Mon titre

1 Introduction

smaller groups, smaller emigration probabilites, both leading to increased within group relatedness are more conducive to the evolution of altruistic behavior. Living next to your kin however also means 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.

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, $1 \le i \le N$. 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 ωb, while altruists pay a fecundity cost ωc. 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

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

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

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

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

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

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).

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

$$\partial_\omega \mathbb{E}\left[\overline{X}\right] = \mathsf{b}\left(\beta_{\mathrm{D}} - \beta_{\mathrm{I}}\right) - \mathsf{c}\left(\gamma_{\mathrm{D}} - \gamma_{\mathrm{I}}\right), \tag{10}$$

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.

3.2 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}:

$$Q_{ij} = \begin{cases} 1 & \text{when } i = j; \\ Q_{\mathrm{in}} & \text{when } i \neq j \text{ and both sites are in the same deme;} \\ Q_{\mathrm{out}} & \text{when sites } i \text{ and } j \text{ are in different demes.} \end{cases} \tag{11}$$

3.2.1 Moran updating

$$Q_{\text{in}}^{\text{M}} = \frac{(1-\mu)\big(m+\mu(d(1-m)-1)\big)}{(1-\mu)m(d\mu(n-1)+1)+(d-1)\mu(\mu(n-1)+1)}, \tag{12a}$$

$$Q_{\text{out}}^{\text{M}} = \frac{(1-\mu)m}{(1-\mu)m(d\mu(n-1)+1)+(d-1)\mu(\mu(n-1)+1)}. \tag{12b}$$

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

$$Q_{\text{in}}^{\text{WF}} = \frac{-d+M_1+M_2}{(n-1)d+M_1+M_2}, \tag{13a}$$

$$Q_{\text{out}}^{\text{WF}} = \frac{-\frac{1}{d-1}M_1+M2}{(n-1)d+M_1+M_2}, \tag{13b}$$

with

$$M_1 = \frac{d-1}{1-\frac{(1-\mu)^2(d(1-m)-1)^2}{(d-1)^2}}, \text{ and} \tag{13c}$$

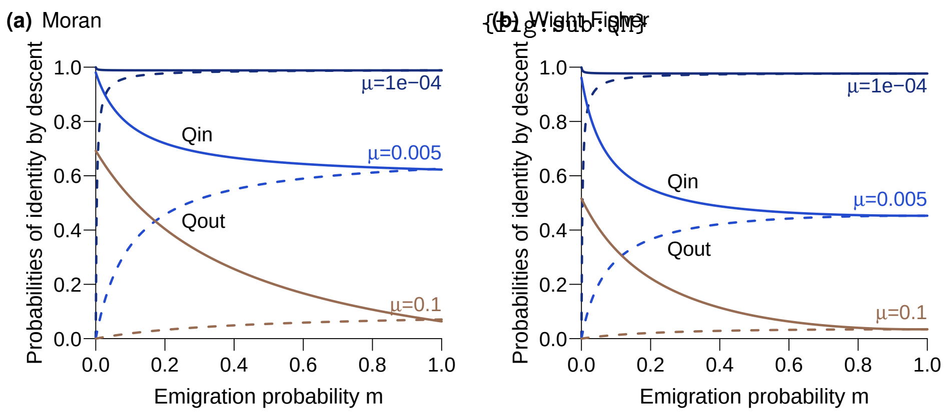
$$M_2 = \frac{1}{1-(1-\mu)^2}. \tag{13d}$$

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

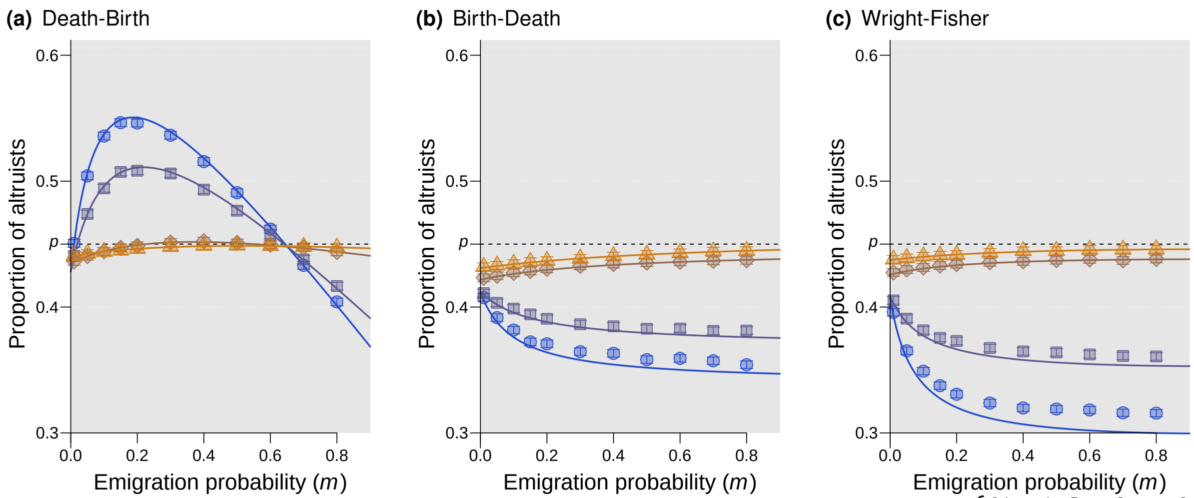
Also, because more sites (all of them, actually) are updated at each time step, Q_{in} is lower for the Wright-Fisher updating than for a Moran updating, under which only one site is updated at each time step (see figure 1).

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



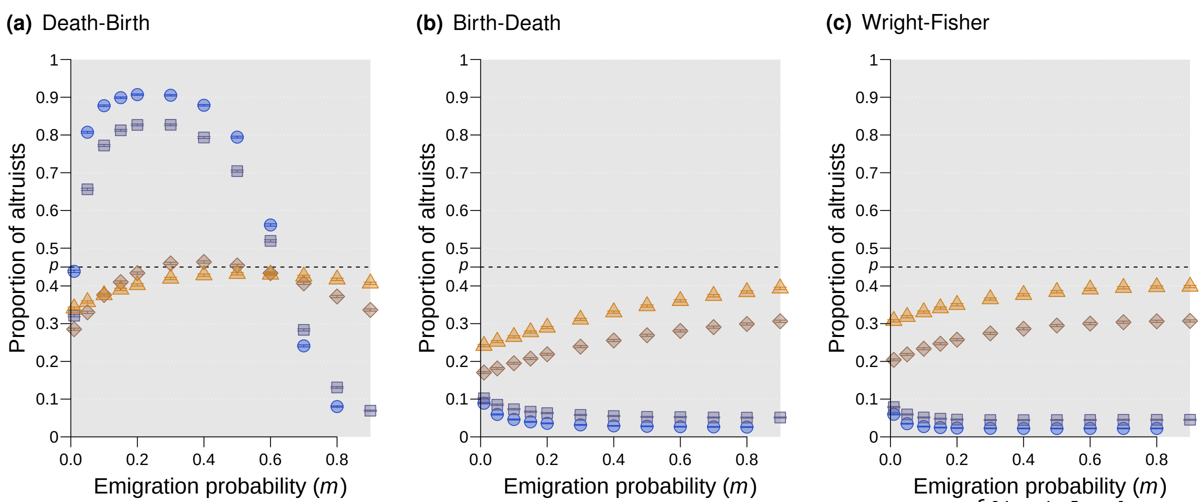
{fig:Q}

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.



{fig:island_weaksel}

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.



{fig:island_strongsel}

Figure 3: Strong selection

4 Figures

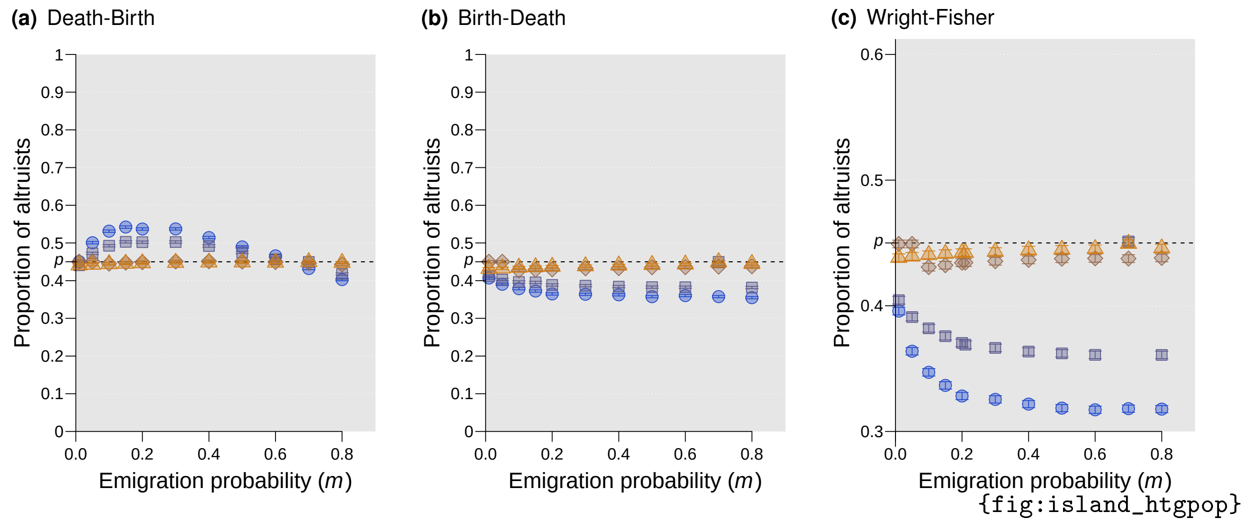


Figure 4: Weak selection, heterogeneous population

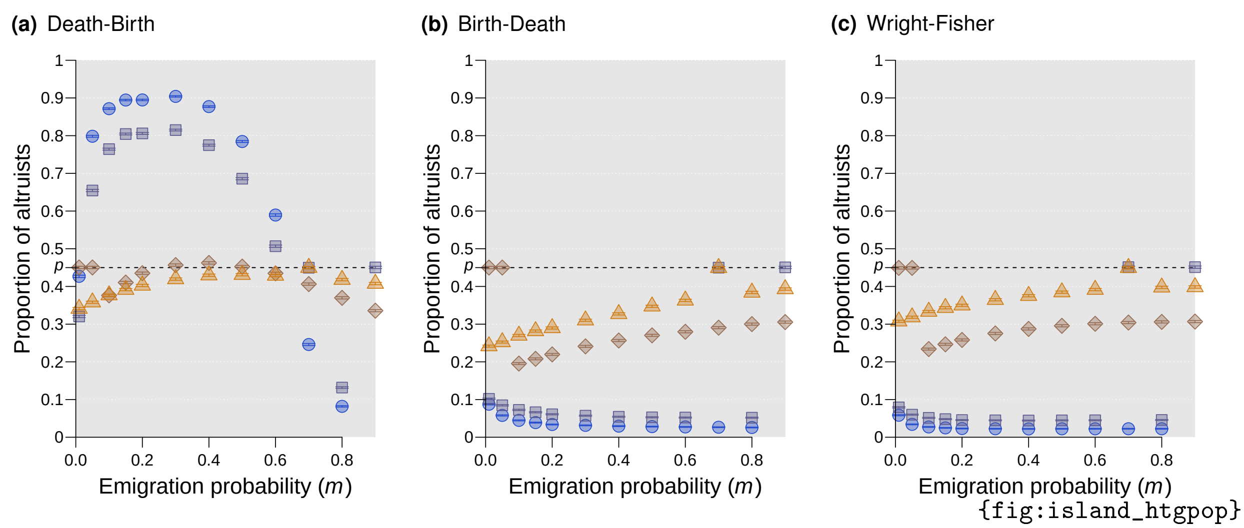


Figure 5: Strong selection, heterogeneous population

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

$$\begin{aligned} Y_{\text{self}} &:= Y_{i,i} && \text{(14a)} \\ Y_{\text{in}} &:= Y_{i,j}, \quad i \text{ and } j \neq i \text{ in the same deme;} && \text{(14b)} \\ Y_{\text{out}} &:= Y_{i,j}, \quad i \text{ and } j \text{ in different demes.} && \text{(14c)} \end{aligned}$$

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

$$\mathbb{E}\left[\overline{X}\right] = p + \delta \frac{p(1-p)}{\mu} \left[\mathsf{b}\,(\beta^D - \beta^I) - \mathsf{c}\,(\gamma^D - \gamma^I) \right]. \tag{15}$$

Moran, Birth-Death

$$\begin{aligned} \beta^D_{\text{BD}} &= \sum_{k,\ell=1}^{N} \frac{1-\mu}{N} e_{kl} Q_{lk} \\ &= \sum_{k=1}^{N} \frac{1-\mu}{N} \Big(e_{\text{self}} + (n-1) e_{\text{in}} Q_{\text{in}} + (N-n) e_{\text{out}} Q_{\text{out}} \Big) \\ &= (1-\mu) \Big(e_{\text{self}} + (n-1) e_{\text{in}} Q_{\text{in}} + (N-n) e_{\text{out}} Q_{\text{out}} \Big). \end{aligned} \tag{16a}$$

$$
\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} \Bigg[\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) \Bigg] \\
&\quad + \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}} \\
&\qquad + \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}} \\
&\qquad + \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] \\
&\quad - \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}} \\
&\quad + (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}} \\
&\quad + (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}} \\
&\quad - \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). \quad (16b)
\end{aligned}
$$

$$
\gamma^D_{\mathrm{BD}} = 1 - \mu. \tag{16c}
$$

$$
\begin{aligned}
\gamma^I_{\mathrm{BD}} &= \frac{1}{N} \sum_{j,k=1}^{N} \left(d_{kj} - \frac{\mu}{N} \right) Q_{jk} \\
&= \frac{1}{N} \sum_{j=1}^{N} \left[d_{\mathrm{self}} - \frac{\mu}{N} + (n-1) \left(d_{\mathrm{in}} - \frac{\mu}{N} \right) Q_{\mathrm{in}} + (N-n) \left(d_{\mathrm{out}} - \frac{\mu}{N} \right) Q_{\mathrm{out}} \right] \\
&= d_{\mathrm{self}} + (n-1) d_{\mathrm{in}} Q_{\mathrm{in}} + (N-n) d_{\mathrm{out}} Q_{\mathrm{out}} \\
&\quad - \frac{\mu}{N} \left(1 + (n-1) Q_{\mathrm{in}} + (N-n) Q_{\mathrm{out}} \right) \qquad (16d)
\end{aligned}
$$

Moran, Death-Birth

$$\begin{aligned}\beta_{\mathrm{DB}}^{D} &= \frac{1-\mu}{N}\sum_{j,k=1}^{N} Q_{jk}e_{jk} = \beta_{\mathrm{BD}}^{D}\\ &= (1-\mu)\Big(e_{\mathrm{self}} + (n-1)e_{\mathrm{in}}Q_{\mathrm{in}} + (N-n)e_{\mathrm{out}}Q_{\mathrm{out}}\Big).\end{aligned} \tag{17a}$$

$$\beta_{\mathrm{DB}}^{I} = \frac{1-\mu}{N}\sum_{i,j,k,l=1}^{N} d_{ji}d_{li}e_{kl}Q_{jk} \tag{17b}$$

Presented in the table in the appendix.

$$\gamma_{\mathrm{DB}}^{D} = 1-\mu = \gamma_{\mathrm{BD}}^{D}. \tag{17c}$$

$$\begin{aligned}\gamma_{\mathrm{DB}}^{I} &= (1-\mu)\sum_{i,j,k=1}^{N}\frac{d_{ji}d_{ki}}{N}Q_{jk}\\ &= \frac{1-\mu}{N}\sum_{j=1}^{N}\sum_{i=1}^{N}\Big(d_{ji}d_{ji} + \sum_{\substack{k\neq j\\ k\in G_j}} d_{ji}d_{ki}Q_{\mathrm{in}} + \sum_{k\notin G_j} d_{ji}d_{ki}Q_{\mathrm{out}}\Big)\\ &= \frac{1-\mu}{N}\sum_{j=1}^{N}\Big[d_{\mathrm{self}}d_{\mathrm{self}} + (n-1)d_{\mathrm{in}}d_{\mathrm{in}} + (N-n)d_{\mathrm{out}}d_{\mathrm{out}}\\ &\quad + (n-1)\Big(d_{\mathrm{self}}d_{\mathrm{in}} + d_{\mathrm{in}}d_{\mathrm{self}} + (n-2)d_{\mathrm{in}}d_{\mathrm{in}} + (N-n)d_{\mathrm{out}}d_{\mathrm{out}}\Big)Q_{\mathrm{in}}\\ &\quad + (N-n)\Big(d_{\mathrm{self}}d_{\mathrm{out}} + (n-1)d_{\mathrm{in}}d_{\mathrm{out}} + d_{\mathrm{out}}d_{\mathrm{self}} + (n-1)d_{\mathrm{out}}d_{\mathrm{in}} + (N-2n)d_{\mathrm{out}}d_{\mathrm{out}}\Big)Q_{\mathrm{out}}\Big]\end{aligned} \tag{17d}$$

Probabilities of identity by descent

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

Moran For $i =\neq j$,

$$Q_{ij} = \frac{1-\mu}{2}\sum_{k=1}^{N}\big(d_{kj}Q_{ki} + d_{ki}Q_{kj}\big). \tag{18a}$$

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

$$\begin{aligned}
Q_{\text{in}} &= \frac{1-\mu}{2}\Big((d_{\text{in}} + d_{\text{self}} Q_{\text{in}}) + (d_{\text{self}} Q_{\text{in}} + d_{\text{in}}) \\
&\qquad + (n-2)\,(d_{\text{in}} Q_{\text{in}} + d_{\text{in}} Q_{\text{in}}) + (N-n)\,(d_{\text{out}} Q_{\text{out}} + d_{\text{out}} Q_{\text{out}}) \Big) \\
&= (1-\mu)\Big(d_{\text{in}} + d_{\text{self}} Q_{\text{in}} + (n-2) d_{\text{in}} Q_{\text{in}} + (N-n) d_{\text{out}} Q_{\text{out}} \Big).
\end{aligned} \tag{18b}$$

And for $j \notin G_i$,

$$\begin{aligned}
Q_{\text{out}} &= \frac{1-\mu}{2}\Big((d_{\text{out}} + d_{\text{self}} Q_{\text{out}}) + (n-1)\,(d_{\text{out}} Q_{\text{in}} + d_{\text{in}} Q_{\text{out}}) \\
&\qquad + (d_{\text{self}} Q_{\text{out}} + d_{\text{out}}) + (n-1)\,(d_{\text{in}} Q_{\text{out}} + d_{\text{out}} Q_{\text{in}}) \\
&\qquad + (N-2n)\,(d_{\text{out}} Q_{\text{out}} + d_{\text{out}} Q_{\text{out}}) \Big) \\
&= (1-\mu)\Big(d_{\text{out}} + d_{\text{self}} Q_{\text{out}} + (n-1)\,(d_{\text{out}} Q_{\text{in}} + d_{\text{in}} Q_{\text{out}}) + (N-2n) d_{\text{out}} Q_{\text{out}} \Big)
\end{aligned} \tag{18c}$$

Wright-Fisher For $j \neq i$,

$$Q_{ij} = (1-\mu)^2 \sum_{k,l=1}^{N} d_{ki} d_{lj} Q_{kl}. \tag{19a}$$

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

$$
\begin{aligned}
Q_{\text{in}} = (1-\mu)^2 \Bigg[& \Big(d_{\text{self}} d_{\text{in}} + d_{\text{in}} d_{\text{self}} + (n-2) d_{\text{in}} d_{\text{in}} + (N-n) d_{\text{out}} d_{\text{out}} \Big) \\
& + \Big(d_{\text{self}} d_{\text{self}} + (n-2) d_{\text{self}} d_{\text{in}} \\
& \quad + (n-1) d_{\text{in}} d_{\text{in}} + (n-2) d_{\text{in}} d_{\text{self}} \\
& \quad + (n-2)(n-2) d_{\text{in}} d_{\text{in}} + (N-n)(n-1) d_{\text{out}} d_{\text{out}} \Big) Q_{\text{in}} \\
& + \Big((N-n) d_{\text{self}} d_{\text{out}} + (N-n)(n-1) d_{\text{in}} d_{\text{out}} \\
& \quad + (N-n) d_{\text{out}} d_{\text{self}} + (N-n)(n-1) d_{\text{out}} d_{\text{in}} \\
& \quad + (N-n)(N-2n) d_{\text{out}} d_{\text{out}} \Big) Q_{\text{out}} \Bigg] \\
= (1-\mu)^2 \Bigg[& \Big(2 d_{\text{in}} d_{\text{self}} + (n-2) d_{\text{in}}^2 + (N-n) d_{\text{out}}^2 \Big) \\
& + \Big(d_{\text{self}}^2 + 2(n-2) d_{\text{self}} d_{\text{in}} + (n^2 - 3n + 3) d_{\text{in}}^2 + + (N-n)(n-1) d_{\text{out}}^2 \Big) Q_{\text{in}} \\
& + \Big(2(N-n) d_{\text{self}} d_{\text{out}} + 2(N-n)(n-1) d_{\text{in}} d_{\text{out}} \\
& \quad + (N-n)(N-2n) d_{\text{out}} d_{\text{out}} \Big) Q_{\text{out}} \Bigg]
\end{aligned}
\tag{19b}
$$

And when $j \notin G_i$, we have

$$
\begin{aligned}
Q_{\text{out}} = (1-\mu)^2 \Bigg[& \Big(2 d_{\text{self}} d_{\text{out}} + 2(n-1) d_{\text{in}} d_{\text{out}} + (N-2n) d_{\text{out}}^2 \Big) \\
& + \Big(2(n-1) d_{\text{self}} d_{\text{out}} + 2(n-1)^2 d_{\text{in}} d_{\text{out}} + (N-2n)(n-1) d_{\text{out}}^2 \Big) Q_{\text{in}} \\
& + \Big(d_{\text{self}} d_{\text{self}} + (n-1) d_{\text{self}} d_{\text{in}} + (N-2n) d_{\text{self}} d_{\text{out}} \\
& \quad + (n-1) d_{\text{in}} d_{\text{self}} + (n-1)^2 d_{\text{in}}^2 + (n-1)(N-2n) d_{\text{in}} d_{\text{out}} \\
& \quad + (N-n) d_{\text{out}} d_{\text{self}} + (N-n)(n-1) d_{\text{out}} d_{\text{in}} + (N-n)(N-2n) d_{\text{out}} d_{\text{out}} \Big) Q_{\text{out}} \Bigg].
\end{aligned}
\tag{19c}
$$

PAS FINI

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

$$
\begin{aligned}
d_{\text{self}} = d_{\text{in}} &= \frac{1-m}{n}, && \text{(20a)}\\
d_{\text{out}} &= \frac{m}{N-n}. && \text{(20b)}
\end{aligned}
$$

Without self-replacement

$$
\begin{aligned}
d_{\text{self}} &= 0, && \text{(21a)}\\
d_{\text{in}} &= \frac{1-m}{n-1}, && \text{(21b)}\\
d_{\text{out}} &= \frac{m}{N-n}. && \text{(21c)}
\end{aligned}
$$

B IDB

B.1 Moran

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

$$
\tilde{\mathcal{D}}_{\substack{q_1\\q_2}} = \sum_{l_1=0}^{N_1-1}\sum_{l_2=0}^{N_2-1} \tilde{d}_{\substack{l_1\\l_2}} \exp\left(-\imath\frac{2\pi q_1 l_1}{N_1}\right)\exp\left(-\imath\frac{2\pi q_2 l_2}{N_2}\right) \tag{22a}
$$

$$
\tilde{\mathcal{Q}}_{\substack{r_1\\r_2}} = \frac{1}{N}\sum_{q_1=0}^{N_1-1}\sum_{q_2=0}^{N_2-1} \frac{\mu\lambda'_M}{1-(1-\mu)\tilde{\mathcal{D}}_{\substack{q_1\\q_2}}} \exp\left(\imath\frac{2\pi q_1 r_1}{N_1}\right)\exp\left(\imath\frac{2\pi q_2 r_2}{N_2}\right) \tag{22b}
$$

We have

$$
\begin{aligned}
\tilde{\mathcal{D}}_{\substack{q_1\\q_2}} &= d_{\text{self}} + \sum_{l_2=1}^{N_2-1} d_{\text{in}} \exp\left(-\imath\frac{2\pi q_2 l_2}{N_2}\right) + \sum_{l_1=1}^{N_1-1}\sum_{l_2=0}^{N_2-1} d_{\text{out}} \exp\left(-\imath\frac{2\pi q_1 l_1}{N_1}\right)\exp\left(-\imath\frac{2\pi q_2 l_2}{N_2}\right)\\
&= d_{\text{self}} + \left(\delta_{q_2}(N_2-1) + (1-\delta_{q_2})(-1)\right) d_{\text{in}} + \left(\delta_{q_1}(N_1-1) + (1-\delta_{q_1})(-1)\right)\left(\delta_{q_2} N_2\right) d_{\text{out}}\\
&= d_{\text{self}} + \left(\delta_{q_2} N_2 - 1\right) d_{\text{in}} + \left(\delta_{q_1} N_1 - 1\right)\delta_{q_2} N_2 d_{\text{out}}. && \text{(23a)}
\end{aligned}
$$

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

$$
\begin{aligned}
\tilde{\mathcal{D}}_{\substack{0\\0}} &= 1, && \text{(24a)}\\
\tilde{\mathcal{D}}_{\substack{q_1\\0}} &= 1 - m - \frac{m}{d-1} \quad (q_1 \not\equiv 0 \pmod{N_1}), && \text{(24b)}\\
\tilde{\mathcal{D}}_{\substack{q_1\\q_2}} &= d_{\text{self}} - d_{\text{in}} \quad (q_2 \not\equiv 0 \pmod{N_2}). && \text{(24c)}
\end{aligned}
$$

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

$$\begin{aligned}\tilde{\mathcal{Q}}_{\substack{r_1\\r_2}} &= \frac{\mu\lambda'_M}{N}\Bigg[\frac{1}{1-(1-\mu)\tilde{\mathcal{D}}_{\substack{0\\0}}} + \sum_{q_2=1}^{N_2-1}\frac{1}{1-(1-\mu)\tilde{\mathcal{D}}_{\substack{0\\q_2}}}\exp\left(-\imath\frac{2\pi q_2 r_2}{N_2}\right) + \sum_{q_1=1}^{N_1-1}\frac{1}{1-(1-\mu)\tilde{\mathcal{D}}_{\substack{q_1\\0}}}\exp\left(-\imath\frac{2\pi q_1 r_1}{N_1}\right)\\
&\quad + \sum_{q_1=1}^{N_1-1}\sum_{q_2=1}^{N_2-1}\frac{1}{1-(1-\mu)\tilde{\mathcal{D}}_{\substack{q_1\\q_2}}}\exp\left(-\imath\frac{2\pi q_1 r_1}{N_1}\right)\exp\left(-\imath\frac{2\pi q_2 r_2}{N_2}\right)\Bigg]\\
&= \frac{\mu\lambda'_M}{N}\Bigg[\frac{1}{1-(1-\mu)} + \frac{1}{1-(1-\mu)(d_{\text{self}}-d_{\text{in}})}(\delta_{r_2}N_2-1) + \frac{1}{1-(1-\mu)(1-m-\frac{m}{d-1})}(\delta_{r_1}N_1-1)\\
&\quad + \frac{1}{1-(1-\mu)(d_{\text{self}}-d_{\text{in}})}(\delta_{r_1}N_1-1)(\delta_{r_2}N_2-1)\Bigg]. \qquad (25a)\end{aligned}$$

In particular,

$$\begin{aligned}\tilde{\mathcal{Q}}_{\substack{0\\0}} &= \frac{\mu\lambda'_M}{N}\Bigg[\frac{1}{\mu} + \frac{1}{1-(1-\mu)(d_{\text{self}}-d_{\text{in}})}(n-1) + \frac{1}{1-(1-\mu)(1-m-\frac{m}{d-1})}(D-1)\\
&\quad + \frac{1}{1-(1-\mu)(d_{\text{self}}-d_{\text{in}})}(D-1)(n-1)\Bigg]\\
&= 1. \qquad (25b)\end{aligned}$$

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

$$\begin{aligned}Q_{\text{in}} &= \frac{\mu\lambda'_M}{N}\Bigg[\frac{1}{\mu} + \frac{1}{1-(1-\mu)(d_{\text{self}}-d_{\text{in}})}(-1) + \frac{1}{1-(1-\mu)(1-m-\frac{m}{d-1})}(D-1)\\
&\quad + \frac{1}{1-(1-\mu)(d_{\text{self}}-d_{\text{in}})}(D-1)(-1)\Bigg]. \qquad (25c)\end{aligned}$$

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

$$\begin{aligned}Q_{\text{out}} &= \frac{\mu\lambda'_M}{N}\Bigg[\frac{1}{\mu} + \frac{1}{1-(1-\mu)(d_{\text{self}}-d_{\text{in}})}(-1) + \frac{1}{1-(1-\mu)(1-m-\frac{m}{d-1})}(-1)\\
&\quad + \frac{1}{1-(1-\mu)(d_{\text{self}}-d_{\text{in}})}\Bigg]. \qquad (25d)\end{aligned}$$

B.2 Wright-Fisher

$$
\begin{aligned}
\tilde{\mathcal{Q}}_{\substack{r_1\\r_2}} &= \frac{1}{N}\sum_{q_1=0}^{N_1-1}\sum_{q_2=0}^{N_2-1}\frac{\mu\lambda'_{WF}}{1-(1-\mu)^2(\tilde{\mathcal{D}}_{\substack{q_1\\q_2}})^2}\exp\left(-\imath\frac{2\pi q_1 r_1}{N_1}\right)\exp\left(-\imath\frac{2\pi q_2 r_2}{N_2}\right)\\
&= \frac{1}{N}\Bigg[\frac{\mu\lambda'_{WF}}{1-(1-\mu)^2(\tilde{\mathcal{D}}_{\substack{0\\0}})^2}+\sum_{q_2=1}^{N_2-1}\frac{\mu\lambda'_{WF}}{1-(1-\mu)^2(\tilde{\mathcal{D}}_{\substack{0\\q_2}})^2}\exp\left(-\imath\frac{2\pi q_2 r_2}{N_2}\right)\\
&\quad+\sum_{q_1=1}^{N_1-1}\frac{\mu\lambda'_{WF}}{1-(1-\mu)^2(\tilde{\mathcal{D}}_{\substack{q_1\\0}})^2}\exp\left(-\imath\frac{2\pi q_1 r_1}{N_1}\right)\\
&\quad+\sum_{q_1=1}^{N_1-1}\sum_{q_2=1}^{N_2-1}\frac{\mu\lambda'_{WF}}{1-(1-\mu)^2(\tilde{\mathcal{D}}_{\substack{q_1\\q_2}})^2}\exp\left(-\imath\frac{2\pi q_1 r_1}{N_1}\right)\exp\left(-\imath\frac{2\pi q_2 r_2}{N_2}\right)\Bigg] \qquad (26)\\
&= \frac{\mu\lambda'_{WF}}{N}\Bigg[\frac{1}{1-(1-\mu)^2}+\frac{1}{1-(1-\mu)^2(d_{\text{self}}-d_{\text{in}})^2}(\delta_{q_2}N_2-1)\\
&\quad+\frac{1}{1-(1-\mu)^2(1-m-\frac{m}{d-1})^2}(\delta_{q_1}N_1-1)\\
&\quad+\frac{1}{1-(1-\mu)^2(d_{\text{self}}-d_{\text{in}})^2}(\delta_{q_1}N_1-1)(\delta_{q_2}N_2-1)\Bigg]\\
&= \frac{\mu\lambda'_{WF}}{N}\Bigg[\frac{1}{1-(1-\mu)^2}+\frac{1}{1-(1-\mu)^2(d_{\text{self}}-d_{\text{in}})^2}(\delta_{q_2}N_2-1)\delta_{q_1}N_1\\
&\quad+\frac{1}{1-(1-\mu)^2(1-m-\frac{m}{d-1})^2}(\delta_{q_1}N_1-1)\Bigg]. \qquad (27)
\end{aligned}
$$

To find λ'_{WF}, we solve

$$
1=\frac{\mu\lambda'_{WF}}{N}\left[\frac{1}{1-(1-\mu)^2}+\frac{1}{1-(1-\mu)^2(d_{\text{self}}-d_{\text{in}})^2}(N_2-1)N_1+\frac{1}{1-(1-\mu)^2(1-m-\frac{m}{d-1})^2}(N_1-1)\right]. \tag{28a}
$$

Then,

$$
Q_{\text{in}}=\frac{\mu\lambda'_{WF}}{N}\left[\frac{1}{1-(1-\mu)^2}-\frac{1}{1-(1-\mu)^2(d_{\text{self}}-d_{\text{in}})^2}N_1+\frac{1}{1-(1-\mu)^2(1-m-\frac{m}{d-1})^2}(N_1-1)\right]. \tag{28b}
$$

and

$$
Q_{\text{out}}=\frac{\mu\lambda'_{WF}}{N}\left[\frac{1}{1-(1-\mu)^2}-\frac{1}{1-(1-\mu)^2(1-m-\frac{m}{d-1})^2}\right]. \tag{28c}
$$