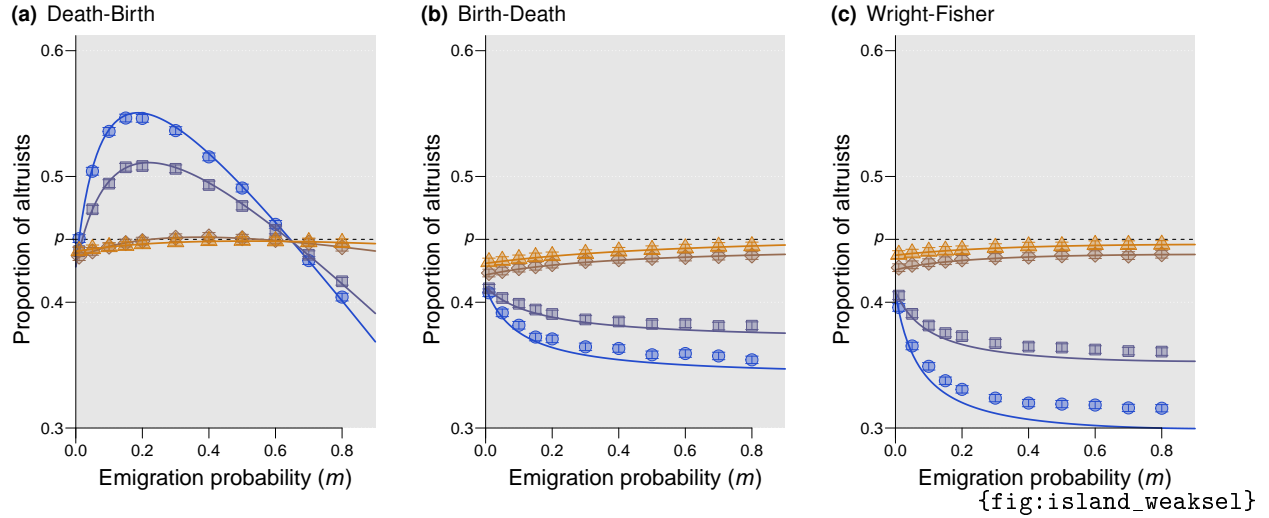


Mon titre

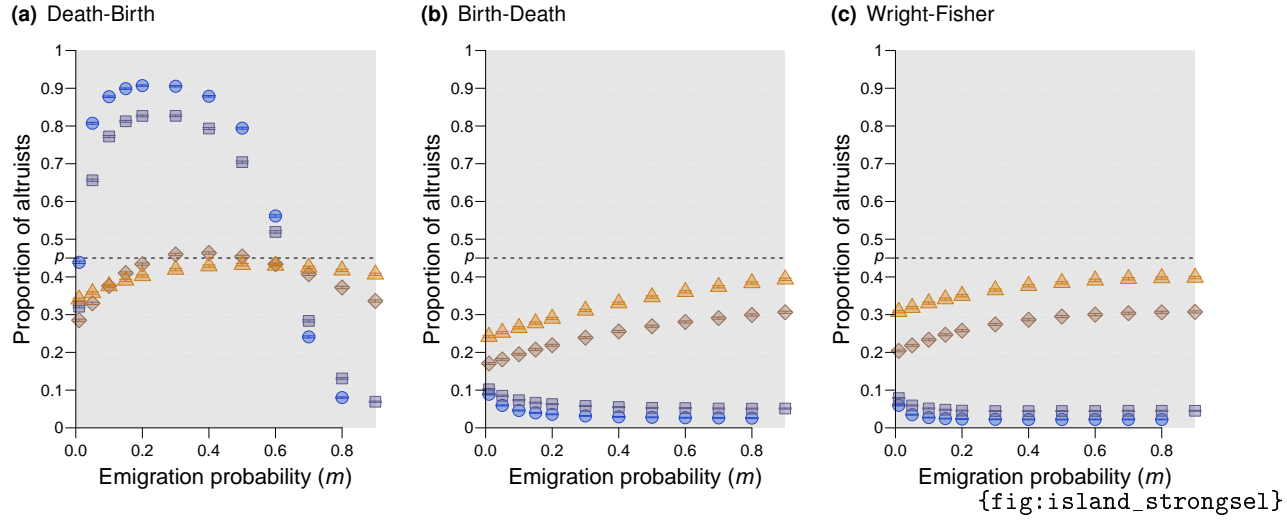


**Figure 1:** Weak selection. Parameters:  $\omega = 0.005$ ,  $b = 15$ ,  $c = 1$ , **ndemes**, **size**, **nreps**. NOTE simulations running with 0.005 for  $\mu$  and with 0.8 for mig.

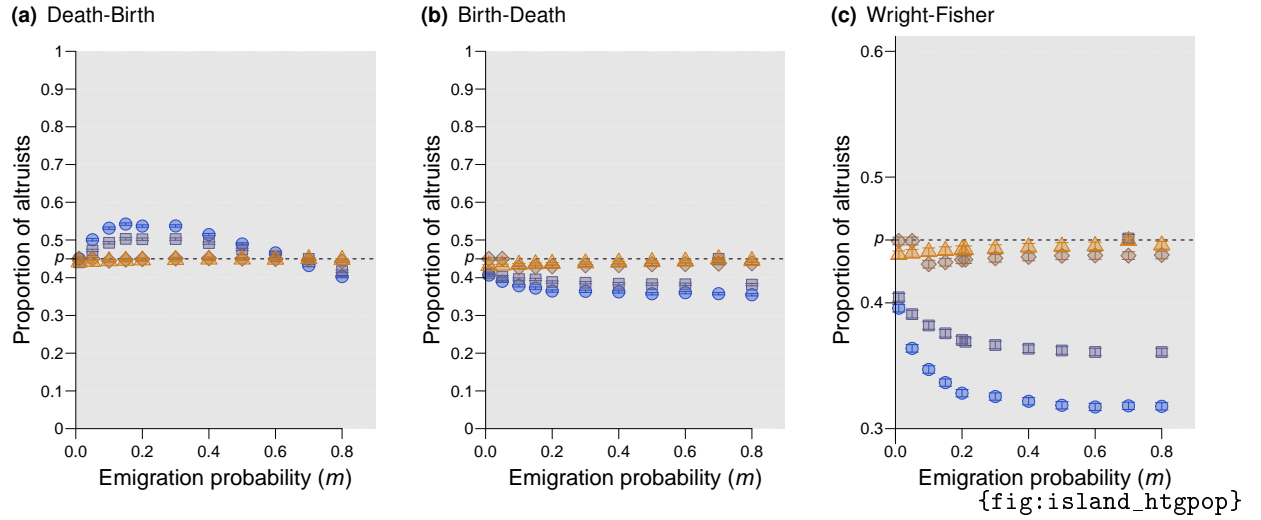
## 1 Introduction

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.

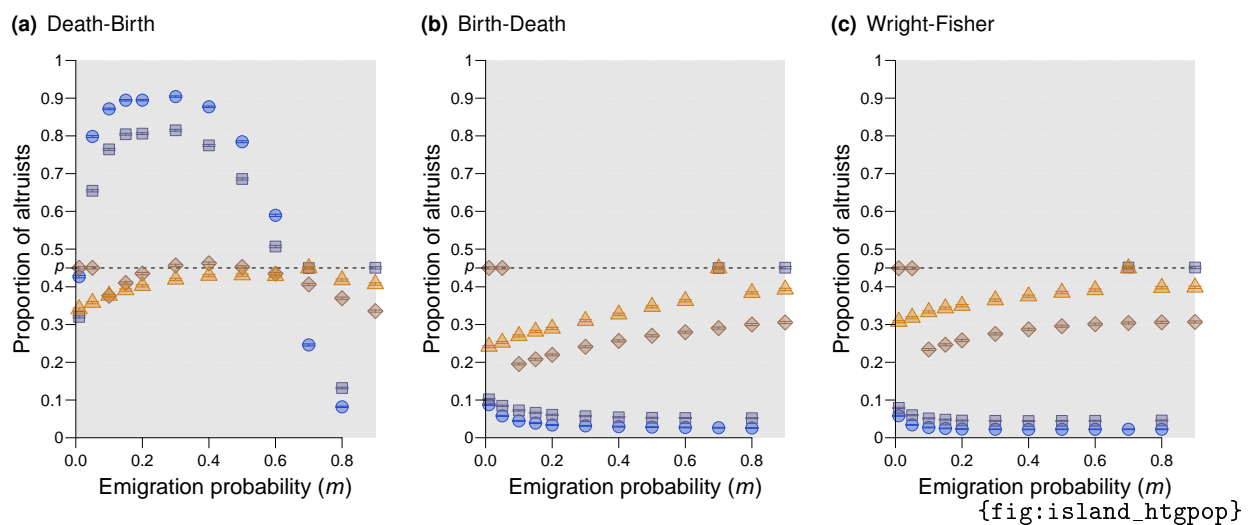
Deriving analytical results often implies making simplifying assumptions. Include simple population structures (but see), weak selection approximations, and rare or absent mutation. Simple pop reduces the dimension / complexity of the system that one has to study; weak selection approximations allow a decomposition of time scales explicuer. 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.



**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 ( $Y = e, d, Q$ ):

$$Y_{\text{self}} := Y_{i,i} \quad (1a)$$

$$Y_{\text{in}} := Y_{i,j}, \quad i \text{ and } j \neq i \text{ in the same deme}; \quad (1b)$$

$$Y_{\text{out}} := Y_{i,j}, \quad i \text{ and } j \text{ in different demes.} \quad (1c)$$

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

$$\mathbb{E}[\bar{X}] = p + \delta \frac{p(1-p)}{\mu} [b(\beta^D - \beta^I) - c(\gamma^D - \gamma^I)]. \quad (2)$$

### Moran, Birth-Death

$$\begin{aligned} \beta_{\text{BD}}^D &= \sum_{k,\ell=1}^N \frac{1-\mu}{N} e_{k\ell} Q_{\ell k} \\ &= \sum_{k=1}^N \frac{1-\mu}{N} (e_{\text{self}} + (n-1)e_{\text{in}}Q_{\text{in}} + (N-n)e_{\text{out}}Q_{\text{out}}) \\ &= (1-\mu) (e_{\text{self}} + (n-1)e_{\text{in}}Q_{\text{in}} + (N-n)e_{\text{out}}Q_{\text{out}}). \end{aligned} \quad (3a)$$

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

$$\gamma_{\text{BD}}^D = 1 - \mu. \quad (3c)$$

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

### Moran, Death-Birth

$$\begin{aligned}\beta_{\text{DB}}^D &= \frac{1-\mu}{N} \sum_{j,k=1}^N Q_{jk} e_{jk} = \beta_{\text{BD}}^D \\ &= (1-\mu) \left( e_{\text{self}} + (n-1) e_{\text{in}} Q_{\text{in}} + (N-n) e_{\text{out}} Q_{\text{out}} \right).\end{aligned}\quad (4a)$$

$$\beta_{\text{DB}}^I = \frac{1-\mu}{N} \sum_{i,j,k,l=1}^N d_{ji} d_{li} e_{kl} Q_{jk} \quad (4b)$$

Presented in the table in the appendix.

$$\gamma_{\text{DB}}^D = 1 - \mu = \gamma_{\text{BD}}^D. \quad (4c)$$

$$\begin{aligned}\gamma_{\text{DB}}^I &= (1-\mu) \sum_{i,j,k=1}^N \frac{d_{ji} d_{ki}}{N} Q_{jk} \\ &= \frac{1-\mu}{N} \sum_{j=1}^N \sum_{i=1}^N \left( d_{ji} d_{ji} + \sum_{\substack{k \neq j \\ k \in G_j}} d_{ji} d_{ki} Q_{\text{in}} + \sum_{k \notin G_j} d_{ji} d_{ki} Q_{\text{out}} \right) \\ &= \frac{1-\mu}{N} \sum_{j=1}^N \left[ d_{\text{self}} d_{\text{self}} + (n-1) d_{\text{in}} d_{\text{in}} + (N-n) d_{\text{out}} d_{\text{out}} \right. \\ &\quad \left. + (n-1) \left( d_{\text{self}} d_{\text{in}} + d_{\text{in}} d_{\text{self}} + (n-2) d_{\text{in}} d_{\text{in}} + (N-n) d_{\text{out}} d_{\text{out}} \right) Q_{\text{in}} \right. \\ &\quad \left. + (N-n) \left( d_{\text{self}} d_{\text{out}} + (n-1) d_{\text{in}} d_{\text{out}} + d_{\text{out}} d_{\text{self}} + (n-1) d_{\text{out}} d_{\text{in}} + (N-2n) d_{\text{out}} d_{\text{out}} \right) Q_{\text{out}} \right] \\ &\quad (4d)\end{aligned}$$

### Probabilities of identity by descent

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

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

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

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

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

And for  $j \notin G_i$ ,

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

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

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



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

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

And when  $j \notin G_i$ , we have

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

**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

$$d_{\text{self}} = d_{\text{in}} = \frac{1-m}{n}, \quad (7a)$$

$$d_{\text{out}} = \frac{m}{N-n}. \quad (7b)$$

Without self-replacement

$$d_{\text{self}} = 0, \quad (8a)$$

$$d_{\text{in}} = \frac{1-m}{n-1}, \quad (8b)$$

$$d_{\text{out}} = \frac{m}{N-n}. \quad (8c)$$

## B IDB

### B.1 Moran

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

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

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

We have

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

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

$$\tilde{\mathcal{D}}_0 = 1, \quad (11a)$$

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

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

So for  $\tilde{Q}$ ,

$$\begin{aligned}
\tilde{Q}_{r_1, r_2} &= \frac{\mu \lambda'_M}{N} \left[ \frac{1}{1 - (1 - \mu) \tilde{D}_0} + \sum_{q_2=1}^{N_2-1} \frac{1}{1 - (1 - \mu) \tilde{D}_{q_2}} \exp\left(-i \frac{2\pi q_2 r_2}{N_2}\right) + \sum_{q_1=1}^{N_1-1} \frac{1}{1 - (1 - \mu) \tilde{D}_{q_1}} \exp\left(-i \frac{2\pi q_1 r_1}{N_1}\right) \right. \\
&\quad \left. + \sum_{q_1=1}^{N_1-1} \sum_{q_2=1}^{N_2-1} \frac{1}{1 - (1 - \mu) \tilde{D}_{q_1, q_2}} \exp\left(-i \frac{2\pi q_1 r_1}{N_1}\right) \exp\left(-i \frac{2\pi q_2 r_2}{N_2}\right) \right] \\
&= \frac{\mu \lambda'_M}{N} \left[ \frac{1}{1 - (1 - \mu)} + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})} (\delta_{r_2} N_2 - 1) + \frac{1}{1 - (1 - \mu)(1 - m - \frac{m}{d-1})} (\delta_{r_1} N_1 - 1) \right. \\
&\quad \left. + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})} (\delta_{r_1} N_1 - 1)(\delta_{r_2} N_2 - 1) \right]. \tag{12a}
\end{aligned}$$

In particular,

$$\begin{aligned}
\tilde{Q}_0 &= \frac{\mu \lambda'_M}{N} \left[ \frac{1}{\mu} + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})} (n - 1) + \frac{1}{1 - (1 - \mu)(1 - m - \frac{m}{d-1})} (D - 1) \right. \\
&\quad \left. + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})} (D - 1)(n - 1) \right] \\
&= 1. \tag{12b}
\end{aligned}$$

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

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

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

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

## B.2 Wright-Fisher

$$\begin{aligned}
\tilde{Q}_{r_1 r_2} &= \frac{1}{N} \sum_{q_1=0}^{N_1-1} \sum_{q_2=0}^{N_2-1} \frac{\mu \lambda'_{WF}}{1 - (1-\mu)^2 (\tilde{\mathcal{D}}_{q_1}^2)_{q_2}^2} \exp\left(-i \frac{2\pi q_1 r_1}{N_1}\right) \exp\left(-i \frac{2\pi q_2 r_2}{N_2}\right) \\
&= \frac{1}{N} \left[ \frac{\mu \lambda'_{WF}}{1 - (1-\mu)^2 (\tilde{\mathcal{D}}_0^2)} + \sum_{q_2=1}^{N_2-1} \frac{\mu \lambda'_{WF}}{1 - (1-\mu)^2 (\tilde{\mathcal{D}}_0^2)_{q_2}^2} \exp\left(-i \frac{2\pi q_2 r_2}{N_2}\right) \right. \\
&\quad + \sum_{q_1=1}^{N_1-1} \frac{\mu \lambda'_{WF}}{1 - (1-\mu)^2 (\tilde{\mathcal{D}}_0^2)_{q_1}^2} \exp\left(-i \frac{2\pi q_1 r_1}{N_1}\right) \\
&\quad \left. + \sum_{q_1=1}^{N_1-1} \sum_{q_2=1}^{N_2-1} \frac{\mu \lambda'_{WF}}{1 - (1-\mu)^2 (\tilde{\mathcal{D}}_{q_1}^2)_{q_2}^2} \exp\left(-i \frac{2\pi q_1 r_1}{N_1}\right) \exp\left(-i \frac{2\pi q_2 r_2}{N_2}\right) \right] \quad (13)
\end{aligned}$$

$$\begin{aligned}
&= \frac{\mu \lambda'_{WF}}{N} \left[ \frac{1}{1 - (1-\mu)^2} + \frac{1}{1 - (1-\mu)^2 (d_{\text{self}} - d_{\text{in}})^2} (\delta_{q_2} N_2 - 1) \right. \\
&\quad + \frac{1}{1 - (1-\mu)^2 (1 - m - \frac{m}{d-1})^2} (\delta_{q_1} N_1 - 1) \\
&\quad \left. + \frac{1}{1 - (1-\mu)^2 (d_{\text{self}} - d_{\text{in}})^2} (\delta_{q_1} N_1 - 1) (\delta_{q_2} N_2 - 1) \right] \\
&= \frac{\mu \lambda'_{WF}}{N} \left[ \frac{1}{1 - (1-\mu)^2} + \frac{1}{1 - (1-\mu)^2 (d_{\text{self}} - d_{\text{in}})^2} (\delta_{q_2} N_2 - 1) \delta_{q_1} N_1 \right. \\
&\quad \left. + \frac{1}{1 - (1-\mu)^2 (1 - m - \frac{m}{d-1})^2} (\delta_{q_1} N_1 - 1) \right]. \quad (14)
\end{aligned}$$

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

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

Then,

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

and

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