

Mon titre

# 1 Introduction

In his pioneering work on the evolution of social behavior, Hamilton REF 1964 suggested that limited dispersal would favor the evolution of altruism. This notion, that tighter links between individuals favor altruistic behavior, has been shown to hold in a number of population structures (?subdivided pops?? graphs Ohtsuki etc. The rationale behind this is 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) ; the more viscous the population, the more likely it is that.

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

Deriving analytical results often implies making simplifying assumptions. 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.

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.

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## 34 2 Model and methods

### 35 2.1 Assumptions

36 We consider a population of size  $N$ , subdivided into  $N_D$  demes, each hosting ex-  
 37 actly  $n$  individuals (*ie*, containing  $n$  sites, each of which is occupied by exactly  
 38 1 individual; we have  $nN_D = N$ ). Each site has a unique label  $i$ ,  $1 \leq i \leq N$ . There  
 39 are two types of individuals in the population, altruists and defectors. Reproduc-  
 40 tion is asexual. Parents transmit their strategy to their offspring with probability  
 41  $1 - \mu$ ; this transmission can be genetic or cultural (vertical cultural transmis-  
 42 sion), but for simplicity, we refer to the parameter  $\mu$  as a mutation probability.  
 43 With probability  $\mu$ , offspring do not inherit their strategy from their parent but  
 44 instead get one randomly: with probability  $p$ , they become altruists, with prob-  
 45 ability  $1 - p$  they become defectors. We call the parameter  $p$  the mutation bias.

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

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

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

attention,  
maybe  
rather  
{echar}  
1/(n-1)

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

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

56 Although our assumptions may seem restrictive (unconditional benefits, addi-  
 57 tive effects), the same fecundities are obtained with a generic fecundity func-  
 58 tion, after linearization, under the assumption that altruists and defectors are  
 59 phenotypically close (see **APPENDIX** for details).

60 Offspring remain in the parental deme with probability  $1 - m$ ; when they  
 61 do, they land on any site of the deme with equal probability (including the very  
 62 site of their parent). With probability  $m$ , offspring emigrate to a different deme,

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

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

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

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

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

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

## 79 3 Results

### 80 3.1 Expected proportion of altruists

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

in a table?

93 new individual,

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

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

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

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

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

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

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

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

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

115 Now, we use the assumption of weak selection ( $\omega \ll 1$ ) and consider the first-  
 116 order expansion of eq. (6) for  $\omega$  close to 0. First, we note that in the absence  
 117 of selection ( $\omega = 0$ ), the population is at a mutation-drift balance, and the ex-  
 118 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  
 119 bias. Secondly, we further expand derivatives of  $B_{ji}$  and  $D_i$  using the chain rule,

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

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

128 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  
 129 the expected state of the pair of sites  $(i, j)$ , evaluated in the absence of selection  
 130 ( $\omega = 0$ ). We can also replace these terms by

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

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

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

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

137 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).

## 138 3.2 Identity by descent

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

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

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

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

### 148 3.2.1 Moran updating

{eq:QM}

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

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

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

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

### 158 3.2.2 Wright-Fisher updating

{eq:QWF}

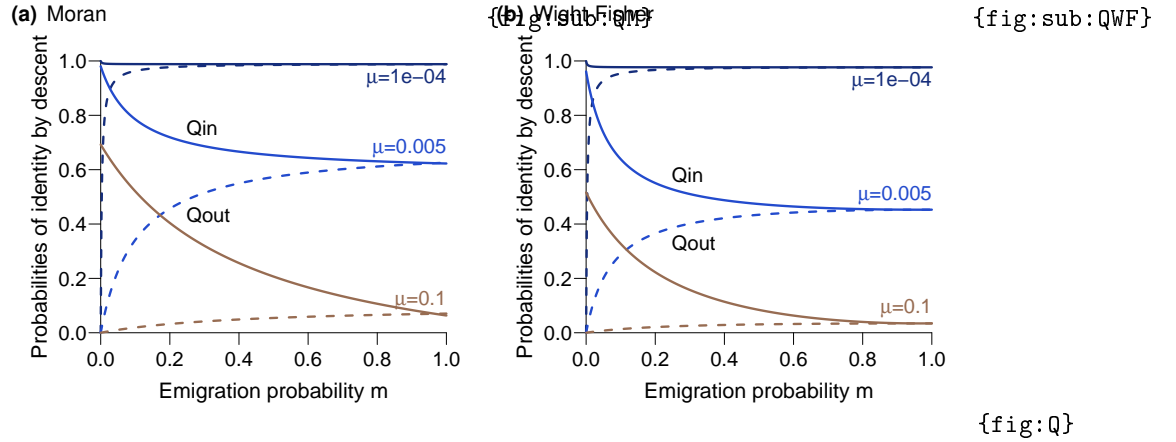
$$Q_{\text{in}}^{\text{WF}} = \frac{-d + M_1 + M_2}{(n - 1)d + M_1 + M_2}, \quad (12a)$$

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

159 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  $\mu$  ( $10^{-4}$ , 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 ( $\beta_D$ ) decreases, while the direct (costly) effects ( $\gamma_D$ ) 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

202 identical-by-descent to it; we obtain

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

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

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

### 212 3.3.3 Moran Death-Birth

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

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

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

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

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

name

### 226 3.3.4 Wright-Fisher

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

## 235 3.4 Identifying threshold values of the mutation probability $\mu$

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

### 241 3.4.1 Moran Birth-Death

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

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

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

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### 248 3.4.2 Moran Death-Birth

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

255 Combining these results, we write

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

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

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attention  
order of  
limits

appendix

### 261 3.4.3 Wright-Fisher

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

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

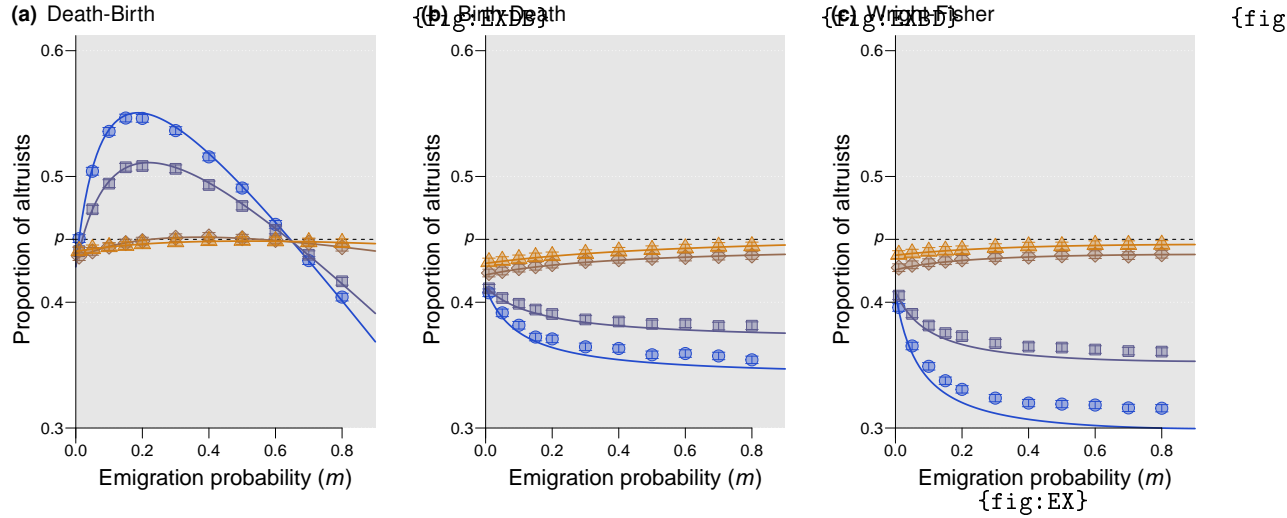
265 and it is a minimum otherwise (see figure 2(c)).

## 266 3.5 Relaxing key assumptions

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

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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  $\mu$  and with 0.8 for mig.

## 4 Discussion

Adding non zero mutation probability altruism increases with emigration.

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

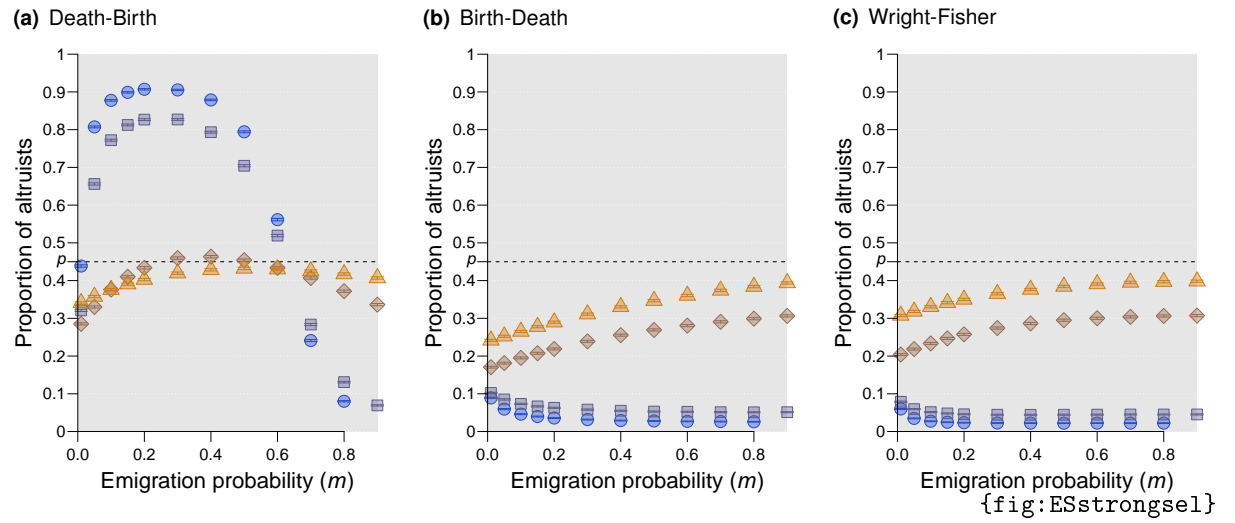
Go back to the decomposition of the different terms, we see that increase of  $\mathbb{E}[\bar{X}]$  with  $m$  is driven by the  $\beta_1$  term. To simplify the explanations, let us consider that the number of demes is large: in this case,  $Q_{\text{out}}$  is vanishingly small and so terms involving 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.

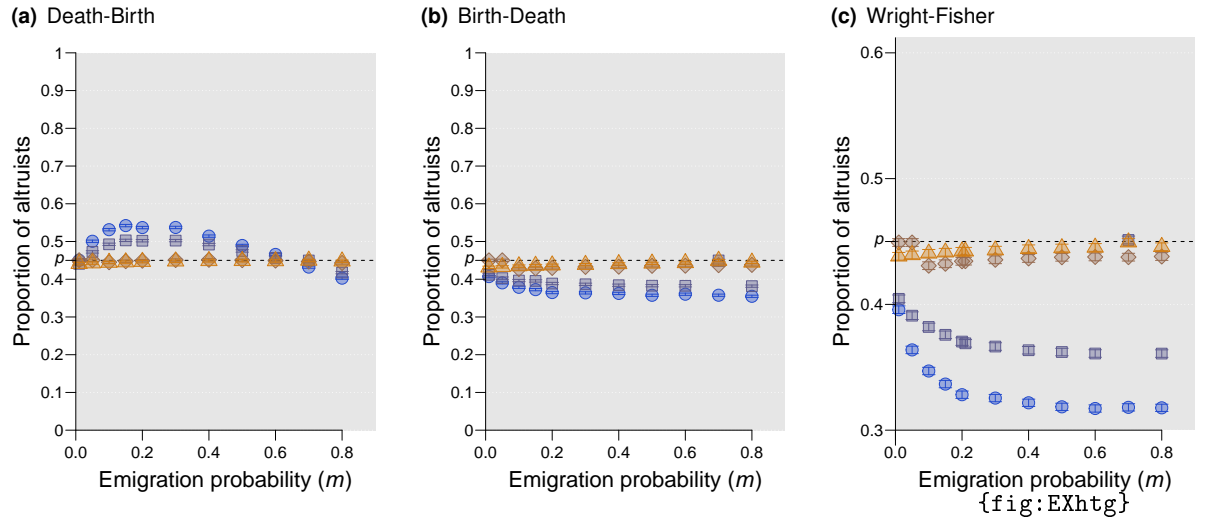
Difference with Steve Frank:  $R$  was a model parameter, *i.e.*, the same for different emigration probabilities.

Voter model

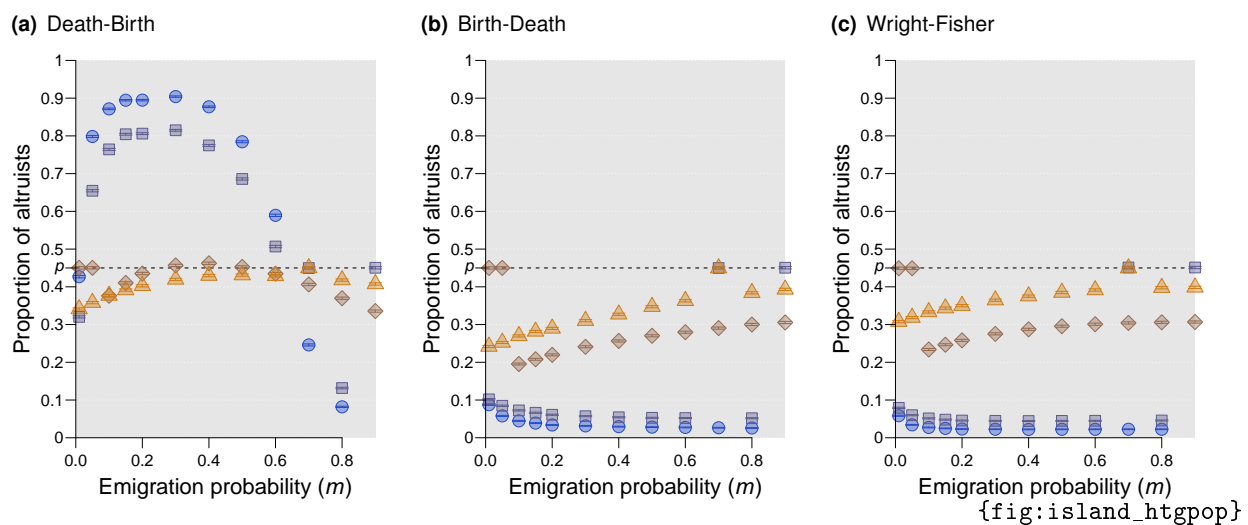
## Supplementary figures



**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



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

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

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

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

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

298      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

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

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

299 Presented in the table in the appendix.

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

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

### 300 Probabilities of identity by descent

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

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

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

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

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

304 And for  $j \notin G_i$ ,

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

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

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

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

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

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

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

308 **PAS FINI**

## 309 **Appendix**

310 All combinations for  $i, j, k, l$ . Notation:  $(i, j)$  means that  $i$  and  $j$  are in the same  
311 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	$j \notin G_i$	$k \notin G_i, G_j$	$l \notin G_i, G_j, G_k$	$(i), (j), (k), (l)$	$(N - n)(N - 2n)(N - 3n)$	$d_{\text{out}}$	$d_{\text{out}}$	$e_{\text{out}}$	$Q_{\text{out}}$

## 312 **A Island model**

313 With self replacement

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

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

314 Without self-replacement

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

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

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

## 315 **B IDB**

### 316 **B.1 Moran**

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

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

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

318 We have

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

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

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

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

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

320 So for  $\tilde{Q}$ ,

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

321 In particular,

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

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

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

324 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

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

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

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

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

327 Then,

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

328 and

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