

Mon titre

# 1 Introduction

smaller groups, smaller emigration probabilities, 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 expliciter. 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  $\mu$  as a mutation probability. With probability  $\mu$ , 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  $\omega b$ , while altruists pay a fecundity cost  $\omega c$ . The parameter  $\omega$  scales the relative effect of social interactions on fecundity, and is assumed to be small ( $\omega \ll 1$ ). For instance, in a deme with  $k$  altruists, an altruist has a fecundity equal to  $1 + \omega((k - 1)b - c)$ , while a defector has a fecundity

equal to  $1 + \omega kb$ . Although these assumptions may seem restrictive, 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).

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

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

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

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

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  $\bar{X}(t) = \sum_{i=1}^N X_i(t)$ . 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?

$$D_i = \sum_{j=1}^N B_{ij} \quad (2)$$

holds for all sites  $i$ .

really needed?

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

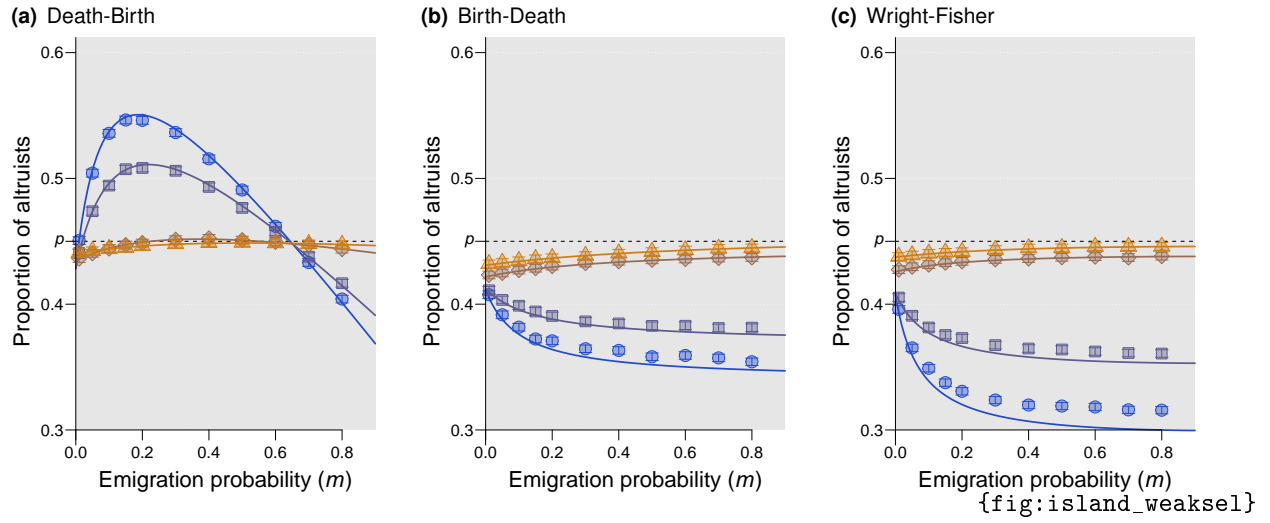
$$\mathbb{E}[\bar{X}(t+1)|\mathbf{X}(t)] = \frac{1}{N} \sum_{i=1}^N \left[ \sum_{j=1}^N B_{ij} (X_j(1-\mu) + \mu p) + (1-D_i)X_i \right]. \quad (3a) \quad \{\text{eq:conditionalchange}\}$$

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  $i$ .

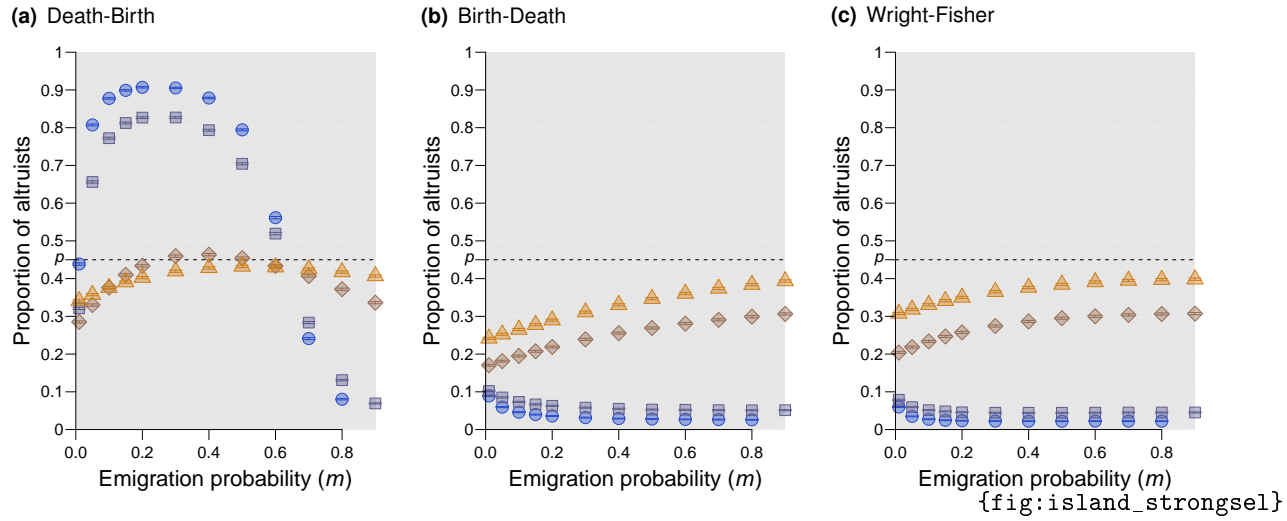
Given that there is no absorbing population state (a lost strategy can always be recreated by mutation), there is a stationary distribution of population states, and the expected frequency of altruists does not change anymore; we denote by  $\xi(\mathbf{X}, \omega, \mu)$  the probability that the population is in state  $\mathbf{X}$ , given the strength of selection  $\omega$  and the mutation probability  $\mu$ . Taking the expectation of eq. (3a) ( $\mathbb{E}[\bar{X}] = \sum_{\mathbf{X} \in \Omega} \bar{X} \xi(\mathbf{X}, \omega, \mu)$ ), we obtain, after reorganizing:

$$0 = \frac{1}{N} \sum_{\mathbf{X} \in \Omega} \sum_{i=1}^N \left[ \sum_{j=1}^N B_{ij} (X_j(1-\mu) + \mu p) - D_i X_i \right] \xi(\mathbf{X}, \omega, \mu). \quad (4) \quad \{\text{eq:statdist}\}$$

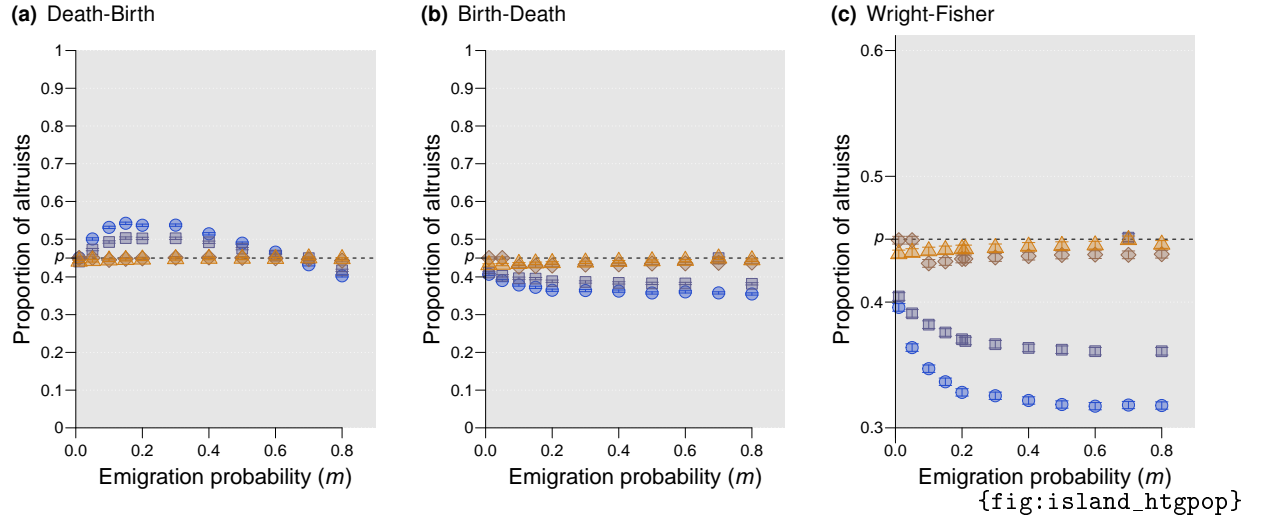
Now, we use the assumption of weak selection ( $\omega \ll 1$ )



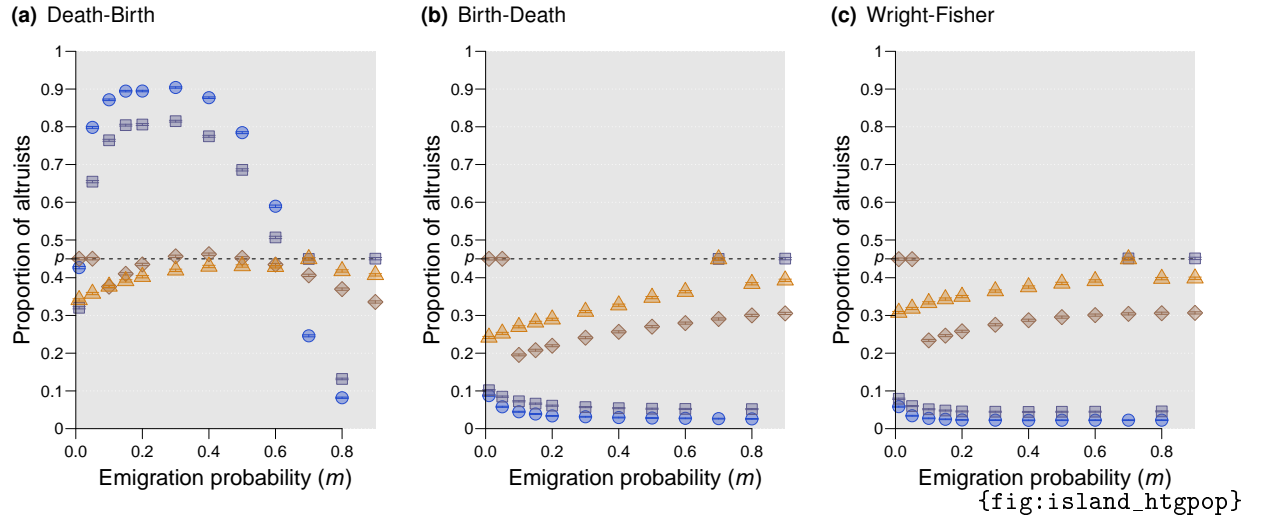
**Figure 1:** Weak selection. Parameters:  $\omega = 0.005$ ,  $b = 15$ ,  $c = 1$ , **ndemes**, **size**, **nreps**. NOTE simulations running with 0.005 for  $\mu$  and with 0.8 for mig.



**Figure 2:** Strong selection



**Figure 3:** Weak selection, heterogeneous population



**Figure 4:** Strong selection, heterogeneous population

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

$$Y_{\text{self}} := Y_{i,i} \quad (5a)$$

$$Y_{\text{in}} := Y_{i,j}, \quad i \text{ and } j \neq i \text{ in the same deme}; \quad (5b)$$

$$Y_{\text{out}} := Y_{i,j}, \quad i \text{ and } j \text{ in different demes.} \quad (5c)$$

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

$$\mathbb{E}[\bar{X}] = p + \delta \frac{p(1-p)}{\mu} [b(\beta^D - \beta^I) - c(\gamma^D - \gamma^I)]. \quad (6)$$

### Moran, Birth-Death

$$\begin{aligned} \beta_{\text{BD}}^D &= \sum_{k,\ell=1}^N \frac{1-\mu}{N} e_{k\ell} Q_{\ell k} \\ &= \sum_{k=1}^N \frac{1-\mu}{N} (e_{\text{self}} + (n-1)e_{\text{in}}Q_{\text{in}} + (N-n)e_{\text{out}}Q_{\text{out}}) \\ &= (1-\mu) (e_{\text{self}} + (n-1)e_{\text{in}}Q_{\text{in}} + (N-n)e_{\text{out}}Q_{\text{out}}). \end{aligned} \quad (7a)$$

$$\begin{aligned}
\beta_{\text{BD}}^I &= \sum_{j,k,l=1}^N \left( \frac{d_{lj}}{N} - \frac{\mu}{N^2} \right) e_{kl} Q_{jk} \\
&= \frac{1}{N} \sum_{j=1}^N \left[ \left( \sum_{l=1}^N d_{lj} e_{jl} \right) + \sum_{\substack{k \in G_j \\ k \neq j}} \left( \sum_{l=1}^N d_{lj} e_{kl} Q_{\text{in}} Q_{\text{in}} \right) + \sum_{k \notin G_j} \sum_{l=1}^N d_{lj} (e_{kl} Q_{\text{out}} Q_{\text{out}}) \right] \\
&\quad + \frac{\mu}{N^2} \sum_{j=1}^N \left( \sum_{l=1}^N e_{kl} \right) \left( \sum_{k=1}^N Q_{jk} \right) \\
&= \frac{1}{N} \sum_{j=1}^N \left[ d_{\text{self}} e_{\text{self}} + (n-1) d_{\text{in}} e_{\text{in}} + (N-n) d_{\text{out}} e_{\text{out}} \right. \\
&\quad + \sum_{\substack{k \in G_j \\ k \neq j}} (d_{\text{in}} e_{\text{self}} + d_{\text{self}} e_{\text{in}} + (n-2) d_{\text{in}} e_{\text{in}} + (N-n) d_{\text{out}} e_{\text{out}}) Q_{\text{in}} \\
&\quad + \sum_{k \notin G_j} (d_{\text{self}} e_{\text{out}} + (n-1) d_{\text{in}} e_{\text{out}} + d_{\text{out}} e_{\text{self}} + (n-1) d_{\text{out}} e_{\text{in}} + (N-2n) d_{\text{out}} e_{\text{out}}) Q_{\text{out}} \left. \right] \\
&\quad - \frac{\mu}{N} (1 + (n-1) Q_{\text{in}} + (N-n) Q_{\text{out}}) (e_{\text{self}} + (n-1) e_{\text{in}} + (N-n) e_{\text{out}}) \\
&= d_{\text{self}} e_{\text{self}} + (n-1) d_{\text{in}} e_{\text{in}} + (N-n) d_{\text{out}} e_{\text{out}} \\
&\quad + (n-1) (d_{\text{in}} e_{\text{self}} + d_{\text{self}} e_{\text{in}} + (n-2) d_{\text{in}} e_{\text{in}} + (N-n) d_{\text{out}} e_{\text{out}}) Q_{\text{in}} \\
&\quad + (N-n) (d_{\text{self}} e_{\text{out}} + (n-1) d_{\text{in}} e_{\text{out}} + d_{\text{out}} e_{\text{self}} + (n-1) d_{\text{out}} e_{\text{in}} + (N-2n) d_{\text{out}} e_{\text{out}}) Q_{\text{out}} \\
&\quad - \frac{\mu}{N} (1 + (n-1) Q_{\text{in}} + (N-n) Q_{\text{out}}) (e_{\text{self}} + (n-1) e_{\text{in}} + (N-n) e_{\text{out}}). \quad (7b)
\end{aligned}$$

$$\gamma_{\text{BD}}^D = 1 - \mu. \quad (7c)$$

$$\begin{aligned}
\gamma_{\text{BD}}^I &= \frac{1}{N} \sum_{j,k=1}^N \left( d_{kj} - \frac{\mu}{N} \right) Q_{jk} \\
&= \frac{1}{N} \sum_{j=1}^N \left[ d_{\text{self}} - \frac{\mu}{N} + (n-1) \left( d_{\text{in}} - \frac{\mu}{N} \right) Q_{\text{in}} + (N-n) \left( d_{\text{out}} - \frac{\mu}{N} \right) Q_{\text{out}} \right] \\
&= d_{\text{self}} + (n-1) d_{\text{in}} Q_{\text{in}} + (N-n) d_{\text{out}} Q_{\text{out}} \\
&\quad - \frac{\mu}{N} (1 + (n-1) Q_{\text{in}} + (N-n) Q_{\text{out}}) \quad (7d)
\end{aligned}$$



### Moran, Death-Birth

$$\begin{aligned}\beta_{\text{DB}}^D &= \frac{1-\mu}{N} \sum_{j,k=1}^N Q_{jk} e_{jk} = \beta_{\text{BD}}^D \\ &= (1-\mu) \left( e_{\text{self}} + (n-1) e_{\text{in}} Q_{\text{in}} + (N-n) e_{\text{out}} Q_{\text{out}} \right).\end{aligned}\quad (8a)$$

$$\beta_{\text{DB}}^I = \frac{1-\mu}{N} \sum_{i,j,k,l=1}^N d_{ji} d_{li} e_{kl} Q_{jk} \quad (8b)$$

Presented in the table in the appendix.

$$\gamma_{\text{DB}}^D = 1 - \mu = \gamma_{\text{BD}}^D. \quad (8c)$$

$$\begin{aligned}\gamma_{\text{DB}}^I &= (1-\mu) \sum_{i,j,k=1}^N \frac{d_{ji} d_{ki}}{N} Q_{jk} \\ &= \frac{1-\mu}{N} \sum_{j=1}^N \sum_{i=1}^N \left( d_{ji} d_{ji} + \sum_{\substack{k \neq j \\ k \in G_j}} d_{ji} d_{ki} Q_{\text{in}} + \sum_{k \notin G_j} d_{ji} d_{ki} Q_{\text{out}} \right) \\ &= \frac{1-\mu}{N} \sum_{j=1}^N \left[ d_{\text{self}} d_{\text{self}} + (n-1) d_{\text{in}} d_{\text{in}} + (N-n) d_{\text{out}} d_{\text{out}} \right. \\ &\quad \left. + (n-1) \left( d_{\text{self}} d_{\text{in}} + d_{\text{in}} d_{\text{self}} + (n-2) d_{\text{in}} d_{\text{in}} + (N-n) d_{\text{out}} d_{\text{out}} \right) Q_{\text{in}} \right. \\ &\quad \left. + (N-n) \left( d_{\text{self}} d_{\text{out}} + (n-1) d_{\text{in}} d_{\text{out}} + d_{\text{out}} d_{\text{self}} + (n-1) d_{\text{out}} d_{\text{in}} + (N-2n) d_{\text{out}} d_{\text{out}} \right) Q_{\text{out}} \right] \end{aligned} \quad (8d)$$

### Probabilities of identity by descent

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

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

$$Q_{ij} = \frac{1-\mu}{2} \sum_{k=1}^N (d_{kj} Q_{ki} + d_{ki} Q_{kj}). \quad (9a)$$

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

$$\begin{aligned}
Q_{\text{in}} &= \frac{1-\mu}{2} \left( (d_{\text{in}} + d_{\text{self}} Q_{\text{in}}) + (d_{\text{self}} Q_{\text{in}} + d_{\text{in}}) \right. \\
&\quad \left. + (n-2) (d_{\text{in}} Q_{\text{in}} + d_{\text{in}} Q_{\text{in}}) + (N-n) (d_{\text{out}} Q_{\text{out}} + d_{\text{out}} Q_{\text{out}}) \right) \\
&= (1-\mu) \left( d_{\text{in}} + d_{\text{self}} Q_{\text{in}} + (n-2) d_{\text{in}} Q_{\text{in}} + (N-n) d_{\text{out}} Q_{\text{out}} \right). \tag{9b}
\end{aligned}$$

And for  $j \notin G_i$ ,

$$\begin{aligned}
Q_{\text{out}} &= \frac{1-\mu}{2} \left( (d_{\text{out}} + d_{\text{self}} Q_{\text{out}}) + (n-1) (d_{\text{out}} Q_{\text{in}} + d_{\text{in}} Q_{\text{out}}) \right. \\
&\quad \left. + (d_{\text{self}} Q_{\text{out}} + d_{\text{out}}) + (n-1) (d_{\text{in}} Q_{\text{out}} + d_{\text{out}} Q_{\text{in}}) \right. \\
&\quad \left. + (N-2n) (d_{\text{out}} Q_{\text{out}} + d_{\text{out}} Q_{\text{out}}) \right) \\
&= (1-\mu) \left( d_{\text{out}} + d_{\text{self}} Q_{\text{out}} + (n-1) (d_{\text{out}} Q_{\text{in}} + d_{\text{in}} Q_{\text{out}}) + (N-2n) d_{\text{out}} Q_{\text{out}} \right) \tag{9c}
\end{aligned}$$

**Wright-Fisher** For  $j \neq i$ ,

$$Q_{ij} = (1-\mu)^2 \sum_{k,l=1}^N d_{ki} d_{lj} Q_{kl}. \tag{10a}$$

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

$$\begin{aligned}
Q_{\text{in}} &= (1 - \mu)^2 \left[ \left( d_{\text{self}} d_{\text{in}} + d_{\text{in}} d_{\text{self}} + (n - 2) d_{\text{in}} d_{\text{in}} + (N - n) d_{\text{out}} d_{\text{out}} \right) \right. \\
&\quad + \left( d_{\text{self}} d_{\text{self}} + (n - 2) d_{\text{self}} d_{\text{in}} \right. \\
&\quad \quad + (n - 1) d_{\text{in}} d_{\text{in}} + (n - 2) d_{\text{in}} d_{\text{self}} \\
&\quad \quad \left. + (n - 2)(n - 2) d_{\text{in}} d_{\text{in}} + (N - n)(n - 1) d_{\text{out}} d_{\text{out}} \right) Q_{\text{in}} \\
&\quad + \left( (N - n) d_{\text{self}} d_{\text{out}} + (N - n)(n - 1) d_{\text{in}} d_{\text{out}} \right. \\
&\quad \quad + (N - n) d_{\text{out}} d_{\text{self}} + (N - n)(n - 1) d_{\text{out}} d_{\text{in}} \\
&\quad \quad \left. + (N - n)(N - 2n) d_{\text{out}} d_{\text{out}} \right) Q_{\text{out}} \Big] \\
&= (1 - \mu)^2 \left[ \left( 2 d_{\text{in}} d_{\text{self}} + (n - 2) d_{\text{in}}^2 + (N - n) d_{\text{out}}^2 \right) \right. \\
&\quad + \left( d_{\text{self}}^2 + 2(n - 2) d_{\text{self}} d_{\text{in}} + (n^2 - 3n + 3) d_{\text{in}}^2 + (N - n)(n - 1) d_{\text{out}}^2 \right) Q_{\text{in}} \\
&\quad + \left( 2(N - n) d_{\text{self}} d_{\text{out}} + 2(N - n)(n - 1) d_{\text{in}} d_{\text{out}} \right. \\
&\quad \quad \left. + (N - n)(N - 2n) d_{\text{out}} d_{\text{out}} \right) Q_{\text{out}} \Big] \tag{10b}
\end{aligned}$$

And when  $j \notin G_i$ , we have

$$\begin{aligned}
Q_{\text{out}} &= (1 - \mu)^2 \left[ \left( 2 d_{\text{self}} d_{\text{out}} + 2(n - 1) d_{\text{in}} d_{\text{out}} + (N - 2n) d_{\text{out}}^2 \right) \right. \\
&\quad + \left( 2(n - 1) d_{\text{self}} d_{\text{out}} + 2(n - 1)^2 d_{\text{in}} d_{\text{out}} + (N - 2n)(n - 1) d_{\text{out}}^2 \right) Q_{\text{in}} \\
&\quad + \left( d_{\text{self}} d_{\text{self}} + (n - 1) d_{\text{self}} d_{\text{in}} + (N - 2n) d_{\text{self}} d_{\text{out}} \right. \\
&\quad \quad + (n - 1) d_{\text{in}} d_{\text{self}} + (n - 1)^2 d_{\text{in}}^2 + (n - 1)(N - 2n) d_{\text{in}} d_{\text{out}} \\
&\quad \quad \left. + (N - n) d_{\text{out}} d_{\text{self}} + (N - n)(n - 1) d_{\text{out}} d_{\text{in}} + (N - n)(N - 2n) d_{\text{out}} d_{\text{out}} \right) Q_{\text{out}} \Big]. \tag{10c}
\end{aligned}$$

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

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

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

## A Island model

With self replacement

$$d_{\text{self}} = d_{\text{in}} = \frac{1-m}{n}, \quad (11a)$$

$$d_{\text{out}} = \frac{m}{N-n}. \quad (11b)$$

Without self-replacement

$$d_{\text{self}} = 0, \quad (12a)$$

$$d_{\text{in}} = \frac{1-m}{n-1}, \quad (12b)$$

$$d_{\text{out}} = \frac{m}{N-n}. \quad (12c)$$

## B IDB

### B.1 Moran

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

$$\tilde{\mathcal{D}}_{q_1} = \sum_{q_2} \sum_{l_1=0}^{N_1-1} \sum_{l_2=0}^{N_2-1} \tilde{d}_{l_1} \exp\left(-i \frac{2\pi q_1 l_1}{N_1}\right) \exp\left(-i \frac{2\pi q_2 l_2}{N_2}\right) \quad (13a)$$

$$\tilde{\mathcal{Q}}_{r_1} = \frac{1}{N} \sum_{q_1=0}^{N_1-1} \sum_{q_2=0}^{N_2-1} \frac{\mu \lambda'_M}{1 - (1-\mu) \tilde{\mathcal{D}}_{q_1}} \exp\left(i \frac{2\pi q_1 r_1}{N_1}\right) \exp\left(i \frac{2\pi q_2 r_2}{N_2}\right) \quad (13b)$$

We have

$$\begin{aligned} \tilde{\mathcal{D}}_{q_1} &= d_{\text{self}} + \sum_{l_2=1}^{N_2-1} d_{\text{in}} \exp\left(-i \frac{2\pi q_2 l_2}{N_2}\right) + \sum_{l_1=1}^{N_1-1} \sum_{l_2=0}^{N_2-1} d_{\text{out}} \exp\left(-i \frac{2\pi q_1 l_1}{N_1}\right) \exp\left(-i \frac{2\pi q_2 l_2}{N_2}\right) \\ &= d_{\text{self}} + (\delta_{q_2}(N_2-1) + (1-\delta_{q_2})(-1)) d_{\text{in}} + (\delta_{q_1}(N_1-1) + (1-\delta_{q_1})(-1)) (\delta_{q_2} N_2) d_{\text{out}} \\ &= d_{\text{self}} + (\delta_{q_2} N_2 - 1) d_{\text{in}} + (\delta_{q_1} N_1 - 1) \delta_{q_2} N_2 d_{\text{out}}. \end{aligned} \quad (14a)$$

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

$$\tilde{\mathcal{D}}_0 = 1, \quad (15a)$$

$$\tilde{\mathcal{D}}_{q_1} = 1 - m - \frac{m}{d-1} \quad (q_1 \not\equiv 0 \pmod{N_1}), \quad (15b)$$

$$\tilde{\mathcal{D}}_{q_1} = d_{\text{self}} - d_{\text{in}} \quad (q_2 \not\equiv 0 \pmod{N_2}). \quad (15c)$$



So for  $\tilde{Q}$ ,

$$\begin{aligned}
\tilde{Q}_{r_1, r_2} &= \frac{\mu \lambda'_M}{N} \left[ \frac{1}{1 - (1 - \mu) \tilde{D}_0} + \sum_{q_2=1}^{N_2-1} \frac{1}{1 - (1 - \mu) \tilde{D}_{q_2}} \exp\left(-i \frac{2\pi q_2 r_2}{N_2}\right) + \sum_{q_1=1}^{N_1-1} \frac{1}{1 - (1 - \mu) \tilde{D}_{q_1}} \exp\left(-i \frac{2\pi q_1 r_1}{N_1}\right) \right. \\
&\quad \left. + \sum_{q_1=1}^{N_1-1} \sum_{q_2=1}^{N_2-1} \frac{1}{1 - (1 - \mu) \tilde{D}_{q_1, q_2}} \exp\left(-i \frac{2\pi q_1 r_1}{N_1}\right) \exp\left(-i \frac{2\pi q_2 r_2}{N_2}\right) \right] \\
&= \frac{\mu \lambda'_M}{N} \left[ \frac{1}{1 - (1 - \mu)} + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})} (\delta_{r_2} N_2 - 1) + \frac{1}{1 - (1 - \mu)(1 - m - \frac{m}{d-1})} (\delta_{r_1} N_1 - 1) \right. \\
&\quad \left. + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})} (\delta_{r_1} N_1 - 1)(\delta_{r_2} N_2 - 1) \right]. \tag{16a}
\end{aligned}$$

In particular,

$$\begin{aligned}
\tilde{Q}_0 &= \frac{\mu \lambda'_M}{N} \left[ \frac{1}{\mu} + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})} (n - 1) + \frac{1}{1 - (1 - \mu)(1 - m - \frac{m}{d-1})} (D - 1) \right. \\
&\quad \left. + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})} (D - 1)(n - 1) \right] \\
&= 1. \tag{16b}
\end{aligned}$$

We find  $\lambda'_M$  using the above equation. When  $r_1 = 0$ , the two individuals are in the same deme. They are different when  $r_2 \neq 0$ :

$$\begin{aligned}
Q_{\text{in}} &= \frac{\mu \lambda'_M}{N} \left[ \frac{1}{\mu} + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})} (-1) + \frac{1}{1 - (1 - \mu)(1 - m - \frac{m}{d-1})} (D - 1) \right. \\
&\quad \left. + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})} (D - 1)(-1) \right]. \tag{16c}
\end{aligned}$$

And when  $r_1 \neq 0$ , the two individuals are in different demes:

$$\begin{aligned}
Q_{\text{out}} &= \frac{\mu \lambda'_M}{N} \left[ \frac{1}{\mu} + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})} (-1) + \frac{1}{1 - (1 - \mu)(1 - m - \frac{m}{d-1})} (-1) \right. \\
&\quad \left. + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})} \right]. \tag{16d}
\end{aligned}$$

## B.2 Wright-Fisher

$$\begin{aligned}
\tilde{Q}_{r_1 r_2} &= \frac{1}{N} \sum_{q_1=0}^{N_1-1} \sum_{q_2=0}^{N_2-1} \frac{\mu \lambda'_{WF}}{1 - (1-\mu)^2 (\tilde{\mathcal{D}}_{q_1}^2)_{q_2}^2} \exp\left(-i \frac{2\pi q_1 r_1}{N_1}\right) \exp\left(-i \frac{2\pi q_2 r_2}{N_2}\right) \\
&= \frac{1}{N} \left[ \frac{\mu \lambda'_{WF}}{1 - (1-\mu)^2 (\tilde{\mathcal{D}}_0^2)} + \sum_{q_2=1}^{N_2-1} \frac{\mu \lambda'_{WF}}{1 - (1-\mu)^2 (\tilde{\mathcal{D}}_0^2)_{q_2}^2} \exp\left(-i \frac{2\pi q_2 r_2}{N_2}\right) \right. \\
&\quad + \sum_{q_1=1}^{N_1-1} \frac{\mu \lambda'_{WF}}{1 - (1-\mu)^2 (\tilde{\mathcal{D}}_0^2)_{q_1}^2} \exp\left(-i \frac{2\pi q_1 r_1}{N_1}\right) \\
&\quad \left. + \sum_{q_1=1}^{N_1-1} \sum_{q_2=1}^{N_2-1} \frac{\mu \lambda'_{WF}}{1 - (1-\mu)^2 (\tilde{\mathcal{D}}_{q_1}^2)_{q_2}^2} \exp\left(-i \frac{2\pi q_1 r_1}{N_1}\right) \exp\left(-i \frac{2\pi q_2 r_2}{N_2}\right) \right] \quad (17)
\end{aligned}$$

$$\begin{aligned}
&= \frac{\mu \lambda'_{WF}}{N} \left[ \frac{1}{1 - (1-\mu)^2} + \frac{1}{1 - (1-\mu)^2 (d_{\text{self}} - d_{\text{in}})^2} (\delta_{q_2} N_2 - 1) \right. \\
&\quad + \frac{1}{1 - (1-\mu)^2 (1 - m - \frac{m}{d-1})^2} (\delta_{q_1} N_1 - 1) \\
&\quad \left. + \frac{1}{1 - (1-\mu)^2 (d_{\text{self}} - d_{\text{in}})^2} (\delta_{q_1} N_1 - 1) (\delta_{q_2} N_2 - 1) \right] \\
&= \frac{\mu \lambda'_{WF}}{N} \left[ \frac{1}{1 - (1-\mu)^2} + \frac{1}{1 - (1-\mu)^2 (d_{\text{self}} - d_{\text{in}})^2} (\delta_{q_2} N_2 - 1) \delta_{q_1} N_1 \right. \\
&\quad \left. + \frac{1}{1 - (1-\mu)^2 (1 - m - \frac{m}{d-1})^2} (\delta_{q_1} N_1 - 1) \right]. \quad (18)
\end{aligned}$$

To find  $\lambda'_{WF}$ , we solve

$$1 = \frac{\mu \lambda'_{WF}}{N} \left[ \frac{1}{1 - (1-\mu)^2} + \frac{1}{1 - (1-\mu)^2 (d_{\text{self}} - d_{\text{in}})^2} (N_2 - 1) N_1 + \frac{1}{1 - (1-\mu)^2 (1 - m - \frac{m}{d-1})^2} (N_1 - 1) \right]. \quad (19a)$$

Then,

$$Q_{\text{in}} = \frac{\mu \lambda'_{WF}}{N} \left[ \frac{1}{1 - (1-\mu)^2} - \frac{1}{1 - (1-\mu)^2 (d_{\text{self}} - d_{\text{in}})^2} N_1 + \frac{1}{1 - (1-\mu)^2 (1 - m - \frac{m}{d-1})^2} (N_1 - 1) \right]. \quad (19b)$$

and

$$Q_{\text{out}} = \frac{\mu \lambda'_{WF}}{N} \left[ \frac{1}{1 - (1-\mu)^2} - \frac{1}{1 - (1-\mu)^2 (1 - m - \frac{m}{d-1})^2} \right]. \quad (19c)$$