Mon titre

1 Introduction

Hamilton 1964 viscous (low dispersal) "giving-traits" more common in viscous population. Notion that tighter links between individuals favors the evolution of altruism has been shown to hold (othsuki et autres). The rationale behind this is that altruism is favored when altruists interact more with altruists than defectors do; the more viscous the population, the more likely it is that

Yet, living next to your kin also implies competing against them; 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. With generations are synchronous (Wright-Fisher model), in infinite populations, Talor REF has shown that compensation + Gardner and Rodrigues + other Taylor.

Deriving analytical results often implies making simplifying assumptions. Include simple population structures (but see), weak selection approximations, and rare or absent mutation. Simple pop reduces the dimension / complexity of the system that one has to study; weak selection approximations allow a decomposition of time scales expliquer. Say what mutation means, fidelity of parent-offspring transmission. Here, we relax the assumption of rare or absent mutation and explore how imperfect strategy transmission from parents to their offspring affect the evolution of altruistic behavior in subdivided populations.

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.* , containing n sites, each of which is occupied by exactly 1 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. 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 p, they become altruists, with probability $1-p$ they become defectors. We call the parameter p the mutation bias.

Social interactions take place within each deme; each individual interacts with the $n-1$ other deme members. We assume that social interactions affect individual fecundity, whose baseline is set to 1. Each interaction with an altruist increases an individual's fecundity by $\omega \mathrm{b}$, while altruists pay a fecundity cost $\omega \mathrm{c}$

(and $\mathsf{c} \leq \mathsf{b}$). The parameter ω scales the relative effect of social interactions on fecundity, and is assumed to be small ($\omega \ll 1$).

Denoting by e_{ij} the interaction probability between individuals living at sites i and j, we have

attention, maybe rather 1 than $1/(n-1)$

$$e_{ij} = \begin{cases} 0 & \text{if } i = j; \\ \frac{1}{n-1} & \text{if } i \neq j \text{ and both sites are in the same deme;} \\ 0 & \text{if the two sites are in different demes.} \end{cases} \tag{1}$$ {eq:defE}

Given our assumptions and with this notation, the fecundity of the individual living at site k is given by

$$f_k(\mathbf{X}, \omega) = 1 + \omega \left(\sum_{\ell=1}^{N} e_{\ell k} \mathsf{b} X_\ell - \mathsf{c} X_k \right). \tag{2}$$

Although our assumptions may seem restrictive (unconditional benefits, additive effects), the same fecundities are obtained with a generic fecundity function, after linearization, under the assumption that altruists and defectors are phenotypically close (see APPENDIX for details).

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

$$d_{ij} = \begin{cases} d_{\text{in}} = \frac{1-m}{n} & \text{if both sites are in the same deme;} \\ d_{\text{out}} = \frac{m}{(N_D - 1)n} & \text{if the two sites are in different demes.} \end{cases} \tag{3}$$ {eq:defD}

The way the population is updated from one time step to the next depends on the chosen life-cycle (updating rule). 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.

3 Results

3.1 Expected proportion of altruists

We want to compute the expected proportion of altruists in the population. Some steps can be done without specifying the life-cycle. 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 $B_{ji}(X(t),\omega)$, 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. We denote by $D_i(X(t),\omega)$ (D_i for simplicity) the probability that the individual living at site i at time t has been replaced (*i. e.* , died) at time $t+1$. Both quantities depend on the chosen life-cycle. Since a dead individual is immediately replaced by one new individual, in a table?

$$D_i = \sum_{j=1}^{N} B_{ij} \tag{4a}$$ {eq:DBequiv}

holds for all sites i. The structure of the population is also such that in the absence of selection ($\omega = 0$), all individuals have the same probability of dying and the same probability of having successful offspring (*i. e.* , offspring that become adults), so that really needed?

$$D_i^0 = \sum_{j=1}^{N} B_{ji}^0 = B^*, \tag{4b}$$ {eq:DBRV}

where the ^{0} subscript means that the quantities are evaluated for $\omega = 0$; 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 with eq. (4a) 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

$$\mathbb{E}\left[\overline{X}(t+1)|\mathbf{X}(t)\right] = \frac{1}{N}\sum_{i=1}^{N}\left[\sum_{j=1}^{N} B_{ij}\left(X_j(1-\mu)+\mu p\right) + (1-D_i)X_i\right]. \tag{5a}$$ {eq:conditionalchange}

The first term within the brackets corresponds to births; the type of the individual living at i at time $t+1$ then depends on the type of its parent (living at site j), and on whether mutation occurred. The second term corresponds to the survival of the individual living at site i.

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, and the expected frequency of altruists does not change anymore; we denote by $\xi(\mathbf{X}, \omega, \mu)$ the probability that the population is in state $\mathbf{X}$, given the strength of selection ω and the mutation probability μ. Taking the expectation of eq. (5a) ($\mathbb{E}\left[\overline{X}\right] = \sum_{X \in \Omega} \overline{X} \xi(\mathbf{X}, \omega, \mu)$), we obtain, after reorganizing:

$$0 = \frac{1}{N} \sum_{X \in \Omega} \sum_{i=1}^{N} \left[\sum_{j=1}^{N} B_{ij} \left(X_j (1-\mu) + \mu p \right) - D_i X_i \right] \xi(\mathbf{X}, \omega, \mu). \tag{6}$$ {eq:statdist}

Now, we use the assumption of weak selection ($\omega \ll 1$) and consider the first-order expansion of eq. (6) for ω close to 0. First, we note that in the absence of selection ($\omega = 0$), the population is at a mutation-drift balance, and the expected state of every site i is then $\mathbb{E}_0\left[X_i\right] = \sum_{X \in \Omega} X_i \xi(X, 0, \mu) = p$, the mutation bias. Secondly, we further expand derivatives of B_{ji} and D_i using the chain rule, using the variables f_k ($1 \le k \le N$), corresponding to individual fecundities (also, recall that $f_k = 1$ when $\omega = 0$). Finally, we use the shorthand notation ∂_x to denote $\left.\frac{\partial}{\partial x}\right|_{x=0}$. Thirdly, we note that for all the life-cycles that we consider, the number of deaths in the population during one time step does not depend on population composition (exactly 1 death for the Moran life-cycles, and exactly N for the Wright-Fisher life-cycle), so that $\partial_\omega \sum_{i,j=1}^{N} B_{ij}$ does not depend on ω. After simplification and reorganization, the first order expansion of eq. (6) yields

$$\begin{aligned} 0 = &\frac{1}{N} \sum_{i,k=1}^{N} \Bigg[\left. \frac{\partial \left(\sum_{j=1}^{N} (1-\mu) B_{ji} - D_i \right)}{\partial f_k} \right|_{f_k=1} \\ &\qquad \times \left(\sum_{\ell=1}^{N} e_{\ell k} \mathrm{b} \sum_{X \in \Omega} X_\ell X_i \xi(\mathbf{X}, 0, \mu) - c \sum_{X \in \Omega} X_k X_i \xi(\mathbf{X}, 0, \mu) \right) \Bigg] \\ &- B^* \mu \left. \frac{\partial \mathbb{E}\left[\overline{X}\right]}{\partial \omega} \right|_{\omega=0} + O\left(\omega^2\right). \end{aligned} \tag{7}$$ {eq:weaksel1}

The terms $\sum_{X \in \Omega} X_i X_j \xi(\mathbf{X}, 0, \mu)$, that we will also denote by P_{ij}, correspond to the expected state of the pair of sites (i, j), evaluated in the absence of selection

($\omega = 0$). We can also replace these terms by

$$Q_{ij} = \frac{P_{ij} - p^2}{p(1-p)}; \tag{8}$$

{eq:QP}

recursions on P_{ij} will 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.

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

$$\mathbb{E}\left[\overline{X}\right] = p + \omega\,\partial_\omega \mathbb{E}\left[\overline{X}\right] + O\left(\omega^2\right), \tag{9}$$

{eq:EXgeneric}

where $\partial_\omega \mathbb{E}\left[\overline{X}\right]$ is a shorthand notation for $\left.\frac{\partial \mathbb{E}\left[\overline{X}\right]}{\partial \omega}\right|_{\omega=0}$, which is given by eq. (7).

3.2 Identity by descent

We need to find equations for the expected state of pairs of sites (P_{ij}) and probabilities of identity by descent (Q_{ij}), quantities that are evaluated in the absence of selection (*i. e.* , for $\omega = 0$). To do so, we follow the same steps as in the previous section: we first write expectations at the next time step given a current state, and we then take the expectation of this. Here we focus on identity by descent Q_{ij}, but expectations of the state of pairs of sites P_{ij} are simply recovered using eq. (8). appendix

Because of the structure of the population, there are only three different values of Q_{ij}:

$$Q_{ij} = \begin{cases} 1 & \text{when } i = j; \\ Q_{\text{in}} & \text{when } i \neq j \text{ and both sites are in the same deme;} \\ Q_{\text{out}} & \text{when sites } i \text{ and } j \text{ are in different demes.} \end{cases} \tag{10}$$

3.2.1 Moran updating

{eq:QM}

$$Q^{\mathrm{M}}_{\text{in}} = \frac{(1-\mu)\left(m + \mu(d(1-m)-1)\right)}{(1-\mu)m(d\mu(n-1)+1) + (d-1)\mu(\mu(n-1)+1)}, \tag{11a}$$

$$Q^{\mathrm{M}}_{\text{out}} = \frac{(1-\mu)m}{(1-\mu)m(d\mu(n-1)+1) + (d-1)\mu(\mu(n-1)+1)}. \tag{11b}$$

The probability that two different deme-mates are identical by descent, Q_{in}^{M}, monotonically decreases with the emigration probability m, while $Q_{\text{out}}^{\text{M}}$ monotonically increases with m (see figure 1(a)).

We confirm that Q_{in}^{M} and $Q_{\text{out}}^{\text{M}}$ are equal to 1 when the mutation probability μ tends to 0; in the absence of mutation indeed, the population ends up fixed for one of the two types, and all individuals are identical by descent. However, trouble arises if we also want to consider infinite population (when the number of demes $N_D \to \infty$), because the order of limits matters. For instance, $\lim_{d\to\infty} Q_{\text{out}}^{M} = 0$.

3.2.2 Wright-Fisher updating

{eq:QWF}

$$Q_{\text{in}}^{\text{WF}} = \frac{-d + M_1 + M_2}{(n-1)d + M_1 + M_2}, \tag{12a}$$

$$Q_{\text{out}}^{\text{WF}} = \frac{-\frac{1}{d-1} M_1 + M2}{(n-1)d + M_1 + M_2}, \tag{12b}$$

with

$$M_1 = \frac{d-1}{1 - \frac{(1-\mu)^2 (d(1-m)-1)^2}{(d-1)^2}}, \text{ and} \tag{12c}$$

$$M_2 = \frac{1}{1-(1-\mu)^2}. \tag{12d}$$

Here, $Q_{\text{in}}^{\text{WF}}$ decreases until $m = m_c = \frac{d-1}{d}$, then increases again, while Q_{out}^{WF} follows the opposite pattern. The threshold value m_c corresponds to an emigration probability so high that an individual's offspring is as likely to land in its parent's deme as in any other deme.

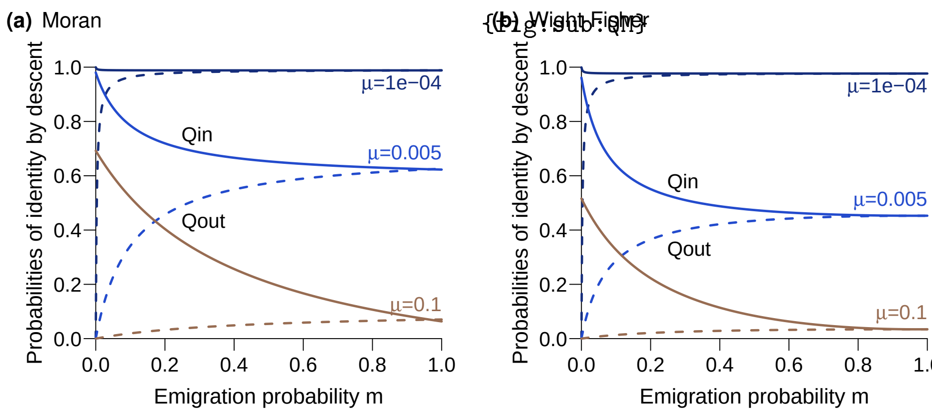
The two probabilities of identity by descent go to 1 when $\mu \to 1$. When the number of demes is very large ($d \to \infty$) blabal

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 (see figure 1).

3.3 Expected frequencies of altruists for each life-cycle

For each of the life-cycles that we consider, we can express $\partial_\omega \mathbb{E}\left[\overline{X}\right]$ as follows:

$$\partial_\omega \mathbb{E}\left[\overline{X}\right] = \frac{p(1-p)}{\mu}\left[\mathsf{b}\left(\beta_{\text{D}} - \beta_{\text{I}}\right) - \mathsf{c}\left(\gamma_{\text{D}} - \gamma_{\text{I}}\right)\right], \tag{13}$$ {eq:dEXgeneric}



{fig:sub:QM} {fig:sub:QWF}

{fig:Q}

Figure 1: 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), for different values of the mutation probability μ (10^{-4}, 0.005, 0.1), and for the two types of life-cycles: Moran (a) and Wright-Fisher (b). Other parameters: $n = 4$ individuals per deme, $N_D = 30$ demes.

where the subscript $_{\mathrm{D}}$ refers to “direct” effects, and the subscript $_{\mathrm{I}}$ to “indirect” effects. These indirect effects correspond to (kin) competition: by providing a benefit to a deme-mate and thereby increasing its fecundity, a focal altruist indirectly harms others by reducing their relative fecundity. Similarly, paying a fecundity cost indirectly helps others because it increases their relative fecundities.

3.3.1 Direct effects

Direct effects are similar for the three life-cycles; the only difference is the value of probabilities of identity by descent Q, that differ between Moran and Wright-Fisher life-cycles, as seen in the previous section: {eq:directeffects}

$$\beta_{\mathrm{D}}^{\mathrm{BD}} = \beta_{\mathrm{D}}^{\mathrm{DB}} = \left(1-\mu\right) Q_{\mathrm{in}}^{\mathrm{M}}, \tag{14a}$$ {eq:bBDD}

$$\beta_{\mathrm{D}}^{\mathrm{WF}} = \left(1-\mu\right) Q_{\mathrm{in}}^{\mathrm{WF}}; \tag{14b}$$ {eq:bWFD}

$$\gamma_{\mathrm{D}}^{\mathrm{BD}} = \gamma_{\mathrm{D}}^{\mathrm{BD}} = \gamma_{\mathrm{D}}^{\mathrm{WF}} = 1-\mu. \tag{14c}$$ {eq:cBDD}

For both benefits and costs, direct effects only count when there is no mutation $(1-\mu)$. Direct effects of benefits (b) only count if the interaction takes place with an individual who is identical by descent; interactions occurs only within demes, hence the presence of Q_{in} in eq. (14a) and eq. (14b). The direct effect of the fecundity cost c however does not depend on the type of interactant.

As seen in the previous section, $Q_{\mathrm{in}}^{\mathrm{M}}$ and $Q_{\mathrm{in}}^{\mathrm{WF}}$ decrease with the emigration probability m (actually only until $m = \frac{d-1}{d}$ for the latter). Consequently, the magnitude of the direct (beneficial) effects of benefits b provided by altruists (β_{D}) decreases, while the direct (costly) effects (γ_{D}) due to the direct cost of altruism c are constant. As a result, if we only consider direct effects, more emigration m is detrimental to the evolution of altruistic behaviour. But there are also indirect effects at play.

3.3.2 Indirect effects

Indirect effects are collateral effects on other individuals; they depend on the type of life-cycle, but always involve individuals who are identical by descent.

Moran Birth-Death Changing the fecundity of a focal individual has two types of indirect effects on others: *i*) it affects their probability of being the one chosen to reproduce – this affects all individuals in the population who are identical by descent to the focal, and *ii*) it affects their probability of dying because the number of offspring landing in their site changes – this affects individuals in the population who can send offspring at the same locations as the focal and are identical-by-descent to it; we obtain

$$
\begin{aligned}
\beta_{\mathrm{I}}^{\mathrm{BD}} &= (1-m)\left(\frac{n-1}{n}Q_{\mathrm{in}}^{\mathrm{M}}+\frac{1}{n}\right)+m\,Q_{\mathrm{out}}^{\mathrm{M}}-\mu\frac{1+(n-1)Q_{\mathrm{in}}^{\mathrm{M}}+n(d-1)Q_{\mathrm{out}}^{\mathrm{M}}}{nd} \\
&= \gamma_{\mathrm{D}}^{\mathrm{BD}}.
\end{aligned}
\tag{15a}
$$

{eq:bBDI}

The formulas are the same for the indirect effects associated to b and to c; in other words, the balance between the two indirect effects remains the same when the emigration probability changes. The term $\left(\frac{n-1}{n}Q_{\mathrm{in}}^{\mathrm{M}}+\frac{1}{n}\right)$, which we will see appear again later, corresponds to the probability that two individuals sampled with replacement from the same deme are identical by descent. Indirect effects are indeed also felt by the focal individual itself (*e. g.* , increasing the fecundity of another individual implies decreasing one's own relative fecundity).

Replacing Q_{in} and Q_{out} by their formula for the Moran life-cycle (eq. (11)), we see that both are decreasing functions of the emigration probability m.

3.3.3 Moran Death-Birth

With this life-cycle, death comes first and every individual in the population has the same survival probability ($1/N$). The indirect consequences of changing a focal individual's fecundity affect all individuals who can send their offspring to the same locations are the focal, and are identical by descent to it. We obtain

$$
\begin{aligned}
\beta_{\mathrm{I}}^{\mathrm{DB}} = (1-\mu)\Bigg[&\left(\frac{1}{n}+\frac{(n-1)Q_{\mathrm{in}}^{\mathrm{M}}}{n}\right)\left((1-m)^2+\frac{m^2}{(d-1)}\right) \\
&+m\left(2(1-m)+(d-2)\frac{m}{(d-1)}\right)Q_{\mathrm{out}}^{\mathrm{M}}\Bigg] \\
= \gamma_{\mathrm{I}}^{\mathrm{DB}}&
\end{aligned}
\tag{15b}
$$

{eq:bDBI}

The first term within the brackets in eq. (15b) corresponds individuals from the same deme whose offspring either does not emigrate, or emigrate to the same deme, and the second term, to individuals from different demes who end up in the same location (either one of their demes, or a third deme).

Here again, $\beta_{\mathrm{I}} = \gamma_{\mathrm{I}}$, so the balance between the two does not change when the emigration probability m increases.

Replacing Q_{in} and Q_{out} by their formulas given in eq. (11), we can see that $\beta_{\mathrm{I}} = \gamma_{\mathrm{I}}$ first decreases with the emigration probability m, and increases again after a threshold value m'_c (given in the appendix; $m'_c < (d-1)/d$). name

3.3.4 Wright-Fisher

Generations are synchronous, and all individuals again all have the same survival probability (now equal to 0). As a result, the formulas for $\beta_{\mathrm{I}}^{\mathrm{WF}}$ and $\gamma_{\mathrm{I}}^{\mathrm{WF}}$ are the same as $\beta_{\mathrm{I}}^{\mathrm{DB}}$ and $\gamma_{\mathrm{I}}^{\mathrm{WF}}$, except that instead of $Q_{\mathrm{in}}^{\mathrm{M}}$ and $Q_{\mathrm{out}}^{\mathrm{M}}$, we need to use $Q_{\mathrm{in}}^{\mathrm{WF}}$ and $Q_{\mathrm{out}}^{\mathrm{WF}}$ (given in eq. (12)). Once this is done, we see that $\beta_{\mathrm{I}}^{\mathrm{WF}} = \gamma_{\mathrm{I}}^{\mathrm{WF}} =$ first decreases with the emigration probability m, and increases again after the threshold value $m_c = (d-1)/d$ (which was identified previously as the emigration probability such that offspring have an equal chance of landing in their natal deme or in any other deme).

3.4 Identifying threshold values of the mutation probability μ

In the previous section, we investigated the impact of changes in the emigration probability m on each of the terms that make up the expected frequency of altruists $\mathbb{E}[\overline{X}]$. Now we need to combine these different terms to focus on the quantity we are eventually interested in, $\mathbb{E}[\overline{X}]$. The rather lengthy formulas that we obtain are relegated to the appendix, and we concentrate here on the results.

3.4.1 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; μ_c^{BD} is given by

$$\mu_c^{\mathrm{BD}} = 1 - \frac{\mathsf{b} - \mathsf{c} + \sqrt{(\mathsf{b}-\mathsf{c})\left(4\mathsf{b}(nd)^2 + \mathsf{b} - \mathsf{c}\right)}}{2\mathsf{b}nd} \tag{16}$$

{eq:mucBD}

This result is illustrated in figure 2(b).

donner la valeur

3.4.2 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. 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. (17) 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

$$\mu_c^{\mathrm{DB}} = \begin{cases} \dfrac{\mathsf{b}-(n+1)\mathsf{c}}{(n-1)\mathsf{c}-(2n-1)\mathsf{b}} & \text{if } \mathsf{b} < \mathsf{c}(n+1), \\ 0 & \text{otherwise.} \end{cases} \tag{17}$$

{eq:mucDB}

The expected frequency of altruists $\mathbb{E}\left[\overline{X}\right]$ reaches a maximum for an emigration probability m_c^{DB} (whose complicatedequation is in the appendix), as can be seen in figure 2(a). The limit of this critical emigration probability m_c^{DB} when $\mu \to 0$ is 0: we recover the result that more emigration is detrimental to the evolution of altruism when the mutation probability is either null or vanishingly small.

do

attention order of limits

appendix

3.4.3 Wright-Fisher

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

$$\mu_c^{\mathrm{WF}} = 1 - \sqrt{1 - \frac{\mathsf{c}}{\mathsf{b}}}, \tag{18}$$

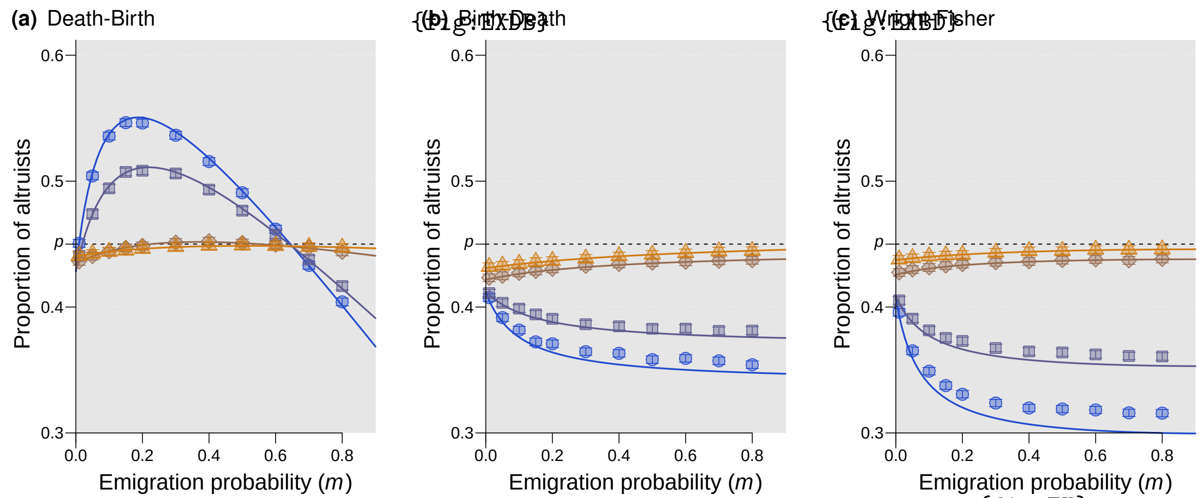
and it is a minimum otherwise (see figure 2(c)).

3.5 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. The patterns that we identified hold when selection is strong (see figure **??**, done with $\omega = 0.1$), but also when the demes have different sizes. Deme sizes are drawn randomly at the beginning of a simulation; the range from 1 to 5 individuals per deme and the average size is 4 individuals as in the other figures.. Here as well, the same patterns hold as those obtained with a homogeneous structure (figure S2). Addeffect of d_{self}.

le pb c'est ptet simplement que 1 individu ca pose probleme!

todo



{fig:EX}

Figure 2: Weak selection. Parameters: $\omega = 0.005$, $b = 15$, $c = 1$, ndemes, size, nreps. NOTE simulations running with 0.005 for mu and with 0.8 for mig.

4 Discussion

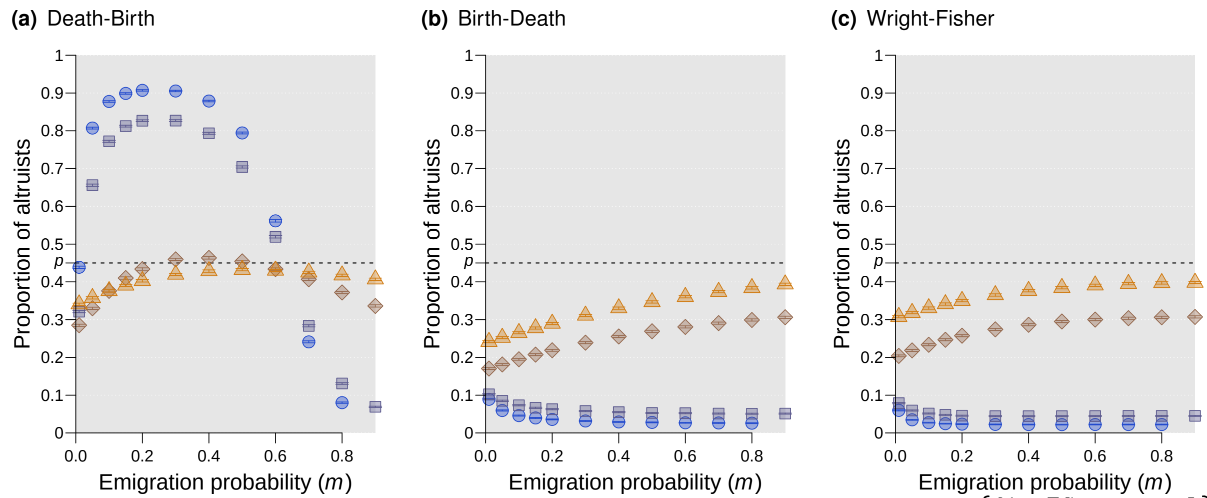
Adding non zero mutation probability altruism increases with emigration.

Quantitative measure of the success of altruism: $\mathbb{E}[\overline{X}]$. Qualitative measure commonly used is whether greater than p: no effect on BD and WF, but still effect on DB.

Go back to the decomposition of the different terms, we see that increase of $\mathbb{E}[\overline{X}]$ with m is driven by the β_{I} term. To simplify the explanations, let us consider that the number of demes is large: in this case, Q_{out} is vanishingly small and so terms involving it can be omitted. Let us also assume that there is no direct cost to being an altruist ($c = 0$).

Problems of orders of limits, especially when $d \to \infty$ and $\mu \to 0$. Need to specify how small the mutation probability is compared to the size of the population.

Supplementary figures



{fig:ESstrongsel}

Figure S1: Equivalent of figure 2 but with strong selection ($\omega = 0.1$); all other parameters and legend are identical to those of figure 2.

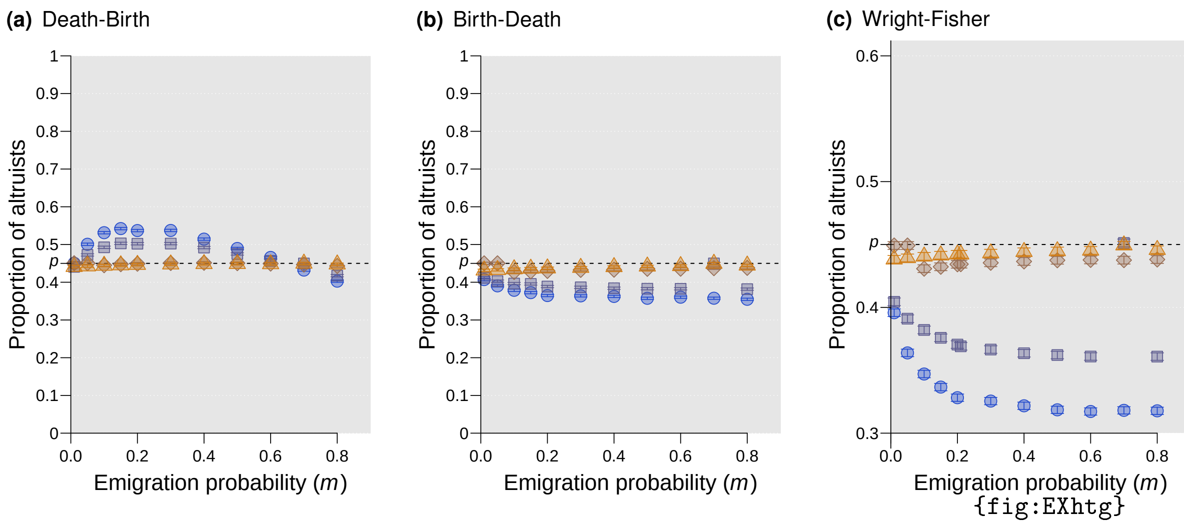
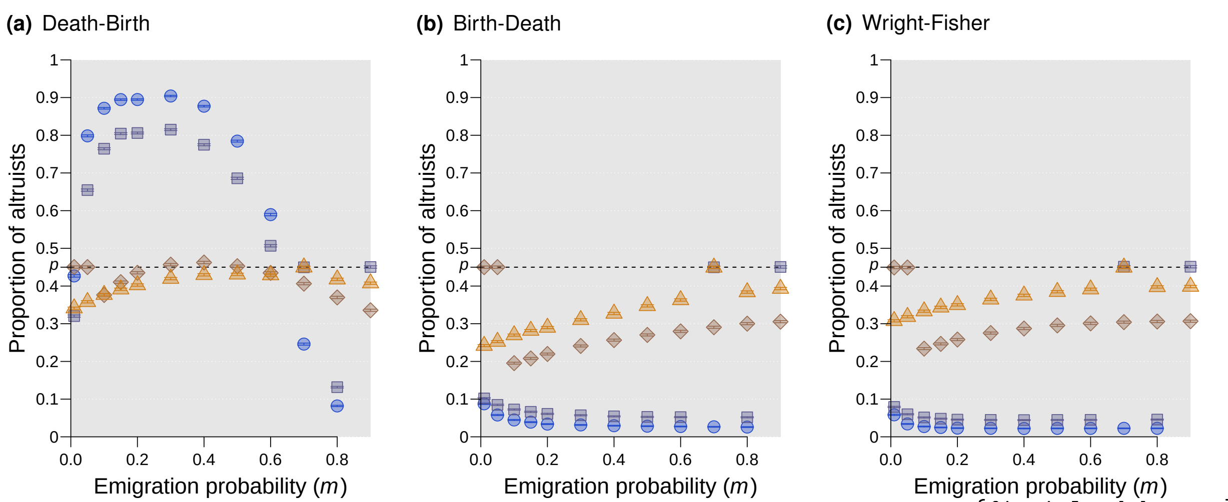


Figure S2: Equivalent of figure 2 but with a heterogeneous population structure: deme sizes range form 1 to 5 individuals per deme, the average deme size is 4 as in figure 2; all other parameters and legend are identical to those of figure 2.



{fig:island_htgpop}

Figure S3: Strong selection, heterogeneous population

Adaptation of my equations to a subdivided population. Notation, for a quantity Y that depends on two sites ($Y = e, d, Q$):

$$Y_{\text{self}} := Y_{i,i} \tag{.1a}$$
$$Y_{\text{in}} := Y_{i,j}, \quad i \text{ and } j \neq i \text{ in the same deme;} \tag{.1b}$$
$$Y_{\text{out}} := Y_{i,j}, \quad i \text{ and } j \text{ in different demes.} \tag{.1c}$$

For a site i, G_i denotes the deme the site belongs to, and notation $j \in G_i$ means that sites i and j are in the same deme.

The expected frequency of altruists in the population is given by

$$\mathbb{E}\left[\overline{X}\right] = p + \delta \frac{p(1-p)}{\mu} \left[\mathsf{b}\,(\beta^D - \beta^I) - \mathsf{c}\,(\gamma^D - \gamma^I) \right]. \tag{.2}$$

Moran, Birth-Death

$$\begin{aligned}
\beta^D_{\text{BD}} &= \sum_{k,\ell=1}^{N} \frac{1-\mu}{N} e_{kl} Q_{lk} \\
&= \sum_{k=1}^{N} \frac{1-\mu}{N} \Big(e_{\text{self}} + (n-1) e_{\text{in}} Q_{\text{in}} + (N-n) e_{\text{out}} Q_{\text{out}} \Big) \\
&= (1-\mu) \Big(e_{\text{self}} + (n-1) e_{\text{in}} Q_{\text{in}} + (N-n) e_{\text{out}} Q_{\text{out}} \Big).
\end{aligned} \tag{.3a}$$

$$
\begin{aligned}
\beta^I_{\mathrm{BD}} =& \sum_{j,k,l=1}^{N} \left(\frac{d_{lj}}{N} - \frac{\mu}{N^2}\right) e_{kl} Q_{jk} \\
=& \frac{1}{N} \sum_{j=1}^{N} \left[\left(\sum_{l=1}^{N} d_{lj} e_{jl} \right) + \sum_{\substack{k \in G_j \\ k \neq j}} \left(\sum_{l=1}^{N} d_{lj} e_{kl} Q_{\mathrm{in}} Q_{\mathrm{in}} \right) + \sum_{k \notin G_j} \sum_{l=1}^{N} d_{lj} \left(e_{kl} Q_{\mathrm{out}} Q_{\mathrm{out}} \right) \right] \\
& + \frac{\mu}{N^2} \sum_{j=1}^{N} \left(\sum_{l=1}^{N} e_{kl} \right) \left(\sum_{k=1}^{N} Q_{jk} \right) \\
=& \frac{1}{N} \sum_{j=1}^{N} \Bigg[d_{\mathrm{self}} e_{\mathrm{self}} + (n-1) d_{\mathrm{in}} e_{\mathrm{in}} + (N-n) d_{\mathrm{out}} e_{\mathrm{out}} \\
& \quad + \sum_{\substack{k \in G_j \\ k \neq j}} \left(d_{\mathrm{in}} e_{\mathrm{self}} + d_{\mathrm{self}} e_{\mathrm{in}} + (n-2) d_{\mathrm{in}} e_{\mathrm{in}} + (N-n) d_{\mathrm{out}} e_{\mathrm{out}} \right) Q_{\mathrm{in}} \\
& \quad + \sum_{k \notin G_j} \left(d_{\mathrm{self}} e_{\mathrm{out}} + (n-1) d_{\mathrm{in}} e_{\mathrm{out}} + d_{\mathrm{out}} e_{\mathrm{self}} + (n-1) d_{\mathrm{out}} e_{\mathrm{in}} + (N-2n) d_{\mathrm{out}} e_{\mathrm{out}} \right) Q_{\mathrm{out}} \Bigg] \\
& - \frac{\mu}{N} \left(1 + (n-1) Q_{\mathrm{in}} + (N-n) Q_{\mathrm{out}}\right) \left(e_{\mathrm{self}} + (n-1) e_{\mathrm{in}} + (N-n) e_{\mathrm{out}}\right) \\
=& d_{\mathrm{self}} e_{\mathrm{self}} + (n-1) d_{\mathrm{in}} e_{\mathrm{in}} + (N-n) d_{\mathrm{out}} e_{\mathrm{out}} \\
& + (n-1) \left(d_{\mathrm{in}} e_{\mathrm{self}} + d_{\mathrm{self}} e_{\mathrm{in}} + (n-2) d_{\mathrm{in}} e_{\mathrm{in}} + (N-n) d_{\mathrm{out}} e_{\mathrm{out}} \right) Q_{\mathrm{in}} \\
& + (N-n) \left(d_{\mathrm{self}} e_{\mathrm{out}} + (n-1) d_{\mathrm{in}} e_{\mathrm{out}} + d_{\mathrm{out}} e_{\mathrm{self}} + (n-1) d_{\mathrm{out}} e_{\mathrm{in}} + (N-2n) d_{\mathrm{out}} e_{\mathrm{out}} \right) Q_{\mathrm{out}} \\
& - \frac{\mu}{N} \left(1 + (n-1) Q_{\mathrm{in}} + (N-n) Q_{\mathrm{out}}\right) \left(e_{\mathrm{self}} + (n-1) e_{\mathrm{in}} + (N-n) e_{\mathrm{out}}\right). \qquad (.3b)
\end{aligned}
$$

$$
\gamma^D_{\mathrm{BD}} = 1 - \mu. \qquad (.3c)
$$

$$
\begin{aligned}
\gamma^I_{\mathrm{BD}} =& \frac{1}{N} \sum_{j,k=1}^{N} \left(d_{kj} - \frac{\mu}{N} \right) Q_{jk} \\
=& \frac{1}{N} \sum_{j=1}^{N} \left[d_{\mathrm{self}} - \frac{\mu}{N} + (n-1) \left(d_{\mathrm{in}} - \frac{\mu}{N} \right) Q_{\mathrm{in}} + (N-n) \left(d_{\mathrm{out}} - \frac{\mu}{N} \right) Q_{\mathrm{out}} \right] \\
=& d_{\mathrm{self}} + (n-1) d_{\mathrm{in}} Q_{\mathrm{in}} + (N-n) d_{\mathrm{out}} Q_{\mathrm{out}} \\
& - \frac{\mu}{N} \left(1 + (n-1) Q_{\mathrm{in}} + (N-n) Q_{\mathrm{out}}\right) \qquad (.3d)
\end{aligned}
$$

Moran, Death-Birth

$$\beta^D_{\mathrm{DB}} = \frac{1-\mu}{N}\sum_{j,k=1}^{N} Q_{jk}e_{jk} = \beta^D_{\mathrm{BD}}$$
$$= (1-\mu)\Big(e_{\mathrm{self}} + (n-1)e_{\mathrm{in}}Q_{\mathrm{in}} + (N-n)e_{\mathrm{out}}Q_{\mathrm{out}}\Big). \tag{.4a}$$

$$\beta^I_{\mathrm{DB}} = \frac{1-\mu}{N}\sum_{i,j,k,l=1}^{N} d_{ji}d_{li}e_{kl}Q_{jk} \tag{.4b}$$

283 Presented in the table in the appendix.

$$\gamma^D_{\mathrm{DB}} = 1-\mu = \gamma^D_{\mathrm{BD}}. \tag{.4c}$$

$$\gamma^I_{\mathrm{DB}} = (1-\mu)\sum_{i,j,k=1}^{N}\frac{d_{ji}d_{ki}}{N}Q_{jk}$$
$$= \frac{1-\mu}{N}\sum_{j=1}^{N}\sum_{i=1}^{N}\Big(d_{ji}d_{ji} + \sum_{\substack{k\neq j\\ k\in G_j}} d_{ji}d_{ki}Q_{\mathrm{in}} + \sum_{k\notin G_j} d_{ji}d_{ki}Q_{\mathrm{out}}\Big)$$
$$= \frac{1-\mu}{N}\sum_{j=1}^{N}\Big[d_{\mathrm{self}}d_{\mathrm{self}} + (n-1)d_{\mathrm{in}}d_{\mathrm{in}} + (N-n)d_{\mathrm{out}}d_{\mathrm{out}}$$
$$+ (n-1)\Big(d_{\mathrm{self}}d_{\mathrm{in}} + d_{\mathrm{in}}d_{\mathrm{self}} + (n-2)d_{\mathrm{in}}d_{\mathrm{in}} + (N-n)d_{\mathrm{out}}d_{\mathrm{out}}\Big)Q_{\mathrm{in}}$$
$$+ (N-n)\Big(d_{\mathrm{self}}d_{\mathrm{out}} + (n-1)d_{\mathrm{in}}d_{\mathrm{out}} + d_{\mathrm{out}}d_{\mathrm{self}} + (n-1)d_{\mathrm{out}}d_{\mathrm{in}} + (N-2n)d_{\mathrm{out}}d_{\mathrm{out}}\Big)Q_{\mathrm{out}}\Big] \tag{.4d}$$

284 Probabilities of identity by descent

285 WF est faux. Il faut utiliser les formules Fourier...!

286 **Moran** For $i =\neq j$,

$$Q_{ij} = \frac{1-\mu}{2}\sum_{k=1}^{N}\left(d_{kj}Q_{ki} + d_{ki}Q_{kj}\right). \tag{.5a}$$

For $j \neq i$, $j \in G_i$,

$$\begin{aligned}
Q_{\text{in}} &= \frac{1-\mu}{2}\Big((d_{\text{in}} + d_{\text{self}} Q_{\text{in}}) + (d_{\text{self}} Q_{\text{in}} + d_{\text{in}}) \\
&\qquad + (n-2)\,(d_{\text{in}} Q_{\text{in}} + d_{\text{in}} Q_{\text{in}}) + (N-n)\,(d_{\text{out}} Q_{\text{out}} + d_{\text{out}} Q_{\text{out}}) \Big) \\
&= (1-\mu)\Big(d_{\text{in}} + d_{\text{self}} Q_{\text{in}} + (n-2) d_{\text{in}} Q_{\text{in}} + (N-n) d_{\text{out}} Q_{\text{out}} \Big).
\end{aligned} \tag{.5b}$$

And for $j \notin G_i$,

$$\begin{aligned}
Q_{\text{out}} &= \frac{1-\mu}{2}\Big((d_{\text{out}} + d_{\text{self}} Q_{\text{out}}) + (n-1)\,(d_{\text{out}} Q_{\text{in}} + d_{\text{in}} Q_{\text{out}}) \\
&\qquad + (d_{\text{self}} Q_{\text{out}} + d_{\text{out}}) + (n-1)\,(d_{\text{in}} Q_{\text{out}} + d_{\text{out}} Q_{\text{in}}) \\
&\qquad + (N-2n)\,(d_{\text{out}} Q_{\text{out}} + d_{\text{out}} Q_{\text{out}}) \Big) \\
&= (1-\mu)\Big(d_{\text{out}} + d_{\text{self}} Q_{\text{out}} + (n-1)\,(d_{\text{out}} Q_{\text{in}} + d_{\text{in}} Q_{\text{out}}) + (N-2n) d_{\text{out}} Q_{\text{out}} \Big)
\end{aligned} \tag{.5c}$$

Wright-Fisher For $j \neq i$,

$$Q_{ij} = (1-\mu)^2 \sum_{k,l=1}^{N} d_{ki} d_{lj} Q_{kl}. \tag{.6a}$$

When $j \neq i$, $j \in G_i$,

$$
\begin{aligned}
Q_{\text{in}} = (1-\mu)^2 \Big[& \Big(d_{\text{self}} d_{\text{in}} + d_{\text{in}} d_{\text{self}} + (n-2) d_{\text{in}} d_{\text{in}} + (N-n) d_{\text{out}} d_{\text{out}} \Big) \\
& + \Big(d_{\text{self}} d_{\text{self}} + (n-2) d_{\text{self}} d_{\text{in}} \\
& \quad + (n-1) d_{\text{in}} d_{\text{in}} + (n-2) d_{\text{in}} d_{\text{self}} \\
& \quad + (n-2)(n-2) d_{\text{in}} d_{\text{in}} + (N-n)(n-1) d_{\text{out}} d_{\text{out}} \Big) Q_{\text{in}} \\
& + \Big((N-n) d_{\text{self}} d_{\text{out}} + (N-n)(n-1) d_{\text{in}} d_{\text{out}} \\
& \quad + (N-n) d_{\text{out}} d_{\text{self}} + (N-n)(n-1) d_{\text{out}} d_{\text{in}} \\
& \quad + (N-n)(N-2n) d_{\text{out}} d_{\text{out}} \Big) Q_{\text{out}} \Big] \\
= (1-\mu)^2 \Big[& \Big(2 d_{\text{in}} d_{\text{self}} + (n-2) d_{\text{in}}^2 + (N-n) d_{\text{out}}^2 \Big) \\
& + \Big(d_{\text{self}}^2 + 2(n-2) d_{\text{self}} d_{\text{in}} + (n^2-3n+3) d_{\text{in}}^2 + +(N-n)(n-1) d_{\text{out}}^2 \Big) Q_{\text{in}} \\
& + \Big(2(N-n) d_{\text{self}} d_{\text{out}} + 2(N-n)(n-1) d_{\text{in}} d_{\text{out}} \\
& \quad + (N-n)(N-2n) d_{\text{out}} d_{\text{out}} \Big) Q_{\text{out}} \Big]
\end{aligned} \tag{.6b}
$$

And when $j \notin G_i$, we have

$$
\begin{aligned}
Q_{\text{out}} = (1-\mu)^2 \Big[& \Big(2 d_{\text{self}} d_{\text{out}} + 2(n-1) d_{\text{in}} d_{\text{out}} + (N-2n) d_{\text{out}}^2 \Big) \\
& + \Big(2(n-1) d_{\text{self}} d_{\text{out}} + 2(n-1)^2 d_{\text{in}} d_{\text{out}} + (N-2n)(n-1) d_{\text{out}}^2 \Big) Q_{\text{in}} \\
& + \Big(d_{\text{self}} d_{\text{self}} + (n-1) d_{\text{self}} d_{\text{in}} + (N-2n) d_{\text{self}} d_{\text{out}} \\
& \quad + (n-1) d_{\text{in}} d_{\text{self}} + (n-1)^2 d_{\text{in}}^2 + (n-1)(N-2n) d_{\text{in}} d_{\text{out}} \\
& \quad + (N-n) d_{\text{out}} d_{\text{self}} + (N-n)(n-1) d_{\text{out}} d_{\text{in}} + (N-n)(N-2n) d_{\text{out}} d_{\text{out}} \Big) Q_{\text{out}} \Big].
\end{aligned} \tag{.6c}
$$

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Appendix

All combinations for i, j, k, l. Notation: (i, j) means that i and j are in the same deme, but are different; G_i refers to the deme containing site i.

	j	k	l	Notation	Count	d_{ji}	d_{li}	e_{kl}	Q_{jk}
1	$j=i$	$k=i$	$l=i$	$(i=j=k=l)$	1	d_{self}	d_{self}	e_{self}	1
2	$j=i$	$k=i$	$l \neq i; l \in G_i$	$(i=j=k,l)$	$n-1$	d_{self}	d_{in}	e_{in}	1
3	$j=i$	$k=i$	$l \notin G_i$	$(i=j=k),(l)$	$N-n$	d_{self}	d_{out}	e_{out}	1
4	$j=i$	$k \neq i; k \in G_i$	$l=i$	$(i=j=l,k)$	$n-1$	d_{self}	d_{self}	e_{in}	Q_{in}
5	$j=i$	$k \neq i; k \in G_i$	$l=k$	$(i=j,k=l)$	$n-1$	d_{self}	d_{in}	e_{self}	Q_{in}
6	$j=i$	$k \neq i; k \in G_i$	$l \neq i,k; l \in G_i$	$(i=j,k,l)$	$(n-1)(n-2)$	d_{self}	d_{in}	e_{in}	Q_{in}
7	$j=i$	$k \neq i; k \in G_i$	$l \notin G_i$	$(i=j,k),(l)$	$(n-1)(N-n)$	d_{self}	d_{out}	e_{out}	Q_{in}
8	$j=i$	$k \notin G_i$	$l=i=j$	$(i=j=l),(k)$	$(N-n)$	d_{self}	d_{self}	e_{out}	Q_{out}
9	$j=i$	$k \notin G_i$	$l \neq i, l \in G_i$	$(i=j,l),(k)$	$(N-n)(n-1)$	d_{self}	d_{in}	e_{out}	Q_{out}
10	$j=i$	$k \notin G_i$	$l=k$	$(i=j),(k=l)$	$(N-n)$	d_{self}	d_{out}	e_{self}	Q_{out}
11	$j=i$	$k \notin G_i$	$l \neq k; l \in G_k$	$(i=j),(k,l)$	$(N-n)(n-1)$	d_{self}	d_{out}	e_{in}	Q_{out}
12	$j=i$	$k \notin G_i$	$l \notin G_i, G_k$	$(i=j),(k),(l)$	$(N-n)(N-2n)$	d_{self}	d_{out}	e_{out}	Q_{out}
13	$j \neq i, j \in G_i$	$k=i$	$l=i$	$(i=k=l,j)$	$(n-1)$	d_{in}	d_{self}	e_{self}	Q_{in}
14	$j \neq i, j \in G_i$	$k=i$	$l=j$	$(i=k,j=l)$	$(n-1)$	d_{in}	d_{in}	e_{in}	Q_{in}
15	$j \neq i, j \in G_i$	$k=i$	$l \neq i,j; l \in G_i$	$(i=k,j,l)$	$(n-1)(n-2)$	d_{in}	d_{in}	e_{in}	Q_{in}
16	$j \neq i, j \in G_i$	$k=i$	$l \notin G_i$	$(i=k,j),(l)$	$(n-1)(N-n)$	d_{in}	d_{out}	e_{out}	Q_{in}
17	$j \neq i, j \in G_i$	$k=j$	$l=i$	$(i=l,j=k)$	$(n-1)$	d_{in}	d_{self}	e_{in}	1
18	$j \neq i, j \in G_i$	$k=j$	$l=j$	$(i,j=k=l)$	$(n-1)$	d_{in}	d_{in}	e_{self}	1
19	$j \neq i, j \in G_i$	$k=j$	$l \neq i,j; l \in G_i$	$(i,j=k,l)$	$(n-1)(n-2)$	d_{in}	d_{in}	e_{in}	1
20	$j \neq i, j \in G_i$	$k=j$	$l \notin G_i$	$(i,j=k),(l)$	$(n-1)(N-n)$	d_{in}	d_{out}	e_{out}	1
21	$j \neq i, j \in G_i$	$k \neq i,j; k \in G_i$	$l=i$	$(i=l,j,k)$	$(n-1)(n-2)$	d_{in}	d_{self}	e_{in}	Q_{in}
22	$j \neq i, j \in G_i$	$k \neq i,j; k \in G_i$	$l=j$	$(i,j=l,k)$	$(n-1)(n-2)$	d_{in}	d_{in}	e_{in}	Q_{in}
23	$j \neq i, j \in G_i$	$k \neq i,j; k \in G_i$	$l=k$	$(i,j,k=l)$	$(n-1)(n-2)$	d_{in}	d_{in}	e_{self}	Q_{in}
24	$j \neq i, j \in G_i$	$k \neq i,j; k \in G_i$	$l \neq i,j,k; l \in G_i$	(i,j,k,l)	$(n-1)(n-2)(n-3)$	d_{in}	d_{in}	e_{in}	Q_{in}
25	$j \neq i, j \in G_i$	$k \neq i,j; k \in G_i$	$l \notin G_i$	$(i,j,k),(l)$	$(n-1)(n-2)(N-n)$	d_{in}	d_{out}	e_{out}	Q_{in}

	j	k	l	Notation	Count	d_{ji}	d_{li}	e_{kl}	Q_{jk}
26	$j \neq i; j \in G_i$	$k \notin G_i$	$l = i$	$(i = l, j), (k)$	$(n-1)(N-n)$	d_{in}	d_{self}	e_{out}	Q_{out}
27	$j \neq i; j \in G_i$	$k \notin G_i$	$l = j$	$(i, j = l), (k)$	$(n-1)(N-n)$	d_{in}	d_{in}	e_{out}	Q_{out}
28	$j \neq i; j \in G_i$	$k \notin G_i$	$l \neq i, j; l \in G_i$	$(i, j, l), (k)$	$(n-1)(N-n)(n-2)$	d_{in}	d_{in}	e_{out}	Q_{out}
29	$j \neq i; j \in G_i$	$k \notin G_i$	$l = k$	$(i, j), (k = l)$	$(n-1)(N-n)$	d_{in}	d_{out}	e_{self}	Q_{out}
30	$j \neq i; j \in G_i$	$k \notin G_i$	$l \neq k; l \in G_k$	$(i, j), (k, l)$	$(n-1)(N-n)(n-1)$	d_{in}	d_{out}	e_{in}	Q_{out}
31	$j \neq i; j \in G_i$	$k \notin G_i$	$l \notin G_i, G_k$	$(i, j), (k), (l)$	$(n-1)(N-n)(N-2n)$	d_{in}	d_{out}	e_{out}	Q_{out}
32	$j \notin G_i$	$k = i$	$l = i$	$(i = k = l), (j)$	$(N-n)$	d_{out}	d_{self}	e_{self}	Q_{out}
33	$j \notin G_i$	$k = i$	$l \neq i; l \in G_i$	$(i = k, l), (j)$	$(N-n)(n-1)$	d_{out}	d_{in}	e_{in}	Q_{out}
34	$j \notin G_i$	$k = i$	$l = j$	$(i = k), (j = l)$	$(N-n)$	d_{out}	d_{out}	e_{out}	Q_{out}
35	$j \notin G_i$	$k = i$	$l \neq j; l \in G_j$	$(i = k), (j, l)$	$(N-n)(n-1)$	d_{out}	d_{out}	e_{out}	Q_{out}
36	$j \notin G_i$	$k = i$	$l \notin G_i, G_j$	$(i = k), (j), (l)$	$(N-n)(N-2n)$	d_{out}	d_{out}	e_{out}	Q_{out}
37	$j \notin G_i$	$k \neq i; k \in G_i$	$l = i$	$(i = l, k), (j)$	$(N-n)(n-1)$	d_{out}	d_{self}	e_{in}	Q_{out}
38	$j \notin G_i$	$k \neq i; k \in G_i$	$l = k$	$(i, k = l), (j)$	$(N-n)(n-1)$	d_{out}	d_{in}	e_{self}	Q_{out}
39	$j \notin G_i$	$k \neq i; k \in G_i$	$l \neq i, k; l \in G_i$	$(i, k, l), (j)$	$(N-n)(n-1)(n-2)$	d_{out}	d_{in}	e_{in}	Q_{out}
40	$j \notin G_i$	$k \neq i; k \in G_i$	$l = j$	$(i, k), (j = l)$	$(N-n)(n-1)$	d_{out}	d_{out}	e_{out}	Q_{out}
41	$j \notin G_i$	$k \neq i; k \in G_i$	$l \neq j; l \in G_j$	$(i, k), (j, l)$	$(N-n)(n-1)(n-1)$	d_{out}	d_{out}	e_{out}	Q_{out}
42	$j \notin G_i$	$k \neq i; k \in G_i$	$l \notin G_i, G_j$	$(i, k), (j), (l)$	$(N-n)(n-1)(N-2n)$	d_{out}	d_{out}	e_{out}	Q_{out}
43	$j \notin G_i$	$k = j$	$l = i$	$(i = l), (j = k)$	$(N-n)$	d_{out}	d_{self}	e_{out}	1
44	$j \notin G_i$	$k = j$	$l \neq i; l \in G_i$	$(i, l), (j = k)$	$(N-n)(n-1)$	d_{out}	d_{in}	e_{out}	1
45	$j \notin G_i$	$k = j$	$l = j$	$(i), (j = k = l)$	$(N-n)$	d_{out}	d_{out}	e_{self}	1
46	$j \notin G_i$	$k = j$	$l \neq j; l \in G_j$	$(i), (j = k, l)$	$(N-n)(n-1)$	d_{out}	d_{out}	e_{in}	1
47	$j \notin G_i$	$k = j$	$l \notin G_i, G_j$	$(i), (j = k), (l)$	$(N-n)(N-2n)$	d_{out}	d_{out}	e_{out}	1

	j	k	l	Notation	Count	d_{ji}	d_{li}	e_{kl}	Q_{jk}
48	$j \notin G_i$	$k \neq j; k \in G_j$	$l = i$	$(i = l), (j, k)$	$(N-n)(n-1)$	d_{out}	d_{self}	e_{out}	Q_{in}
49	$j \notin G_i$	$k \neq j; k \in G_j$	$l \neq i; l \in G_i$	$(i, l), (j, k)$	$(N-n)(n-1)(n-1)$	d_{out}	d_{in}	e_{out}	Q_{in}
50	$j \notin G_i$	$k \neq j; k \in G_j$	$l = j$	$(i), (j = l, k)$	$(N-n)(n-1)$	d_{out}	d_{out}	e_{in}	Q_{in}
51	$j \notin G_i$	$k \neq j; k \in G_j$	$l = k$	$(i), (j, k = l)$	$(N-n)(n-1)$	d_{out}	d_{out}	e_{self}	Q_{in}
52	$j \notin G_i$	$k \neq j; k \in G_j$	$l \neq j, k; l \in G_j$	$(i), (j, k, l)$	$(N-n)(n-1)(n-2)$	d_{out}	d_{out}	e_{in}	Q_{in}
53	$j \notin G_i$	$k \neq j; k \in G_j$	$l \notin G_i, G_j$	$(i), (j, k), (l)$	$(N-n)(n-1)(N-2n)$	d_{out}	d_{out}	e_{out}	Q_{in}
54	$j \notin G_i$	$k \notin G_i, G_j$	$l = i$	$(i = l), (j), (k)$	$(N-n)(N-2n)$	d_{out}	d_{self}	e_{out}	Q_{out}
55	$j \notin G_i$	$k \notin G_i, G_j$	$l \neq i; l \in G_i$	$(i, l), (j), (k)$	$(N-n)(N-2n)(n-1)$	d_{out}	d_{in}	e_{out}	Q_{out}
56	$j \notin G_i$	$k \notin G_i, G_j$	$l = j$	$(i), (j = l), (k)$	$(N-n)(N-2n)$	d_{out}	d_{out}	e_{out}	Q_{out}
57	$j \notin G_i$	$k \notin G_i, G_j$	$l \neq j; l \in G_j$	$(i), (j, l), (k)$	$(N-n)(N-2n)(n-1)$	d_{out}	d_{out}	e_{out}	Q_{out}
58	$j \notin G_i$	$k \notin G_i, G_j$	$l = k$	$(i), (j), (k = l)$	$(N-n)(N-2n)$	d_{out}	d_{out}	e_{self}	Q_{out}
59	$j \notin G_i$	$k \notin G_i, G_j$	$l \neq k; l \in G_k$	$(i), (j), (k, l)$	$(N-n)(N-2n)(n-1)$	d_{out}	d_{out}	e_{in}	Q_{out}
60	$j \notin G_i$	$k \notin G_i, G_j$	$l \notin G_i, G_j, G_k$	$(i), (j), (k), (l)$	$(N-n)(N-2n)(N-3n)$	d_{out}	d_{out}	e_{out}	Q_{out}

A Island model

With self replacement

$$d_{\text{self}} = d_{\text{in}} = \frac{1-m}{n}, \tag{A.7a}$$

$$d_{\text{out}} = \frac{m}{N-n}. \tag{A.7b}$$

Without self-replacement

$$d_{\text{self}} = 0, \tag{A.8a}$$

$$d_{\text{in}} = \frac{1-m}{n-1}, \tag{A.8b}$$

$$d_{\text{out}} = \frac{m}{N-n}. \tag{A.8c}$$

B IDB

B.1 Moran

Using the formulas for a 2D graph in REF Debarre 2017,

$$\tilde{\mathcal{D}}_{\substack{q_1\\q_2}} = \sum_{l_1=0}^{N_1-1}\sum_{l_2=0}^{N_2-1} \tilde{d}_{\substack{l_1\\l_2}} \exp\left(-\imath\frac{2\pi q_1 l_1}{N_1}\right)\exp\left(-\imath\frac{2\pi q_2 l_2}{N_2}\right) \tag{B.9a}$$

$$\tilde{\mathcal{Q}}_{\substack{r_1\\r_2}} = \frac{1}{N}\sum_{q_1=0}^{N_1-1}\sum_{q_2=0}^{N_2-1} \frac{\mu\lambda'_M}{1-(1-\mu)\tilde{\mathcal{D}}_{\substack{q_1\\q_2}}} \exp\left(\imath\frac{2\pi q_1 r_1}{N_1}\right)\exp\left(\imath\frac{2\pi q_2 r_2}{N_2}\right) \tag{B.9b}$$

We have

$$\begin{aligned}
\tilde{\mathcal{D}}_{\substack{q_1\\q_2}} &= d_{\text{self}} + \sum_{l_2=1}^{N_2-1} d_{\text{in}} \exp\left(-\imath\frac{2\pi q_2 l_2}{N_2}\right) + \sum_{l_1=1}^{N_1-1}\sum_{l_2=0}^{N_2-1} d_{\text{out}} \exp\left(-\imath\frac{2\pi q_1 l_1}{N_1}\right)\exp\left(-\imath\frac{2\pi q_2 l_2}{N_2}\right)\\
&= d_{\text{self}} + \left(\delta_{q_2}(N_2-1) + (1-\delta_{q_2})(-1)\right) d_{\text{in}} + \left(\delta_{q_1}(N_1-1) + (1-\delta_{q_1})(-1)\right)\left(\delta_{q_2}N_2\right) d_{\text{out}}\\
&= d_{\text{self}} + \left(\delta_{q_2}N_2 - 1\right) d_{\text{in}} + \left(\delta_{q_1}N_1 - 1\right)\delta_{q_2}N_2 d_{\text{out}}.
\end{aligned} \tag{B.10a}$$

Whether there is self-replacement or not, we have $N_1 = D$ and $N_2 = n$, and

$$\tilde{\mathcal{D}}_{\substack{0\\0}} = 1, \tag{B.11a}$$

$$\tilde{\mathcal{D}}_{\substack{q_1\\0}} = 1 - m - \frac{m}{d-1} \quad (q_1 \not\equiv 0 \pmod{N_1}), \tag{B.11b}$$

$$\tilde{\mathcal{D}}_{\substack{q_1\\q_2}} = d_{\text{self}} - d_{\text{in}} \quad (q_2 \not\equiv 0 \pmod{N_2}). \tag{B.11c}$$

So for $\tilde{\mathcal{Q}}$,

$$\begin{aligned}\tilde{\mathcal{Q}}_{\substack{r_1\\r_2}} = \frac{\mu\lambda'_M}{N}\Bigg[&\frac{1}{1-(1-\mu)\tilde{\mathcal{D}}_{\substack{0\\0}}} + \sum_{q_2=1}^{N_2-1}\frac{1}{1-(1-\mu)\tilde{\mathcal{D}}_{\substack{0\\q_2}}}\exp\left(-\imath\frac{2\pi q_2 r_2}{N_2}\right) + \sum_{q_1=1}^{N_1-1}\frac{1}{1-(1-\mu)\tilde{\mathcal{D}}_{\substack{q_1\\0}}}\exp\left(-\imath\frac{2\pi q_1 r_1}{N_1}\right)\\
&+\sum_{q_1=1}^{N_1-1}\sum_{q_2=1}^{N_2-1}\frac{1}{1-(1-\mu)\tilde{\mathcal{D}}_{\substack{q_1\\q_2}}}\exp\left(-\imath\frac{2\pi q_1 r_1}{N_1}\right)\exp\left(-\imath\frac{2\pi q_2 r_2}{N_2}\right)\Bigg]\\
= \frac{\mu\lambda'_M}{N}\Bigg[&\frac{1}{1-(1-\mu)} + \frac{1}{1-(1-\mu)(d_{\text{self}}-d_{\text{in}})}(\delta_{r_2}N_2-1) + \frac{1}{1-(1-\mu)(1-m-\frac{m}{d-1})}(\delta_{r_1}N_1-1)\\
&+\frac{1}{1-(1-\mu)(d_{\text{self}}-d_{\text{in}})}(\delta_{r_1}N_1-1)(\delta_{r_2}N_2-1)\Bigg]. \end{aligned} \tag{B.12a}$$

In particular,

$$\begin{aligned}\tilde{\mathcal{Q}}_{\substack{0\\0}} = \frac{\mu\lambda'_M}{N}\Bigg[&\frac{1}{\mu} + \frac{1}{1-(1-\mu)(d_{\text{self}}-d_{\text{in}})}(n-1) + \frac{1}{1-(1-\mu)(1-m-\frac{m}{d-1})}(D-1)\\
&+\frac{1}{1-(1-\mu)(d_{\text{self}}-d_{\text{in}})}(D-1)(n-1)\Bigg]\\
= 1.&\end{aligned} \tag{B.12b}$$

We find λ'_M using the above equation. When $r_1 = 0$, the two individuals are in the same deme. They are different when $r_2 \not\equiv 0$:

$$\begin{aligned}Q_{\text{in}} = \frac{\mu\lambda'_M}{N}\Bigg[&\frac{1}{\mu} + \frac{1}{1-(1-\mu)(d_{\text{self}}-d_{\text{in}})}(-1) + \frac{1}{1-(1-\mu)(1-m-\frac{m}{d-1})}(D-1)\\
&+\frac{1}{1-(1-\mu)(d_{\text{self}}-d_{\text{in}})}(D-1)(-1)\Bigg].\end{aligned} \tag{B.12c}$$

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

$$\begin{aligned}Q_{\text{out}} = \frac{\mu\lambda'_M}{N}\Bigg[&\frac{1}{\mu} + \frac{1}{1-(1-\mu)(d_{\text{self}}-d_{\text{in}})}(-1) + \frac{1}{1-(1-\mu)(1-m-\frac{m}{d-1})}(-1)\\
&+\frac{1}{1-(1-\mu)(d_{\text{self}}-d_{\text{in}})}\Bigg].\end{aligned} \tag{B.12d}$$

B.2 Wright-Fisher

$$
\begin{aligned}
\tilde{\mathcal{Q}}_{\substack{r_1\\r_2}} &= \frac{1}{N}\sum_{q_1=0}^{N_1-1}\sum_{q_2=0}^{N_2-1}\frac{\mu\lambda'_{WF}}{1-(1-\mu)^2(\tilde{\mathcal{D}}_{\substack{q_1\\q_2}})^2}\exp\left(-\imath\frac{2\pi q_1 r_1}{N_1}\right)\exp\left(-\imath\frac{2\pi q_2 r_2}{N_2}\right)\\
&= \frac{1}{N}\Bigg[\frac{\mu\lambda'_{WF}}{1-(1-\mu)^2(\tilde{\mathcal{D}}_{\substack{0\\0}})^2}+\sum_{q_2=1}^{N_2-1}\frac{\mu\lambda'_{WF}}{1-(1-\mu)^2(\tilde{\mathcal{D}}_{\substack{0\\q_2}})^2}\exp\left(-\imath\frac{2\pi q_2 r_2}{N_2}\right)\\
&\quad+\sum_{q_1=1}^{N_1-1}\frac{\mu\lambda'_{WF}}{1-(1-\mu)^2(\tilde{\mathcal{D}}_{\substack{q_1\\0}})^2}\exp\left(-\imath\frac{2\pi q_1 r_1}{N_1}\right)\\
&\quad+\sum_{q_1=1}^{N_1-1}\sum_{q_2=1}^{N_2-1}\frac{\mu\lambda'_{WF}}{1-(1-\mu)^2(\tilde{\mathcal{D}}_{\substack{q_1\\q_2}})^2}\exp\left(-\imath\frac{2\pi q_1 r_1}{N_1}\right)\exp\left(-\imath\frac{2\pi q_2 r_2}{N_2}\right)\Bigg] \qquad \text{(B.13)}\\
&= \frac{\mu\lambda'_{WF}}{N}\Bigg[\frac{1}{1-(1-\mu)^2}+\frac{1}{1-(1-\mu)^2(d_{\text{self}}-d_{\text{in}})^2}(\delta_{q_2}N_2-1)\\
&\quad+\frac{1}{1-(1-\mu)^2(1-m-\frac{m}{d-1})^2}(\delta_{q_1}N_1-1)\\
&\quad+\frac{1}{1-(1-\mu)^2(d_{\text{self}}-d_{\text{in}})^2}(\delta_{q_1}N_1-1)(\delta_{q_2}N_2-1)\Bigg]\\
&= \frac{\mu\lambda'_{WF}}{N}\Bigg[\frac{1}{1-(1-\mu)^2}+\frac{1}{1-(1-\mu)^2(d_{\text{self}}-d_{\text{in}})^2}(\delta_{q_2}N_2-1)\delta_{q_1}N_1\\
&\quad+\frac{1}{1-(1-\mu)^2(1-m-\frac{m}{d-1})^2}(\delta_{q_1}N_1-1)\Bigg]. \qquad \text{(B.14)}
\end{aligned}
$$

To find λ'_{WF}, we solve

$$1=\frac{\mu\lambda'_{WF}}{N}\left[\frac{1}{1-(1-\mu)^2}+\frac{1}{1-(1-\mu)^2(d_{\text{self}}-d_{\text{in}})^2}(N_2-1)N_1+\frac{1}{1-(1-\mu)^2(1-m-\frac{m}{d-1})^2}(N_1-1)\right]. \qquad \text{(B.15a)}$$

Then,

$$Q_{\text{in}}=\frac{\mu\lambda'_{WF}}{N}\left[\frac{1}{1-(1-\mu)^2}-\frac{1}{1-(1-\mu)^2(d_{\text{self}}-d_{\text{in}})^2}N_1+\frac{1}{1-(1-\mu)^2(1-m-\frac{m}{d-1})^2}(N_1-1)\right]. \qquad \text{(B.15b)}$$

and

$$Q_{\text{out}}=\frac{\mu\lambda'_{WF}}{N}\left[\frac{1}{1-(1-\mu)^2}-\frac{1}{1-(1-\mu)^2(1-m-\frac{m}{d-1})^2}\right]. \qquad \text{(B.15c)}$$