boils down to the following 5 equations:

$$\text{Cov}[S_a, P_A]' = (1 - m)\text{Cov}[S_a, P_A] - (1 - m)p_A(1 - p_A)(V[S_a] - \text{Cov}[S_a, S_A])$$

$$\text{Cov}[S_A, P_A]' = (1 - m)\text{Cov}[S_A, P_A] + (1 - m)p_A(1 - p_A)(V[S_A] - \text{Cov}[S_a, S_A])$$

$$\begin{aligned} V[P_A]' &= (1 - m)^2 V[P_A] + 2(1 - m)^2 p_A(1 - p_A)(\text{Cov}[S_A, P_A] - \text{Cov}[S_a, P_A]) + \frac{p_A(1 - p_A)}{N} \\ &\quad + (p_A(1 - p_A))^2 (1 - m)^2 (V[S_A] + V[S_a] - 2\text{Cov}[S_a, S_A]) \end{aligned}$$

$$V[P_M]' = (1 - m)^2 V[P_M] + \frac{p_M(1 - p_M)}{N}$$

$$V[D]' = (1 - m)^2 (1 - \psi)^2 V[D] + \frac{p_A(1 - p_A)p_M(1 - p_M)}{N}$$

where the prime denotes the variables taken at the next generation. Note that in the following we eliminate the expected value  $\langle \cdot \rangle$  for simplicity, but all the spatial moments are, in reality, *expected*

values of spatial moments. These five moments equilibrate to (the star denotes an equilibrium value):

$$\text{Cov}[S_a, P_A]^* = -\frac{(1-m)p_A(1-p_A)}{m} (V[S_a] - \text{Cov}[S_a, S_A])$$

$$\text{Cov}[S_A, P_A]^* = \frac{(1-m)p_A(1-p_A)}{m} (V[S_A] - \text{Cov}[S_a, S_A])$$

$$V[P_A]^* = \frac{p_A(1-p_A)}{(2-m)mN} + \frac{(1-m)^2(p_A(1-p_A))^2}{m^2} (V[S_A] + V[S_a] - 2\text{Cov}[S_a, S_A])$$

$$V[P_M]^* = \frac{p_M(1-p_M)}{(2-m)mN}$$

$$V[D]^* = \frac{p_A(1-p_A)p_M(1-p_M)}{N(1-(1-m)^2(1-\phi)^2)}$$

## C1.2. Equations for the average variables

Under the second order approximation no linkage disequilibrium is generated (i.e. the linkage decays according to equation  $d' = d(1 - \psi)$ ) and the frequency of the modifier does not change through time. In other words, these two variables change under the action of very small forces and it is necessary to derive approximations to the next order to understand the evolution of the modifier of dispersal (see section C2 below).

In contrast, the average allele frequency at the selected locus changes as:

$$\begin{aligned} p'_A = & p_A + p_A(1-p_A)(s_A - s_a)(1 - (1-p_A)s_a - p_A s_A) + (1-m)^2 p_A(1-p_A)((1 \\ & - p_A)V[S_a] - p_A V[S_A] - \text{Cov}[S_a, S_A](1 - 2p_A)) + ((2-m)m(1-p_A) - (1 \\ & - 2p_A))\text{Cov}[S_a, P_A] + (1 - 2p_A + (2-m)m p_A)\text{Cov}[S_A, P_A] \end{aligned}$$

Plugging the appropriate equilibrium expressions for the moments given above and simplifying, yields:

$$\begin{aligned}
p'_A = & p_A + p_A(1 - p_A)(s_A - s_a)(1 - (1 - p_A)s_a - p_A s_A) \\
& + p_A(1 - p_A) \frac{1 - m}{m} (V[S_A](1 - (2 - m)p_A) + V[S_a](1 - m - (2 - m)p_A) \\
& - \text{Cov}[S_a, S_A](2 - m)(1 - 2p_A))
\end{aligned}$$

In this expression, the first term represents selection at the level of the metapopulation. It will tend to bring  $p_A$  to 1 or 0 depending on the sign of  $(s_A - s_a)$ , determining which allele is favoured at the scale of the metapopulation. However, the second term which depends on the heterogeneity of selection may stabilize the allele frequency towards an intermediate value.

We found  $p_A$  stabilizes to:

$$p_A^* = \frac{(1 - m)(V[S_A] + V[S_a](1 - m) - \text{Cov}[S_a, S_A](2 - m)) + m(1 - s_a)(s_A - s_a)}{(2 - m)(1 - m)(V[S_a] + V[S_A] - 2\text{Cov}[S_a, S_A]) + m(s_A - s_a)^2}$$

We conducted a stability analysis on  $p_A^*$  (not shown) and found this inner equilibrium is stable whenever it lies in the interval  $[0,1]$ . The above expression can thus be used to derive general conditions for the maintenance of polymorphism. Yet, for the sake of simplicity, we focus in a more restrictive set of assumptions where  $V[S_a] = V[S_A] = V_S$  and  $\text{Cov}[S_a, S_A] = \rho V_S$ , where  $\rho$  measures the spatial correlation between selection coefficients acting on the alleles  $a$  and  $A$ . Furthermore, we can assume without loss of generality that  $s_a = 0$  (the baseline fecundity  $f$  can always be rescaled such that  $s_a = 0$ ), and denote  $s_A = \delta_s$ . In such case the equilibrium allele frequency reduces to:

$$p_A^* = \frac{(2 - m)(1 - m)(1 - \rho)V_S + m \delta_s}{2(2 - m)(1 - m)(1 - \rho)V_S + m \delta_s^2}$$

we find the polymorphic equilibrium is stable if and only if:

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

, which is equation (1) of the main text.

In terms of the migration rate, this condition reads:

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

, which is equation (2) of the main text.

## **C2. Third order approximation**

To study the dynamics of the modifier locus we account for generation of linkage disequilibrium and we develop our approximations to the third order. There are now equations for the 3 average variables and 43 moments to compute. The equations for the moments are linear.

We apply the separation of time scale argument and solve for an equilibrium solution for the 43 moments. Note that in the following the star now denotes an equilibrium value of the third order approximation. Only 20 moments have non-null values to the third order. However, explicit solutions in the general case for this set of linear equations are lengthy and not very insightful. We thus focus on several simplifying scenarios we detail below. We conduct a full analysis in a very specific scenario (scenario 1). Then we relax some of the assumptions in turn and examine the consequences of these more general scenarios for the evolution of migration (scenarios 2-4).

### **C2.1 Scenario 1: perfect negative trade-off and selection is balanced**

This is the most specific scenario. Here, we assume that the selection is balanced at the metapopulation level, i.e.  $\delta_s = 0$  (equivalently,  $s_A = s_a = 0$ ). Yet, there is some variance in selection among populations,  $V_S$ . We assume the tradeoff between the performances of the two

alleles is  $\rho = -1$  (perfect negative trade-off). We also assume that the distribution of selection coefficients is not skewed (all third order moments of selection coefficients are zero). Under these more restrictive assumptions, only 12 spatial moments are not zero. These 12 moments are  $\text{Cov}[S_a, P_A]$  and  $\text{Cov}[S_A, P_A]$ ,  $\text{Cov}[S_a, P_M]$  and  $\text{Cov}[S_A, P_M]$ ,  $\text{Cov}[S_a, D]$  and  $\text{Cov}[S_A, D]$ ,  $\text{Cov}[P_A, P_M]$ ,  $\text{Cov}[P_A, D]$ ,  $\text{Cov}[P_M, D]$  and, finally, the three spatial variances  $V[P_A]$ ,  $V[P_M]$  and  $V[D]$ . Note that in this scenario, we have  $s_{i,a} = -s_{i,A}$  for all demes  $i$  and therefore  $\text{Cov}[S_a, P_A] = -\text{Cov}[S_A, P_A]$  and  $\text{Cov}[S_a, D] = -\text{Cov}[S_A, D]$ .

We will not write down the recursions for all spatial moments but only the few spatial moments that we will need in the following to describe the evolution of the modifier. First, the average frequency of the modifier of migration changes as such:

$$\begin{aligned} p'_M &= p_M + 2(1 - \phi)\text{Cov}[S_A, D] + \Delta m(1 - m)V[P_M] \\ &\quad - (\Delta m + m(2 - m - \Delta m))(1 - 2p_A)\text{Cov}[S_A, P_M] + \Delta m(1 - m)p_M(1 \\ &\quad - p_M)(1 - 2p_A)^2V_S \end{aligned}$$

The first term in the expression above is indirect selection on the modifier and expresses the fact that genotype with higher migration rates are less well adapted. The second term is an automatic advantage to migration due to kin selection. The two latter terms will not be important in this scenario because  $p_A$  converges to  $1/2$  which is a stable equilibrium.

To obtain an equilibrium expression for  $\text{Cov}[S_A, D]$ , we need to solve for the joined dynamics of  $\text{Cov}[S_A, D]$  and  $\text{Cov}[S_A, P_A]$ . The latter moment describes how local selection covaries with the allele frequency. We show in Supplementary Information D that this moment,  $\text{Cov}[S_A, P_A]$ , is proportional to local adaptation. The system of recursions for these moments is:

$$\begin{aligned} \text{Cov}[S_A, P_A]' &= (1 - m - \Delta m p_M)\text{Cov}[S_A, P_A] - \Delta m(1 - \phi)\text{Cov}[S_A, D] + 2p_A(1 - p_A)(1 \\ &\quad - m - \Delta m p_M)V_S \end{aligned}$$

$$\begin{aligned} \text{Cov}[S_A, D]' &= (1 - \phi)(1 - m - \Delta m(1 - p_M))\text{Cov}[S_A, D] - \Delta m p_M(1 - p_M)\text{Cov}[S_A, P_A] \\ &\quad - 2\Delta m p_A(1 - p_A)p_M(1 - p_M)V_S \end{aligned}$$

This system yields the following equilibrium values:

$$\text{Cov}[S_A, P_A]^* \approx \frac{1 - m}{m} 2p_A(1 - p_A)V_S$$

$$\text{Cov}[S_A, D]^* \approx -\frac{2 \Delta m p_M(1 - p_M)p_A(1 - p_A)V_S}{m(1 - (1 - \phi)(1 - m))}$$

Second, the recursion for the spatial variance of the modifier frequency is:

$$\begin{aligned} V[P_M]' &= (1 - m) \left( 1 - m - 2\Delta m(1 - p_M) \right) V[P_M] \\ &\quad + 2 \Delta m(1 - m) p_M(1 - p_M)(1 - 2p_A)\text{Cov}[S_A, P_M] + \frac{p_M(1 - p_M)}{N} \end{aligned}$$

This expression is slightly more complicated than the expression above, and in particular reveals that the covariances between local selection and the modifier can affect the variance at the modifier locus. However, as mentioned above in this scenario  $p_A$  converges to  $1/2$ , so these terms will cancel.

Replacing in the expression for  $p_M'$  with the equilibrium expressions for the moments, we find the modifier evolves as:

$$\begin{aligned} p_M' &= p_M + \Delta m p_M(1 - p_M) \left( \underbrace{-\frac{(1 - \phi)V_S}{m((m + \Delta m)(1 - \phi) + \phi) + \Delta m \phi p_M}}_{\text{local adaptation effect}} \right. \\ &\quad \left. + \frac{(1 - m)}{\underbrace{(2 - m)mN + 2N(1 - p_M)(1 - m)\Delta m}_{\text{kin selection effect}}} \right) \end{aligned}$$

The selection gradient is a sum of two terms. The first term is selection for less migration because of local adaptation. The second, positive term is selection for more migration under the action of kin selection.

Neglecting the terms involving the effect of the modifier  $\Delta m$  in the denominators of the above equation, the selection gradient can be approximated as:

$$\frac{\Delta m}{m} \left( -\frac{(1-\phi)V_S}{m(1-\phi) + \phi} + \frac{1-m}{(2-m)N} \right)$$

The migration rates that cancel the selection gradient are:

$$m_{\pm} = \frac{1-2\phi}{2(1-\phi)} + \frac{N V_S}{2} \pm \frac{1}{2(1-\phi)} \sqrt{1 - (1-\phi)N V_S(6 - 4\phi - (1-\phi)N V_S)}$$

For simplicity we call these roots  $m_-$  and  $m_+$ . In order to find an evolutionarily stable migration rate (ESMR), we looked at when the above roots were real and between 0 and 1. Indeed, because the selection gradient is positive if and only if

$$-m^2(1-\phi) + m(1-2\phi + (1-\phi)N V_S) + \phi - 2(1-\phi)N V_S > 0$$

, the selection gradient is positive between the two roots. Thus knowledge of whether real roots exist and where they are relative to 0 and 1 is sufficient to determine what are the evolutionarily stable migration rates. We found three scenarios were possible:

$$1/ N V_S < \frac{\phi}{2(1-\phi)}: m = m_+ \text{ is the only ES MR.}$$

$$2/ \frac{\phi}{2(1-\phi)} < N V_S < 2 - 2\sqrt{\frac{2-\phi}{1-\phi}} + \frac{1}{1-\phi}: \text{ the ES MR are } m = 0 \text{ and } m = m_+, \text{ depending on the}$$

initial conditions. Specifically, if the initial migration rate is smaller than  $m_-$ , the ES MR is 0, and it is  $m_+$  otherwise.

3/  $N V_S > 2 - 2 \sqrt{\frac{2-\phi}{1-\phi}} + \frac{1}{1-\phi}$ : the ESMR is  $m = 0$ .

## C2.2. Scenario 2: imperfect trade-off and selection is balanced

Here we extend on scenario 1 by considering the possibility that the performance of the two alleles do not trade-offs perfectly across environments, i.e.,  $\text{Cov}[S_a, S_A] = \rho V_S$ . We still assume that selection is balanced at the level of the metapopulation, i.e.  $s_a = s_A = 0$ . We are interested in how  $\rho$  influences the evolution of the modifier of migration. As in the first scenario, the average allele frequency at the selected locus converges to  $1/2$  which is a stable equilibrium.

In this scenario the modifier frequency evolves as:

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

The last term above cancels because  $p_A$  equilibrates to  $1/2$ .

We found  $\text{Cov}[S_A, D] - \text{Cov}[S_a, D]$  equilibrates to:

$$\text{Cov}[S_A, D]^* - \text{Cov}[S_a, D]^* = - \frac{2 V_S \Delta m (1-\rho) p_A (1-p_A) p_M (1-p_M)}{m(m + \Delta m + \phi - (m + \Delta m)\phi) + \Delta m \phi p_M}$$

Which can be approximated, neglecting the small terms in  $\Delta m$  in the denominator, as:

$$\text{Cov}[S_A, D]^* - \text{Cov}[S_a, D]^* = - \frac{2 V_S \Delta m (1-\rho) p_A (1-p_A) p_M (1-p_M)}{m(m + \phi(1-m))}$$

The recursion for the spatial variance of the modifier frequency is:

$$\begin{aligned}
V[P_M]' &= (1 - m) \left( 1 - m - 2\Delta m(1 - p_M) \right) V[P_M] \\
&\quad - 2 \Delta m(1 - m) p_M(1 - p_M) \left( (1 - p_A) \text{Cov}[S_a, P_M] + p_A \text{Cov}[S_A, P_M] \right) \\
&\quad + \frac{p_M(1 - p_M)}{N}
\end{aligned}$$

This expression is slightly more complicated than the expression above, and in particular reveals that the covariances between local selection and the modifier may affect the variance at the modifier locus. The equilibrium values of these two covariances are:

$$\text{Cov}[S_a, P_M]^* \approx -\frac{\Delta m}{m} p_M(1 - p_M) V_S (\rho p_A + (1 - p_A))$$

$$\text{Cov}[S_A, P_M]^* \approx -\frac{\Delta m}{m} p_M(1 - p_M) V_S (p_A + \rho(1 - p_A))$$

The equilibrium is:

$$V[P_M]^* \approx \frac{p_M(1 - p_M)}{m(2 - m)} \left( \frac{1}{N} + \Delta m^2 p_M(1 - p_M) V_S \frac{1 - m}{m} (1 - 2(1 - \rho)p_A(1 - p_A)) \right)$$

The second term in the equilibrium expression above vanishes when  $\rho = -1$  and  $p_A = 1/2$ .

But even when  $\rho > -1$  and  $p_A \neq 1/2$  this second term is much smaller than the first term (it is of order 4) and can therefore be neglected.

Finally, the third term in the in the equation for the dynamics of the modifier reads:

$$(1 - p_A) \text{Cov}[S_a, P_M]^* + p_A \text{Cov}[S_A, P_M]^* \approx -\frac{\Delta m}{m} V_S p_M(1 - p_M) (1 - 2(1 - \rho)p_A(1 - p_A))$$

Replacing for the equilibrium expressions of the moments and of the selected allele frequency

$p_A^* = 1/2$ , we find the modifier evolves as:

$$p'_M \approx p_M + \Delta m p_M (1 - p_M) \left( \underbrace{-\frac{(1 - \rho)(1 - \phi)}{2m(m(1 - \phi) + \phi)} V_S}_{\text{local adaptation effect}} + \underbrace{\frac{1 - m}{(2 - m)m N}}_{\text{kin selection effect}} - \underbrace{\frac{1}{2}(1 + \rho)V_S}_{\text{habitat heterogeneity effect}} \right)$$

Where the first term corresponds to indirect selection on the modifier through covariance between the linkage and selection, the second corresponds to direction selection induced by kin selection and the third to direct selection induced by the covariance between selection and the frequency of the modifier.

### C2.3. Scenario 3: perfect trade-off and asymmetric selection

Here we extend on scenario 1 by considering the possibility that one allele is superior to the other at the scale of the metapopulation, that is  $\delta_S > 0$ . We still assume that  $\rho = -1$ . We are interested in how  $\delta_S$  influences the evolution of the modifier of migration. Contrary to the first scenario, in this scenario the average allele frequency at the selected locus converges to  $p_A^* = \frac{2(2-m)(1-m)V_S + m\delta_S}{4(2-m)(1-m)V_S + m\delta_S^2}$  which is a stable equilibrium if and only if  $V_S > \frac{m(1-\delta_S)\delta_S}{2(2-m)(1-m)}$ .

Under this scenario, the modifier frequency evolves as:

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

This expression is quite complicated. One noteworthy difference with the other scenarios is that the average linkage disequilibrium in the metapopulation may drive the evolution of the modifier (term in  $\delta_s(1 - \phi)D_t$ ). However, when solving for the equilibrium values of the average linkage and the spatial moments, we found that the term in  $D_t$  cancels (little linkage is generated in the metapopulation), and that the term in  $\text{Cov}[P_A, P_M]$  cancels as well (note that there is an intimate link between  $D_t$  and  $\text{Cov}[P_A, P_M]$ , as a spatial covariance in allele frequency across loci generates linkage disequilibrium upon migration). When solving explicitly for the evolution of the modifier by plugging in the equilibrium expressions for the moments, we obtain:

$$p'_M \approx p_M + \Delta m p_M(1 - p_M) \left( \underbrace{-\frac{4(1 - \phi) p_A^*(1 - p_A^*)}{m(m + \phi - m \phi)} V_S}_{\text{local adaptation effect}} + \underbrace{\frac{1 - m}{m(2 - m)N}}_{\text{kin selection effect}} - \underbrace{\frac{V_S(1 - 2 p_A^*)^2}{\text{habitat heterogeneity effect}}}_{\text{habitat heterogeneity effect}} \right)$$

The last step to obtain an explicit expression for the moments is to replace the equilibrium expression for  $p_A$ ,  $p_A^* = \frac{2(2-m)(1-m)V_S + m \delta_s}{4(2-m)(1-m)V_S + m \delta_s^2}$ . We don't write the full expression here because it is quite cumbersome.

In this scenario, polymorphism at the selected locus is not necessarily maintained. If  $p_A^*$  is not within the  $[0,1]$  interval, then polymorphism is lost, we have  $p_A^* = 1$  (because we considered  $\delta_s > 0$ ) and the modifier will evolve according to:

$$p'_M \approx p_M + \Delta m p_M(1 - p_M) \left( \frac{1 - m}{m(2 - m)N} - V_S \right)$$

That is, kin selection favors migration while heterogeneity in selection, which is actually heterogeneity in habitat quality because one allele is fixed, counterselects migration. Such

dynamics results in an evolutionarily stable migration rate at  $m^* = \frac{2}{1+2N V_S + \sqrt{1+4N^2 V_S^2}}$ .

#### C2.4. Scenario 4: changing selective pressure

Here we extend scenario 1 by considering the possibility that the selective coefficients  $s_{i,a}$  and  $s_{i,A}$  may change through time in an arbitrary fashion. As in scenario 1, we consider  $\rho = -1$  and  $s_a = s_A = 0$ . In a changing environment, the equation for the change in the modifier remains the same as in scenario 1. Moreover, because the spatial variance at the modifier does not depend on selection in our model, we only need to consider how changing selection affects the covariance between selection and the linkage disequilibrium.

The dynamics of this spatial moment is given by the following system of equations:

$$\begin{aligned} \text{Cov}[S_{A,t+1}, P_{A,t+1}] &= (1 - m - \Delta m p_M) \text{Cov}[S_{A,t+1}, P_{A,t}] - \Delta m (1 - \phi) \text{Cov}[S_{A,t+1}, D_t] \\ &\quad + 2p_A(1 - p_A)(1 - m - \Delta m p_M) \text{Cov}[S_{A,t+1}, S_{A,t}] \end{aligned}$$

$$\begin{aligned} \text{Cov}[S_{A,t+1}, D_{t+1}] &= (1 - \phi)(1 - m - \Delta m(1 - p_M)) \text{Cov}[S_{A,t+1}, D_t] \\ &\quad - \Delta m p_M(1 - p_M) \text{Cov}[S_{A,t+1}, P_{A,t}] - 2 \Delta m p_A(1 - p_A) p_M(1 \\ &\quad - p_M) \text{Cov}[S_{A,t+1}, S_{A,t}] \end{aligned}$$

These equations reveal that  $\text{Cov}[S_{A,t+1}, P_{A,t+1}]$  will be of order  $\epsilon^2$  and  $\text{Cov}[S_{A,t+1}, D_{t+1}]$  of order  $\epsilon^3$  (see also section C.2.1). The term  $\Delta m (1 - \phi) \text{Cov}[S_{A,t+1}, D_t]$  in the equation for

$\text{Cov}[S_{A,t+1}, P_{A,t+1}]$ , and the term  $-\Delta m(1 - p_M)\text{Cov}[S_{A,t+1}, D_t]$  in the equation for  $\text{Cov}[S_{A,t+1}, D_{t+1}]$  can thus be neglected, simplifying the above recursions in:

$$\begin{aligned} \text{Cov}[S_{A,t}, P_{A,t}] &= (1 - m - \Delta m p_M)\text{Cov}[S_{A,t}, P_{A,t-1}] + 2p_A(1 - p_A)(1 - m \\ &\quad - \Delta m p_M)\text{Cov}[S_{A,t}, S_{A,t-1}] \end{aligned}$$

$$\begin{aligned} \text{Cov}[S_{A,t}, D_t] &= (1 - \phi)(1 - m)\text{Cov}[S_{A,t}, D_{t-1}] - \Delta m p_M(1 - p_M)\text{Cov}[S_{A,t}, P_{A,t-1}] \\ &\quad - 2 \Delta m p_A(1 - p_A)p_M(1 - p_M)\text{Cov}[S_{A,t}, S_{A,t-1}] \end{aligned}$$

The first equation can thus be solved explicitly as:

$$\text{Cov}[S_{A,t}, P_{A,t}] = 2p_A(1 - p_A) \sum_{j=1}^{\infty} (1 - m - \Delta m p_M)^j \text{Cov}[S_{A,t}, S_{A,t-j}]$$

Similarly, one can show that:

$$\text{Cov}[S_{A,t}, P_{A,t}] = -2p_A(1 - p_A) \sum_{j=1}^{\infty} (1 - m - \Delta m p_M)^j \text{Cov}[S_{A,t}, S_{A,t-j}]$$

For the second recursion, we need the equilibrium expressions for any moment of the form  $\text{Cov}[S_{A,t}, P_{A,t-\tau}]$ , which reads:

$$\text{Cov}[S_{A,t}, P_{A,t-\tau}] = 2p_A(1 - p_A) \sum_{j=1}^{\infty} (1 - m - \Delta m p_M)^j \text{Cov}[S_{A,t}, S_{A,t-\tau-j}]$$

Finally, the equilibrium expression for the moment  $\text{Cov}[S_{A,t}, D_t]$  reads:

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

Note that this derivation also assumes a separation of time scale between the change in the spatial moments and the change in the average allele frequencies  $p_A$  and  $p_M$ . The change in allele frequency is assumed to be much slower than the change in the spatial moments. The only difference between the case where selection does not change in time is due to the fact that the spatial moments fluctuate together with the fluctuations of selection coefficients.

Although the above expression for  $\text{Cov}[S_{A,t}, D_t]$  seems complicated, in many scenarios of environmental change, the sums can be simplified once the appropriate spatial covariance  $\text{Cov}[S_{A,t}, S_{A,t-\tau-j}]$  is plugged in the expression. For example, in the case of a periodical change in selection, assuming selection is  $s_{i,a} = s_{max} \sin[\beta t + \tau_i]$  and  $s_{i,A} = -s_{max} \sin[\beta t + \tau_i]$ , and further assuming that there are many demes and fluctuations are not synchronized across demes, we can approximate  $\text{Cov}[S_{A,t}, S_{A,t-\tau-j}]$  as the temporal autocovariance, i.e.  $\text{Cov}[S_{A,t}, S_{A,t-\tau-j}] = \frac{1}{2} s_{max}^2 \cos[\beta(\tau + j)]$ . In this case we obtain:

$$\begin{aligned} & \text{Cov}[S_{A,t}, D_t] \\ &= \frac{-s_{max}^2 \Delta m p_M (1 - p_M) ((1 - m)(2 - \phi) + (-2 + (2 - m)m(1 - \phi) + \phi) \cos[\beta])}{(2 - (2 - m)m - 2(1 - m) \cos[\beta]) (2 - 2m(1 - \phi)^2 + m^2(1 - \phi)^2 - (2 - \phi)\phi - 2(1 - m)(1 - \phi) \cos[\beta])} \end{aligned}$$

This expression is identical to one obtained in a slightly different way in Blanquart and Gandon (2011). With rapid periodical fluctuations, indirect selection on the modifier can actually favor more migration.

Our framework also allows us to consider a case where selection fluctuates in a random autocorrelated way, such that  $s_{i,A,t+1} = \alpha s_{i,A,t} + (1 - \alpha)\epsilon$ , where  $\epsilon$  is drawn in a random distribution. In this scenario, assuming  $s_{i,a,t} = -s_{i,A,t}$ , that there are many demes and that the environmental variation is not correlated across demes, we can replace the spatial covariance  $\text{Cov}[S_{A,t}, S_{A,t-\tau-j}]$  by the temporal autocovariance,  $\text{Cov}[S_{A,t}, S_{A,t-\tau-j}] = \frac{(1-\alpha)^2}{1-\alpha^2} \nu \alpha^{j+\tau}$ , where  $\nu$

is the variance of the random variable  $\epsilon$ . The spatial variance of selection in this scenario is

$$V_S = \frac{(1-\alpha)^2}{1-\alpha^2} \nu. \text{ In this scenario we obtain:}$$

$$\text{Cov}[S_{A,t}, D_t] = -\frac{V_S \alpha}{2(1 - \alpha(1 - m)(1 - \phi))(1 - \alpha(1 - m))} \Delta m p_M (1 - p_M)$$

This is always negative. Finally, note that in the limit case where selection does not vary in time we recover the equilibrium values given in sections C.2.1.

It is interesting to note that lower levels of autocorrelation lead to the disappearance of the evolutionary bistability. In particular, in the absence of recombination (i.e.  $\phi = 0$ ) the above expression can be used with equation (7) to show that there is a threshold value of

autocorrelation,  $\alpha_c = \sqrt{\frac{1}{3} + \frac{2}{3\sqrt{3}}} \approx 0.84$ , below which evolutionary bistability vanishes. For larger

levels of recombination this threshold value is even higher.

# Supplementary Information D. Measuring differentiation in populations

## D1. Neutral and selected variation

The spatial variance at the modifier locus is mainly due to genetic drift and is given by (see C.1.1):

$$V[P_M]^* \approx \frac{p_M(1-p_M)}{(2-m)mN}$$

A classical measure of differentiation at the modifier locus is population differentiation at a neutral locus, noted  $F_{ST}^{neut}$  (Roze and Rousset 2008):

$$F_{ST}^{neut} = \frac{V[P_M]^*}{p_M(1-p_M)} \approx \frac{1}{(2-m)mN}$$

Similarly one can derive a measure of differentiation at the selected locus  $F_{ST}^{sel}$ :

$$F_{ST}^{sel} = \frac{V[P_A]^*}{p_A(1-p_A)} \approx F_{ST}^{neut} + p_A(1-p_A) \frac{(1-m)^2}{m^2} (V[S_A] + V[S_a] - 2\text{Cov}[S_a, S_A])$$

In the following we show that the latter term  $p_A(1-p_A) \frac{(1-m)^2}{m^2} (V[S_A] + V[S_a] - 2\text{Cov}[S_a, S_A])$  in the expression above is proportional to a measure of local adaptation.

## D2. Local adaptation

Local adaptation can be defined as the difference between the fitness populations achieve in sympatry and the fitness they achieve in allopatry (Blanquart *et al.* 2013). Fitness in sympatry is the mean fitness of the metapopulation. For example, if in the experiment the fecundity is taken as a proxy for fitness, it is:

$$\begin{aligned}
\bar{W} &= E[p_{i,A,t}f(1 + s_{A,i,t}) + (1 - p_{i,A,t})f(1 + s_{a,i,t})] \\
&= fE[p_{i,A,t} + p_{i,A,t}s_{A,i,t} + 1 - p_{i,A,t} + s_{a,i,t} - p_{i,A,t}s_{a,i,t}] \\
&= f(p_{A,t} + p_{A,t}s_{A,t} + 1 - p_{A,t} + s_{a,t} - p_{A,t}s_{a,t} + \text{Cov}[S_A, P_A] - \text{Cov}[S_a, P_A]) \\
&= f(1 + p_{A,t}s_{A,t} + (1 - p_{A,t})s_{a,t} + \text{Cov}[S_A, P_A] - \text{Cov}[S_a, P_A])
\end{aligned}$$

The mean fitness in allopatry is calculated over all possible pairs of transplant ( $i \rightarrow j$ ) (including the sympatric transplant: we calculate local adaptation “sympatric vs. total” rather than local adaptation “sympatric vs. allopatric”):

$$\begin{aligned}
\bar{W}_{total} &= E_{i \rightarrow j}^S [p_{i,A,t}f(1 + s_{A,j,t}) + (1 - p_{i,A,t})f(1 + s_{a,j,t})] \\
&= f(1 + p_{A,t}s_{A,t} + (1 - p_{A,t})s_{a,t})
\end{aligned}$$

Overall, local adaptation is thus:

$$\lambda = (\bar{W} - \bar{W}_{total})/\bar{W}$$

Under the assumption that selection is weak this yields:

$$\lambda \approx (\bar{W} - \bar{W}_{total})/f = \text{Cov}[S_A, P_A] - \text{Cov}[S_a, P_A]$$

Plugging the equilibrium expressions obtained in C1.1., we find:

$$\lambda = p_A(1 - p_A) \frac{1 - m}{m} (V[S_A] + V[S_a] - 2\text{Cov}[S_a, S_A])$$

which is always positive.

# Supplementary Information E: details of evolutionary simulations

## E1. Maintenance of polymorphism:

To test for the maintenance of polymorphism, we simulated the life cycle described in part 1.1 in 100 populations of  $N = 1000$  individuals, without the modifier of migration ( $\Delta m = 0$ ). The system was left to evolve during 1000 generations, at which point the average allele frequency at the selected locus had equilibrated. We recorded the average allele frequency over the last 100 generations and over 10 replicates runs. We consider polymorphism is maintained when this average was smaller than 0.99.

## E2. Evolution of the migration rate:

To investigate the evolution of the rate of migration, we simulated the life cycle described in part 1.1 with 100 populations of  $N = 100$  individuals. We assume 101 alleles with migration rates  $\{0, 0.01, 0.02, \dots, 1\}$  at the modifier locus. Mutation occurs at a rate  $\mu = 0.001$  at the modifier locus and follows a stepping stone model, where a genotype may mutate to the genotype with the immediately greater or smaller mutation rate. For each set of parameters tested, we let the system evolve for  $6 \cdot 10^5$  generations. We recorded the average migration rate in the metapopulation at 100 points taken every 1000 generations in the last  $10^5$  generations. To assess the presence of bistability, we ran two sets of simulations, one starting with a population fixed with the “no migration” modifier allele ( $m = 0$ ) and one starting with a population fixed with the “full migration” modifier allele ( $m = 1$ ). Last, we ran at least three replicates for each of these situations.

We ran these simulations across various values of  $V_S$ , the recombination rate  $\phi$ , the trade-off  $\rho$  and asymmetry in selection  $\delta_S$ . Lastly, to test for the influence of local population size, we ran simulations with  $N = 1000$  individuals per deme and mutation rate  $\mu = 10^{-4}$  for one set of parameters (fig. 5).