

Mon titre

1 Introduction

In his pioneering work on the evolution of social behavior, Hamilton suggested that altruistic behavior would be associated to limited dispersal (Hamilton, 1964, p.10). This notion, that tighter links between individuals favor the evolution of altruism, has been shown to hold in a number of population structures (see *eg.* Ohtsuki et al., 2006; Taylor et al., 2007; Lehmann et al., 2007). The rationale that altruism is favored when altruists interact more with altruists than defectors do (are related or assorted REF Fletcher Doebeli correlated Hamilton 1975 in Okasha) , a condition that is met in viscous populations, *ie*, populations with limited dispersal.

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Yet, living next to your kin also implies competing against them; the evolution of social traits hence depends on the balance between the positive effects of interactions with related individuals and the detrimental consequences of kin competition. With generations are synchronous (Wright-Fisher model), in infinite populations, Talor REF has shown that compensation + Gardner and Rodrigues + other Taylor.

Deriving analytical results often implies making simplifying assumptions. A large number of studies on the evolution of altruistic behavior assume simple population structures (typically, homogeneous populations REF TDW + infinite population sizes (*eg*, regular structures but see Allen), weak selection approximations, and rare or absent mutation. Simple population structures help reduce the dimensionality of the system that one has to study: for instance, if the structure of the population is homogeneous such that all sites behave the same way in expectation, then we only need to consider how one site behaves. Weak selection approximations allow a decomposition of time scales expliciter. Finally, parent-offspring strategy transmission is commonly assumed to be perfect, a probability of mutation being sometimes introduced in finite populations, under the assumption that it is vanishingly small, in order to compute key quantities such as probabilities of identity by descent REF TAYLOR. . Say what mutation means, fidelity of parent-offspring transmission.

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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, focusing on the effect of population viscosity.

2 Model and methods

2.1 Assumptions

We consider a population of size N , subdivided into N_D demes, each hosting exactly n individuals (*ie*, containing n sites, each of which is occupied by exactly 1 individual; we have $nN_D = N$). Each site has a unique label i , $1 \leq i \leq N$. There are two types of individuals in the population, altruists and defectors. Reproduction is asexual. Parents transmit their strategy to their offspring with probability $1 - \mu$; this transmission can be genetic or cultural (vertical cultural transmission), but for simplicity, we refer to the parameter μ as a mutation probability. With probability μ , offspring do not inherit their strategy from their parent but instead get one randomly: with probability p , they become altruists, with probability $1 - p$ they become defectors. We call the parameter p the mutation bias.

Social interactions take place within each deme; each individual interacts with the $n - 1$ other deme members. We assume that social interactions affect individual fecundity, whose baseline is set to 1. Each interaction with an altruist increases an individual's fecundity by ωb , while altruists pay a fecundity cost ωc (and $c \leq b$). The parameter ω scales the relative effect of social interactions on fecundity, and is assumed to be small ($\omega \ll 1$).

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

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

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1/(n-1)

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

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

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,

64 chosen uniformly at random among the other demes. Denoting by d_{ij} the prob-
 65 ability of moving from site i to site j , we have

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

66 The way the population is updated from one time step to the next depends
 67 on the chosen life-cycle (updating rule). We will specifically explore three dif-
 68 ferent life-cycles. At the beginning of each step of each life-cycle, all individuals
 69 produce offspring, that can be mutated; then these juveniles move, within the
 70 parental deme or outside of it, and land on a site. The next events occurring
 71 during the time step depend on the life-cycle:

72 **Moran Birth-Death** : One of the newly created juveniles is chosen at random; it
 73 kills the adult who was living at the site, and replaces it; all other juveniles
 74 die.

75 **Moran Death-Birth** : One of the adults is chosen to die (uniformly at random
 76 among all adults). It is replaced by one of the juveniles who had landed in
 77 its site. All other juveniles die.

78 **Wright-Fisher** : All the adults die. At each site of the entire population, one of
 79 the juveniles that landed there is chosen and establishes at the site.

80 3 Results

81 3.1 Expected proportion of altruists

82 We want to compute the expected proportion of altruists in the population. Some
 83 steps can be done without specifying the life-cycle. We represent the state of the
 84 population at a given time t using indicator variables $X_i(t)$, $1 \leq i \leq N$, equal
 85 to 1 if the individual living at site i at time t is an altruist, and equal to 0 if it is
 86 a defector; these indicator variables are gathered in a N -long vector $\mathbf{X}(t)$. The
 87 set of all possible population states is $\Omega = \{0, 1\}^N$. The proportion of altruists in
 88 the population is written $\bar{X}(t) = \sum_{i=1}^N X_i(t)$. We denote by $B_{ji}(X(t), \omega)$, written
 89 B_{ji} for simplicity, the probability that the individual at site j at time $t+1$ is the
 90 newly established offspring of the individual living at site i at time t . We denote
 91 by $D_i(X(t), \omega)$ (D_i for simplicity) the probability that the individual living at site
 92 i at time t has been replaced (*i.e.*, died) at time $t+1$. Both quantities depend on
 93 the chosen life-cycle. Since a dead individual is immediately replaced by one

in a table?

94 new individual,

$$D_i = \sum_{j=1}^N B_{ij} \quad (4a) \quad \{\text{eq:DBequiv}\}$$

95 holds for all sites i . The structure of the population is also such that in the ab-
 96 sence of selection ($\omega = 0$), all individuals have the same probability of dying and
 97 the same probability of having successful offspring (*i.e.*, offspring that become
 98 adults), so that

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

99 where the ⁰ subscript means that the quantities are evaluated for $\omega = 0$; this also
 100 implies that B_{ij}^0 and D_i^0 do not depend on the state \mathbf{X} of the population. For the
 101 Moran life-cycles, $B^* = 1/N$, while for the Wright-Fisher life-cycle, $B^* = 1$. (The
 102 difference with eq. (4a) is that we are now considering offspring produced by i
 103 landing on j).

104 Given that the population is in state $\mathbf{X}(t)$ at time t , the expected frequency of
 105 altruists at time $t + 1$ is given by

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

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

110 Given that there is no absorbing population state (a lost strategy can always
 111 be recreated by mutation), there is a stationary distribution of population states,
 112 and the expected frequency of altruists does not change anymore; we denote by
 113 $\xi(\mathbf{X}, \omega, \mu)$ the probability that the population is in state \mathbf{X} , given the strength of
 114 selection ω and the mutation probability μ . Taking the expectation of eq. (5a)
 115 ($\mathbb{E}[\bar{X}] = \sum_{\mathbf{X} \in \Omega} \bar{X} \xi(\mathbf{X}, \omega, \mu)$), we obtain, after reorganizing:

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

116 Now, we use the assumption of weak selection ($\omega \ll 1$) and consider the first-
 117 order expansion of eq. (6) for ω close to 0. First, we note that in the absence
 118 of selection ($\omega = 0$), the population is at a mutation-drift balance, and the ex-
 119 pected state of every site i is then $\mathbb{E}_0[X_i] = \sum_{\mathbf{X} \in \Omega} X_i \xi(\mathbf{X}, 0, \mu) = p$, the mutation
 120 bias. Secondly, we further expand derivatives of B_{ji} and D_i using the chain rule,

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121 using the variables f_k ($1 \leq k \leq N$), corresponding to individual fecundities (also,
 122 recall that $f_k = 1$ when $\omega = 0$). **Finally, we use the shorthand notation ∂_x to de-**
 123 **note $\frac{\partial}{\partial x} \Big|_{x=0}$.** Thirdly, we note that for all the life-cycles that we consider, the
 124 number of deaths in the population during one time step does not depend on
 125 population composition (exactly 1 death for the Moran life-cycles, and exactly
 126 N for the Wright-Fisher life-cycle), so that $\partial_\omega \sum_{i,j=1}^N B_{ij}$ does not depend on ω .
 127 After simplification and reorganization, the first order expansion of eq. (6) yields
 128

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

129 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
 130 the expected state of the pair of sites (i, j) , evaluated in the absence of selection
 131 ($\omega = 0$). We can also replace these terms by

$$Q_{ij} = \frac{P_{ij} - p^2}{p(1-p)}; \tag{8} \quad \{\text{eq:QP}\}$$

132 recursions on P_{ij} will reveal that Q_{ij} can be interpreted as a probability of iden-
 133 tity by descent, *i.e.*, the probability that the individuals at sites i and j have a
 134 common ancestor and that no mutation has occurred on either lineage since
 135 the ancestor.

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

$$\mathbb{E}[\bar{X}] = p + \omega \partial_\omega \mathbb{E}[\bar{X}] + O(\omega^2), \tag{9} \quad \{\text{eq:EXgeneric}\}$$

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

139 3.2 Identity by descent

140 We need to find equations for the expected state of pairs of sites (P_{ij}) and prob-
 141 abilities of identity by descent (Q_{ij}), quantities that are evaluated in the absence
 142 of selection (*i.e.*, for $\omega = 0$). To do so, we follow the same steps as in the previous

143 section: we first write expectations at the next time step given a current state,
 144 and we then take the expectation of this. Here we focus on identity by descent
 145 Q_{ij} , but expectations of the state of pairs of sites P_{ij} are simply recovered using
 146 eq. (8).

147 Because of the structure of the population, there are only three different val-
 148 ues of Q_{ij} :

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

149 3.2.1 Moran updating

{eq:QM}

$$Q_{\text{in}}^{\text{M}} = \frac{(1 - \mu)(m + \mu(d(1 - m) - 1))}{(1 - \mu)m(d\mu(n - 1) + 1) + (d - 1)\mu(\mu(n - 1) + 1)}, \quad (11a)$$

$$Q_{\text{out}}^{\text{M}} = \frac{(1 - \mu)m}{(1 - \mu)m(d\mu(n - 1) + 1) + (d - 1)\mu(\mu(n - 1) + 1)}. \quad (11b)$$

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

153 We confirm that Q_{in}^{M} and $Q_{\text{out}}^{\text{M}}$ are equal to 1 when the mutation probabilit-
 154 ity μ tends to 0; in the absence of mutation indeed, the population ends up
 155 fixed for one of the two types, and all individuals are identical by descent. How-
 156 ever, trouble arises if we also want to consider infinite population (when the
 157 number of demes $N_D \rightarrow \infty$), because the order of limits matters. For instance,
 158 $\lim_{d \rightarrow \infty} Q_{\text{out}}^{\text{M}} = 0$.

159 3.2.2 Wright-Fisher updating

{eq:QWF}

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

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

160 with

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

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

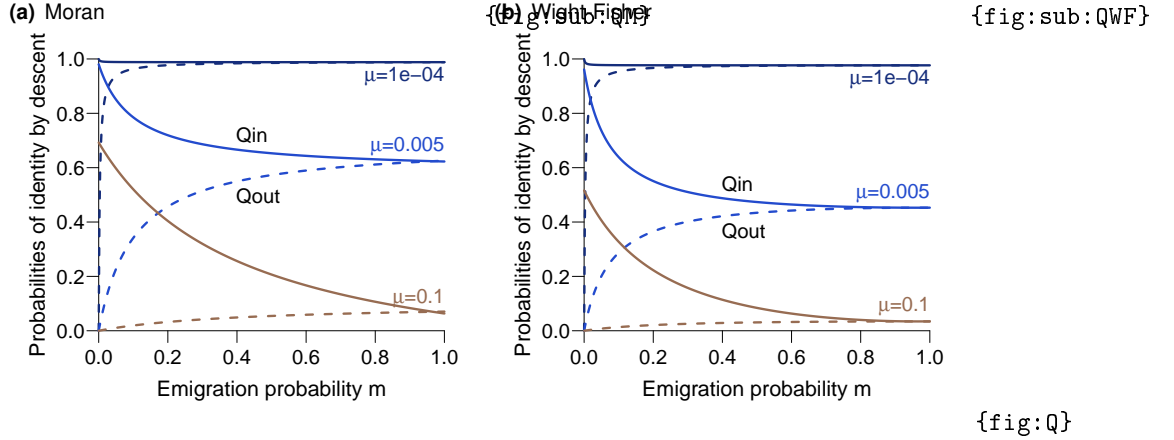


Figure 1: Probabilities of identity by descent, for two different individuals within the same deme (Q_{in} , full curves) and two individuals in different demes (Q_{out} , dashed curves), for different values of the mutation probability μ (10^{-4} , 0.005, 0.1), and for the two types of life-cycles: Moran (a) and Wright-Fisher (b). Other parameters: $n = 4$ individuals per deme, $N_D = 30$ demes.

Here, Q_{in}^{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 $\mu \rightarrow 1$. When the number of demes is very large ($d \rightarrow \infty$) **blabal**

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

3.3 Expected frequencies of altruists for each life-cycle

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

$$\partial_{\omega} \mathbb{E}[\bar{X}] = \frac{p(1-p)}{\mu} [b(\beta_D - \beta_I) - c(\gamma_D - \gamma_I)], \quad (13) \quad \{\text{eq:dEXgeneric}\}$$

where the subscript D refers to “direct” effects, and the subscript I to “indirect” effects. These indirect effects correspond to (kin) competition: by providing a

benefit to a deme-mate and thereby increasing its fecundity, a focal altruist indirectly harms others by reducing their relative fecundity. Similarly, paying a fecundity cost indirectly helps others because it increases their relative fecundities.

3.3.1 Direct effects

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

{eq:directeffects}

$$\beta_D^{BD} = \beta_D^{DB} = (1 - \mu) Q_{in}^M, \quad (14a) \quad \{\text{eq:bBDD}\}$$

$$\beta_D^{WF} = (1 - \mu) Q_{in}^{WF}; \quad (14b) \quad \{\text{eq:bWFD}\}$$

$$\gamma_D^{BD} = \gamma_D^{DB} = \gamma_D^{WF} = 1 - \mu. \quad (14c) \quad \{\text{eq:cBDD}\}$$

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

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

3.3.2 Indirect effects

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

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

203 identical-by-descent to it; we obtain

$$\begin{aligned}\beta_I^{\text{BD}} &= (1-m) \left(\frac{n-1}{n} Q_{\text{in}}^{\text{M}} + \frac{1}{n} \right) + m Q_{\text{out}}^{\text{M}} - \mu \frac{1 + (n-1) Q_{\text{in}}^{\text{M}} + n(d-1) Q_{\text{out}}^{\text{M}}}{nd} \\ &= \gamma_D^{\text{BD}}.\end{aligned}\quad (15a) \quad \{\text{eq:bBDI}\}$$

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

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

213 3.3.3 Moran Death-Birth

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

$$\begin{aligned}\beta_I^{\text{DB}} &= (1-\mu) \left[\left(\frac{1}{n} + \frac{(n-1) Q_{\text{in}}^{\text{M}}}{n} \right) \left((1-m)^2 + \frac{m^2}{(d-1)} \right) \right. \\ &\quad \left. + m \left(2(1-m) + (d-2) \frac{m}{(d-1)} \right) Q_{\text{out}}^{\text{M}} \right] \\ &= \gamma_I^{\text{DB}}\end{aligned}\quad (15b) \quad \{\text{eq:bDBI}\}$$

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

222 Here again, $\beta_I = \gamma_I$, so the balance between the two does not change when
223 the emigration probability m increases.

224 Replacing Q_{in} and Q_{out} by their formulas given in eq. (11), we can see that
225 $\beta_I = \gamma_I$ first decreases with the emigration probability m , and increases again
226 after a threshold value m'_c (given in the appendix; $m'_c < (d-1)/d$).

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227 3.3.4 Wright-Fisher

228 Generations are synchronous, and all individuals again all have the same sur-
 229 vival probability (now equal to 0). As a result, the formulas for β_1^{WF} and γ_1^{WF} are
 230 the same as β_1^{DB} and γ_1^{WF} , except that instead of Q_{in}^{M} and $Q_{\text{out}}^{\text{M}}$, we need to use
 231 $Q_{\text{in}}^{\text{WF}}$ and $Q_{\text{out}}^{\text{WF}}$ (given in eq. (12)). Once this is done, we see that $\beta_1^{\text{WF}} = \gamma_1^{\text{WF}} =$
 232 first decreases with the emigration probability m , and increases again after the
 233 threshold value $m_c = (d - 1)/d$ (which was identified previously as the emigra-
 234 tion probability such that offspring have an equal chance of landing in their na-
 235 tal deme or in any other deme).

236 3.4 Identifying threshold values of the mutation probability μ

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

242 3.4.1 Moran Birth-Death

243 For this life-cycle, we find that the expected frequency of altruists $\mathbb{E}[\bar{X}]$ is a mono-
 244 tonic function of the emigration probability m ; the direction of the change de-
 245 pends on the value of the mutation probability μ compared to a threshold value
 246 μ_c^{BD} . When $\mu < \mu_c^{\text{BD}}$, $\mathbb{E}[\bar{X}]$ decreases with m , while when $\mu > \mu_c^{\text{BD}}$, $\mathbb{E}[\bar{X}]$ increases
 247 with m ; μ_c^{BD} is given by

$$\mu_c^{\text{BD}} = 1 - \frac{b - c + \sqrt{(b - c)(4b(nd)^2 + b - c)}}{2bnd} \quad (16) \quad \{\text{eq:mucBD}\}$$

248 This result is illustrated in figure 2(b).

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249 3.4.2 Moran Death-Birth

250 The relationship between $\mathbb{E}[\bar{X}]$ and m is a bit more complicated for this life-
 251 cycle. For simplicity, we concentrate on what happens starting from low emi-
 252 gration probabilities. If the benefits b provided by altruists are relatively low
 253 ($b < c(n + 1)$), $\mathbb{E}[\bar{X}]$ initially increases with m provided the mutation probability
 254 μ is greater than a threshold value μ_c^{DB} given in eq. (17) below; otherwise, when
 255 the benefits are high enough, $\mathbb{E}[\bar{X}]$ initially increases with m for any value of μ .

256 Combining these results, we write

$$\mu_c^{\text{DB}} = \begin{cases} \frac{b - (n+1)c}{(n-1)c - (2n-1)b} & \text{if } b < c(n+1), \\ 0 & \text{otherwise.} \end{cases} \quad (17) \quad \{\text{eq:mucDB}\}$$

257 The expected frequency of altruists $\mathbb{E}[\bar{X}]$ reaches a maximum for an emigration
 258 probability m_c^{DB} (whose complicated equation is in the **appendix**), as can be seen
 259 in figure 2(a). The limit of this critical emigration probability m_c^{DB} when $\mu \rightarrow 0$ is
 260 0: we recover the result that more emigration is detrimental to the evolution of
 261 altruism when the mutation probability is either null or vanishingly small.

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262 3.4.3 Wright-Fisher

263 The expected frequency of altruists in the population reaches an extremum when
 264 $m = m_c^{\text{WF}} = \frac{d-1}{d}$. This extremum is a maximum when the mutation probability
 265 is higher than a threshold value μ_c^{WF} given by

$$\mu_c^{\text{WF}} = 1 - \sqrt{1 - \frac{c}{b}}, \quad (18)$$

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

267 3.5 Relaxing key assumptions

268 To derive our analytical results, we had to make a number of simplifying as-
 269 sumptions, such as the fact that selection is weak ($\omega \ll 1$), and the fact that the
 270 structure of the population is regular (all demes have the same size n). We ex-
 271 plored with numerical simulations the effect of relaxing these key assumptions.
 272 The patterns that we identified hold when selection is strong (see figure ??, done
 273 with $\omega = 0.1$), but also when the demes have different sizes. Deme sizes are
 274 drawn randomly at the beginning of a simulation; the range from 1 to 5 individ-
 275 uals per deme and the average size is 4 individuals as in the other figures.. Here
 276 as well, the same patterns hold as those obtained with a homogeneous structure
 277 (figure S2). Addeffect of d_{self} .

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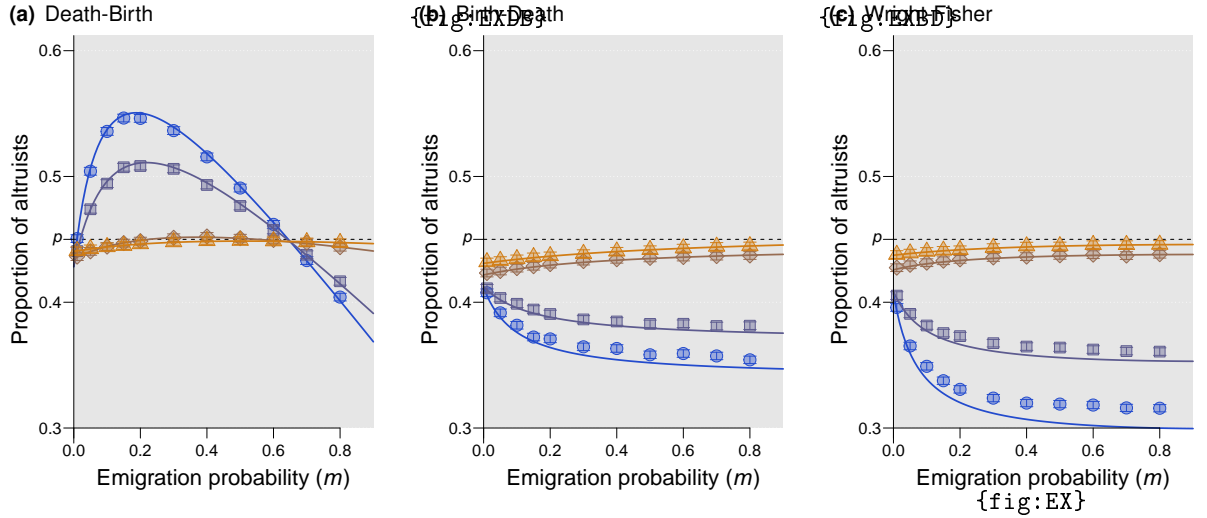


Figure 2: Weak selection. Parameters: $\omega = 0.005$, $b = 15$, $c = 1$, **ndemes**, **size**, **nreps**. NOTE simulations running with 0.005 for μ and with 0.8 for mig.

4 Discussion

Adding non zero mutation probability altruism increases with emigration.

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

Go back to the decomposition of the different terms, we see that increase of $\mathbb{E}[\bar{X}]$ with m is driven by the β_1 term. To simplify the explanations, let us consider that the number of demes is large: in this case, Q_{out} is vanishingly small and so terms involving it can be omitted. Let us also assume that there is no direct cost to being an altruist ($c = 0$).

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

Difference with Steve Frank: R was a model parameter, *i.e.*, the same for different emigration probabilities.

Voter model

294 **References**

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Supplementary figures

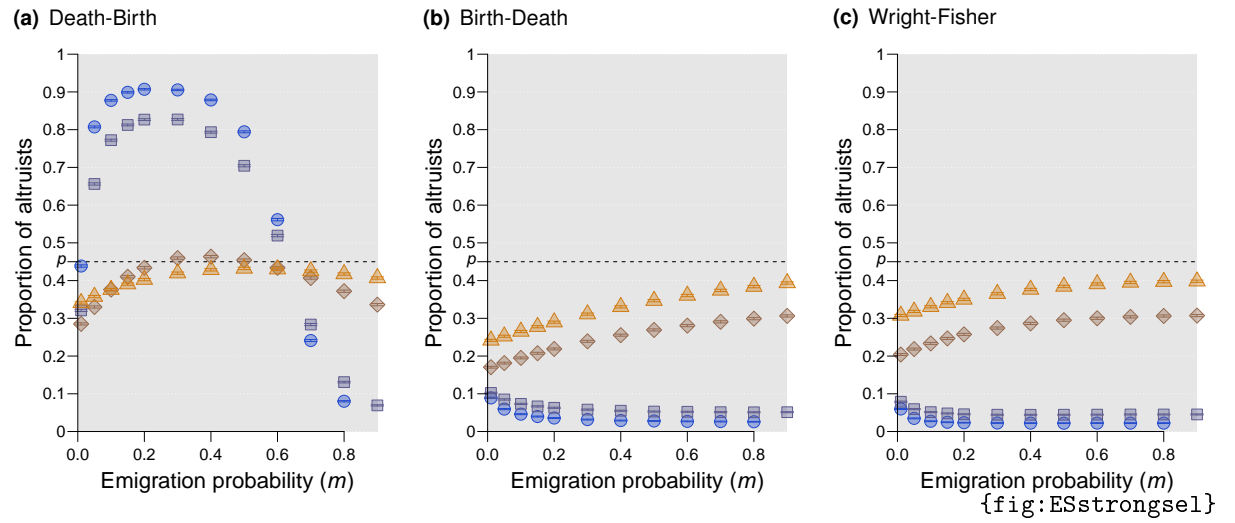


Figure S1: Equivalent of figure 2 but with strong selection ($\omega = 0.1$); all other parameters and legend are identical to those of figure 2.

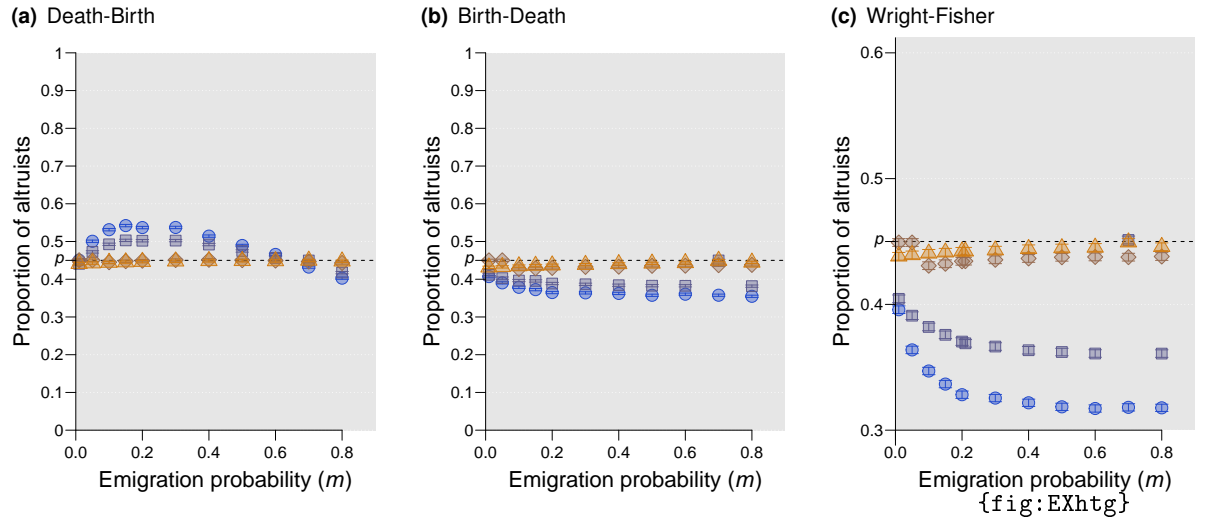


Figure S2: Equivalent of figure 2 but with a heterogeneous population structure: deme sizes range from 1 to 5 individuals per deme, the average deme size is 4 as in figure 2; all other parameters and legend are identical to those of figure 2.

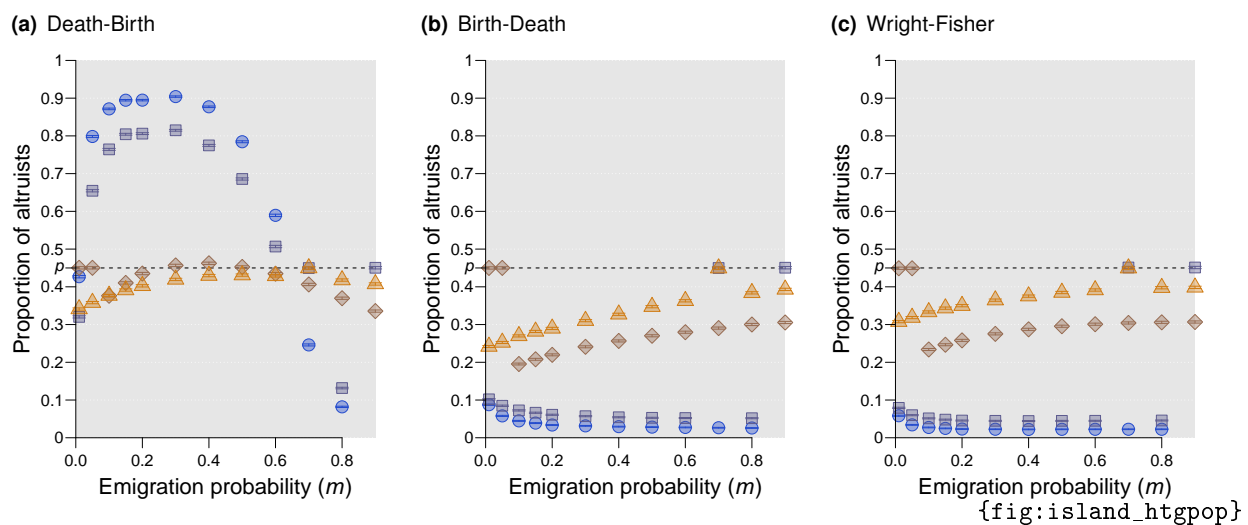


Figure S3: Strong selection, heterogeneous population

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

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

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

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

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

310 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

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

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

311 Presented in the table in the appendix.

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

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

312 Probabilities of identity by descent

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

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

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

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

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

316 And for $j \notin G_i$,

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

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

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

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

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

319 And when $j \notin G_i$, we have

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

320 **PAS FINI**

321 **Appendix**

322 All combinations for i, j, k, l . Notation: (i, j) means that i and j are in the same
323 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}

324 **A Island model**

325 With self replacement

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

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

326 Without self-replacement

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

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

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

327 **B IDB**

328 **B.1 Moran**

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

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

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

330 We have

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

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

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

$$\tilde{\mathcal{D}}_0 = 1 - m - \frac{m}{d-1} \quad (q_1 \not\equiv 0 \pmod{N_1}), \quad (\text{B.11b})$$

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

332 So for \tilde{Q} ,

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

333 In particular,

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

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

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

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

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

B.2 Wright-Fisher

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

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

338 To find λ'_{WF} , we solve

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

339 Then,

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

340 and

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