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Article Title: Imperfect strategy transmission can reverse the role of population viscosity on the evolution of altruism .

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Abstract

Population viscosity, *i.e.*, low emigration out of the natal deme, leads to high within-deme relatedness, which is beneficial to the evolution of altruistic behavior when social interactions take place among deme-mates. At the same time however, it increases competition among related individuals. The evolution of altruism depends on the balance between these opposite effects. This balance is already known to be affected by details of the life-cycle; we show here that it further depends on the fidelity of strategy transmission from parents to their offspring. We consider different life-cycles (Wright-Fisher, with synchronous non-overlapping generations, Moran Death-Birth and Moran Birth-Death, both with exactly one individual dying and reproducing at each time step) and we identify thresholds of parent-offspring strategy transmission inaccuracy, above which the effect of population viscosity on the frequency of altruists maintained in the population qualitatively changes. Analytical predictions are first obtained analytically under weak selection and equal deme sizes, then confirmed with

stochastic simulations relaxing these assumptions. This result challenges the notion that the evolution of 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. This 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.

1 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.* Ohtsuki et al., 2006; Taylor et al., 2007a; Lehmann et al., 2007). The rationale 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). 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.

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; Taylor et al., 2007b; Tarnita & Taylor, 2014) or absent mutation (for models assuming infinite population sizes, or models concentrating on fixation probabilities 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 struc-

tured 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. 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.

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 it 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.

2 Model and methods

2.1 Assumptions

We consider a population of size N, subdivided into N_D demes, each 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 $\mathbf{X}$. For a given population state $\mathbf{X}$, the proportion of altruists is $\overline{X} = \sum_{i=1}^{N} X_i$. All symbols are summarized in table S1.

Reproduction is asexual. Parents transmit their strategy to their offspring with probability $1 - \mu$; this transmission can be genetic or cultural (vertical cultural transmission), but for simplicity, we refer to the parameter μ as a mutation probability. With probability μ, offspring do not inherit their strategy from their

parent but instead get one randomly: with probability ν, they become altruists, with probability $1-\nu$ they become defectors. We call the parameter ν the mutation bias.

An individual of type X_k expresses a social phenotype $\phi_k = \delta X_k$, where δ is assumed to be small ($\delta \ll 1$). Social interactions take place within each deme, benefits are shared with the $n-1$ other deme-mates. We assume that social interactions affect individual fecundity; f_k denotes the fecundity of the individual at site k. We denote by b the marginal effect of a deme-mate's phenotype on the fecundity of a focal individual, and by $-\mathsf{c}$ the marginal effect of a focal individual's phenotype on its own fecundity ($\mathsf{c} \leq \mathsf{b}$).

Offspring remain in the parental deme with probability $1-m$; when they do, they land on any site of the deme with equal probability (including the very site of their parent). With probability m, offspring emigrate to a different deme, chosen uniformly at random among the other demes. Denoting by d_{ij} the probability of moving from site i to site j, we have

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

with $0 < m < 1 - \frac{1}{N_D}$ (the upper bound implies $d_{\text{in}} > d_{\text{out}}$).

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

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

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.

2.2 Methods

2.2.1 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 this quantity and consider large times t. After this, we write a first order expansion for phenotypic differences δ close to 0 (this corresponds to weak selection approximation).

The formula involves quantities that can be identified as neutral probabilities of identity by descent Q_{ij}, *i.e.*, the probability that individuals living at site i and j share a common ancestor and that no mutation occurred on either lineage

since that ancestor, in a model with no selection ($\omega = 0$; this is the "mutation definition" of identity by descent (Rousset & Billiard, 2000).)

These neutral probabilities of identity by descent depend on the chosen life-cycle, and are also computed by taking the long-term expectation of conditional expectations after one time step (see Appendix B.1 and B.2).

All the results obtained analytically were checked numerically using specific population structures (see supplementary Mathematica file (Wolfram Research, Inc., 2017).)

2.2.2 Stochastic simulations

We also ran stochastic simulations (coded in `C`). The simulations were run for 10^8 generations (one generation is one time step for the Wright-Fisher life-cycle, and N time steps for the Moran life-cycles). For each set of parameters and life-cycle, using R (R Core Team, 2015), we estimated the long-term frequency of altruists by sampling the population every 10^3 generations and computing the average frequency of altruists.

All scripts are available at

`https://github.com/flodebarre/SocEvolSubdivPop/tree/master/Programs`

3 Results

3.1 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, $\mathbb{E}\left[\overline{X}\right]$, can be approximated as

$$\mathbb{E}\left[\overline{X}\right] \approx \nu + \frac{\delta}{\mu B^*}\nu(1-\nu)(1-Q_{\text{out}})\times \left[\underbrace{\frac{\partial W}{\partial f_\bullet}(-\mathsf{c}) + \frac{\partial W}{\partial f_{\text{in}}}\mathsf{b}}_{-\mathcal{C}} + \underbrace{\left(\frac{\partial W}{\partial f_\bullet}\mathsf{b} + (n-1)\frac{\partial W}{\partial f_{\text{in}}}(-\mathsf{c}) + (n-2)\frac{\partial W}{\partial f_{\text{in}}}\mathsf{b}\right)}_{\mathcal{B}}\underbrace{\frac{Q_{\text{in}}-Q_{\text{out}}}{1-Q_{\text{out}}}}_{R}\right], \quad (3)$$

{eq:EXapprox}

with W as defined in eq. (2). (Calculations leading to eq. (3) are presented in Appendix A.)

The mutation bias ν 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 effects of interactions between individuals, which is assumed to be small. 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 effects on an individual's fitness of the change of a deme-mate's phenotype. 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.2. The formulas of probabilities of identity by descent are more complicated, so not substituted, but they can be found in eq. (B.32) and eq. (B.36). 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 secondary (subscript S) effects . Primary effects correspond to unmediated, direct 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, competition. They correspond to what was called "direct" and "indirect" effects in (Débarre et al., 2014; Débarre, 2017), but the terminology was updated

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for more consistency with other authors. All equations are of the form

$$\mathbb{E}[\overline{X}] \approx \nu + \frac{\delta}{\mu}\nu(1-\nu)(1-Q_{\text{out}})\left[\underbrace{\begin{pmatrix}-\mathcal{C}_{\text{P}}\\ -\mathcal{C}_{\text{S}}\end{pmatrix}}_{-\mathcal{C}} + \underbrace{\begin{pmatrix}\mathcal{B}_{\text{P}}\\ +\mathcal{B}_{\text{S}}\end{pmatrix}}_{\mathcal{B}}\underbrace{\frac{Q_{\text{in}}-Q_{\text{out}}}{1-Q_{\text{out}}}}_{R}\right]. \tag{4}$$ {eq:EXBD}

Moran Birth-Death With the Birth-Death life-cycle, eq. (3) becomes

$$\mathbb{E}[\overline{X}] \approx \nu + \frac{\delta}{\mu}\nu(1-\nu)(1-Q^{\text{M}}_{\text{out}})\times$$
$$\left[\underbrace{\begin{pmatrix}(1-\mu)(-\mathsf{c})\\ +(\mathsf{b}-\mathsf{c})\left(\frac{\mu}{N}-\frac{1-m}{n}\right)\end{pmatrix}}_{-\mathcal{C}^{\text{BD}}} + \underbrace{\begin{pmatrix}(1-\mu)\mathsf{b}\\ +(\mathsf{b}-\mathsf{c})(n-1)\left(\frac{\mu}{N}-\frac{1-m}{n}\right)\end{pmatrix}}_{\mathcal{B}^{\text{BD}}}\underbrace{\frac{Q^{\text{M}}_{\text{in}}-Q^{\text{M}}_{\text{out}}}{1-Q^{\text{M}}_{\text{out}}}}_{R^{\text{M}}}\right], \tag{5}$$ {eq:EXBD}

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.*, $m < (N_D - 1)/N_D$).

Moran Death-Birth With the Death-Birth life-cycle, eq. (3) becomes

$$\mathbb{E}[\overline{X}] \approx \nu + \frac{\delta}{\mu}\nu(1-\nu)(1-Q^{\text{M}}_{\text{out}})\times$$
$$\left[\underbrace{\begin{pmatrix}(1-\mu)(-\mathsf{c})\\ -(\mathsf{b}-\mathsf{c})(1-\mu)\left(\frac{(1-m)^2}{n}+\frac{m^2}{N-n}\right)\end{pmatrix}}_{-\mathcal{C}^{\text{DB}}} + \underbrace{\begin{pmatrix}(1-\mu)\mathsf{b}\\ -(\mathsf{b}-\mathsf{c})(n-1)(1-\mu)\left(\frac{(1-m)^2}{n}+\frac{m^2}{N-n}\right)\end{pmatrix}}_{\mathcal{B}^{\text{DB}}}\underbrace{\frac{Q^{\text{M}}_{\text{in}}-Q^{\text{M}}_{\text{out}}}{1-Q^{\text{M}}_{\text{out}}}}_{R^{\text{M}}}\right],$$

(6) {eq:EXDB}

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 a $1-\mu$ term in all terms. The primary effects (first lines in the parentheses) remain the same as with the Birth-Death

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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

$$\mathbb{E}\left[\overline{X}\right] \approx v + \frac{\delta}{\mu} v(1-v)(1-Q_{\text{out}}^{\text{WF}}) \times \left[\underbrace{\begin{pmatrix} (1-\mu)(-\mathsf{c}) \\ -(\mathsf{b}-\mathsf{c})(1-\mu)\left(\frac{(1-m)^2}{n} + \frac{m^2}{N-n}\right) \end{pmatrix}}_{-\mathcal{C}^{\text{WF}}} + \underbrace{\begin{pmatrix} (1-\mu)\mathsf{b} \\ -(\mathsf{b}-\mathsf{c})(n-1)(1-\mu)\left(\frac{(1-m)^2}{n} + \frac{m^2}{N-n}\right) \end{pmatrix}}_{\mathcal{B}^{\text{WF}}} \underbrace{\frac{Q_{\text{in}}^{\text{WF}} - Q_{\text{out}}^{\text{WF}}}{1-Q_{\text{out}}^{\text{WF}}}}_{R^{\text{WF}}} \right], \tag{7}$$

{eq:EXWF}

The only – but important – different between eq. (7) and eq. (6) is the value of the probabilities of identity by descent, because the number of individuals that are updated at each time step differs.

3.2 Primary effects

Let us first focus on primary effects, shown on the first lines in the parentheses in eq. (5)–eq. (7). 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, the relatedness terms R^{M} and R^{WF} decrease with m (keeping $m < \frac{N_D-1}{N_D}$.) Consequently, Figure R ignoring 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.

3.3 Changes with the emigration probability m

For the three life-cycles, the secondary effects are negative (with $0 < m < \frac{N_D-1}{N_D}$) and they increase with the emigration probability m. In other words, these detrimental secondary effects weaken when the emigration probability increases. This 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 $\mathbb{E}[\overline{X}]$, and on how this is affected by the (in)fideliy of parent-offspring transmission μ (see Figure 1).

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

3.3.1 Moran Birth-Death

For this life-cycle, we find that the expected frequency of altruists $\mathbb{E}[\overline{X}]$ 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 $\mu < \mu_c^{\mathrm{BD}}$, $\mathbb{E}[\overline{X}]$ decreases with m, while when $\mu > \mu_c^{\mathrm{BD}}$, $\mathbb{E}[\overline{X}]$ increases with m. The critical value μ_c^{BD} is given by

$$\mu_c^{\mathrm{BD}} = 1 - \frac{\mathsf{b}-\mathsf{c}+\sqrt{(\mathsf{b}-\mathsf{c})\left(4\mathsf{b}N^2+\mathsf{b}-\mathsf{c}\right)}}{2\mathsf{b}N} \tag{8}$$

{eq:mucBD}

(recall that N is the total size of the population, $N = nN_D$.) This result is illustrated in figure 1(b); with the parameters of the figure, $\mu_c^{\mathrm{BD}} \approx 0.026$.

given value for large N

3.3.2 Moran Death-Birth

The relationship between $\mathbb{E}[\overline{X}]$ and m is a bit more complicated for this life-cycle. For simplicity, we concentrate on what happens starting from low emigration probabilities (*i.e.*, on the sign of the slope of $\mathbb{E}[\overline{X}]$ as a function of m when $m \to 0$). If the benefits b provided by altruists are relatively low ($\mathsf{b} < \mathsf{c}(n+1)$),

$\mathbb{E}[\overline{X}]$ initially increases with m provided the mutation probability μ is greater than a threshold value μ_c^{DB} given in eq. (9) below; otherwise, when the benefits are high enough, $\mathbb{E}[\overline{X}]$ initially increases with m for any value of μ. Combining these results, we write

$$\mu_c^{\mathrm{DB}} = \begin{cases} \dfrac{(n+1)\mathsf{c}-\mathsf{b}}{(2n-1)\mathsf{b}-(n-1)\mathsf{c}} & \text{if } \mathsf{b} < \mathsf{c}(n+1), \\ 0 & \text{otherwise.} \end{cases} \tag{9}$$ {eq:mucDB}

comment on condition 1 whether altruist can be maintained

In figure 1(a), the parameters are such that $\mu_c^{\mathrm{DB}} = 0$.

The expected frequency of altruists $\mathbb{E}[\overline{X}]$ then reaches a maximum at an emigration probability m_c^{DB} (whose complicated equation is given in the supplementary Mathematica file), as can be seen in figure 1(a). When the mutation probability gets close to 0 ($\mu \to 0$), m_c^{DB} also gets close to 0,

3.3.3 Wright-Fisher

The expected frequency of altruists in the population reaches an extremum at the highest admissible emigration value $m = m_c^{\mathrm{WF}} = \frac{N_D-1}{N_D}$. This extremum is a maximum when the mutation probability is higher than a threshold value μ_c^{WF} given by

$$\mu_c^{\mathrm{WF}} = 1 - \sqrt{1 - \frac{\mathsf{c}}{\mathsf{b}}}, \tag{10}$$

and it is a minimum otherwise. With the parameters of figure 1(c), $\mu_c^{\mathrm{WF}} = 0.034$.

3.4 Relaxing key assumptions

To derive our analytical results, we had to make a number of simplifying assumptions, such as the fact that selection is weak ($\omega \ll 1$), and the fact that the structure of the population is regular (all demes have the same size n). We explored with numerical simulations the effect of relaxing these key assumptions. When

selection is strong, the patterns that we identified not only still hold but are even more marked, as shown on figure S1.

To relax the assumption of equal deme sizes, we randomly drew deme sizes at the beginning of simulations, with sizes ranging from 2 to 6 individuals and on average $\overline{n} = 4$ individuals per deme as previously. As shown in figure S2, the patterns initially obtained with a homogeneous population structure are robust when the structure is heterogeneous.

For the Moran model, it may seem odd that an offspring can replace its own parent (which can occur since $d_{ii} \neq 0$). Figure S3, plotted with dispersal probabilities 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.

4 Discussion

remove direct/indirect effects

discuss effects of n and N_D

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 1(b)–(c)) or favorable (Taylor et al., 2007a, and dashed lines in figure 1(a)) to the evolution of altruistic behavior.

Quantitative vs. qualitative measures

We used a quantitative measure, the expected frequency of altruists in the population ($\mathbb{E}[\overline{X}]$), to explore how non-zero mutation probabilities altered the impact of population viscosity. Often however, 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 1). 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, altruism can be favored only at intermediate emigration probabilities (figure 1(a)): increased emigration can still favor the evolution of altruism under this qualitative criterion.

The result is due to indirect (/secondary) effects

To explain how the frequency of altruists can increase with the emigration probability m, let us go back to the decomposition of the expected frequency of altruists in the population $\mathbb{E}[\overline{X}]$ into different terms (eq. (3)). For all the life-cycles that we consider, the direct effect of helping others (β_{D}) decreases with emigration m, while the direct effect of the cost of helping (γ_{D}) does not change with m. If we (erroneously) considered only direct effects, we would conclude that the expected proportion of altruists decreases with the emigration probability

m, because an increase in m reduces the probability that two interactants (two deme-mates in this model) are identical by descent. But this explanation ignores indirect, competitive, effects. In the three life-cycles that we considered, $\beta_{\mathrm{I}} = \gamma_{\mathrm{I}}$, so the overall indirect effects are given by $(-(\mathsf{b}-\mathsf{c})\beta_{\mathrm{I}})$. Hence, any increase of $\mathbb{E}\left[\overline{X}\right]$ with m is driven by β_{I}. Indirect effects correspond to competition: helping another individual indirectly harms others – even the individual who is providing help is indirectly harmed. This competition can be diluted by increasing the emigration probability m. The overall effect of m on the expected frequency of altruists depends on the balance between direct and indirect effects. This balance depends on the fidelity of parent-offspring transmission (μ), in particular because probabilities of identity by descent depend on μ.

Indirect (secondary) effects are less straightforward to understand than direct (/primary) effects, yet they play a crucial role for social evolution in spatially structured populations. Competition among relatives is for instance behind 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 (Grafen & Archetti, 2008; Débarre et al., 2014). Secondary effects are also behind the evolution of social behaviors such as spite (West & Gardner, 2010).

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 ($\delta \ll 0$). 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 order in which these limits are taken matters, *i.e.*, one needs to specify how small μ, but also ω, 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.

Interactions and dispersal graphs

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 S4 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.

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 (Parvinen, 2013; Mullon et al., 2017). The assumptions of these studies however differ 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.

References

Alizon, S. & Taylor, P. 2008: Empty sites can promote altruistic behavior. Evolution 62(6):1335–1344.

Allen, B.; Lippner, G.; Chen, Y.-T.; Fotouhi, B.; Momeni, N.; Yau, S.-T. & Nowak, M. A. 2017: Evolutionary dynamics on any population structure. Nature 544(7649):227–230.

Allen, B.; Traulsen, A.; Tarnita, C. E. & Nowak, M. A. 2012: How mutation affects evolutionary games on graphs. Journal of Theoretical Biology 299:97 – 105. Evolution of Cooperation.

Brockhurst, M. A.; Buckling, A. & Gardner, A. 2007: Cooperation peaks at intermediate disturbance. Current Biology 17(9):761–765.

Cockerham, C. C. & Weir, B. 1987: Correlations, descent measures: drift with migration and mutation. Proceedings of the National Academy of Sciences 84(23):8512–8514.

Débarre, F. 2017: Fidelity of parent-offspring transmission and the evolution of social behavior in structured populations. Journal of Theoretical Biology 420:26 – 35.

Débarre, F.; Hauert, C. & Doebeli, M. 2014: Social evolution in structured populations. Nature Communications 5.

Fletcher, J. A. & Doebeli, M. 2009: A simple and general explanation for the evolution of altruism. Proceedings of the Royal Society B: Biological Sciences 276(1654):13–19.

Frank, S. A. 1997: The Price equation, Fisher's fundamental theorem, kin selection, and causal analysis. Evolution 51(6):1712–1729.

Frank, S. A. 2010: Microbial secretor–cheater dynamics. Philosophical Transactions of the Royal Society of London B: Biological Sciences 365(1552):2515–2522.

Grafen, A. & Archetti, M. 2008: Natural selection of altruism in inelastic viscous homogeneous populations. Journal of Theoretical Biology 252(4):694 – 710.

Hamilton, W. 1964: The genetical evolution of social behaviour. i. Journal of Theoretical Biology 7(1):1 – 16.

Hamilton, W. D. 1975: Innate social aptitudes of man: an approach from evolutionary genetics. Biosocial anthropology 53:133–55.

Lehmann, L.; Keller, L. & Sumpter, D. J. T. 2007: The evolution of helping and harming on graphs: the return of the inclusive fitness effect. Journal of Evolutionary Biology 20(6):2284–2295.

Lehmann, L. & Rousset, F. 2014: The genetical theory of social behaviour. Philosophical Transactions of the Royal Society of London B: Biological Sciences 369(1642).

Leturque, H. & Rousset, F. 2002: Dispersal, kin competition, and the ideal free distribution in a spatially heterogeneous population. Theoretical Population Biology 62(2):169 – 180.

Lion, S. 2016: Moment equations in spatial evolutionary ecology. Journal of theoretical biology 405:46–57.

Mullon, C.; Keller, L. & Lehmann, L. 2017: Co-evolution of dispersal with behaviour favours social polymorphism. bioRxiv .

Mullon, C. & Lehmann, L. 2014: The robustness of the weak selection approximation for the evolution of altruism against strong selection. Journal of evolutionary biology 27(10):2272–2282.

Ohtsuki, H.; Hauert, C.; Lieberman, E. & Nowak, M. A. 2006: A simple rule for the evolution of cooperation on graphs and social networks. Nature 441(7092):502–505.

Parvinen, K. 2013: Joint evolution of altruistic cooperation and dispersal in a metapopulation of small local populations. Theoretical population biology 85:12–19.

R Core Team. 2015: R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rodrigues, A. M. M. & Gardner, A. 2012: Evolution of helping and harming in heterogeneous populations. Evolution 66(7):2065–2079.

Rousset, F. & Billiard, S. 2000: A theoretical basis for measures of kin selection in subdivided populations: finite populations and localized dispersal. Journal of Evolutionary Biology 13(5):814–825.

Sample, C. & Allen, B. 2017: The limits of weak selection and large population size in evolutionary game theory. Journal of mathematical biology pages 1–33.

Tarnita, C. E. & Taylor, P. D. 2014: Measures of relative fitness of social behaviors in finite structured population models. The American Naturalist 184(4):477–488.

Taylor, P. 1992a: Altruism in viscous populations—an inclusive fitness model. Evolutionary ecology 6(4):352–356.

Taylor, P.; Lillicrap, T. & Cownden, D. 2011: Inclusive fitness analysis on mathematical groups. Evolution 65(3):849–859.

Taylor, P. D. 1992b: Inclusive fitness in a homogeneous environment. Proceedings of the Royal Society of London. Series B: Biological Sciences 249(1326):299–302.

Taylor, P. D.; Day, T. & Wild, G. 2007a: Evolution of cooperation in a finite homogeneous graph. Nature 447(7143):469–472.

Taylor, P. D.; Day, T. & Wild, G. 2007b: From inclusive fitness to fixation probability in homogeneous structured populations. Journal of Theoretical Biology 249(1):101 – 110.

Taylor, P. D. & Irwin, A. J. 2000: Overlapping generations can promote altruistic behavior. Evolution 54(4):1135–1141.

Van Cleve, J. 2015: Social evolution and genetic interactions in the short and long term. Theoretical Population Biology 103:2 – 26.

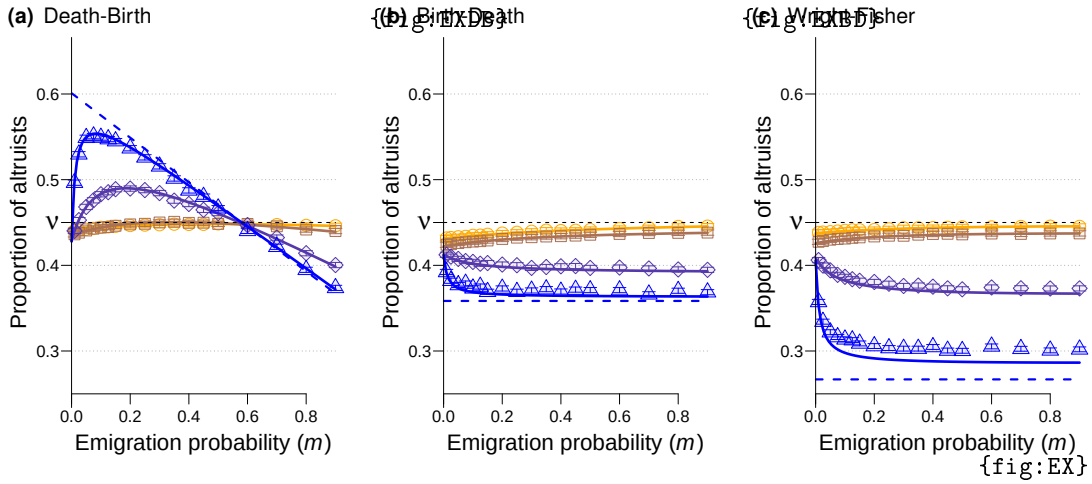
West, S. A. & Gardner, A. 2010: Altruism, spite, and greenbeards. Science 327(5971):1341–1344.

West, S. A.; Pen, I. & Griffin, A. S. 2002: Cooperation and competition between relatives. Science 296(5565):72–75.

Wilson, D. S.; Pollock, G. B. & Dugatkin, L. A. 1992: Can altruism evolve in purely viscous populations? Evolutionary Ecology 6(4):331–341.

Wolfram Research, Inc. 2017: Mathematica, Version 11.1. Champaign, IL, 2017.

Figures

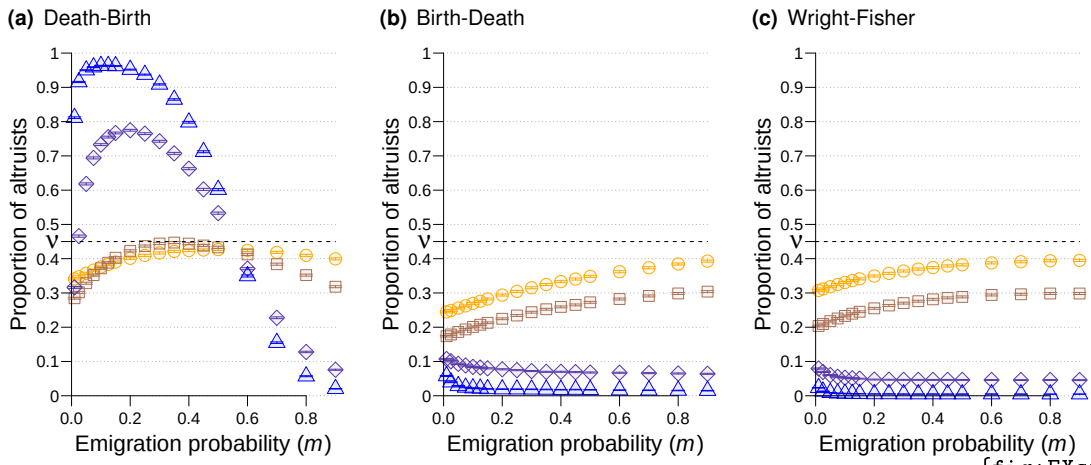


{fig:EXDB} {fig:EXBD} {fig:EXWF}

{fig:EX}

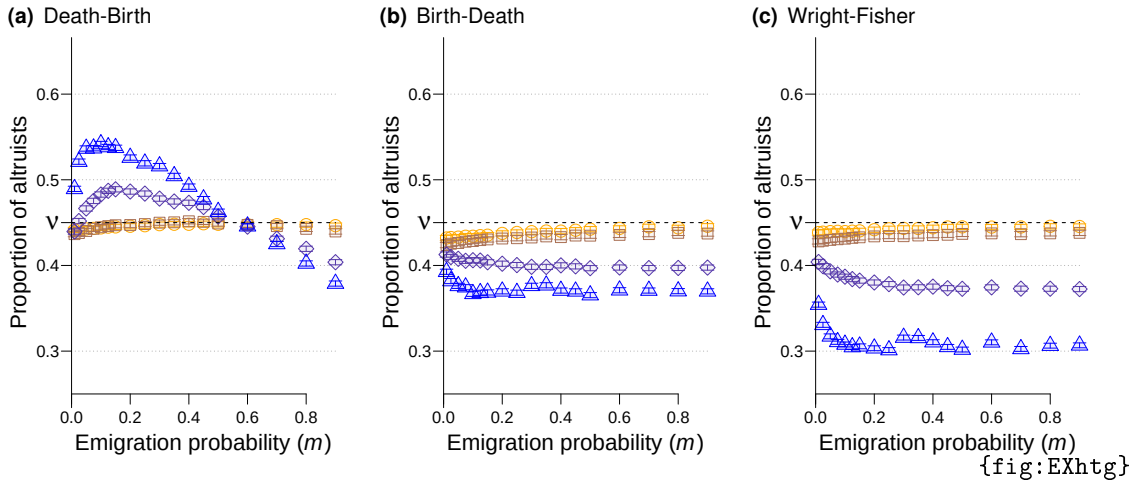
Figure 1: Expected proportion of altruists under weak selection, as a function of the emigration probability m, for different mutation values ($\mu = 0.001$ (blue, dots), 0.01 (purple, squares), 0.1 (brown, diamonds), 0.25 (orange, triangles); the dashed blue lines correspond to $\mu = 0$) and different 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: $\omega = 0.005$, $\nu = 0.45$, $b = 15$, $c = 1$, $n = 4$ individuals per deme, $N_D = 15$ demes.

Supplementary figures



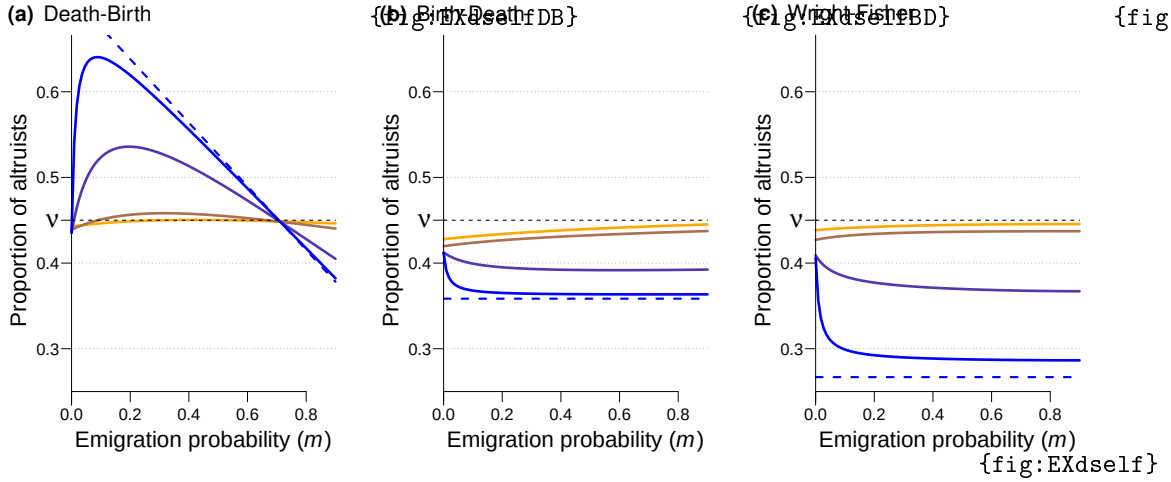
{fig:EXstrongsel}

Figure S1: Equivalent of figure 1 (simulations only) but with strong selection ($\omega = 0.1$); please note the change of scale on the vertical axis. All other parameters and legends are identical to those of figure 1 (increasing mutation probabilities from blue dots to orange triangles).



{fig:EXhtg}

Figure S2: Equivalent of figure 1 (simulations only) but with a heterogeneous population structure: deme sizes range form 1 to 5 individuals per deme, the average deme size is 4 as in figure 1; all other parameters and legend are identical to those of figure 1.



{fig:EXdselfDB} {fig:EXdselfBD} {fig:EXdselfW

{fig:EXdself}

Figure S3: Equivalent of figure 1 (analysis only), with no self-replacement ($d_{ii} = d_{\text{self}} = 0$ for all sites).

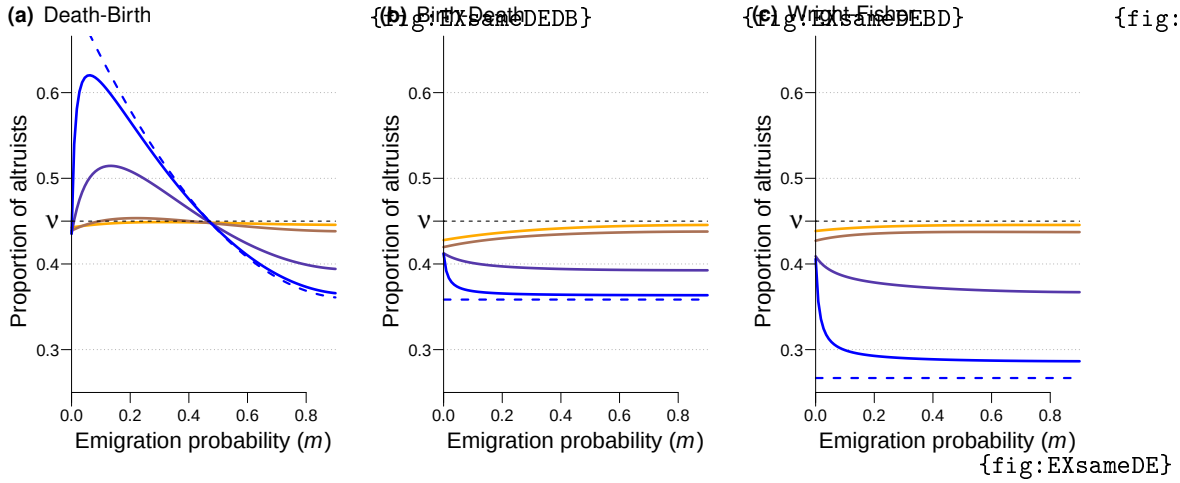


Figure S4: Equivalent of figure 1 (analysis only), with equal dispersal and interaction graphs (*i.e.*, no self-replacement [$d_{ii} = d_{\text{self}} = 0$ for all sites], and a proportion m of the interactions occurring outside of the home deme).

Supplementary Table

b	Fecundity benefit given by altruists to social interactants
c	Fecundity cost paid by altruists
d_{ij}	Dispersal probability from site i to site j
e_{ij}	Interaction probability from site i to site j
n	Deme size
N_D	Number of demes
N	Total population size ($N = N_D n$)
m	Emigration probability
Q_{ij}	(Long-term) Probability of identity by descent of individuals at sites i and j
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.)
β	Term associated to the benefits b
γ	Term associated to the costs c
μ	Mutation probability
ν	Mutation bias: probability that mutant is altruist
ω	Parameter scaling the relative effect of social interactions on fecundity
D	Subscript corresponding to direct/primary effects
I	Subscript corresponding to indirect/secondary effects
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 $i = j$
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

{tab:symbols}

Table S1: List of symbols. "r.v." means *random variable*.

Appendix

A Expected frequency of altruists {sec:app:EX}

A.1 For a generic life-cycle {sec:app:generic}

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 S2 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

{tab:BD}

Table S2: 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,

$$D_i = \sum_{j=1}^N B_{ij} \tag{A.1a}$$

{eq:DBequiv}

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

$$D_i^0 = \sum_{j=1}^{N} B_{ji}^0 = B_i^0 =: B^*, \tag{A.1b}$$ {eq:DBRV}

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. (A.1b) and eq. (A.1a) 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

$$\mathbb{E}\left[\overline{X}(t+1)|\mathbf{X}(t)\right] = \frac{1}{N}\sum_{i=1}^{N}\left[B_i(1-\mu)X_i + (1-D_i)X_i + B_i\mu\nu\right]. \tag{A.2a}$$ {eq:conditionalchange}

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), which ever 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. (A.2a) ($\mathbb{E}\left[\overline{X}\right] = \sum_{X\in\Omega}\overline{X}\xi(\mathbf{X},\delta,\mu)$), we obtain, after reorganizing:

$$0 = \frac{1}{N}\sum_{X\in\Omega}\left[\sum_{i=1}^{N}\left(B_i(1-\mu)X_i - D_iX_i\right) + \sum_{i=1}^{N}B_i\mu\nu\right]\xi(\mathbf{X},\delta,\mu). \tag{A.3}$$ {eq:statdist}

Now, we use the assumption of weak selection ($\delta \ll 1$) and consider the first-order expansion of eq. (A.3) 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. (A.3) vanishes when we take its derivative with respect to δ, for the life-cycles that we consider.

The first order expansion of eq. (A.3) yields

$$0 = \frac{\delta}{N}\sum_{i=1}^{N}\left[\sum_{X\in\Omega}\left(\frac{\partial B_i}{\partial\delta}(1-\mu) - \frac{\partial D_i}{\partial\delta}\right)X_i\xi(\mathbf{X},0,\mu) - \sum_{X\in\Omega}\mu B^*X_i\frac{\partial\xi}{\partial\delta}\right] + O\left(\delta^2\right), \tag{A.4}$$ {eq:weaksel0}

where the derivatives are evaluated at $\delta = 0$, and where we used eq. (A.1b) to simplify the second term. For conciseness, we define

$$W_i = (1-\mu)B_i + (1-D_i), \tag{A.5}$$ {eq:app:defW}

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. (A.4) as

$$\delta\mu B^* \frac{\partial \mathbb{E}\left[\overline{X}\right]}{\partial\delta} = \frac{\delta}{N}\sum_{i=1}^{N} \mathbb{E}_0\left[\frac{\partial W_i}{\partial\delta} X_i\right] + O\left(\delta^2\right). \tag{A.6}$$ {eq:weaksel0reorg}

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

$$\begin{aligned}\frac{\partial W_i}{\partial\delta} &= \sum_{k=1}^{N} \frac{\partial W_i}{\partial\phi_k}\frac{\partial\phi_k}{\partial\delta} \\ &= \sum_{k=1}^{N} \frac{\partial W_i}{\partial\phi_k} X_k,\end{aligned} \tag{A.7}$$ {eq:totalproba1}

by definition of ϕ_k, and where the first derivative is evaluated for all $\phi_i = 0$. With the notation $P_{ij} = \mathbb{E}_0\left[X_i X_j\right]$, eq. (A.6) becomes

$$\delta\mu B^* \frac{\partial \mathbb{E}\left[\overline{X}\right]}{\partial\delta} = \frac{\delta}{N}\sum_{i=1}^{N}\sum_{k=1}^{N} \frac{\partial W_i}{\partial\phi_k} P_{ik} + O\left(\delta^2\right). \tag{A.8}$$ {eq:weaksel1}

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 since the size of the population is fixed ($\sum_{i=1}^{N}(B_i - D_i) = 0$), and since 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)

$$\frac{\partial W_i}{\partial\phi_i} + (n-1)\frac{\partial W_i}{\partial\phi_{\text{in}}} + (N-n)\frac{\partial W_i}{\partial\phi_{\text{out}}} = 0. \tag{A.9}$$ {eq:derivsumW}

With this, eq. (A.8) becomes

$$\delta\mu B^* \frac{\partial \mathbb{E}\left[\overline{X}\right]}{\partial\delta} = \frac{\delta}{N}\sum_{i=1}^{N}\left(\frac{\partial W_i}{\partial\phi_i} + (n-1)\frac{\partial W_i}{\partial\phi_{\text{in}}}\frac{P_{\text{in}} - P_{\text{out}}}{P_{ii} - P_{\text{out}}}\right)(P_{ii} - P_{\text{out}}) + O\left(\delta^2\right). \tag{A.10}$$ {eq:weaksel1CBRP}

We can also replace the P terms by

$$P_{ij} = \nu^2 + \nu(1-\nu)Q_{ij}. \tag{A.11}$$ {eq:QP}

In Appendix B.1, we will see that recursions on P_{ij} reveal that Q_{ij} can be interpreted as a probability of identity by descent, *i.e.*, the probability that the individuals at sites i and j have a common ancestor and that no mutation has occurred on either lineage since the ancestor. Eq. (A.10) becomes

$$\delta\mu B^* \frac{\partial \mathbb{E}\left[\overline{X}\right]}{\partial \delta} = \frac{\delta}{N}\sum_{i=1}^{N}\left(\underbrace{\frac{\partial W_i}{\partial \phi_i}}_{-\mathcal{C}} + \underbrace{(n-1)\frac{\partial W_i}{\partial \phi_{\text{in}}}}_{\mathcal{B}}\underbrace{\frac{Q_{\text{in}}-Q_{\text{out}}}{1-Q_{\text{out}}}}_{R}\right)(1-Q_{\text{out}})\nu(1-\nu) + O\left(\delta^2\right). \tag{A.12}$$ {eq:weaksel1CBR}

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

$$\frac{\partial W_i}{\partial \phi_k} = \sum_{\ell=1}^{N}\frac{\partial W_i}{\partial f_\ell}\frac{\partial f_\ell}{\partial \phi_k}. \tag{A.13}$$

With our notation, and given that social interactions take place within demes and affect fecundity, we have {eq:derivf}

$$\left.\frac{\partial f_\ell}{\partial \phi_\ell}\right|_{\delta=0} = -\mathsf{c}, \tag{A.14a}$$

$$\left.\frac{\partial f_\ell}{\partial \phi_{\text{in}}}\right|_{\delta=0} = \frac{\mathsf{b}}{n-1}, \tag{A.14b}$$

$$\left.\frac{\partial f_\ell}{\partial \phi_{\text{out}}}\right|_{\delta=0} = 0. \tag{A.14c}$$

Eq. (A.12) then becomes (using notation $\bullet$ to refer to the focal individual itself, and where $W = W_i$, since the derivatives are the same for all i):

$$\begin{aligned}\delta\mu B^* \frac{\partial \mathbb{E}\left[\overline{X}\right]}{\partial \delta} &= \delta\nu(1-\nu)(1-Q_{\text{out}})\times \\ &\left(\underbrace{\frac{\partial W}{\partial f_\bullet}(-\mathsf{c}) + \frac{\partial W}{\partial f_{\text{in}}}\mathsf{b}}_{-\mathcal{C}} + \underbrace{\left(\frac{\partial W}{\partial f_\bullet}\mathsf{b} + (n-1)\frac{\partial W}{\partial f_{\text{in}}}(-\mathsf{c}) + (n-2)\frac{\partial W}{\partial f_{\text{in}}}\mathsf{b}\right)}_{\mathcal{B}}\underbrace{\frac{Q_{\text{in}}-Q_{\text{out}}}{1-Q_{\text{out}}}}_{R}\right) + O\left(\delta^2\right).\end{aligned} \tag{A.15}$$ {eq:weaksel2}

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

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

$$\mathbb{E}\left[\overline{X}\right] = \nu + \delta\left.\frac{\partial \mathbb{E}\left[\overline{X}\right]}{\partial \delta}\right|_{\delta=0} + O\left(\delta^2\right), \tag{A.16}$$ {eq:EXgeneric}

where $\left.\frac{\partial \mathbb{E}\left[\overline{X}\right]}{\partial \delta}\right|_{\delta=0}$ is obtained from eq. (A.15). We then need to replace the B_i and

D_i terms by their formulas for each life-cycle (given in table S2).

A.2 Derivatives for the specific life-cycles

{sec:app:dW}

Using the formulas presented in table S2, and the definition of $W = W_i$ given in eq. (A.5), we obtain the following equations:

{eq:dWBD}

Moran Birth-Death

$$\left.\frac{\partial W^{\mathrm{BD}}}{\partial f_{\bullet}}\right|_{\delta=0} = (1-\mu)\left(\frac{1}{N}-\frac{1}{N^2}\right)-\left(\frac{1-m}{nN}-\frac{1}{N^2}\right) = \frac{1-\mu}{N}+\frac{\mu}{N^2}-\frac{1-m}{nN}, \tag{A.17a}$$

$$\left.\frac{\partial W^{\mathrm{BD}}}{\partial f_{\mathrm{in}}}\right|_{\delta=0} = (1-\mu)\left(-\frac{1}{N^2}\right)-\left(\frac{1-m}{nN}-\frac{1}{N^2}\right) = \frac{\mu}{N^2}-\frac{1-m}{nN}. \tag{A.17b}$$

{eq:dWDB}

Moran Death-Birth

$$\left.\frac{\partial W^{\mathrm{DB}}}{\partial f_{\bullet}}\right|_{\delta=0} = \frac{1-\mu}{N}\left[1-\left(\frac{(1-m)^2}{n}+\frac{m^2}{N-n}\right)\right], \tag{A.18a}$$

$$\left.\frac{\partial W^{\mathrm{DB}}}{\partial f_{\mathrm{in}}}\right|_{\delta=0} = -\frac{1-\mu}{N}\left(\frac{(1-m)^2}{n}+\frac{m^2}{N-n}\right). \tag{A.18b}$$

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

{eq:dWWF}

Wright-Fisher

$$\left.\frac{\partial W^{\mathrm{WF}}}{\partial f_{\bullet}}\right|_{\delta=0} = (1-\mu)\left[1-\left(\frac{(1-m)^2}{n}+\frac{m^2}{N-n}\right)\right], \tag{A.19a}$$

$$\left.\frac{\partial W^{\mathrm{WF}}}{\partial f_{\mathrm{in}}}\right|_{\delta=0} = -(1-\mu)\left(\frac{(1-m)^2}{n}+\frac{m^2}{N-n}\right). \tag{A.19b}$$

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

B Probabilities of identity by descent

B.1 Expected state of pairs of sites and probabilities of identity by descent

{sec:app:IBD}

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 $\mathbb{E}\left[\overline{X}\right]$, P_{ij} is the quantity that appears, but most studies use Q_{ij}. Both are evaluated in the absence of selection ($\omega = 0$).

B.1.1 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. (B.20)), 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. (B.20)):

$$\begin{aligned}\mathbb{E}\left[X_i X_j(t+1)|X(t)=\mathbf{X}\right] =& X_i X_j \left(1 - \sum_{k=1}^{N} \frac{1}{N}\left(d_{ki}+d_{kj}\right)\left((1-X_k)(1-\mu)+\mu(1-\nu)\right)\right) \\ &+ X_i(1-X_j)\sum_{k=1}^{N}\frac{1}{N}d_{kj}\left(X_k(1-\mu)+\mu\nu\right) \\ &+ X_j(1-X_i)\sum_{k=1}^{N}\frac{1}{N}d_{ki}\left(X_k(1-\mu)+\mu\nu\right).\end{aligned} \tag{B.20}$$

{eq:app:PijM1}

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

$$P_{ij} = \frac{1}{2}\left(\sum_{k=1}^{N}(1-\mu)\left(d_{kj}P_{ki}+d_{ki}P_{kj}\right)\right) + \mu\nu^2 \qquad (i \neq j), \tag{B.21}$$

{eq:app:PijM}

while $P_{ii} = \nu$.

Now we substitute $P_{ij} = \nu^2 + \nu(1-\nu)Q_{ij}$ in eq. (B.21), we obtain

$$Q_{ij} = \frac{1}{2}\sum_{k=1}^{N}(1-\mu)\left(d_{ki}Q_{kj}+d_{kj}Q_{ki}\right), \tag{B.22}$$

{eq:app:QijM}

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 ($1-\mu$).

B.1.2 Wright-Fisher model

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

$$\begin{aligned}\mathbb{E}\big[X_i X_j(t+1)|X(t)=\mathbf{X}\big] = \sum_{k,\ell=1}^{N} d_{ki}d_{\ell j}\Big(&X_k X_\ell (1-\mu+\mu\nu)^2 \\ &+ (X_k(1-X_\ell)+(1-X_k)X_\ell)\,(1-\mu+\mu\nu)(\mu\nu) \\ &+ (1-X_k)(1-X_\ell)(\mu\nu)^2\Big)\end{aligned} \tag{B.23}$$

{eq:app:PijWF1}

The first term of eq. (B.23) corresponds to both parents being altruists, and having altruist offspring; the second line corresponds to exactly one parent being altruist, and the third line to both parents being non-altruists (in this latter case, the two offspring have to be both mutants to be altruists).
Taking the expectation and simplifying, we obtain

$$P_{ij} = \sum_{k,\ell=1}^{N} \big(P_{kl}(1-\mu)^2\big) + (2-\mu)\mu\nu^2. \tag{B.24}$$

{eq:app:PijWF}

Replacing P_{ij} by $\nu^2+\nu(1-\nu)Q_{ij}$, eq. (B.24) becomes

$$Q_{ij} = \sum_{k,\ell=1}^{N} d_{ki}d_{\ell j}Q_{k\ell}(1-\mu)^2. \tag{B.25}$$

{eq:app:QijWF}

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

B.2 Probabilities of identity by descent in a subdivided population {sec:app:Qsubdiv}

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}:

$$Q_{ij} = \begin{cases} 1 & \text{when } i = j; \\ Q_{\text{in}} & \text{when } i \neq j \text{ and both sites are in the same deme;} \\ Q_{\text{out}} & \text{when sites } i \text{ and } j \text{ are in different demes.} \end{cases} \tag{B.26}$$

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 $\tilde{d}_{\substack{i_1\\i_2}}$ and $\tilde{Q}_{\substack{i_1\\i_2}}$, 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.*, $\tilde{d}_{\substack{i_1\\i_2}} = d_{\substack{j_1\ j_1+i_1\\j_2'\ j_2+i_2}}$.)

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

B.2.1 Moran model

In Débarre (2017), it was shown that

$$\tilde{\mathcal{Q}}_{\substack{r_1\\r_2}} = \frac{1}{N} \sum_{q_1=0}^{N_1-1} \sum_{q_2=0}^{N_2-1} \frac{\mu\lambda'_M}{1-(1-\mu)\tilde{\mathcal{D}}_{\substack{q_1\\q_2}}} \exp\left(\imath \frac{2\pi q_1 r_1}{N_1}\right) \exp\left(\imath \frac{2\pi q_2 r_2}{N_2}\right) \tag{B.27a}$$ {eq:app:Q2DM}

with

$$\tilde{\mathcal{D}}_{\substack{q_1\\q_2}} = \sum_{\ell_1=0}^{N_1-1} \sum_{\ell_2=0}^{N_2-1} \tilde{d}_{\substack{\ell_1\\\ell_2}} \exp\left(-\imath \frac{2\pi q_1 \ell_1}{N_1}\right) \exp\left(-\imath \frac{2\pi q_2 \ell_2}{N_2}\right), \tag{B.27b}$$ {eq:app:D2D}

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

$$\begin{aligned} \tilde{\mathcal{D}}_{\substack{q_1\\q_2}} &= d_{\text{self}} + \sum_{\ell_2=1}^{N_2-1} d_{\text{in}} \exp\left(-\imath \frac{2\pi q_2 \ell_2}{N_2}\right) + \sum_{\ell_1=1}^{N_1-1} \sum_{\ell_2=0}^{N_2-1} d_{\text{out}} \exp\left(-\imath \frac{2\pi q_1 \ell_1}{N_1}\right) \exp\left(-\imath \frac{2\pi q_2 \ell_2}{N_2}\right) \\ &= d_{\text{self}} + \left(\delta_{q_2}(N_2-1) + (1-\delta_{q_2})(-1)\right) d_{\text{in}} + \left(\delta_{q_1}(N_1-1) + (1-\delta_{q_1})(-1)\right)\left(\delta_{q_2} N_2\right) d_{\text{out}} \\ &= d_{\text{self}} + \left(\delta_{q_2} N_2 - 1\right) d_{\text{in}} + \left(\delta_{q_1} N_1 - 1\right) \delta_{q_2} N_2 d_{\text{out}}. \end{aligned} \tag{B.28a}$$

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

$$\tilde{\mathcal{D}}_{\substack{0\\0}} = 1, \tag{B.29a}$$

$$\tilde{\mathcal{D}}_{\substack{q_1\\0}} = 1 - m - \frac{m}{d-1} \quad (q_1 \not\equiv 0 \pmod{N_1}), \tag{B.29b}$$

$$\tilde{\mathcal{D}}_{\substack{q_1\\q_2}} = d_{\text{self}} - d_{\text{in}} \quad (q_2 \not\equiv 0 \pmod{N_2}). \tag{B.29c}$$

So for $\tilde{\mathcal{Q}}$, using system (B.29) in eq. (B.27a),

$$\begin{aligned}
\tilde{\mathcal{Q}}_{\substack{r_1\\r_2}} = \frac{\mu\lambda'_M}{N}\Bigg[&\frac{1}{1-(1-\mu)\tilde{\mathcal{D}}_{\substack{0\\0}}} + \sum_{q_2=1}^{N_2-1}\frac{1}{1-(1-\mu)\tilde{\mathcal{D}}_{\substack{0\\q_2}}}\exp\left(-\imath\frac{2\pi q_2 r_2}{N_2}\right)\\
&+\sum_{q_1=1}^{N_1-1}\frac{1}{1-(1-\mu)\tilde{\mathcal{D}}_{\substack{q_1\\0}}}\exp\left(-\imath\frac{2\pi q_1 r_1}{N_1}\right)\\
&+\sum_{q_1=1}^{N_1-1}\sum_{q_2=1}^{N_2-1}\frac{1}{1-(1-\mu)\tilde{\mathcal{D}}_{\substack{q_1\\q_2}}}\exp\left(-\imath\frac{2\pi q_1 r_1}{N_1}\right)\exp\left(-\imath\frac{2\pi q_2 r_2}{N_2}\right)\Bigg]\\
= \frac{\mu\lambda'_M}{N}\Bigg[&\frac{1}{1-(1-\mu)} + \frac{1}{1-(1-\mu)(d_{\text{self}}-d_{\text{in}})}(\delta_{r_2}N_2-1)\\
&+\frac{1}{1-(1-\mu)(1-m-\frac{m}{d-1})}(\delta_{r_1}N_1-1)\\
&+\frac{1}{1-(1-\mu)(d_{\text{self}}-d_{\text{in}})}(\delta_{r_1}N_1-1)(\delta_{r_2}N_2-1)\Bigg].
\end{aligned} \tag{B.30}$$ {eq:app:Q2DMsol}

In particular,

$$\begin{aligned}
\tilde{\mathcal{Q}}_{\substack{0\\0}} = \frac{\mu\lambda'_M}{N}\Bigg[&\frac{1}{\mu} + \frac{1}{1-(1-\mu)(d_{\text{self}}-d_{\text{in}})}(n-1) + \frac{1}{1-(1-\mu)(1-m-\frac{m}{d-1})}(D-1)\\
&+\frac{1}{1-(1-\mu)(d_{\text{self}}-d_{\text{in}})}(D-1)(n-1)\Bigg]\\
= 1.
\end{aligned} \tag{B.31a}$$ {eq:app:Q2D1}

We find λ'_M using the eq. (B.31a). Going back to eq. (B.30), when $r_1 = 0$, the two individuals are in the same deme. They are different when $r_2 \not\equiv 0$, and so:

$$\begin{aligned}
Q_{\text{in}} = \frac{\mu\lambda'_M}{N}\Bigg[&\frac{1}{\mu} + \frac{1}{1-(1-\mu)(d_{\text{self}}-d_{\text{in}})}(-1) + \frac{1}{1-(1-\mu)(1-m-\frac{m}{d-1})}(D-1)\\
&+\frac{1}{1-(1-\mu)(d_{\text{self}}-d_{\text{in}})}(D-1)(-1)\Bigg].
\end{aligned} \tag{B.31b}$$

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

$$Q_{\text{out}} = \frac{\mu\lambda'_M}{N}\left[\frac{1}{\mu} + \frac{1}{1-(1-\mu)(d_{\text{self}}-d_{\text{in}})}(-1) + \frac{1}{1-(1-\mu)(1-m-\frac{m}{d-1})}(-1) + \frac{1}{1-(1-\mu)(d_{\text{self}}-d_{\text{in}})}\right]. \tag{B.31c}$$

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

$$Q^{\text{M}}_{\text{in}} = \frac{(1-\mu)\left(m+\mu(N_D(1-m)-1)\right)}{(1-\mu)m(N_D\mu(n-1)+1)+(N_D-1)\mu(\mu(n-1)+1)}, \tag{B.32a}$$

$$Q^{\text{M}}_{\text{out}} = \frac{(1-\mu)m}{(1-\mu)m(N_D\mu(n-1)+1)+(N_D-1)\mu(\mu(n-1)+1)}. \tag{B.32b}$$

The probability that two different deme-mates are identical by descent, Q^{M}_{in}, decreases monotonically with the emigration probability m, while $Q^{\text{M}}_{\text{out}}$ monotonically increases with m (see figure S5(a)).

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

B.2.2 Wright-Fisher

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

$$\tilde{Q}^{r_1}_{r_2} = \frac{1}{N}\sum_{q_1=0}^{N_1-1}\sum_{q_2=0}^{N_2-1}\frac{\mu\lambda'_{WF}}{1-(1-\mu)^2(\tilde{\mathcal{D}}^{q_1}_{q_2})^2}\exp\left(-\imath\frac{2\pi q_1 r_1}{N_1}\right)\exp\left(-\imath\frac{2\pi q_2 r_2}{N_2}\right), \tag{B.33}$$

with $\tilde{\mathcal{D}}$ given in eq. (B.27b). In a subdivided population, with $N_1 = N_D$ and $N_2 = n$, this becomes

$$\begin{aligned}
\tilde{\mathcal{Q}}_{r_2}^{r_1} = \frac{1}{N}\Bigg[& \frac{\mu\lambda'_{WF}}{1-(1-\mu)^2(\tilde{\mathcal{D}}_{\substack{0\\0}})^2} + \sum_{q_2=1}^{N_2-1} \frac{\mu\lambda'_{WF}}{1-(1-\mu)^2(\tilde{\mathcal{D}}_{\substack{0\\q_2}})^2} \exp\left(-\imath\frac{2\pi q_2 r_2}{N_2}\right) \\
& + \sum_{q_1=1}^{N_1-1} \frac{\mu\lambda'_{WF}}{1-(1-\mu)^2(\tilde{\mathcal{D}}_{\substack{q_1\\0}})^2} \exp\left(-\imath\frac{2\pi q_1 r_1}{N_1}\right) \\
& + \sum_{q_1=1}^{N_1-1}\sum_{q_2=1}^{N_2-1} \frac{\mu\lambda'_{WF}}{1-(1-\mu)^2(\tilde{\mathcal{D}}_{\substack{q_1\\q_2}})^2} \exp\left(-\imath\frac{2\pi q_1 r_1}{N_1}\right)\exp\left(-\imath\frac{2\pi q_2 r_2}{N_2}\right)\Bigg] \\
= \frac{\mu\lambda'_{WF}}{N}\Bigg[& \frac{1}{1-(1-\mu)^2} + \frac{1}{1-(1-\mu)^2(d_{\text{self}}-d_{\text{in}})^2}(\delta_{q_2}N_2-1) \\
& + \frac{1}{1-(1-\mu)^2(1-m-\frac{m}{d-1})^2}(\delta_{q_1}N_1-1) \\
& + \frac{1}{1-(1-\mu)^2(d_{\text{self}}-d_{\text{in}})^2}(\delta_{q_1}N_1-1)(\delta_{q_2}N_2-1)\Bigg] \\
= \frac{\mu\lambda'_{WF}}{N}\Bigg[& \frac{1}{1-(1-\mu)^2} + \frac{1}{1-(1-\mu)^2(d_{\text{self}}-d_{\text{in}})^2}(\delta_{q_2}N_2-1)\delta_{q_1}N_1 \\
& + \frac{1}{1-(1-\mu)^2(1-m-\frac{m}{d-1})^2}(\delta_{q_1}N_1-1)\Bigg].
\end{aligned} \tag{B.34}$$

{eq:app:Q2DWFsol}

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

$$1 = \frac{\mu\lambda'_{WF}}{N}\left[\frac{1}{1-(1-\mu)^2} + \frac{1}{1-(1-\mu)^2(d_{\text{self}}-d_{\text{in}})^2}(N_2-1)N_1 + \frac{1}{1-(1-\mu)^2(1-m-\frac{m}{d-1})^2}(N_1-1)\right]. \tag{B.35a}$$

Then from eq. (B.34) we deduce

$$Q_{\text{in}} = \frac{\mu\lambda'_{WF}}{N}\left[\frac{1}{1-(1-\mu)^2} - \frac{1}{1-(1-\mu)^2(d_{\text{self}}-d_{\text{in}})^2}N_1 + \frac{1}{1-(1-\mu)^2(1-m-\frac{m}{d-1})^2}(N_1-1)\right]. \tag{B.35b}$$

and

$$Q_{\text{out}} = \frac{\mu\lambda'_{WF}}{N}\left[\frac{1}{1-(1-\mu)^2} - \frac{1}{1-(1-\mu)^2(1-m-\frac{m}{d-1})^2}\right]. \tag{B.35c}$$

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

$$Q_{\text{in}}^{\text{WF}} = \frac{-N_D + M_1 + M_2}{(n-1)N_D + M_1 + M_2}, \tag{B.36a}$$

$$Q_{\text{out}}^{\text{WF}} = \frac{-\frac{1}{N_D-1}M_1 + M2}{(n-1)N_D + M_1 + M_2}, \tag{B.36b}$$

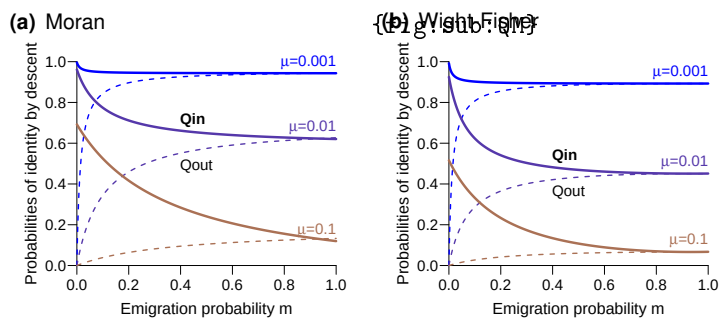
with

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

(These formulas are compatible with, *e.g.*, results presented by Cockerham & Weir (1987), adapted for haploid individuals).
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} follows the opposite pattern. The threshold value m_c^{WF} corresponds to an emigration probability so high that $d_{\text{in}} = d_{\text{out}}$.

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

Also, because more sites (all of them, actually) are updated at each time step, Q_{in} is lower for the Wright-Fisher updating than for a Moran updating, under which only one site is updated at each time step (compare figure S5(a) and S5(b)).



{fig:sub:QMF} {fig:sub:QWF}

{fig:Q}

Figure S5: 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.