Imperfect strategy transmission can reverse the role of population viscosity on the evolution of altruism

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1 Abstract

2 Population viscosity, *i.e.*, low emigration out of the natal deme, leads to high

3 within-deme relatedness, which is beneficial to the evolution of altruistic behav-

4 ior when social interactions take place among deme-mates. However, a detri-

5 mental side-effect of low emigration is the increase in competition among re-

6 lated individuals. The evolution of altruism depends on the balance between

7 these opposite effects. This balance is already known to be affected by details

8 of the life-cycle; we show here that it further depends on the fidelity of strategy

9 transmission from parents to their offspring. We consider different life-cycles

10 and identify thresholds of parent-offspring strategy transmission inaccuracy, above

11 which higher emigration can increase the frequency of altruists maintained in

12 the population. Predictions were first obtained analytically assuming weak se-

13 lection and equal deme sizes, then confirmed with stochastic simulations relax-

14 ing these assumptions. This result challenges the notion that the evolution of

15 altruism requires limited dispersal.

Impact Summary

The evolution of altruistic behavior has fascinated and puzzled evolutionary biologists for a long time: how can a strategy whereby individuals help others at their own cost be maintained in a population? One answer is the fact that altruists may interact with other altruists more often than non-altruists do, a situation made possible by spatial structure and low emigration. Low emigration indeed means that an individual is mostly surrounded by related individuals; when social strategies are faithfully transmitted from parents to offspring, and social interactions are local as well, then altruists interact mainly with other altruists. However, this also means that related individuals have to compete against each other. Whether altruism eventually evolves depends on the balance between these beneficial and detrimental consequences of low emigration. Previous work has shown that the balance depends on the life-cycle that the population undergoes; under nearly perfect strategy transmission, low emigration goes from being neutral to the evolution of altruism (when generations are synchronous and non-overlapping) to favorable. In this work, we show that this conclusion qualitatively changes when offspring do not necessarily adopt their parent's strategy, that is, when strategy transmission is imperfect. Such imperfect transmission can be due to mutation when transmission is genetic, but also to imperfect vertical cultural transmission. We identify thresholds of strategy transmission infidelity, above which higher emigration is more conducive to the evolution of altruism than low emigration. The predictions are first obtained mathematically under the restrictive assumptions that selection is weak and that all demes have the same size, but are then confirmed with computer simulations relaxing these assumptions. This work shows that the evolution of altruism does not require – and even can be hampered by – low emigration.

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Introduction

In his pioneering work on the evolution of social behavior, Hamilton suggested that altruistic behavior would be associated to limited dispersal (Hamilton, 1964, p. 10). This notion, that tighter links between individuals favor the evolution of altruism, has been shown to hold in a number of population structures (see *e.g.* Lehmann et al., 2007; Ohtsuki et al., 2006; Taylor et al., 2007a). The rationale is that altruism is favored when altruists interact more with altruists than defectors do (Hamilton, 1975, p. 141; Fletcher & Doebeli, 2009), a condition that is met in viscous populations, *i.e.*, populations with limited dispersal.

Yet, living next to your kin also implies competing against them (West et al., 2002), which is detrimental to the evolution of altruism. The evolution of social traits hence depends on the balance between the positive effects of interactions with related individuals and the detrimental consequences of kin competition. Under specific conditions, the two effects can even compensate each other, thereby annihilating the impact of population viscosity on the evolution of altruism. First identified with computer simulations (Wilson et al., 1992), this cancellation result was analyzed by Taylor (1992a) in a model with synchronous generations (*i.e.*, Wright-Fisher model) and a subdivided population of constant, infinite size. The cancellation result was later extended to heterogeneous populations (Rodrigues & Gardner, 2012, with synchronous generations and infinite population size), and other life-cycles, with generic regular population structures (Taylor et al., 2011, with synchronous generations but also with continuous generations and Birth-Death updating). However, small changes in the model's assumptions, such as overlapping generations (Taylor & Irwin, 2000) or the presence of empty sites (Alizon & Taylor, 2008) can tip the balance back in the favor of altruism. This high dependence on life-cycle specificities highlights the difficulty of making general statements about the role of spatial structure on the evolution of altruism. In this study, we will consider three different life-cycles:

Wright-Fisher, where the whole population is renewed at each time step, and two Moran life-cycles (Birth-Death and Death-Birth), where a single individual dies and is replaced at each time step. These life-cycles are classically used in studies on altruism in structured populations, and are already known to have different outcomes in models with perfect parent-offspring transmission (*e.g.*, Lehmann et al., 2007; Ohtsuki et al., 2006; Rousset, 2004; Taylor, 1992a, 2010).

A large number of studies on the evolution of social behavior consider simple population structures (typically, homogeneous populations *sensu* Taylor et al. (2007a)) and often also infinite population sizes (but see Allen et al., 2017, for results on any structure). These studies also make use of weak selection approximations, and commonly assume rare (*e.g.*, Leturque & Rousset, 2002; Tarnita & Taylor, 2014; Taylor et al., 2007b) or absent mutation (for models assuming infinite population sizes, or models concentrating on fixation probabilities; see Lehmann & Rousset, 2014; Van Cleve, 2015, for recent reviews). Often, these simplifying assumptions are a necessary step towards obtaining explicit analytical results. Although artificial, simple population structures (*e.g.*, regular graphs, or subdivided populations with demes of equal sizes) help reduce the dimensionality of the system under study, in particular when the structure of the population displays symmetries such that all sites behave the same way in expectation. Weak selection approximations are crucial for disentangling spatial moments (Lion, 2016), that is, changes in global *vs.* local frequencies (though they can in some cases be relaxed, as in Mullon & Lehmann, 2014). Mutation, however, is usually ignored by classical models of inclusive fitness because these models assume infinite population sizes, so that there is no need to add mechanisms that restore genetic diversity (Tarnita & Taylor, 2014). In populations of finite size, this diversifying effect can be obtained thanks to mutation.

When strategy transmission is purely genetic, it makes sense to assume that mutation is relatively weak. A social strategy can however also be culturally

transmitted from parent to offspring, in which case "rebellion" (as in Frank's Rebellious Child Model (Frank, 1997)) does not have to be rare. Imperfect strategy transmission can alter evolutionary dynamics, in particular in spatially structured populations (see *e.g.*, Allen et al., 2012; Débarre, 2017, for graph-structured populations). Here, we want to explore the consequences of imperfect strategy transmission from parents to their offspring on the evolution of altruistic behavior in subdivided populations[1]. The question was tackled by Frank (1997), but with a non fully dynamic model. His method, done "in the spirit of comparative statics" (p.1721), precluded the exploration of the effects of population viscosity on the evolution altruism.

For each of the three life-cycles that we consider, we compute the expected (*i.e.*, long-term) frequency of altruists maintained in a subdivided population, and investigate how this frequency is affected by mutation and emigration. We find that, contrary to what happens with perfect strategy transmission, higher emigration can increase the expected frequency of altruists in the population.

Model and methods

Assumptions

We consider a population of size N, subdivided into N_D demes connected by dispersal, each deme hosting exactly n individuals (*i.e.*, each deme contains n sites, each of which is occupied by exactly one individual; we have $nN_D = N$). Each site has a unique label i, $1 \leq i \leq N$. There are two types of individuals in the population, altruists and defectors. The type of the individual living at site i ($1 \leq i \leq N$) is given by an indicator variable X_i, equal to 1 if the individual is an altruist, and to 0 if it is a defector. The state of the entire population is given by a N-long vector **X**. For a given population state **X**, the proportion of altruists is

---

[1] Note that for the sake of concision, we use the word "mutation" throughout the paper, keeping in mind that strategy transmission does not have to be genetic.

123    $\overline{X} = \sum_{i=1}^{N} X_i$. All symbols are summarized in table A1.

124   Reproduction is asexual. Parents transmit their strategy to their offspring

125   with probability $1 - \mu$; this transmission can be genetic or cultural (vertical cul-

126   tural transmission), but for simplicity, we refer to the parameter μ as a mutation

127   probability. With probability μ, offspring do not inherit their strategy from their

128   parent but instead get one randomly: with probability ν, they become altruists,

129   with probability $1 - \nu$ they become defectors. We call the parameter ν the muta-

130   tion bias.

131   An individual of type X_k expresses a social phenotype $\phi_k = \delta X_k$, where δ is

132   assumed to be small ($\delta \ll 1$). Social interactions take place within each deme,

133   benefits are shared with the $n - 1$ other deme-mates. We assume that social in-

134   teractions affect individual fecundity; f_k denotes the fecundity of the individual

135   at site k. We denote by b the sum of the marginal effects of deme-mates' phe-

136   notypes on the fecundity of a focal individual, and by $-$c the marginal effect of

137   a focal individual's phenotype on its own fecundity (c $\leq$ b; see system (A14) for

138   formal definitions).

139   Offspring remain in the parental deme with probability $1 - m$; when they

140   do, they land on any site of the deme with equal probability (including the very

141   site of their parent). With probability m, offspring emigrate to a different deme,

142   chosen uniformly at random among the other demes. Denoting by d_{ij} the prob-

143   ability of moving from site i to site j, we have

$$
d_{ij} = \begin{cases} d_{\text{in}} = \frac{1-m}{n} & \text{if both sites are in the same deme;} \\[2mm] d_{\text{out}} = \frac{m}{(N_D-1)n} & \text{if the two sites are in different demes,} \end{cases} \tag{1}
$$

144   with $0 < m < 1 - \frac{1}{N_D}$. (This upper bound is here to ensure that within-deme

145   relatedness R, which will be defined later in the article, remains positive.)

146   We denote by $B_i = B_i(\mathbf{X}, \delta)$ the expected number of successful offspring of the

147   individual living at site i (successful means alive at the next time step), and by

$D_i = D_i(\mathbf{X}, \delta)$ the probability that the individual living at site i dies. Both depend on the state of the population $\mathbf{X}$, but also on the way the population is updated from one time step to the next, *i.e.*, on the chosen life-cycle (also called updating rule). We also define

$$W_i := (1 - \mu)B_i + 1 - D_i, \tag{2}$$

which is a definition of fitness were only unmutated offspring are counted.

We will specifically explore three different life-cycles. At the beginning of each step of each life-cycle, all individuals produce offspring, that can be mutated; then these juveniles move, within the parental deme or outside of it, and land on a site. The next events occurring during the time step depend on the life-cycle:

Moran Birth-Death : One of the newly created juveniles is chosen at random; it kills the adult who was living at the site, and replaces it; all other juveniles die.

Moran Death-Birth : One of the adults is chosen to die (uniformly at random among all adults). It is replaced by one of the juveniles who had landed in its site. All other juveniles die.

Wright-Fisher : All the adults die. At each site of the entire population, one of the juveniles that landed there is chosen and establishes at the site.

Methods

Analytical part

The calculation steps to obtain the expected (*i.e.*, long-term) proportion of altruists are given in Appendix A. They go as follows: first, we write an equation for the expected frequency of altruists in the population at time $t + 1$, conditional on the composition of the population at time t; we then take the expectation of

172 this quantity and consider large times t. After this, we write a first order expan-

173 sion for phenotypic differences δ close to 0 (this corresponds to weak selection

174 approximation).

175   The formula involves quantities that can be identified as neutral probabili-

176 ties of identity by descent Q_{ij}, *i.e.*, the probability that individuals living at site

177 i and j share a common ancestor and that no mutation occurred on either lin-

178 eage since that ancestor, in a model with no selection ($\delta = 0$; this is the "muta-

179 tion definition" of identity by descent (Rousset & Billiard, 2000).) In a subdivided

180 population like ours, there are three possible values of Q_{ij}:

$$
Q_{ij} = \begin{cases}
1 & \text{when } i = j, \\
Q_{\text{in}} & \text{when } i \neq j \text{ and both sites are in the same deme,} \\
Q_{\text{out}} & \text{when both sites are in different demes.}
\end{cases}
\tag{3}
$$

181 These neutral probabilities of identity by descent depend on the chosen life-

182 cycle, and are also computed by taking the long-term expectation of conditional

183 expectations after one time step (see Appendix B and B and supplementary Math-

184 ematica file (Wolfram Research, Inc., 2017).)

Stochastic simulations

186 We also ran stochastic simulations (coded in C). The simulations were run for 10^8

187 generations (one generation is one time step for the Wright-Fisher life-cycle, and

188 N time steps for the Moran life-cycles). For each set of parameters and life-cycle,

189 using R (R Core Team, 2015), we estimated the long-term frequency of altruists

190 by sampling the population every 10^3 generations and computing the average

191 frequency of altruists. All scripts are available at

192 `https://flodebarre.github.io/SocEvolSubdivPop/`

Results

Expected frequencies of altruists for each life-cycle

For each of the life-cycles that we consider, the expected frequency of altruists in the population, $\mathbb{E}[\overline{X}]$, can be approximated as

$$
\mathbb{E}[\overline{X}] \approx v + \frac{\delta}{\mu B^*} v(1-v)(1-Q_{\text{out}}) \times
$$

$$
\left[\underbrace{\frac{\partial W}{\partial f_\bullet}(-c) + \frac{\partial W}{\partial f_{\text{in}}}b}_{-\mathcal{C}} + \underbrace{\left(\frac{\partial W}{\partial f_\bullet}b + (n-1)\frac{\partial W}{\partial f_{\text{in}}}(-c) + (n-2)\frac{\partial W}{\partial f_{\text{in}}}b \right)}_{\mathcal{B}} \underbrace{\frac{Q_{\text{in}} - Q_{\text{out}}}{1 - Q_{\text{out}}}}_{R} \right], \quad (4)
$$

with W as defined in eq. (2). (Calculations leading to eq. (4) are presented in Appendix A; notations are recapitulated in table A1)

The mutation bias v corresponds to the expected proportion of altruists in the population in the absence of selection (*i.e.*, when $\delta = 0$); δ is the parameter that scales the strength of selection ($\delta \ll 1$). The $-\mathcal{C}$ term groups the effects corresponding to the effects of a change of a focal individual's phenotype on its own fitness (with the fitness definition given in eq. (2).) The $\mathcal{B}$ term corresponds to the sum of the effects on an individual's fitness of the change of deme-mates' phenotypes. It is multiplied by R, which is relatedness. Also note the overall $(1 - Q_{\text{out}})$ factor. All of these terms depend on the chosen life-cycle, and on parameters such as the mutation probability μ and the emigration probability m.

We now present the values of these different terms for the three life-cycles under study. The equations are obtained by replacing the derivatives of W by their specific formulas for each life-cycle, which are presented in Appendix A. The formulas of probabilities of identity by descent are more complicated, so not substituted, but they can be found in eq. (A32) and eq. (A36). The additional superscripts correspond to the life-cycles (WF: Wright-Fisher, M: Moran (either), DB: Moran Death-Birth, BD: Moran Birth-Death.) Finally, for each life-cycle, we further decompose the $-\mathcal{C}$ and $\mathcal{B}$ terms into primary (subscript P) and sec-

ondary (subscript S) effects (West & Gardner, 2010). Primary effects correspond to unmediated consequences of interactions (they are included in $\frac{\partial W}{\partial f_\bullet}$), while secondary effects correspond to consequences of interactions mediated by other individuals, including competition. Primary and secondary effects correspond to what was called "direct" and "indirect" effects, respectively, in Débarre (2017); Débarre et al. (2014), but the terminology was updated for more consistency with other authors. All equations are of the form

$$\mathbb{E}\big[\overline{X}\big] \approx v + \frac{\delta}{\mu} v(1-v)(1-Q_{\text{out}})\bigg[\underbrace{\begin{pmatrix} -\mathcal{C}_{\text{P}} \\ -\mathcal{C}_{\text{S}} \end{pmatrix}}_{-\mathcal{C}} + \underbrace{\begin{pmatrix} \mathcal{B}_{\text{P}} \\ +\mathcal{B}_{\text{S}} \end{pmatrix}}_{\mathcal{B}} \underbrace{\frac{Q_{\text{in}} - Q_{\text{out}}}{1 - Q_{\text{out}}}}_{R} \bigg]. \tag{5}$$

Moran Birth-Death   With the Birth-Death life-cycle, eq. (4) becomes

$$\mathbb{E}\big[\overline{X}\big] \approx v + \frac{\delta}{\mu} v(1-v)(1-Q_{\text{out}}^{\text{M}}) \times$$

$$\bigg[\underbrace{\begin{pmatrix} (1-\mu)(-\mathsf{c}) \\ +(\mathsf{b}-\mathsf{c})\left(\dfrac{\mu}{N} - \dfrac{1-m}{n}\right) \end{pmatrix}}_{-\mathcal{C}^{\text{BD}}} + \underbrace{\begin{pmatrix} (1-\mu)\mathsf{b} \\ +(\mathsf{b}-\mathsf{c})(n-1)\left(\dfrac{\mu}{N} - \dfrac{1-m}{n}\right) \end{pmatrix}}_{\mathcal{B}^{\text{BD}}} \underbrace{\frac{Q_{\text{in}}^{\text{M}} - Q_{\text{out}}^{\text{M}}}{1 - Q_{\text{out}}^{\text{M}}}}_{R^{\text{M}}} \bigg], \tag{6}$$

The secondary effects (second line in the parentheses) include competitive effects on the probability of reproducing, and consequences of social interactions on the probability that a given individual dies. Note that the secondary effects remain negative for the realistic range of emigration values that we consider (*i.e.*, $m < 1 - 1/N_D$).

Moran Death-Birth   With the Death-Birth life-cycle, eq. (4) becomes

$$
\mathbb{E}\big[\overline{X}\big] \approx \nu + \frac{\delta}{\mu}\nu(1-\nu)(1-Q_{\text{out}}^{\text{M}}) \times
$$

$$
\Bigg[\underbrace{\left(\begin{array}{c} (1-\mu)(-\mathsf{c}) \\ -(\mathsf{b}-\mathsf{c})(1-\mu)\left(\frac{(1-m)^2}{n}+\frac{m^2}{N-n}\right) \end{array} \right)}_{-\mathcal{C}^{\text{DB}}} + \underbrace{\left(\begin{array}{c} (1-\mu)\mathsf{b} \\ -(\mathsf{b}-\mathsf{c})(n-1)(1-\mu)\left(\frac{(1-m)^2}{n}+\frac{m^2}{N-n}\right) \end{array} \right)}_{\mathcal{B}^{\text{DB}}} \underbrace{\frac{Q_{\text{in}}^{\text{M}}-Q_{\text{out}}^{\text{M}}}{1-Q_{\text{out}}^{\text{M}}}}_{R^{\text{M}}} \Bigg],
$$

$$(7)$$

With this life-cycle, Death occurs first, and the probability of dying is independent from the state of the population (since we assume that social interactions affect fecundity. We can therefore factor $(1-\mu)$ in all terms. The primary effects (first lines in the parentheses) remain the same as with the Birth-Death life-cycle. However, the Death-Birth life-cycle leads to different secondary effects compared to the Birth-Death life-cycle: competition occurs at a different scale (Grafen & Archetti, 2008). Finally, with this life-cycle as we defined it, the probabilities of identity by descent are the same as with the Birth-Death model.

Wright-Fisher

$$
\mathbb{E}\big[\overline{X}\big] \approx \nu + \frac{\delta}{\mu}\nu(1-\nu)(1-Q_{\text{out}}^{\text{WF}}) \times
$$

$$
\Bigg[\underbrace{\left(\begin{array}{c} (1-\mu)(-\mathsf{c}) \\ -(\mathsf{b}-\mathsf{c})(1-\mu)\left(\frac{(1-m)^2}{n}+\frac{m^2}{N-n}\right) \end{array} \right)}_{-\mathcal{C}^{\text{WF}}} + \underbrace{\left(\begin{array}{c} (1-\mu)\mathsf{b} \\ -(\mathsf{b}-\mathsf{c})(n-1)(1-\mu)\left(\frac{(1-m)^2}{n}+\frac{m^2}{N-n}\right) \end{array} \right)}_{\mathcal{B}^{\text{WF}}} \underbrace{\frac{Q_{\text{in}}^{\text{WF}}-Q_{\text{out}}^{\text{WF}}}{1-Q_{\text{out}}^{\text{WF}}}}_{R^{\text{WF}}} \Bigg],
$$

$$(8)$$

The only – but important – different between eq. (8) and eq. (7) is the value of the probabilities of identity by descent, because the number of individuals that are updated at each time step differs.

Primary effects

Let us first focus on primary effects, shown on the first lines in the parentheses in eq. (6)–eq. (8). They are the same for the three life-cycles that we consider, and they do not depend on the emigration probability m. At the same time, as shown on figure 1, the relatedness terms R^{M} and R^{WF} decrease with m (keeping $m < 1 - \frac{1}{N_D}$; see figure 1) Consequently, if we ignored secondary effects, we would conclude that even with imperfect strategy transmission ($\mu > 0$), increasing the emigration probability m decreases the expected frequency of altruists in the population (as our intuition may suggest already.) However, secondary effects play a role as well.

Changes with the emigration probability m

For the three life-cycles, the secondary effects are negative (with $0 < m < 1 - \frac{1}{N_D}$) and they increase with the emigration probability m. In other words, these detrimental secondary effects weaken when the emigration probability increases. This effect goes against the reduction of relatedness R as m increases. Hence, we need to consider the entire equations to know the overall effect of the emigration probability m on the expected frequency of altruists $\mathbb{E}\left[\overline{X}\right]$ and on how it is affected by the (in)fideliy of parent-offspring transmission μ (see Figure 2).

The rather lengthy formulas that we obtain are relegated to the Appendix and supplementary Mathematica file, and we concentrate here on the results.

Moran Birth-Death

For the Moran Birth-Death life-cycle, we find that the expected frequency of altruists $\mathbb{E}\left[\overline{X}\right]$ is a monotonic function of the emigration probability m; the direction of the change depends on the value of the mutation probability μ compared to a threshold value μ_c^{BD}. When $\mu < \mu_c^{\mathrm{BD}}$, $\mathbb{E}\left[\overline{X}\right]$ decreases with m, while when

$\mu > \mu_c^{\mathrm{BD}}$, $\mathbb{E}\big[\overline{X}\big]$ increases with m. The critical value μ_c^{BD} is given by

$$\mu_c^{\mathrm{BD}} = 1 - \frac{\mathsf{b} - \mathsf{c} + \sqrt{(\mathsf{b}-\mathsf{c})\left(4\mathsf{b}N^2 + \mathsf{b} - \mathsf{c}\right)}}{2\mathsf{b}N} \tag{9}$$

(recall that N is the total size of the population, $N = nN_D$.) This result is illustrated in figure 2(b); with the parameters of the figure, $\mu_c^{\mathrm{BD}} \approx 0.026$. The threshold value increases with both deme size n and number of demes N_D, up to a maximum value $1 - \sqrt{1 - \mathsf{c}/\mathsf{b}}$ (equal to 0.034 with our parameters.)

With this life-cycle however, the expected frequency of altruists $\mathbb{E}\big[\overline{X}\big]$ remains lower than ν, its value in the absence of selection (*i.e.*, when $\delta = 0$).

Moran Death-Birth

The relationship between $\mathbb{E}\big[\overline{X}\big]$ and m is a bit more complicated for the Moran Death-Birth life-cycle. For simplicity, we concentrate on what happens starting from low emigration probabilities (*i.e.*, on the sign of the slope of $\mathbb{E}\big[\overline{X}\big]$ as a function of m when $m \to 0$). If the benefits b provided by altruists are relatively low ($\mathsf{b} < \mathsf{c}(n+1)$), $\mathbb{E}\big[\overline{X}\big]$ initially increases with m provided the mutation probability μ is greater than a threshold value μ_c^{DB} given in eq. (10) below; otherwise, when the benefits are high enough, $\mathbb{E}\big[\overline{X}\big]$ initially increases with m for any value of μ. Combining these results, we write

$$\mu_c^{\mathrm{DB}} = \begin{cases} \dfrac{(n+1)\mathsf{c} - \mathsf{b}}{(2n-1)\mathsf{b} - (n-1)\mathsf{c}} & \text{if } \mathsf{b} < \mathsf{c}(n+1), \\[2ex] 0 & \text{otherwise.} \end{cases} \tag{10}$$

When $\mathsf{b} < \mathsf{c}(n+1)$, the mutation threshold does not depend on the number of demes N_D, but increases when the size of the demes n increases. In figure 2(a), the parameters are such that $\mu_c^{\mathrm{DB}} = 0$.

When $\mu > \mu_c^{\mathrm{DB}}$, the expected frequency of altruists $\mathbb{E}\big[\overline{X}\big]$ reaches a maximum at an emigration probability m_c^{DB} (whose complicated equation is given in the

₂₈₇ supplementary Mathematica file), as can be seen in figure 2(a). When the muta-

₂₈₈ tion probability gets close to 0 ($\mu \to 0$), m_c^{DB} also gets close to 0.

₂₈₉ With the Death-Birth life-cycle, the expected frequency of altruists is higher

₂₉₀ than its neutral value ν for intermediate values of the emigration probability m

₂₉₁ (unless $\mu \to 0$, in which case the lower bound tends to 0).

Wright-Fisher

₂₉₃ Under a Wright-Fisher updating, the expected frequency of altruists in the pop-

₂₉₄ ulation reaches an extremum at the highest admissible emigration value $m =$

₂₉₅ $1 - \frac{1}{N_D}$. This extremum is a maximum when the mutation probability is higher

₂₉₆ than a threshold value μ_c^{WF} given by

$$\mu_c^{\text{WF}} = 1 - \sqrt{1 - \frac{c}{b}}, \tag{11}$$

₂₉₇ and it is a minimum otherwise. With the parameters of figure 2(c), $\mu_c^{\text{WF}} = 0.034$.

₂₉₈ With the Wright-Fisher life-cycle however, the expected frequency of altruists

₂₉₉ remains below its value in the absence of selection, ν.

Interpreting the effect of m on $\mathbb{E}[\overline{X}]$

₃₀₁ The result, that higher emigration probabilities can actually favor altruistic be-

₃₀₂ havior, may seem surprising, even though it is confirmed by simulations. The

₃₀₃ result may appear counterintuitive because explanations for the effect of popu-

₃₀₄ lation viscosity on the evolution of altruism often focus on primary effects. The

₃₀₅ role played by secondary effects is harder to grasp. To better understand the role

₃₀₆ played by the mutation probability μ, we now focus on a qualitative condition

₃₀₇ for the evolution of altruism and on the Death-Birth life-cycle:

$$\mathbb{E}[\overline{X}] > \nu \Leftrightarrow R^{\text{M}} > \frac{\mathcal{C}^{\text{DB}}}{\mathcal{B}^{\text{DB}}}. \tag{12}$$

308 (having made sure that $\mathcal{B}^{\text{DB}} > 0$, as shown in the supplementary Mathemati-

309 cal file). With this life-cycle, the $\mathcal{C}^{\text{DB}}/\mathcal{B}^{\text{DB}}$ ratio does not change with the muta-

310 tion probability μ, but it decreases with the emigration probability m ($0 < m <$

311 $1 - 1/N_D$). This decrease of the $\mathcal{C}^{\text{DB}}/\mathcal{B}^{\text{DB}}$ ratio is due to secondary effects (com-

312 petition) diminishing as emigration increases. Relatedness, on the other hand,

313 decreases with both μ and m (see figure 3(a)).

314 When the emigration probability m is vanishingly small, $\lim_{m \to 0} R^{\text{M}} \leq \lim_{m \to 0} \frac{\mathcal{C}^{\text{DB}}}{\mathcal{B}^{\text{DB}}}$,

315 the two only being equal when $\mu = 0$. Hence, it is only when strategy transmis-

316 sion is perfect that condition (12) is satisfied for vanishingly low m. Then, as m

317 increases, the $\frac{\mathcal{C}^{\text{DB}}}{\mathcal{B}^{\text{DB}}}$ ratio and relatedness R do not decrease with the same slope.

318 Provided the mutation probability μ is not too high, *i.e.*, that R initially is not too

319 low already, there can be a range of emigration values m such that condition (12)

320 is satisfied (*i.e.*, the R curve is higher than the $\mathcal{C}/\mathcal{B}$ curve in figure 3(a)).

Relaxing key assumptions

322 To derive our analytical results, we had to make a number of simplifying assump-

323 tions, such as the fact that selection is weak ($\delta \ll 1$), and the fact that the struc-

324 ture of the population is regular (all demes have the same size n). We explored

325 with numerical simulations the effect of relaxing these key assumptions.

326 When selection is strong, the patterns that we identified not only still hold

327 but are even more marked, as shown on figure A1.

328 To relax the assumption of equal deme sizes, we randomly drew deme sizes

329 at the beginning of simulations, with sizes ranging from 2 to 6 individuals and

330 on average $\overline{n} = 4$ individuals per deme as previously. As shown in figure A2, the

331 patterns initially obtained with a homogeneous population structure are robust

332 when the structure is heterogeneous.

333 For the Moran model, it may seem odd that an offspring can replace its own

334 parent (which can occur since $d_{ii} \neq 0$). Figure A3, plotted with dispersal prob-

abilities preventing immediate replacement of one's own parent (for all sites i, $d_{ii} = d_{\text{self}} = 0$; $d_{\text{in}} = (1 - m)/(n - 1)$ for two different sites in the same deme, d_{out} remaining unchanged), confirms that this does affect our conclusions.

The results are obtained in a population of finite size (the figures are done with $N_D = 15$ demes), but still hold when the size of the population is larger (see *e.g.*, figure 3(b), showing the range of emigration and mutation values such that altruism is favored, plotted also for $N_D \to \infty$).

Compared to graphs classically used in evolutionary graph theory (*e.g.*, regular random graphs, grids), the island model is particular because the interaction graph and the dispersal graph are different: interactions take place only within demes ($e_{\text{out}} = 0$), while offspring can disperse out of their natal deme ($d_{\text{out}} > 0$). One may wonder whether our result depends on this difference between the two graphs. Figure A4 shows that the result still holds when the dispersal and interaction graphs are the same. In this figure indeed, we let a proportion m (equal to the dispersal probability) of interactions occur outside of the deme where the individuals live, and set d_{self}, the probability of self replacement, equal to 0, so that the dispersal and interactions graphs are the same. Our conclusions remain unchanged.

Discussion

The expected frequency of altruists in a subdivided population can increase with the probability of emigration

Assuming that the transmission of a social strategy (being an altruist or a defector) from a parent to its offspring could be imperfect, we found that the expected frequency of altruists maintained in a population could increase with the probability m of emigration out of the parental deme, a parameter tuning population viscosity. This result can seem surprising, because it contradicts the conclusions

obtained under the assumption of nearly perfect strategy transmission (*i.e.*, in the case of genetic transmission, when mutation is very weak or absent). Under nearly perfect strategy transmission indeed, increased population viscosity (*i.e.*, decreased emigration probability) is either neutral (Taylor, 1992a, and dashed lines in figures 2(b)–(c)) or favorable (Taylor et al., 2007a, and dashed lines in figure 2(a)) to the evolution of altruistic behavior.

Quantitative vs. qualitative measures

Often, evolutionary success is measured qualitatively, by comparing a quantity (an expected frequency, or, in models with no mutation, a probability of fixation) to the value it would have in the absence of selection. In our model, this amounts to saying that altruism is favored whenever $\mathbb{E}[\overline{X}] > v$ (v is plotted as a horizontal dashed line in figure 2). Some of our conclusions change if we switch to this qualitative measure of evolutionary success: Under the Moran Birth-Death and Wright-Fisher life-cycles, population viscosity does not promote the evolution of altruism – actually, these two life-cycles cannot ever promote altruistic behavior for any regular population structure (Taylor et al., 2011), whichever the probability of mutation (Débarre, 2017). However, under a Moran Death-Birth life-cycle (figure 2(a)), altruism can be favored only at intermediate emigration probabilities. Starting for initially low values of m, increasing the emigration probability can still favor the evolution of altruism under this qualitative criterion (see figure 3(b).)

The result is due to secondary effects

The result, that frequency of altruists can increase with the emigration probability m, may seem counterintuitive. It is the case because verbal explanations for the evolution of altruism often rely on primary effects only. Relatedness R decreases with m, so it may be tempting to conclude that increases in the em-

igration probability m are necessarily detrimental to the evolution of altruism. However, secondary effects play an opposite role, as competition decreases with m. To further explain the relative weight of the detrimental and beneficial consequences of increases in the emigration probability m, let us focus on the Death-Birth life-cycle and consider the qualitative criterion for evolutionary success ($\mathbb{E}[\overline{X}] > v$, *i.e.* $R > \mathcal{C}/\mathcal{B}$; figure 3.)

When parent-offspring strategy transmission is nearly perfect ($\mu \to 0$), for vanishingly small emigration probabilities ($m \to 0$), both R and the $\mathcal{C}/\mathcal{B}$ ratio tend to 1. An increase in the mutation probability μ reduces R while leaving $\mathcal{C}/\mathcal{B}$ unchanged. In other words, for vanishingly small emigration probabilities, altruism is favored by selection only when transmission fidelity is nearly perfect. Let us now consider that benefits b of social interactions are high enough for altruism to be favored at low m when $\mu \to 0$ (as in figure 3(a)). Starting from low values of m, small increases in m have a stronger effect on the $\mathcal{C}/\mathcal{B}$ ratio than on relatedness R: local competition is initially so strong that the beneficial reduction in competition caused by an increase in m initially predominates over the detrimental reduction in relatedness R. The opposite holds for much higher values of m: competition is already small enough that reducing it further does not outweigh the reduction in relatedness R.

Secondary effects are less straightforward to understand than primary effects, and yet they play a crucial role for social evolution in spatially structured populations. Competition among relatives is for instance the reason for Taylor (1992b)'s cancellation result. Similarly, the qualitative differences between the Moran Birth-Death and Moran Death-Birth life-cycles is explained by the different scales of competition that the two life-cycle produce (Débarre et al., 2014; Grafen & Archetti, 2008). Secondary effects are also behind the evolution of social behaviors such as spite (West & Gardner, 2010).

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How small is small and how large is large?

Our results were derived under the assumption of weak selection, assuming that the phenotypic difference between altruists and defectors is small ($\delta \ll 1$). We considered any fidelity of transmission (any μ between 0 and 1) and population size. However, most models considering subdivided populations assume nearly perfect strategy transmission ($\mu \to 0$) and infinite population sizes (number of demes $N_D \to \infty$). The point is technical, but it is important to know that the order in which these limits are taken matters, *i.e.*, one needs to specify how small μ and δ are compared to the inverse size of the population. This remark complements findings by Sample & Allen (2017), who highlighted the quantitative differences between different orders of weak selection and large population limits.

Imperfect transmission and Rebellious Children

Our model bears resemblance to the Rebellious Child Model by Frank (1997), who studied the evolution of a vertically transmitted cultural trait in an asexually reproducing population. In Frank's model, however, relatedness r is treated as a fixed parameter (as acknowledged in the legend of Figure 7 in Frank (1997)). Our model is mechanistic; relatedness r necessarily depends on the mutation probability μ, because probabilities of identity by descent do.

Mutation was also previously included in models investigating the maintenance of cooperative microorganisms in the presence of cheaters (Brockhurst et al., 2007; Frank, 2010). In both of these models however, only loss-of-function mutation was considered, which corresponds to setting the mutation bias at $\nu = 0$ in our model. This means that the all-cheaters state is absorbing; no matter how favored cooperators may otherwise be, in the long run, a finite population will only consist of cheaters.

Cultural transmission

Strategy transmission does not have to be genetic: it can be cultural. In our model, strategy transmission occurs upon reproduction, so this is a case of vertical cultural transmission.

The model could nevertheless be interpreted as a representation of horizontal transmission, if we described reproduction as an instance of an individual convincing another one to update its strategy. The Moran Death-Birth model can be interpreted as a modified imitation scheme (Boyd & Richerson, 2002; Ohtsuki et al., 2006) – with a specific function specifying who is imitated –, with mutation (Kandori et al., 1993). First, we choose uniformly at random an individual who may change its strategy; with probability μ the individual chooses a random strategy (altruistic with probability v), and with probability $1 - \mu$ it imitates another individual. Who is imitated depends on the distance to the focal individual (with probability m it is a random individual in another deme) and on the "fecundities" of those individuals (as shown in table A2). With this interpretation of the updating rule however, there is not reproduction nor death anymore.

It remains to be investigated how imperfect strategy transmission would affect the effect of population viscosity on the evolution of altruism in a model implementing both reproduction and horizontal cultural transmission (as in Lehmann et al., 2008). Such a model could then contrast the effects of impecfect genetic transmission and imperfect horizontal cultural transmission.

Coevolution of dispersal and social behavior

This work also raises the question of what would happen if dispersal (*e.g.,* the emigration probability m) could evolve as well. Recent work on the topic has shown that under some conditions disruptive selection could take place, leading to a polymorphism between sessile altruists and mobile defectors (Mullon et al., 2017; Parvinen, 2013). The assumptions of these studies however differ

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from ours in important ways, in that they consider continuous traits and use an adaptive dynamics framework, where, notably, mutations are assumed to be very rare. It remains to be investigated how non-rare and potentially large mutations would affect their result.

Acknowledgements

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Figures

(a) Moran
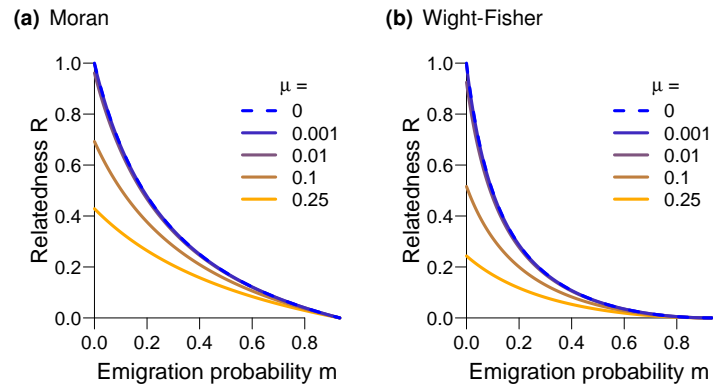
(b) Wight-Fisher

Figure 1: Within-deme relatedness of pairs of individuals, as a function of the emigration probability m, for different values of the mutation probability μ (from 0 [blue] to 0.25 [orange]), and for the two types of life-cycles ((a): Moran, (b): Wright-Fisher). Other parameters: $n = 4$ individuals per deme, $N_D = 15$ demes.

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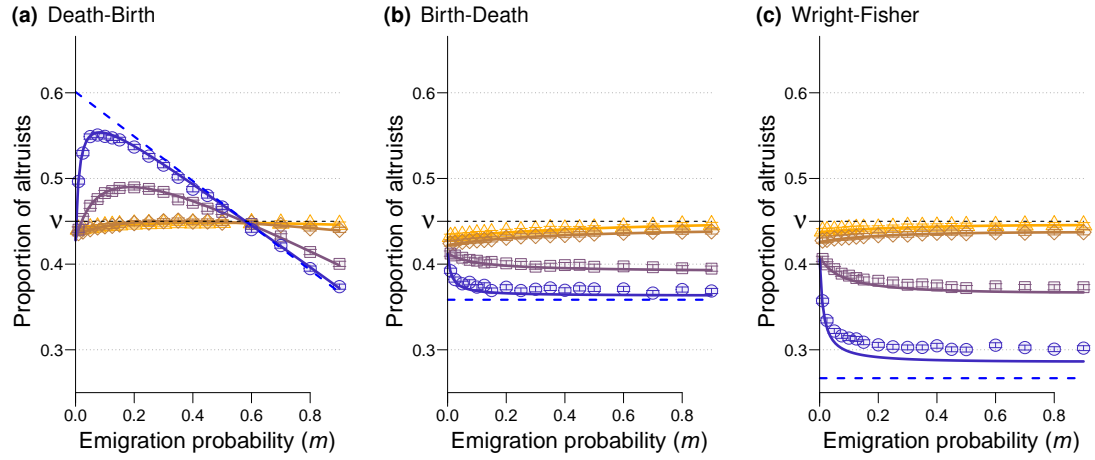
Figure 2: Expected proportion of altruists under weak selection, as a function of the emigration probability m, for different mutation values ($\mu = 0.001$ (blue, dots), 0.01 (purple, squares), 0.1 (brown, diamonds), 0.25 (orange, triangles); the dashed blue lines correspond to $\mu = 0$) and different life-cycles ((a) Moran Death-Birth, (b) Moran Birth Death, (c) Wright-Fisher). The curves are the analytical results, the points are the output of numerical simulations. Parameters: $\delta = 0.005$, $\nu = 0.45$, $b = 15$, $c = 1$, $n = 4$ individuals per deme, $N_D = 15$ demes.
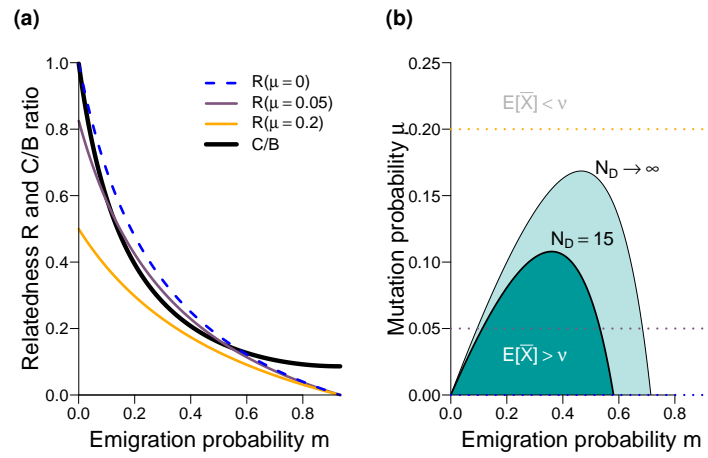
Figure 3: Understanding the effect of emigration m on whether altruism is favored in the Death-Birth life-cycle. (a) Comparison of the $\mathcal{C}/\mathcal{B}$ ratio (thick black curve) and relatedness R (thin curves) for different values of the mutation probability μ (same color code as previously). (b) (m, μ) combinations for which $\mathbb{E}[\overline{X}] > v$. The dotted horizontal lines correspond to the mutation values used in panel (a). Unless specified, all other parameters are the same as in figure 2.

Supplementary figures

(a) Death-Birth   **(b)** Birth-Death   **(c)** Wright-Fisher
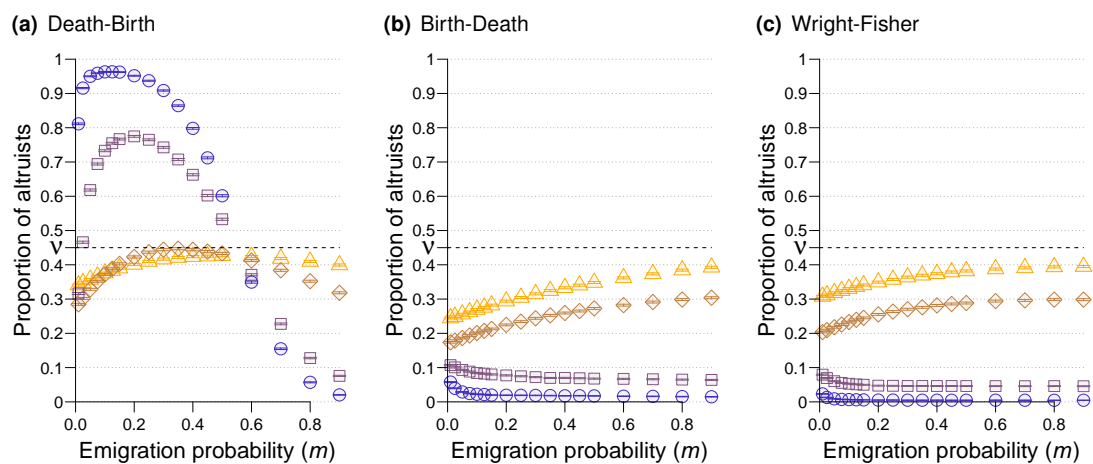
Figure A1: Equivalent of figure 2 (simulations only) but with strong selection ($\delta = 0.1$); please note the change of scale on the vertical axis. All other parameters and legends are identical to those of figure 2 (increasing mutation probabilities from blue dots to orange triangles).
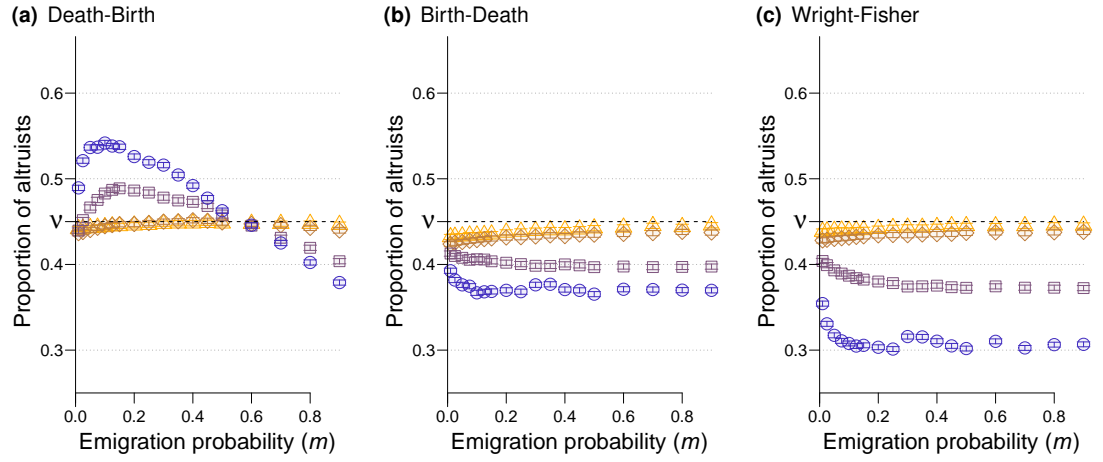
Figure A2: Equivalent of figure 2 (simulations only) but with a heterogeneous population structure: deme sizes range from 1 to 5 individuals per deme, the average deme size is 4 as in figure 2; all other parameters and legend are identical to those of figure 2.
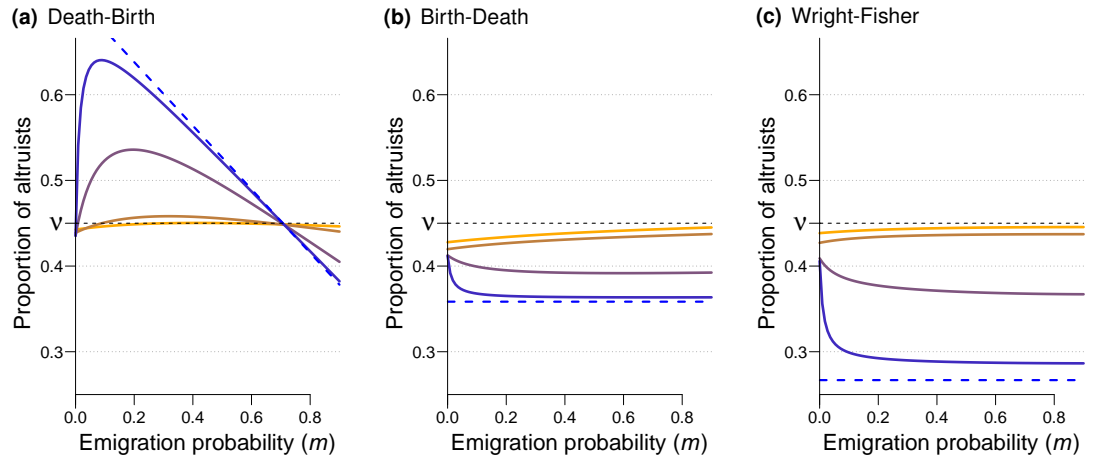
Figure A3: Equivalent of figure 2 (analysis only), with no self-replacement ($d_{ii} = d_{\text{self}} = 0$ for all sites).
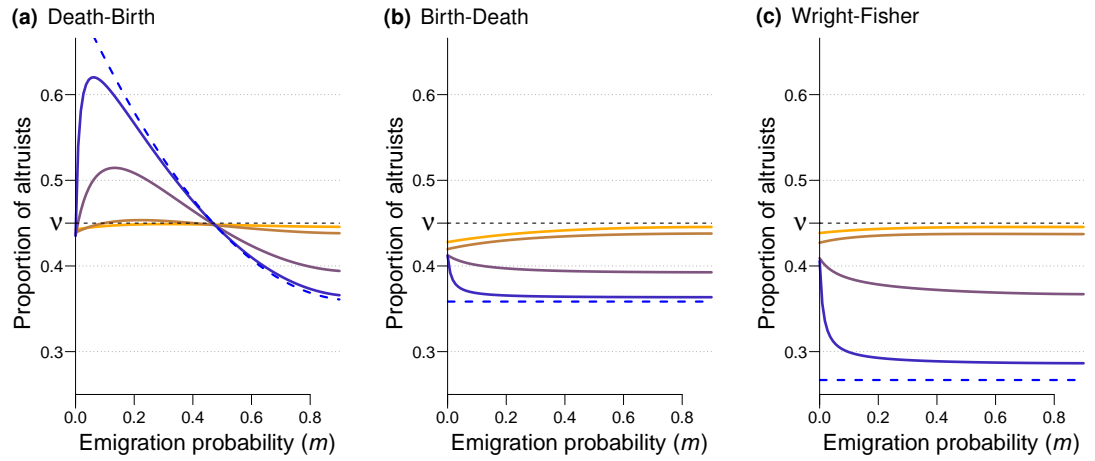
Figure A4: Equivalent of figure 2 (analysis only), with equal dispersal and interaction graphs (*i.e.*, no self-replacement [$d_{ii} = d_{\text{self}} = 0$ for all sites], and a proportion m of the interactions occurring outside of the home deme).

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Supplementary Table

b	Sum of the marginal effects of deme-mates' phenotypes on focal individual's fecundity (benefit)
$\mathcal{B}$	Sum of the marginal effects of deme-mates' phenotypes on the fitness W of a focal individual
B_i	Expected number of successful offspring of the individual living at site i (r.v.)
B^*	Value of B_i for all sites, in the absence of selection ($\delta = 0$)
c	Marginal effect of a focal individual's phenotype on its own fecundity (cost)
$\mathcal{C}$	Marginal effect of an individual's phenotype on its own fitness W
d_{ij}	Dispersal probability from site i to site j
D_i	Probability that the individual currently living at site i is dead at the end of the time step (r.v.)
e_{ij}	Interaction probability from site i to site j
f_i	Fecundity of the individual currently living at site i (r.v.)
n	Deme size
N_D	Number of demes
N	Total population size ($N = N_D n$)
m	Emigration probability
P_{ij}	(Long-term) Expected state of the pair of sites (i,j)
Q_{ij}	(Long-term) Probability of identity by descent of individuals at sites i and j
R	Pairwise within-deme relatedness (see eq. (4))
W_i	Measure of fitness, counting offspring only when unmutated (see eq. (2))
X_i	Indicator variable, equal to 1 if site i is occupied by an altruist, to 0 otherwise (r.v.)
$\overline{X}$	Frequency of altruists in the population (r.v.)
δ	Phenotypic distance between altruists and defectors; strength of selection
ϕ_i	Phenotype of the individual living at site i; $\phi_i = \delta X_i$ (r.v.)
μ	Mutation probability
ν	Mutation bias: probability that mutant is altruist
P	Subscript corresponding to primary effects
S	Subscript corresponding to secondary effects
$\bullet$	Subscript used to denote a focal individual
in	Subscript used when $i \neq j$ and the two sites are in the same deme
out	Subscript used when the two sites i and j are in different demes
self	Subscript used when $i = j$
0	Sub- or superscript meaning that a quantity is evaluated at $\delta = 0$
BD	Superscript corresponding to the Moran Birth-Death model
DB	Superscript corresponding to the Moran Death-Birth model
M	Superscript corresponding to a Moran model
WF	Superscript corresponding to the Wright-Fisher model

Table A1: List of symbols. "r.v." means *random variable*.

Appendix

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A Expected frequency of altruists

For a generic life-cycle

We want to compute the expected proportion of altruists in the population. We represent the state of the population at a given time t using indicator variables $X_i(t)$, $1 \leq i \leq N$, equal to 1 if the individual living at site i at time t is an altruist, and equal to 0 if it is a defector; these indicator variables are gathered in a N-long vector $\mathbf{X}(t)$. The set of all possible population states is $\Omega = \{0,1\}^N$. The proportion of altruists in the population is written $\overline{X}(t) = \sum_{i=1}^{N} X_i(t)$. We denote by $B_{ji}(X(t),\delta)$, written B_{ji} for simplicity, the probability that the individual at site j at time $t+1$ is the newly established offspring of the individual living at site i at time t. The expected number of successful offspring produced by the individual living at site i at time t is given by $B_i = \sum_{j=1}^{N} B_{ji}$. We denote by $D_i(X(t),\delta)$ (D_i for simplicity) the probability that the individual living at site i at time t has been replaced (*i.e.*, died) at time $t+1$. These quantities depend on the chosen life-cycle and on the state of the population; they are given in table A2 for each of the life-cycles that we consider.

Life-cycle	B_{ji}	D_i
Moran Birth-Death	$d_{ij}\dfrac{f_i}{\sum_{k=1}^{N} f_k}$	$\dfrac{\sum_{j=1}^{N} d_{ji} f_j}{\sum_{k=1}^{N} f_k}$
Moran Death-Birth	$\dfrac{1}{N}\dfrac{d_{ij} f_i}{\sum_{k=1}^{N} d_{kj} f_k}$	$\dfrac{1}{N}$
Wright-Fisher	$\dfrac{d_{ij} f_i}{\sum_{k=1}^{N} d_{kj} f_k}$	1

Table A2: Formulas of B_{ji} and D_i for each of the life-cycles that we consider; f_i (shorthand notation for $f_i(X,\delta)$) is the fecundity of the individual living at site i, and d_{ji} is a dispersal probability, given in eq. (1).

Since a dead individual is immediately replaced by one new individual,

$$D_i = \sum_{j=1}^{N} B_{ij} \tag{A1a}$$

holds for all sites i. The structure of the population is also such that in the absence of selection ($\delta = 0$, so that $f_i = 1$ for all sites $1 \leq i \leq N$), all individuals have the same probability of dying and the same probability of having successful offspring (*i.e.*, of having offspring that become adults at the next time step), so that

$$D_i^0 = \sum_{j=1}^{N} B_{ji}^0 = B_i^0 =: B^*, \tag{A1b}$$

where the ^{0} subscript means that the quantities are evaluated for $\delta = 0$. This also implies that B_{ij}^0 and D_i^0 do not depend on the state $\mathbf{X}$ of the population. For the Moran life-cycles, $B^* = 1/N$, while for the Wright-Fisher life-cycle, $B^* = 1$. (The difference between eq. (A1b) and eq. (A1a) is that we are now considering offspring produced by i landing on j).

Given that the population is in state $\mathbf{X}(t)$ at time t, the expected frequency of altruists at time $t + 1$ is given by

$$\mathbb{E}\left[\overline{X}(t+1)|\mathbf{X}(t)\right] = \frac{1}{N}\sum_{i=1}^{N}\left[B_i(1-\mu)X_i + (1-D_i)X_i + B_i\mu\nu\right]. \tag{A2a}$$

The first term within the brackets corresponds to births of unmutated offspring from parents who are altruists (X_i). The second term corresponds to the survival of altruists. The third term corresponds to the births of mutants who became altruists (which occurs with probability ν), whichever the type of the parent.

Given that there is no absorbing population state (a lost strategy can always be recreated by mutation), there is a stationary distribution of population states; the expected frequency of altruists does not change anymore for large times t (realized frequencies of course keep changing). We denote by $\xi(\mathbf{X}, \delta, \mu)$ the probability that the population is in state $\mathbf{X}$, given the strength of selection δ and the mutation probability μ. Taking the expectation of eq. (A2a) ($\mathbb{E}\left[\overline{X}\right] = \sum_{X \in \Omega}\overline{X}\xi(\mathbf{X}, \delta, \mu)$), we obtain, after reorganizing:

$$0 = \frac{1}{N}\sum_{X \in \Omega}\left[\sum_{i=1}^{N}\left(B_i(1-\mu)X_i - D_iX_i\right) + \sum_{i=1}^{N}B_i\mu\nu\right]\xi(\mathbf{X}, \delta, \mu). \tag{A3}$$

Now, we use the assumption of weak selection ($\delta \ll 1$) and consider the first-order expansion of eq. (A3) for δ close to 0. First, we note that in the absence of selection ($\delta = 0$), the population is at a mutation-drift balance; the expected state of every site i is then $\mathbb{E}_0\left[X_i\right] = \sum_{X \in \Omega}X_i\xi(X, 0, \mu) = \nu$ (recall that ν is the mutation bias parameter). Secondly, we note that for all the life-cycles that we consider, the total number of deaths in the population during one time step does not depend on population composition (it is exactly 1 death for the Moran life-cycles, and exactly N for the Wright-Fisher life-cycle), so that $\sum_{i,j=1}^{N}B_{ij}$ does not depend on δ. Consequently, the last term of eq. (A3) vanishes when we take its derivative with respect to δ, for the life-cycles that we consider.

The first order expansion of eq. (A3) yields

$$0 = \frac{\delta}{N}\sum_{i=1}^{N}\left[\sum_{X \in \Omega}\left(\frac{\partial B_i}{\partial \delta}(1-\mu) - \frac{\partial D_i}{\partial \delta}\right)X_i\xi(\mathbf{X}, 0, \mu) - \sum_{X \in \Omega}\mu B^*X_i\frac{\partial \xi}{\partial \delta}\right] + O(\delta^2), \tag{A4}$$

where the derivatives are evaluated at $\delta = 0$, and where we used eq. (A1b) to simplify the second term. For conciseness, we define

$$W_i = (1-\mu)B_i + (1-D_i), \tag{A5}$$

a measure of fitness counting offspring only when they are unmutated. With

this, using the expectation notation, and denoting by $\mathbb{E}_0[\,]$ expectations under $\delta = 0$, we can rewrite and reorganize eq. (A4) as

$$\delta \mu B^* \frac{\partial \mathbb{E}[\overline{X}]}{\partial \delta} = \frac{\delta}{N} \sum_{i=1}^{N} \mathbb{E}_0 \big[\frac{\partial W_i}{\partial \delta} X_i \big] + O(\delta^2). \tag{A6}$$

Now, we use a first time the law of total probabilities, taking individual phenotypes ϕ_k are intermediate variables:

$$\begin{aligned} \frac{\partial W_i}{\partial \delta} &= \sum_{k=1}^{N} \frac{\partial W_i}{\partial \phi_k} \frac{\partial \phi_k}{\partial \delta} \\ &= \sum_{k=1}^{N} \frac{\partial W_i}{\partial \phi_k} X_k, \end{aligned} \tag{A7}$$

by definition of ϕ_k, and where the derivatives are evaluated for all $\phi_i = 0$. With the notation $P_{ij} = \mathbb{E}_0[X_i X_j]$, eq. (A6) becomes

$$\delta \mu B^* \frac{\partial \mathbb{E}[\overline{X}]}{\partial \delta} = \frac{\delta}{N} \sum_{i=1}^{N} \sum_{k=1}^{N} \frac{\partial W_i}{\partial \phi_k} P_{ik} + O(\delta^2). \tag{A8}$$

So far, we have not used the specificities of the population structure that we consider. Once we have fixed a focal individual i, in expectation there are only three types of individuals: the focal itself, $n-1$ other individuals in the focal's deme (denoted by in), and $N-n$ individuals in other demes (denoted by out). We note that given that the size of the population is fixed ($\sum_{i=1}^{N}(B_i - D_i) = 0$), and given that the total number of births does not depend on population composition in the life-cycles that we consider,

$$\sum_{i=1}^{N} \frac{\partial W_i}{\partial \delta} = 0,$$

which we can rewrite as (Rousset & Billiard, 2000)

$$\frac{\partial W_i}{\partial \phi_i} + (n-1) \frac{\partial W_i}{\partial \phi_{\text{in}}} + (N-n) \frac{\partial W_i}{\partial \phi_{\text{out}}} = 0. \tag{A9}$$

With this, eq. (A8) becomes

$$\delta \mu B^* \frac{\partial \mathbb{E}[\overline{X}]}{\partial \delta} = \frac{\delta}{N} \sum_{i=1}^{N} \left(\frac{\partial W_i}{\partial \phi_i} + (n-1) \frac{\partial W_i}{\partial \phi_{\text{in}}} \frac{P_{\text{in}} - P_{\text{out}}}{P_{ii} - P_{\text{out}}} \right) (P_{ii} - P_{\text{out}}) + O(\delta^2). \tag{A10}$$

We can also replace the P terms by

$$\begin{aligned} P_{ij} &= Q_{ij} v + (1 - Q_{ij}) v^2 \\ &= v^2 + v(1-v) Q_{ij}. \end{aligned} \tag{A11}$$

In Appendix B, we will see using recursions on P_{ij} that Q_{ij} can be interpreted as a probability of identity by descent, *i.e.*, the probability that the individuals

653 at sites i and j have a common ancestor and that no mutation has occurred on
654 either lineage since the ancestor. Eq. (A10) becomes

$$\delta\mu B^* \frac{\partial \mathbb{E}[\overline{X}]}{\partial \delta} = \frac{\delta}{N} \sum_{i=1}^{N} \left(\underbrace{\frac{\partial W_i}{\partial \phi_i}}_{-\mathcal{C}} + \underbrace{(n-1)\frac{\partial W_i}{\partial \phi_{\text{in}}}}_{\mathcal{B}} \underbrace{\frac{Q_{\text{in}} - Q_{\text{out}}}{1 - Q_{\text{out}}}}_{R} \right)(1 - Q_{\text{out}})\nu(1-\nu) + O(\delta^2).$$

(A12)

655 We can further decompose the derivatives, now using the fecundities f_ℓ as
656 intermediate variables, *i.e.*,

$$\frac{\partial W_i}{\partial \phi_k} = \sum_{\ell=1}^{N} \frac{\partial W_i}{\partial f_\ell} \frac{\partial f_\ell}{\partial \phi_k}.$$

(A13)

657 With our notation, and given that social interactions take place within demes
658 and affect fecundity, we have

$$\left.\frac{\partial f_\ell}{\partial \phi_\ell}\right|_{\delta=0} = -\mathsf{c},$$

(A14a)

$$\left.\frac{\partial f_\ell}{\partial \phi_{\text{in}}}\right|_{\delta=0} = \frac{\mathsf{b}}{n-1},$$

(A14b)

$$\left.\frac{\partial f_\ell}{\partial \phi_{\text{out}}}\right|_{\delta=0} = 0.$$

(A14c)

659 Eq. (A12) then becomes (using notation • to refer to the focal individual itself,
660 and where $W = W_i$, since the derivatives are the same for all i):

$$\delta\mu B^* \frac{\partial \mathbb{E}[\overline{X}]}{\partial \delta} = \delta\nu(1-\nu)(1 - Q_{\text{out}}) \times$$
$$\left(\underbrace{\frac{\partial W}{\partial f_\bullet}(-\mathsf{c}) + \frac{\partial W}{\partial f_{\text{in}}}\mathsf{b}}_{-\mathcal{C}} + \underbrace{\left(\frac{\partial W}{\partial f_\bullet}\mathsf{b} + (n-1)\frac{\partial W}{\partial f_{\text{in}}}(-\mathsf{c}) + (n-2)\frac{\partial W}{\partial f_{\text{in}}}\mathsf{b} \right)}_{\mathcal{B}} \underbrace{\frac{Q_{\text{in}} - Q_{\text{out}}}{1 - Q_{\text{out}}}}_{R} \right) + O(\delta^2).$$

(A15)

661 (As previously, all derivatives are evaluated at $\delta = 0$.)

662 Finally, we obtain a first-order approximation of the expected frequency of
663 altruists in the population with

$$\mathbb{E}[\overline{X}] = \nu + \delta \left.\frac{\partial \mathbb{E}[\overline{X}]}{\partial \delta}\right|_{\delta=0} + O(\delta^2),$$

(A16)

664 where $\left.\frac{\partial \mathbb{E}[\overline{X}]}{\partial \delta}\right|_{\delta=0}$ is obtained from eq. (A15). We then need to replace the B_i and
665 D_i terms by their formulas for each life-cycle (given in table A2).

Derivatives for the specific life-cycles

667 Using the formulas presented in table A2, and the definition of $W = W_i$ given in
668 eq. (A5), we obtain the following equations:

37   2017-11-09

Moran Birth-Death

$$\left.\frac{\partial W^{\mathrm{BD}}}{\partial f_\bullet}\right|_{\delta=0} = (1-\mu)\left(\frac{1}{N} - \frac{1}{N^2}\right) - \left(\frac{1-m}{nN} - \frac{1}{N^2}\right) = \frac{1-\mu}{N} + \frac{\mu}{N^2} - \frac{1-m}{nN}, \quad \text{(A17a)}$$

$$\left.\frac{\partial W^{\mathrm{BD}}}{\partial f_{\mathrm{in}}}\right|_{\delta=0} = (1-\mu)\left(-\frac{1}{N^2}\right) - \left(\frac{1-m}{nN} - \frac{1}{N^2}\right) = \frac{\mu}{N^2} - \frac{1-m}{nN}. \quad \text{(A17b)}$$

Moran Death-Birth

$$\left.\frac{\partial W^{\mathrm{DB}}}{\partial f_\bullet}\right|_{\delta=0} = \frac{1-\mu}{N}\left[1 - \left(\frac{(1-m)^2}{n} + \frac{m^2}{N-n}\right)\right], \quad \text{(A18a)}$$

$$\left.\frac{\partial W^{\mathrm{DB}}}{\partial f_{\mathrm{in}}}\right|_{\delta=0} = -\frac{1-\mu}{N}\left(\frac{(1-m)^2}{n} + \frac{m^2}{N-n}\right). \quad \text{(A18b)}$$

In addition, for both Moran life-cycles, we have $B_{\mathrm{M}}^* = 1/N$.

Wright-Fisher

$$\left.\frac{\partial W^{\mathrm{WF}}}{\partial f_\bullet}\right|_{\delta=0} = (1-\mu)\left[1 - \left(\frac{(1-m)^2}{n} + \frac{m^2}{N-n}\right)\right], \quad \text{(A19a)}$$

$$\left.\frac{\partial W^{\mathrm{WF}}}{\partial f_{\mathrm{in}}}\right|_{\delta=0} = -(1-\mu)\left(\frac{(1-m)^2}{n} + \frac{m^2}{N-n}\right). \quad \text{(A19b)}$$

For the Wright-Fisher life-cycle, we have $B_{\mathrm{WF}}^* = 1$.

Combining these equations with eq. (A16) and eq. (A15) given eqs. (6)–(8) in the main text.

B Probabilities of identity by descent

Expected state of pairs of sites and probabilities of identity by descent

Here we show the link between the expected state of a pair of sites P_{ij} and probabilities of identity by descent Q_{ij}. In our derivation of $\mathbb{E}[\overline{X}]$, P_{ij} is the quantity that appears, but most studies use Q_{ij}. Both are evaluated in the absence of selection ($\delta = 0$).

Moran model

In a Moran model, exactly one individual dies and one individual reproduces during one time step. Given a state $\mathbf{X}$ at time t, at time $t + 1$ both sites i and $j \neq i$ are occupied by altruists, if *i*) it was the case at time t and neither site was replaced by a non-altruist (first term in eq. (A20)), or *ii*) if exactly one of the two sites was occupied by a non-altruist at time t, but the site was replaced by an altruist (second and third terms of eq. (A20)):

$$
\begin{aligned}
\mathbb{E}\left[X_i X_j(t+1)|X(t) = \mathbf{X}\right] = {} & X_i X_j \left(1 - \sum_{k=1}^{N} \frac{1}{N} \left(d_{ki} + d_{kj}\right)\left((1 - X_k)(1 - \mu) + \mu(1 - \nu)\right)\right) \\
& + X_i(1 - X_j) \sum_{k=1}^{N} \frac{1}{N} d_{kj} \left(X_k(1 - \mu) + \mu\nu\right) \\
& + X_j(1 - X_i) \sum_{k=1}^{N} \frac{1}{N} d_{ki} \left(X_k(1 - \mu) + \mu\nu\right).
\end{aligned}
\tag{A20}
$$

We take the expectation of this quantity, and consider that the stationary distribution is reached ($t \to \infty$); then $\mathbb{E}\left[X_i X_j(t+1)\right] = \mathbb{E}\left[X_i X_j(t)\right]$, and we obtain

$$
P_{ij} = \frac{1}{2} \left(\sum_{k=1}^{N} (1 - \mu)\left(d_{kj} P_{ki} + d_{ki} P_{kj}\right)\right) + \mu\nu^2 \qquad (i \neq j),
\tag{A21}
$$

while $P_{ii} = \nu$.

Now we substitute $P_{ij} = \nu^2 + \nu(1 - \nu)Q_{ij}$ in eq. (A21), we obtain

$$
Q_{ij} = \frac{1}{2} \sum_{k=1}^{N} (1 - \mu)\left(d_{ki} Q_{kj} + d_{kj} Q_{ki}\right),
\tag{A22}
$$

and we realize that Q_{ij} is the probability that the individuals at sites i and $j \neq i$ are identical by descent. To compute it indeed, we need to pick which site was last updated (equal probabilities), then who was the parent (k); the other individual needs to be identical by descent to the parent, and no mutation should have occurred ($1 - \mu$).

₆₉₅ **Wright-Fisher model**

₆₉₆ In a Wright-Fisher model, all individuals are replaced at each time step, so we
₆₉₇ directly consider the state of the parents:

$$\mathbb{E}\big[X_i X_j(t+1)|X(t) = \mathbf{X}\big] = \sum_{k,\ell=1}^{N} d_{ki} d_{\ell j}\bigg(X_k X_\ell (1-\mu+\mu v)^2$$
$$+ (X_k(1-X_\ell) + (1-X_k)X_\ell)(1-\mu+\mu v)(\mu v)$$
$$+ (1-X_k)(1-X_\ell)(\mu v)^2 \bigg) \tag{A23}$$

₆₉₈ The first term of eq. (A23) corresponds to both parents being altruists, and hav-
₆₉₉ ing altruist offspring; the second line corresponds to exactly one parent being
₇₀₀ altruist, and the third line to both parents being non-altruists (in this latter case,
₇₀₁ the two offspring have to be both mutants to be altruists).
₇₀₂ Taking the expectation and simplifying, we obtain

$$P_{ij} = \sum_{k,\ell=1}^{N} \big(P_{kl}(1-\mu)^2 \big) + (2-\mu)\mu v^2. \tag{A24}$$

₇₀₃ Replacing P_{ij} by $v^2 + v(1-v)Q_{ij}$, eq. (A24) becomes

$$Q_{ij} = \sum_{k,\ell=1}^{N} d_{ki} d_{\ell j} Q_{k\ell}(1-\mu)^2. \tag{A25}$$

₇₀₄ Again, Q_{ij} corresponds to a probability of identity by descent: the individuals at
₇₀₅ sites i and j are identical by descent if their parents were and if neither mutated
₇₀₆ $((1-\mu)^2)$.

Probabilities of identity by descent in a subdivided population

Two individuals are said to be identical by descent if there has not been any mutation on either lineage since their common ancestor. Because of the structure of the population, there are only three types of pairs of individuals, and hence three different values of the probabilities of identity by descent of pairs of sites Q_{ij}:

$$Q_{ij} = \begin{cases} 1 & \text{when } i = j; \\ Q_{\text{in}} & \text{when } i \neq j \text{ and both sites are in the same deme;} \\ Q_{\text{out}} & \text{when sites } i \text{ and } j \text{ are in different demes.} \end{cases} \qquad \text{(A26)}$$

The values of Q_{in} and Q_{out} depend on the type of life-cycle that we consider.

Here, we will use formulas derived in Débarre (2017) for "two-dimensional population structures". The name comes from the fact that we only need two types of transformations to go from any site to any other site in the population: permutations on the deme index, and permutations on the within-deme index. We rewrite site labels ($1 \leq i \leq N$) as (ℓ_1, ℓ_2), where ℓ_1 is the index of the deme ($1 \leq \ell_1 \leq N_D$) and ℓ_2 the position of the site within the deme ($1 \leq \ell_2 \leq n$). Then, we introduce notations $\tilde{d}_{i_1 \atop i_2}$ and $\tilde{Q}_{i_1 \atop i_2}$, that correspond to the dispersal probability and probability of identity by descent to a site at distances i_1 and i_2 in the among-demes and within-deme dimensions (e.g., $\tilde{d}_{i_1 \atop i_2} = d_{j_1 \; j_1+i_1 \atop j_2, j_2+i_2}$.)

Also, in this section, we distinguish between $d_{\text{self}} = d_{ii}$ and d_{in} (in the main text, $d_{\text{self}} = d_{\text{in}}$).

Moran model

In Débarre (2017), it was shown that

$$\tilde{Q}_{r_1 \atop r_2} = \frac{1}{N} \sum_{q_1=0}^{N_1-1} \sum_{q_2=0}^{N_2-1} \frac{\mu \lambda'_M}{1-(1-\mu)\tilde{\mathcal{D}}_{q_1 \atop q_2}} \exp\left(\iota \frac{2\pi q_1 r_1}{N_1}\right) \exp\left(\iota \frac{2\pi q_2 r_2}{N_2}\right) \qquad \text{(A27a)}$$

with

$$\tilde{\mathcal{D}}_{q_1 \atop q_2} = \sum_{\ell_1=0}^{N_1-1} \sum_{\ell_2=0}^{N_2-1} \tilde{d}_{\ell_1 \atop \ell_2} \exp\left(-\iota \frac{2\pi q_1 \ell_1}{N_1}\right) \exp\left(-\iota \frac{2\pi q_2 \ell_2}{N_2}\right), \qquad \text{(A27b)}$$

and λ'_M such that $\tilde{Q}_{0 \atop 0} = 1$. Let us first compute $\tilde{\mathcal{D}}_{q_1 \atop q_2}$ in the case of a subdivided population, with $N_1 = N_D$ and $N_2 = n$:

$$\tilde{\mathcal{D}}_{q_1 \atop q_2} = d_{\text{self}} + \sum_{\ell_2=1}^{N_2-1} d_{\text{in}} \exp\left(-\iota \frac{2\pi q_2 \ell_2}{N_2}\right) + \sum_{\ell_1=1}^{N_1-1} \sum_{\ell_2=0}^{N_2-1} d_{\text{out}} \exp\left(-\iota \frac{2\pi q_1 \ell_1}{N_1}\right) \exp\left(-\iota \frac{2\pi q_2 \ell_2}{N_2}\right)$$

$$= d_{\text{self}} + \left(\delta_{q_2}(N_2-1) + (1-\delta_{q_2})(-1)\right) d_{\text{in}} + \left(\delta_{q_1}(N_1-1) + (1-\delta_{q_1})(-1)\right)\left(\delta_{q_2} N_2\right) d_{\text{out}}$$

$$= d_{\text{self}} + \left(\delta_{q_2} N_2 - 1\right) d_{\text{in}} + \left(\delta_{q_1} N_1 - 1\right) \delta_{q_2} N_2 d_{\text{out}}. \qquad \text{(A28a)}$$

730 (δ_q is equal to 1 when q is equal to 0 modulo the relevant dimension, and to 0
731 otherwise). So for the three types of distances that we need to consider (distance
732 0, distance to another deme-mate, distance to individual in another deme), and
733 with $N_1 = N_D$ and $N_2 = n$, we obtain

$$\tilde{\mathcal{D}}_{\substack{0 \\ 0}} = 1, \tag{A29a}$$

$$\tilde{\mathcal{D}}_{\substack{q_1 \\ 0}} = 1 - m - \frac{m}{N_D - 1} \quad (q_1 \not\equiv 0 \pmod{N_1}), \tag{A29b}$$

$$\tilde{\mathcal{D}}_{\substack{q_1 \\ q_2}} = d_{\text{self}} - d_{\text{in}} \quad (q_2 \not\equiv 0 \pmod{N_2}). \tag{A29c}$$

734 So for $\tilde{\mathcal{Q}}$, using system (A29) in eq. (A27a),

$$
\begin{aligned}
\tilde{\mathcal{Q}}_{\substack{r_1 \\ r_2}} &= \frac{\mu \lambda'_M}{N} \Bigg[\frac{1}{1 - (1-\mu)\tilde{\mathcal{D}}_{\substack{0 \\ 0}}} + \sum_{q_2=1}^{N_2-1} \frac{1}{1 - (1-\mu)\tilde{\mathcal{D}}_{\substack{0 \\ q_2}}} \exp\left(-\iota \frac{2\pi q_2 r_2}{N_2}\right) \\
&\quad + \sum_{q_1=1}^{N_1-1} \frac{1}{1 - (1-\mu)\tilde{\mathcal{D}}_{\substack{q_1 \\ 0}}} \exp\left(-\iota \frac{2\pi q_1 r_1}{N_1}\right) \\
&\quad + \sum_{q_1=1}^{N_1-1} \sum_{q_2=1}^{N_2-1} \frac{1}{1 - (1-\mu)\tilde{\mathcal{D}}_{\substack{q_1 \\ q_2}}} \exp\left(-\iota \frac{2\pi q_1 r_1}{N_1}\right) \exp\left(-\iota \frac{2\pi q_2 r_2}{N_2}\right) \Bigg] \\
&= \frac{\mu \lambda'_M}{N} \Bigg[\frac{1}{1 - (1-\mu)} + \frac{1}{1 - (1-\mu)(d_{\text{self}} - d_{\text{in}})} (\delta_{r_2} N_2 - 1) \\
&\quad + \frac{1}{1 - (1-\mu)(1 - m - \frac{m}{N_D - 1})} (\delta_{r_1} N_1 - 1) \\
&\quad + \frac{1}{1 - (1-\mu)(d_{\text{self}} - d_{\text{in}})} (\delta_{r_1} N_1 - 1)(\delta_{r_2} N_2 - 1) \Bigg]. \tag{A30}
\end{aligned}
$$

735 In particular,

$$
\begin{aligned}
\tilde{\mathcal{Q}}_{\substack{0 \\ 0}} &= \frac{\mu \lambda'_M}{N} \Bigg[\frac{1}{\mu} + \frac{1}{1 - (1-\mu)(d_{\text{self}} - d_{\text{in}})} (n-1) + \frac{1}{1 - (1-\mu)(1 - m - \frac{m}{N_D-1})} (N_D - 1) \\
&\quad + \frac{1}{1 - (1-\mu)(d_{\text{self}} - d_{\text{in}})} (N_D - 1)(n-1) \Bigg] \\
&= 1. \tag{A31a}
\end{aligned}
$$

736 We find λ'_M using eq. (A31a). Let's now go back to eq. (A30): when $r_1 = 0$, the two
737 individuals are in the same deme. They are different when $r_2 \not\equiv 0$, and so:

$$
\begin{aligned}
Q_{\text{in}} &= \frac{\mu \lambda'_M}{N} \Bigg[\frac{1}{\mu} + \frac{1}{1 - (1-\mu)(d_{\text{self}} - d_{\text{in}})} (-1) + \frac{1}{1 - (1-\mu)(1 - m - \frac{m}{N_D-1})} (D - 1) \\
&\quad + \frac{1}{1 - (1-\mu)(d_{\text{self}} - d_{\text{in}})} (D - 1)(-1) \Bigg]. \tag{A31b}
\end{aligned}
$$

738 And when $r_1 \not\equiv 0$, the two individuals are in different demes:

$$Q_{\text{out}} = \frac{\mu \lambda'_M}{N} \left[\frac{1}{\mu} + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})}(-1) + \frac{1}{1 - (1 - \mu)(1 - m - \frac{m}{N_D - 1})}(-1) \right.$$

$$\left. + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})} \right]. \tag{A31c}$$

739 With $d_{\text{self}} = d_{\text{in}} = (1 - m)/n$, we eventually obtain:

$$Q_{\text{in}}^{\text{M}} = \frac{(1 - \mu)\left(m + \mu(N_D(1 - m) - 1)\right)}{(1 - \mu)m(N_D\mu(n - 1) + 1) + (N_D - 1)\mu(\mu(n - 1) + 1)}, \tag{A32a}$$

$$Q_{\text{out}}^{\text{M}} = \frac{(1 - \mu)m}{(1 - \mu)m(N_D\mu(n - 1) + 1) + (N_D - 1)\mu(\mu(n - 1) + 1)}. \tag{A32b}$$

740 The probability that two different deme-mates are identical by descent, Q_{in}^{M}, de-
741 creases monotonically with the emigration probability m, while $Q_{\text{out}}^{\text{M}}$ monoton-
742 ically increases with m (see figure A5(a)).

743   When the mutation probability μ is vanishingly small ($\mu \to 0$), both Q_{in}^{M} and
744 $Q_{\text{out}}^{\text{M}}$ are equal to 1: in the absence of mutation indeed, the population ends up
745 fixed for one of the two types, and all individuals are identical by descent. Note
746 that we obtain a different result if we first assumed that the size of the popu-
747 lation is infinite ($N_D \to \infty$), because the order of limits matters; for instance,
748 $\lim_{d \to \infty} Q_{\text{out}}^{M} = 0$.

749 **Wright-Fisher**

750 For the Wright-Fisher updating, the equation for $\tilde{Q}$ is different:

$$\tilde{\mathcal{Q}}_{\substack{r_1 \\ r_2}} = \frac{1}{N} \sum_{q_1 = 0}^{N_1 - 1} \sum_{q_2 = 0}^{N_2 - 1} \frac{\mu \lambda'_{WF}}{1 - (1 - \mu)^2 (\tilde{\mathcal{D}}_{\substack{q_1 \\ q_2}})^2} \exp\left(-\iota \frac{2\pi q_1 r_1}{N_1}\right) \exp\left(-\iota \frac{2\pi q_2 r_2}{N_2}\right), \tag{A33}$$

751 with $\tilde{\mathcal{D}}$ given in eq. (A27b). In a subdivided population, with $N_1 = N_D$ and $N_2 = n$,
752 this becomes

$$
\begin{aligned}
\tilde{\mathcal{Q}}_{\substack{r_1 \\ r_2}} = \frac{1}{N} \Bigg[&\frac{\mu \lambda'_{WF}}{1 - (1-\mu)^2 (\tilde{\mathcal{D}}_{\substack{0 \\ 0}})^2} + \sum_{q_2=1}^{N_2-1} \frac{\mu \lambda'_{WF}}{1 - (1-\mu)^2 (\tilde{\mathcal{D}}_{\substack{0 \\ q_2}})^2} \exp\left(-\iota \frac{2\pi q_2 r_2}{N_2}\right) \\
&+ \sum_{q_1=1}^{N_1-1} \frac{\mu \lambda'_{WF}}{1 - (1-\mu)^2 (\tilde{\mathcal{D}}_{\substack{q_1 \\ 0}})^2} \exp\left(-\iota \frac{2\pi q_1 r_1}{N_1}\right) \\
&+ \sum_{q_1=1}^{N_1-1} \sum_{q_2=1}^{N_2-1} \frac{\mu \lambda'_{WF}}{1 - (1-\mu)^2 (\tilde{\mathcal{D}}_{\substack{q_1 \\ q_2}})^2} \exp\left(-\iota \frac{2\pi q_1 r_1}{N_1}\right) \exp\left(-\iota \frac{2\pi q_2 r_2}{N_2}\right) \Bigg] \\
= \frac{\mu \lambda'_{WF}}{N} \Bigg[&\frac{1}{1 - (1-\mu)^2} + \frac{1}{1 - (1-\mu)^2 (d_{\text{self}} - d_{\text{in}})^2} (\delta_{q_2} N_2 - 1) \\
&+ \frac{1}{1 - (1-\mu)^2 (1 - m - \frac{m}{N_D-1})^2} (\delta_{q_1} N_1 - 1) \\
&+ \frac{1}{1 - (1-\mu)^2 (d_{\text{self}} - d_{\text{in}})^2} (\delta_{q_1} N_1 - 1)(\delta_{q_2} N_2 - 1) \Bigg] \\
= \frac{\mu \lambda'_{WF}}{N} \Bigg[&\frac{1}{1 - (1-\mu)^2} + \frac{1}{1 - (1-\mu)^2 (d_{\text{self}} - d_{\text{in}})^2} (\delta_{q_2} N_2 - 1) \delta_{q_1} N_1 \\
&+ \frac{1}{1 - (1-\mu)^2 (1 - m - \frac{m}{N_D-1})^2} (\delta_{q_1} N_1 - 1) \Bigg].
\end{aligned}
\tag{A34}
$$

753 To find λ'_{WF}, we solve $\tilde{\mathcal{Q}}_{\substack{0 \\ 0}} = 1$, *i.e.*,

$$
1 = \frac{\mu \lambda'_{WF}}{N} \left[\frac{1}{1-(1-\mu)^2} + \frac{1}{1-(1-\mu)^2 (d_{\text{self}} - d_{\text{in}})^2} (N_2-1) N_1 + \frac{1}{1-(1-\mu)^2 (1-m-\frac{m}{N_D-1})^2} (N_1-1) \right].
\tag{A35a}
$$

754 Then from eq. (A34) we deduce

$$
Q_{\text{in}} = \frac{\mu \lambda'_{WF}}{N} \left[\frac{1}{1-(1-\mu)^2} - \frac{1}{1-(1-\mu)^2 (d_{\text{self}} - d_{\text{in}})^2} N_1 + \frac{1}{1-(1-\mu)^2 (1-m-\frac{m}{N_D-1})^2} (N_1-1) \right].
\tag{A35b}
$$

755 and

$$
Q_{\text{out}} = \frac{\mu \lambda'_{WF}}{N} \left[\frac{1}{1-(1-\mu)^2} - \frac{1}{1-(1-\mu)^2 (1-m-\frac{m}{d-1})^2} \right].
\tag{A35c}
$$

756 With $d_{\text{self}} = d_{\text{in}} = (1-m)/n$, we obtain:

$$
Q_{\text{in}}^{\text{WF}} = \frac{-N_D + M_1 + M_2}{(n-1) N_D + M_1 + M_2},
\tag{A36a}
$$

$$
Q_{\text{out}}^{\text{WF}} = \frac{-\frac{1}{N_D-1} M_1 + M2}{(n-1) N_D + M_1 + M_2},
\tag{A36b}
$$

757 with

$$
M_1 = \frac{N_D - 1}{1 - \frac{(1-\mu)^2 (N_D(1-m)-1)^2}{(N_D-1)^2}} \quad \text{and} \quad M_2 = \frac{1}{1 - (1-\mu)^2}.
$$

758 (These formulas are compatible with, *e.g.*, results presented by Cockerham &
759 Weir (1987), adapted for haploid individuals).

760 In the Wright-Fisher life-cycle, $Q_{\text{in}}^{\text{WF}}$ decreases until $m = m_c^{\text{WF}} = \frac{N_D - 1}{N_D}$, while Q_{out}^{WF}
761 follows the opposite pattern. The threshold value m_c^{WF} corresponds to an emi-
762 gration probability so high that $d_{\text{in}} = d_{\text{out}}$.

763 The two probabilities of identity by descent go to 1 when the mutation prob-
764 ability μ is very small ($\mu \to 0$), except if we first assume that the number of demes
765 is very large ($N_D \to \infty$); for instance, with this life-cycle as well, $\lim_{N_D \to \infty} Q_{\text{out}}^{\text{WF}} =$
766 0.

767 Also, because more sites (all of them, actually) are updated at each time
768 step, Q_{in} is lower for the Wright-Fisher updating than for a Moran updating, un-
769 der which only one site is updated at each time step (compare figure A5(a) and
770 A5(b)).
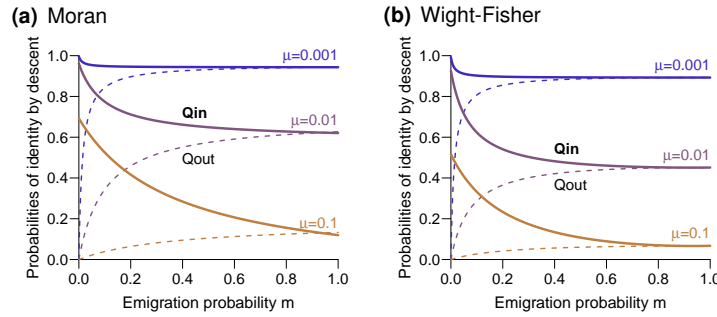
Figure A5: Probabilities of identity by descent, for two different individuals within the same deme (Q_{in}, full curves) and two individuals in different demes (Q_{out}, dashed curves), as a function of the emigration probability m, for different values of the mutation probability μ (0.001, 0.01, 0.1), and for the two types of life-cycles ((a): Moran, (b): Wright-Fisher). Other parameters: $n = 4$ individuals per deme, $N_D = 15$ demes.