

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 *e.g.* 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 (Hamilton, 1975, p. 141; Fletcher & Doebeli, 2009), a condition that is met in viscous populations, *i.e.*, populations with limited dispersal.

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. Under specific conditions, the two effects can even compensate each other, thereby annihilating the impact of population viscosity on the evolution of altruism. First identified with computer simulations (Wilson et al., 1992), this cancellation result was analyzed by Taylor (1992) in a model with synchronous generations (Wright-Fisher model) and a subdivided population of constant, infinite size, and was later extended to heterogeneous populations (Rodrigues & Gardner, 2012, with synchronous generations and infinite population size), and other life-cycles and regular population structures (Taylor et al., 2011, with synchronous generations but also with continuous generations and Birth-Death updating). However, small changes in the model's assumptions, such as overlapping generations (Taylor & Irwin, 2000) or the presence of empty sites (Alizon & Taylor, 2008) can tip the balance back in the favor of altruism. This high dependence on life-cycle specificities highlights the difficulty of making general statements about the role of spatial structure on the evolution of altruism.

Another limitation of mechanistic models is the necessity of simplifying assumptions to obtain analytical results. A large number of studies on the evolution of social behavior consider simple population structures (typically, homogeneous populations *sensu* Taylor et al. (2007)) and often also infinite population sizes (but see Allen et al., 2017, for results on any structure); they make use of weak selection approximations, and commonly assume rare or absent mutation. Simple population structures (*e.g.*, regular graphs, or subdivided populations with demes of equal sizes) help reduce the dimensionality of the system under study: this is for instance the case when the structure of the population displays symmetries such that all sites behave the same way in expectation. Weak selection approximations are also crucial for disentangling spatial moments (Lion, 2016), that is, changes in global *vs.* local frequencies. Finally, as

40 highlighted by Tarnita & Taylor (2014), classical models of inclusive fitness as-
 41 sume infinite population sizes, which maintains diversity; this effect is obtained
 42 thanks to (rare) mutation in finite populations. The aim of this study is to ex-
 43 plore whether and how imperfect strategy transmission from parents to their
 44 offspring affects the impact of population viscosity on the evolution of altruistic
 45 behavior in subdivided populations.

46 When strategy transmission is purely genetic, it makes sense to assume that
 47 mutation is relatively weak. A social strategy can however also be culturally
 48 transmitted from parent to offspring, in which case “rebellion” (as in Frank’s Re-
 49 bellious Child Model (Frank, 1997)) can be frequent. For simplicity though, we
 50 will keep using the word “mutation”, keeping in mind that strategy transmission
 51 does not have to be genetic.

52 In this study, we consider three different life-cycles (Wright-Fisher, Moran
 53 Birth-Death and Moran Death-Birth), compute for each of them the expected
 54 (*i.e.*, long-term) frequency of altruists in the population, and check our findings
 55 with numerical simulations. Our results reveal that imperfect strategy transmis-
 56 sion from parent to offspring can qualitatively alter the way population viscosity
 57 affects the expected frequency of altruists in the population.

cite some-
 where
 (Allen
 et al.,
 2012;
 Débarre,
 2017)

58 2 Model and methods

59 2.1 Assumptions

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

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

77 Denoting by e_{ij} the interaction probability between individuals living at sites i
 78 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
equal
1/(n-1)

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

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

81 Although our assumptions may seem restrictive (fecundity benefits are uncon-
 82 ditional, *i.e.*, the same which ever the type of the recipient; the fecundity effects
 83 are additive, *i.e.*, the effect of interacting with k altruists is k times the effect of
 84 interacting with one altruist), the same fecundities are obtained with a generic
 85 fecundity function, after linearization, under the assumption that altruists and
 86 defectors are phenotypically close (see [APPENDIX](#) for details).

87 Offspring remain in the parental deme with probability $1 - m$; when they
 88 do, they land on any site of the deme with equal probability (including the very
 89 site of their parent). With probability m , offspring emigrate to a different deme,
 90 chosen uniformly at random among the other demes. Denoting by d_{ij} the prob-
 91 ability of moving from site i to site j , we have

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

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

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

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

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

106 **2.2 Methods**

107 **2.2.1 Analytical part**

108 To derive the expected (*i.e.*, long-term) proportion of altruists in the population,
109 we use the toolbox presented in Débarre (2017), which is valid for any regular
110 population and any life-cycle. Calculation steps are given in the **appendix**; they
111 go as follows. First, we write an equation for the expected frequency of altruists
112 in the population at time $t + 1$, conditional on the composition of the population
113 at time t ; we then take the expectation of this quantity, for large times t . After
114 this, we use the assumption that selection is weak ($\omega \ll 1$) and write a first order
115 expansion of the expression that we have obtained. By doing so, we let appear
116 quantities that can be identified as neutral probabilities of identity by descent
117 Q_{ij} , *i.e.*, the probability that individuals living at site i and j share a common
118 ancestor and that no mutation occurred on either lineage since that ancestor, in
119 a model with no selection ($\omega = 0$).

120 These neutral probabilities of identity by descent depend on the chosen life-
121 cycle, and are also computed by taking the long-term expectation of conditional
122 expectations after one time step.

123 **Check results with regular results**

124 **2.2.2 Stochastic simulations**

125 We also run stochastic simulations (coded in C). The simulations are run for 10^8
126 generations (one generation is one time step for the Wright-Fisher life-cycle, and
127 N time steps for the Moran life-cycles). For each set of parameters and life-cycle,
128 we estimate the long-term frequency of altruists by sampling the population every
129 10^3 generations and computing the average frequency of altruists.

**Code
availability**

130 3 Results

131 3.1 Expected proportion of altruists

132 3.2 Identity by descent

133 We need to find equations for the expected state of pairs of sites (P_{ij}) and prob-
 134 abilities of identity by descent (Q_{ij}), quantities that are evaluated in the absence
 135 of selection (*i.e.*, for $\omega = 0$). To do so, we follow the same steps as in the previous
 136 section: we first write expectations at the next time step given a current state,
 137 and we then take the expectation of this. Here we focus on identity by descent
 138 Q_{ij} , but expectations of the state of pairs of sites P_{ij} are simply recovered using
 139 eq. (A.5).

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

$$Q_{ij} = \begin{cases} 1 & \text{when } i = j; \\ Q_{\text{in}} & \text{when } i \neq j \text{ and both sites are in the same deme;} \\ Q_{\text{out}} & \text{when sites } i \text{ and } j \text{ are in different demes.} \end{cases} \quad (4)$$

142 3.2.1 Moran updating

143 Under the Moran life-cycles, probabilities of identity by descent satisfy, for any
 144 pair of sites i and $j \neq i$,

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

145 Each site is equally likely to have been the latest one which was updated (say it
 146 is j); the sum is over the potential parents k , weighted by the dispersal proba-
 147 bilities d_{kj} ; the individuals at sites i and j are identical by descent if i and j 's
 148 parent were (Q_{ki}^M) and if no mutation occurred ($1 - \mu$). We eventually obtain

149 [appendix for calculation steps:](#)

{eq:QM}

$$Q_{\text{in}}^M = \frac{(1-\mu)(m + \mu(d(1-m) - 1))}{(1-\mu)m(d\mu(n-1) + 1) + (d-1)\mu(\mu(n-1) + 1)}, \quad (6a)$$

$$Q_{\text{out}}^M = \frac{(1-\mu)m}{(1-\mu)m(d\mu(n-1) + 1) + (d-1)\mu(\mu(n-1) + 1)}. \quad (6b)$$

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_{out}^M mono-
 152 tonically increases with m (see figure 1(a)).

153 We confirm that Q_{in}^M and Q_{out}^M are equal to 1 when the mutation probability μ 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 $\lim_{d \rightarrow \infty} Q_{\text{out}}^M = 0$.
 158

159 3.2.2 Wright-Fisher updating

160 Under a Wright-Fisher life-cycle, generations are synchronous, all individuals
 161 are replaced at each time step. Probabilities of identity by descent satisfy, for
 162 any pair of sites i and $j \neq i$

$$Q_{ij}^{\text{WF}} = (1 - \mu)^2 \sum_{k, \ell=1}^N d_{ki} d_{\ell j} Q_{kl}^{\text{WF}}. \quad (7)$$

163 The sum is over all possible parents of i and j , weights by the dispersal proba-
 164 bilities to sites i and j ; the individuals at sites i and j are identical by descent if
 165 their parents were $(Q_{k\ell})$ and if neither mutated $((1 - \mu)^2)$.
 166

We then obtain

{eq:QWF}

$$Q_{\text{in}}^{\text{WF}} = \frac{-d + M_1 + M_2}{(n-1)d + M_1 + M_2}, \quad (8a)$$

$$Q_{\text{out}}^{\text{WF}} = \frac{-\frac{1}{d-1} M_1 + M_2}{(n-1)d + M_1 + M_2}, \quad (8b)$$

167 with

$$M_1 = \frac{d-1}{1 - \frac{(1-\mu)^2(d(1-m)-1)^2}{(d-1)^2}} \text{ and } M_2 = \frac{1}{1 - (1-\mu)^2}.$$

168 Here, $Q_{\text{in}}^{\text{WF}}$ decreases until $m = m_c = \frac{d-1}{d}$, then increases again, while $Q_{\text{out}}^{\text{WF}}$
 169 follows the opposite pattern. The threshold value m_c corresponds to an emi-
 170 gration probability so high that an individual's offspring is as likely to land in its
 171 parent's deme as in any other deme.

172 The two probabilities of identity by descent go to 1 when $\mu \rightarrow 1$. When the
 173 number of demes is very large ($d \rightarrow \infty$) blabal

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

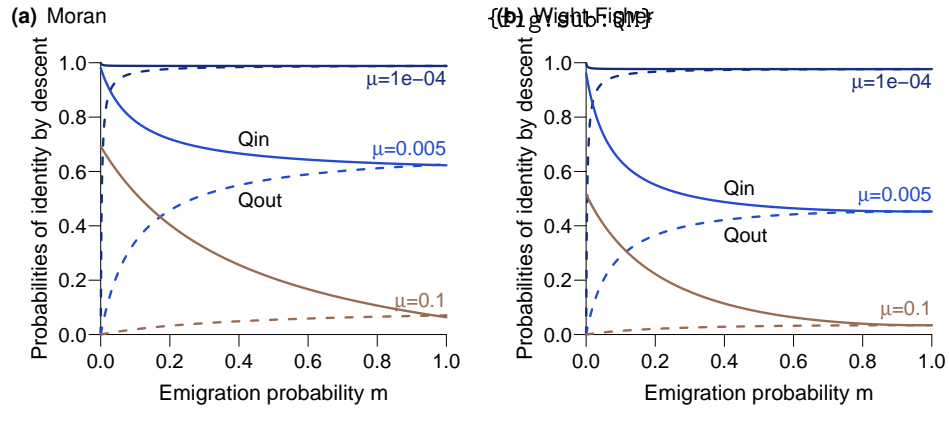


Figure 1: Probabilities of identity by descent, for two different individuals within the same deme (Q_{in} , full curves) and two individuals in different demes (Q_{out} , dashed curves), for different values of the mutation probability μ (10^{-4} , 0.005, 0.1), and for the two types of life-cycles: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

177 3.3 Expected frequencies of altruists for each life-cycle

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

$$\partial_{\omega}\mathbb{E}[\bar{X}] = \frac{p(1-p)}{\mu} [b(\beta_D - \beta_I) - c(\gamma_D - \gamma_I)], \quad (9) \quad \{\text{eq:dEXgeneric}\}$$

179 where the subscript _D refers to “direct” effects, and the subscript _I to “indirect”
 180 effects. These indirect effects correspond to (kin) competition: by providing a
 181 benefit to a deme-mate and thereby increasing its fecundity, a focal altruist in-
 182 directly harms others by reducing their relative fecundity. Similarly, paying a
 183 fecundity cost indirectly helps others because it increases their relative fecundi-
 184 ties.

185 3.3.1 Direct effects

186 Direct effects are similar for the three life-cycles; the only difference is the value
 187 of probabilities of identity by descent Q , that differ between Moran and Wright-
 188 Fisher life-cycles, as seen in the previous section: \{\text{eq:directeffects}\}

$$\beta_D^{BD} = \beta_D^{DB} = (1 - \mu) Q_{\text{in}}^M, \quad (10a) \quad \{\text{eq:bBDD}\}$$

$$\beta_D^{WF} = (1 - \mu) Q_{\text{in}}^{WF}; \quad (10b) \quad \{\text{eq:bWFD}\}$$

$$\gamma_D^{BD} = \gamma_D^{DB} = \gamma_D^{WF} = 1 - \mu. \quad (10c) \quad \{\text{eq:cBDD}\}$$

189 For both benefits and costs, direct effects only count when there is no mutation
 190 $(1 - \mu)$. Direct effects of benefits (b) only count if the interaction takes place
 191 with an individual who is identical by descent; interactions occurs only within
 192 demes, hence the presence of Q_{in} in eq. (10a) and eq. (10b). The direct effect of
 193 the fecundity cost c however does not depend on the type of interactant.

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

201 3.3.2 Indirect effects

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

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

$$\begin{aligned}\beta_1^{\text{BD}} &= (1 - m) \left(\frac{n-1}{n} Q_{\text{in}}^{\text{M}} + \frac{1}{n} \right) + m Q_{\text{out}}^{\text{M}} - \mu \frac{1 + (n-1) Q_{\text{in}}^{\text{M}} + n(d-1) Q_{\text{out}}^{\text{M}}}{nd} \\ &= \gamma_{\text{D}}^{\text{BD}}.\end{aligned}\quad (11a) \quad \{\text{eq: bBDI}\}$$

211 The formulas are the same for the indirect effects associated to b and to c; in
 212 other words, the balance between the two indirect effects remains the same
 213 when the emigration probability changes. The term $\left(\frac{n-1}{n} Q_{\text{in}}^{\text{M}} + \frac{1}{n}\right)$, which we will
 214 see appear again later, corresponds to the probability that two individuals sam-
 215 pled with replacement from the same deme are identical by descent. Indirect
 216 effects are indeed also felt by the focal individual itself (*e.g.*, increasing the fe-
 217 cundity of another individual implies decreasing one's own relative fecundity).

218 Replacing Q_{in} and Q_{out} by their formula for the Moran life-cycle (eq. (6)), we
 219 see that both are decreasing functions of the emigration probability m .

220 3.3.3 Moran Death-Birth

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

$$\begin{aligned}\beta_1^{\text{DB}} &= (1 - \mu) \left[\left(\frac{1}{n} + \frac{(n-1) Q_{\text{in}}^{\text{M}}}{n} \right) \left((1 - m)^2 + \frac{m^2}{(d-1)} \right) \right. \\ &\quad \left. + m \left(2(1 - m) + (d-2) \frac{m}{(d-1)} \right) Q_{\text{out}}^{\text{M}} \right] \\ &= \gamma_{\text{I}}^{\text{DB}}\end{aligned}\quad (11b) \quad \{\text{eq: bDBI}\}$$

225 The first term within the brackets in eq. (11b) corresponds individuals from the
 226 same deme whose offspring either does not emigrate, or emigrate to the same
 227 deme, and the second term, to individuals from different demes who end up in
 228 the same location (either one of their demes, or a third deme).

229 Here again, $\beta_{\text{I}} = \gamma_{\text{I}}$, so the balance between the two does not change when
 230 the emigration probability m increases.

231 Replacing Q_{in} and Q_{out} by their formulas given in eq. (6), we can see that
 232 $\beta_I = \gamma_I$ first decreases with the emigration probability m , and increases again
 233 after a threshold value m'_c (given in the appendix; $m'_c < (d-1)/d$). name

234 3.3.4 Wright-Fisher

235 Generations are synchronous, and all individuals again all have the same sur-
 236 vival probability (now equal to 0). As a result, the formulas for β_I^{WF} and γ_I^{WF} are
 237 the same as β_I^{DB} and γ_I^{WF} , except that instead of Q_{in}^{M} and $Q_{\text{out}}^{\text{M}}$, we need to use
 238 $Q_{\text{in}}^{\text{WF}}$ and $Q_{\text{out}}^{\text{WF}}$ (given in eq. (8)). Once this is done, we see that $\beta_I^{\text{WF}} = \gamma_I^{\text{WF}} =$
 239 first decreases with the emigration probability m , and increases again after the
 240 threshold value $m_c = (d-1)/d$ (which was identified previously as the emigra-
 241 tion probability such that offspring have an equal chance of landing in their na-
 242 tal deme or in any other deme).

243 3.4 Identifying threshold values of the mutation probability μ

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

249 3.4.1 Moran Birth-Death

250 For this life-cycle, we find that the expected frequency of altruists $\mathbb{E}[\bar{X}]$ is a mono-
 251 tonic function of the emigration probability m ; the direction of the change de-
 252 pends on the value of the mutation probability μ compared to a threshold value
 253 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
 254 with m ; μ_c^{BD} is given by

$$\mu_c^{\text{BD}} = 1 - \frac{b - c + \sqrt{(b - c)(4b(nd)^2 + b - c)}}{2bnd} \quad (12) \quad \{\text{eq:}\mu\text{cBD}\}$$

255 This result is illustrated in figure 2(b). donner la
valeur

256 3.4.2 Moran Death-Birth

257 The relationship between $\mathbb{E}[\bar{X}]$ and m is a bit more complicated for this life-
 258 cycle. For simplicity, we concentrate on what happens starting from low em-
 259 igration probabilities. If the benefits b provided by altruists are relatively low

260 ($b < c(n+1)$), $\mathbb{E}[\bar{X}]$ initially increases with m provided the mutation probability
 261 μ is greater than a threshold value μ_c^{DB} given in eq. (13) below; otherwise, when
 262 the benefits are high enough, $\mathbb{E}[\bar{X}]$ initially increases with m for any value of μ .
 263 Combining these results, we write

$$\mu_c^{\text{DB}} = \begin{cases} \frac{b - (n+1)c}{(n-1)c - (2n-1)b} & \text{if } b < c(n+1), \\ 0 & \text{otherwise.} \end{cases} \quad (13) \quad \{\text{eq:mucDB}\}$$

264 The expected frequency of altruists $\mathbb{E}[\bar{X}]$ reaches a maximum for an emigration
 265 probability m_c^{DB} (whose complicated equation is in the **appendix**), as can be seen
 266 in figure 2(a). The limit of this critical emigration probability m_c^{DB} when $\mu \rightarrow 0$ is
 267 0: we recover the result that more emigration is detrimental to the evolution of
 268 altruism when the mutation probability is either null or vanishingly small.

269 3.4.3 Wright-Fisher

270 The expected frequency of altruists in the population reaches an extremum when
 271 $m = m_c^{\text{WF}} = \frac{d-1}{d}$. This extremum is a maximum when the mutation probability
 272 is higher than a threshold value μ_c^{WF} given by

$$\mu_c^{\text{WF}} = 1 - \sqrt{1 - \frac{c}{b}}, \quad (14)$$

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

274 3.5 Relaxing key assumptions

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

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appendix

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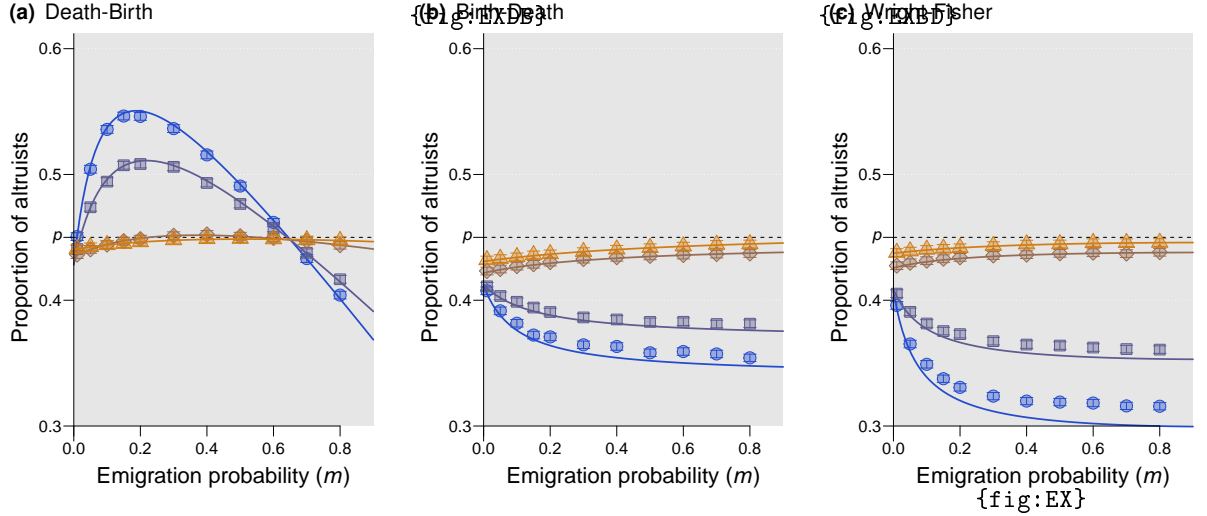


Figure 2: Weak selection. Parameters: $\omega = 0.005$, $b = 15$, $c = 1$, n_{demes} , n_{reps} . NOTE simulations running with 0.005 for μ and with 0.8 for mig.

4 Discussion

Adding non zero mutation probability altruism increases with emigration.

We used a quantitative measure, $\mathbb{E}[\bar{X}]$, to explore how non-zero mutation probabilities altered the impact of population viscosity. Often, evolutionary success is measured qualitatively, by comparing a quantity (an expected frequency, or, in models with no mutation, a probability of fixation) to the value it would have in the absence of selection; in our case, this amount to saying that altruism is favored whenever $\mathbb{E}[\bar{X}] > p$. Under this condition, population viscosity does not promote the evolution of altruism under the Moran Birth-Death and Wright-Fisher (actually, these two life-cycles cannot ever promote altruistic behavior for any regular population structure (Taylor et al., 2011), whichever the probability of mutation (Débarre, 2017)). However, under a Moran Death-Birth life-cycle, altruism can be only favored at intermediate emigration probabilities.

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_I 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

304 specify how small the mutation probability is compared to the size of the popu-
305 lation.

306 Our model bears resemblance to the Rebellious Child Model by Frank (1997),
307 who studied the evolution of a vertically transmitted cultural trait in an asexu-
308 ally reproducing population. In his analysis however, and as acknowledged in
309 the legend of his Figure 7, the model is not fully dynamic because relatedness
310 r is treated as a fixed parameter, which does not depend on mutation. In our
311 mechanistic treatment, r does depend on the mutation probability μ because
312 probabilities of identity by descent do. Mutation was also previously included
313 in models investigating the maintenance of cooperative microorganisms in the
314 presence of cheaters (Brockhurst et al., 2007; Frank, 2010). In both of these mod-
315 els however, only loss-of-function mutation was considered (in our model, this
316 is obtained by setting the mutation bias at $p = 0$). This means that the all-
317 cheaters state is absorbing, and that no matter how favored cooperators may
318 otherwise be, in the long run a finite population will only consist of cheaters.

319 Voter model Ayana Graphs et dire que on peut avoir $e = d$. Faire figure.

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369 **Supplementary figures**

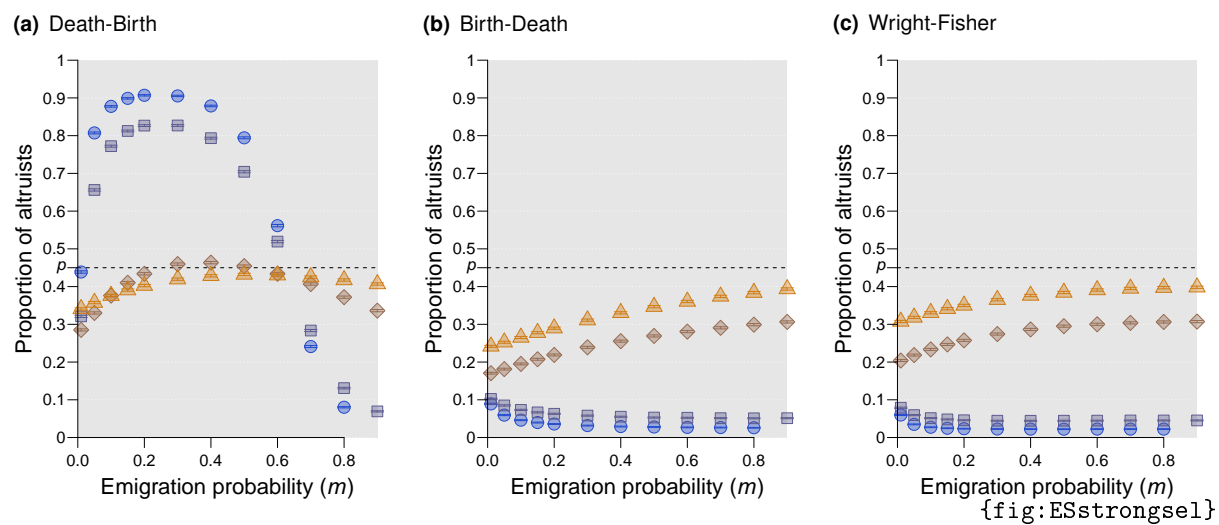


Figure S1: Equivalent of figure 2 but with strong selection ($\omega = 0.1$); all other parameters and legend are identical to those of figure 2.

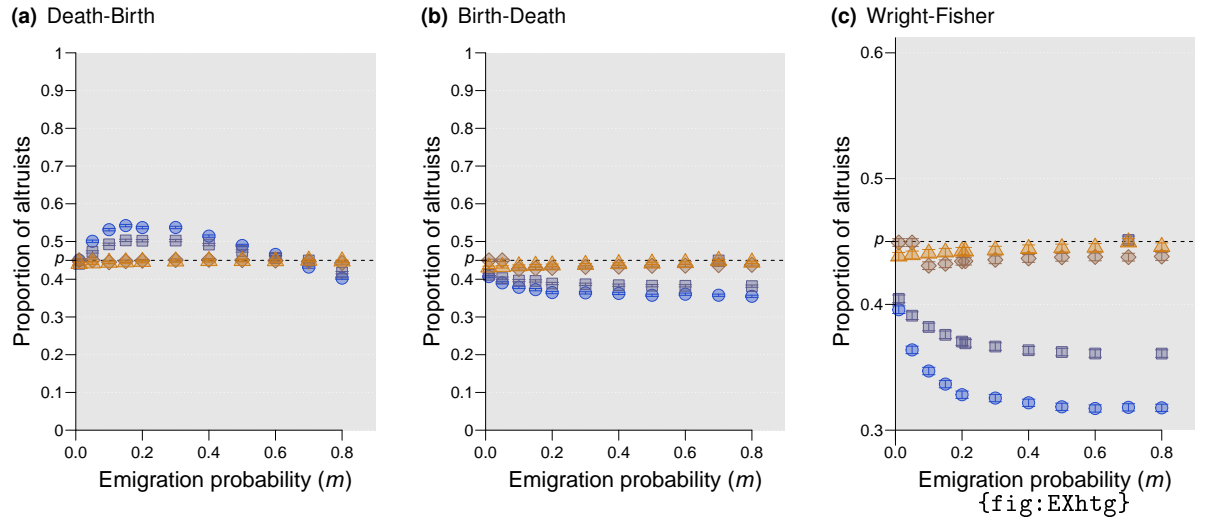


Figure S2: Equivalent of figure 2 but with a heterogeneous population structure: deme sizes range from 1 to 5 individuals per deme, the average deme size is 4 as in figure 2; all other parameters and legend are identical to those of figure 2.

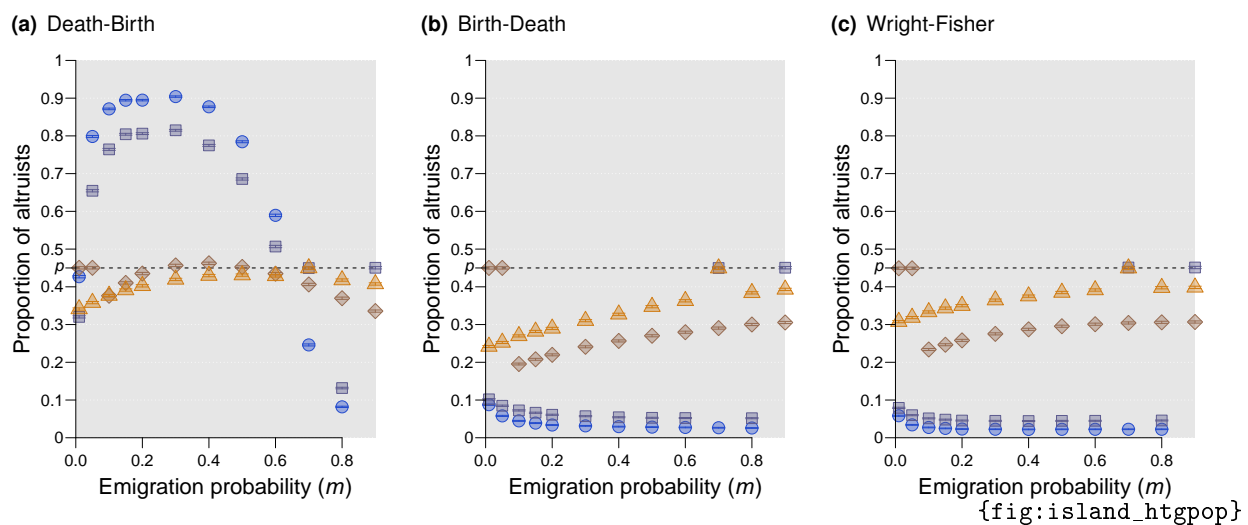


Figure S3: Strong selection, heterogeneous population

A Expected frequency of altruists in the population

{sec:app:EX}

Note: The calculation steps are the same as the ones presented in Débarre (2017); they are presented here so that the article is self-contained, but there are no new results in section XXX.

A.1 For a generic life-cycle

{sec:app:generic}

We want to compute the expected proportion of altruists in the population. Some steps can be done without specifying the life-cycle. We represent the state of the population at a given time t using indicator variables $X_i(t)$, $1 \leq i \leq N$, equal to 1 if the individual living at site i at time t is an altruist, and equal to 0 if it is a defector; these indicator variables are gathered in a N -long vector $\mathbf{X}(t)$. The set of all possible population states is $\Omega = \{0, 1\}^N$. The proportion of altruists in the population is written $\bar{X}(t) = \sum_{i=1}^N X_i(t)$. We denote by $B_{ji}(X(t), \omega)$, written B_{ji} for simplicity, the probability that the individual at site j at time $t + 1$ is the newly established offspring of the individual living at site i at time t . We denote by $D_i(X(t), \omega)$ (D_i for simplicity) the probability that the individual living at site i at time t has been replaced (*i.e.*, died) at time $t + 1$. Both quantities depend on the chosen life-cycle and on the state of the population; they are given in table S1 for each of the life-cycles that we consider.

| Life-cycle | B_{ij} | D_i |
|-------------------|--|--|
| Moran Birth-Death | $d_{ji} \frac{f_j}{\sum_{k=1}^N f_k}$ | $\frac{\sum_{j=1}^N d_{ji} f_j}{\sum_{k=1}^N f_k}$ |
| Moran Death-Birth | $\frac{1}{N} \frac{d_{ji} f_j}{\sum_{k=1}^N d_{ki} f_k}$ | $\frac{1}{N}$ |
| Wright-Fisher | $\frac{d_{ji} f_j}{\sum_{k=1}^N d_{ki} f_k}$ | 1 |

{tab:BD}

Table S1: Formulas of B_{ij} and D_i for each of the life-cycle that we consider; f_i (shorthand notation for $f_i(X, \omega)$) is the fecundity of the individual living at site i , as defined in eq. (2).

Since a dead individual is immediately replaced by one new individual,

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

holds for all sites i . The structure of the population is also such that in the absence of selection ($\omega = 0$, so that $f_i = 1$ for all sites $1 \leq i \leq N$), all individuals have the same probability of dying and the same probability of having successful offspring (*i.e.*, offspring that become adults), so that

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

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

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

$$\mathbb{E}[\bar{X}(t+1)|\mathbf{X}(t)] = \frac{1}{N} \sum_{i=1}^N \left[\sum_{j=1}^N B_{ij} (X_j(1-\mu) + \mu p) + (1 - D_i) X_i \right]. \quad (\text{A.2a}) \quad \{\text{eq:conditionalchange}\}$$

The first term within the brackets corresponds to births: the type of the individual living at i at time $t + 1$ depends on the type of its parent (living at site j), and on whether mutation occurred. The second term in the brackets of eq. (A.2a) corresponds to the survival of the individual living at site i .

Given that there is no absorbing population state (a lost strategy can always be recreated by mutation), there is a stationary distribution of population states, so that the expected frequency of altruists does not change anymore for large times t (realized frequencies of course keep changing). We denote by $\xi(\mathbf{X}, \omega, \mu)$ the probability that the population is in state \mathbf{X} , given the strength of selection ω and the mutation probability μ . Taking the expectation of eq. (A.2a) ($\mathbb{E}[\bar{X}] = \sum_{\mathbf{X} \in \Omega} \bar{X} \xi(\mathbf{X}, \omega, \mu)$), we obtain, after reorganizing:

$$0 = \frac{1}{N} \sum_{\mathbf{X} \in \Omega} \sum_{i=1}^N \left[\sum_{j=1}^N B_{ij} (X_j(1-\mu) + \mu p) - D_i X_i \right] \xi(\mathbf{X}, \omega, \mu). \quad (\text{A.3}) \quad \{\text{eq:statdist}\}$$

Now, we use the assumption of weak selection ($\omega \ll 1$) and consider the first-order expansion of eq. (A.3) for ω close to 0. First, we note that in the absence of selection ($\omega = 0$), the population is at a mutation-drift balance, and the expected state of every site i is then $\mathbb{E}_0[X_i] = \sum_{\mathbf{X} \in \Omega} X_i \xi(\mathbf{X}, 0, \mu) = p$, the mutation bias. Secondly, we further expand derivatives of B_{ji} and D_i thanks to the chain rule, using the variables f_k ($1 \leq k \leq N$), corresponding to individual fecundities (also, recall that $f_k = 1$ when $\omega = 0$). Thirdly, we note that for all the life-cycles that we

418 consider, the number of deaths in the population during one time step does not
 419 depend on population composition (exactly 1 death for the Moran life-cycles,
 420 and exactly N for the Wright-Fisher life-cycle), so that $\partial \sum_{i,j=1}^N B_{ij} / \partial \omega$ does not
 421 depend on ω . After simplification and reorganization, the first order expansion
 422 of eq. (A.3) yields

$$0 = \frac{1}{N} \sum_{i,k=1}^N \left[\frac{\partial \left(\sum_{j=1}^N (1-\mu) B_{ji} - D_i \right)}{\partial f_k} \right]_{f_k=1} \times \left(\sum_{\ell=1}^N e_{\ell k} \mathbf{b} \sum_{X \in \Omega} X_{\ell} X_i \xi(\mathbf{X}, 0, \mu) - c \sum_{X \in \Omega} X_k X_i \xi(\mathbf{X}, 0, \mu) \right) \quad (\text{A.4}) \quad \{\text{eq:weaksel1}\}$$

$$- B^* \mu \frac{\partial \mathbb{E}[\bar{X}]}{\partial \omega} \bigg|_{\omega=0} + O(\omega^2).$$

423 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
 424 the expected state of the pair of sites (i, j) , evaluated in the absence of selection
 425 ($\omega = 0$). We can also replace these terms by

$$P_{ij} = p^2 + p(1-p)Q_{ij}. \quad (\text{A.5}) \quad \{\text{eq:QP}\}$$

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

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

$$\mathbb{E}[\bar{X}] = p + \omega \frac{\partial \mathbb{E}[\bar{X}]}{\partial \omega} \bigg|_{\omega=0} + O(\omega^2), \quad (\text{A.6}) \quad \{\text{eq:EXgeneric}\}$$

432 where $\frac{\partial \mathbb{E}[\bar{X}]}{\partial \omega} \bigg|_{\omega=0}$ is obtained from eq. (A.4). We then need to replace the B_{ij} and
 433 D_j terms by their formulas for each life-cycle (given in table S1), and the d_{ij} and
 434 e_{ij} terms by their formulas (given in eq. (3)) and eq. (1), respectively). For each
 435 life-cycle we can group terms as

$$\frac{\partial \mathbb{E}[\bar{X}]}{\partial \omega} \bigg|_{\omega=0} \approx \frac{p(1-p)}{\mu} [\mathbf{b}(\beta_D - \beta_I) - c(\gamma_D - \gamma_I)], \quad (\text{A.7})$$

436 where D terms come from the numerators of B_{ij} and D_i , and I terms come from
 437 the denominator of B_{ij} and D_i . The values of the different terms for each life-
 438 cycle is given in the main text.

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

$$Y_{\text{self}} := Y_{i,i} \quad (\text{A.8a})$$

$$Y_{\text{in}} := Y_{i,j}, \quad i \text{ and } j \neq i \text{ in the same deme}; \quad (\text{A.8b})$$

$$Y_{\text{out}} := Y_{i,j}, \quad i \text{ and } j \text{ in different demes}. \quad (\text{A.8c})$$

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

443 The expected frequency of altruists in the population is given by

$$\mathbb{E}[\bar{X}] = p + \delta \frac{p(1-p)}{\mu} [\mathbf{b}(\beta_D - \beta_I) - \mathbf{c}(\gamma_D - \gamma_I)]. \quad (\text{A.9})$$

Moran, Birth-Death

$$\begin{aligned} \beta_{\text{BD}}^D &= \sum_{k,\ell=1}^N \frac{1-\mu}{N} e_{k\ell} Q_{\ell k} \\ &= \sum_{k=1}^N \frac{1-\mu}{N} \left(e_{\text{self}} + (n-1)e_{\text{in}}Q_{\text{in}} + (N-n)e_{\text{out}}Q_{\text{out}} \right) \\ &= (1-\mu) \left(e_{\text{self}} + (n-1)e_{\text{in}}Q_{\text{in}} + (N-n)e_{\text{out}}Q_{\text{out}} \right). \end{aligned} \quad (\text{A.10a})$$

$$\begin{aligned}
\beta_{\text{BD}}^I &= \sum_{j,k,l=1}^N \left(\frac{d_{lj}}{N} - \frac{\mu}{N^2} \right) e_{kl} Q_{jk} \\
&= \frac{1}{N} \sum_{j=1}^N \left[\left(\sum_{l=1}^N d_{lj} e_{jl} \right) + \sum_{\substack{k \in G_j \\ k \neq j}} \left(\sum_{l=1}^N d_{lj} e_{kl} Q_{\text{in}} Q_{\text{in}} \right) + \sum_{k \notin G_j} \sum_{l=1}^N d_{lj} (e_{kl} Q_{\text{out}} Q_{\text{out}}) \right] \\
&\quad + \frac{\mu}{N^2} \sum_{j=1}^N \left(\sum_{l=1}^N e_{kl} \right) \left(\sum_{k=1}^N Q_{jk} \right) \\
&= \frac{1}{N} \sum_{j=1}^N \left[d_{\text{self}} e_{\text{self}} + (n-1) d_{\text{in}} e_{\text{in}} + (N-n) d_{\text{out}} e_{\text{out}} \right. \\
&\quad + \sum_{\substack{k \in G_j \\ k \neq j}} (d_{\text{in}} e_{\text{self}} + d_{\text{self}} e_{\text{in}} + (n-2) d_{\text{in}} e_{\text{in}} + (N-n) d_{\text{out}} e_{\text{out}}) Q_{\text{in}} \\
&\quad + \sum_{k \notin G_j} (d_{\text{self}} e_{\text{out}} + (n-1) d_{\text{in}} e_{\text{out}} + d_{\text{out}} e_{\text{self}} + (n-1) d_{\text{out}} e_{\text{in}} + (N-2n) d_{\text{out}} e_{\text{out}}) Q_{\text{out}} \left. \right] \\
&\quad - \frac{\mu}{N} (1 + (n-1) Q_{\text{in}} + (N-n) Q_{\text{out}}) (e_{\text{self}} + (n-1) e_{\text{in}} + (N-n) e_{\text{out}}) \\
&= d_{\text{self}} e_{\text{self}} + (n-1) d_{\text{in}} e_{\text{in}} + (N-n) d_{\text{out}} e_{\text{out}} \\
&\quad + (n-1) (d_{\text{in}} e_{\text{self}} + d_{\text{self}} e_{\text{in}} + (n-2) d_{\text{in}} e_{\text{in}} + (N-n) d_{\text{out}} e_{\text{out}}) Q_{\text{in}} \\
&\quad + (N-n) (d_{\text{self}} e_{\text{out}} + (n-1) d_{\text{in}} e_{\text{out}} + d_{\text{out}} e_{\text{self}} + (n-1) d_{\text{out}} e_{\text{in}} + (N-2n) d_{\text{out}} e_{\text{out}}) Q_{\text{out}} \\
&\quad - \frac{\mu}{N} (1 + (n-1) Q_{\text{in}} + (N-n) Q_{\text{out}}) (e_{\text{self}} + (n-1) e_{\text{in}} + (N-n) e_{\text{out}}).
\end{aligned} \tag{A.10b}$$

$$\gamma_{\text{BD}}^D = 1 - \mu. \tag{A.10c}$$

$$\begin{aligned}
\gamma_{\text{BD}}^I &= \frac{1}{N} \sum_{j,k=1}^N \left(d_{kj} - \frac{\mu}{N} \right) Q_{jk} \\
&= \frac{1}{N} \sum_{j=1}^N \left[d_{\text{self}} - \frac{\mu}{N} + (n-1) \left(d_{\text{in}} - \frac{\mu}{N} \right) Q_{\text{in}} + (N-n) \left(d_{\text{out}} - \frac{\mu}{N} \right) Q_{\text{out}} \right] \\
&= d_{\text{self}} + (n-1) d_{\text{in}} Q_{\text{in}} + (N-n) d_{\text{out}} Q_{\text{out}} \\
&\quad - \frac{\mu}{N} (1 + (n-1) Q_{\text{in}} + (N-n) Q_{\text{out}})
\end{aligned} \tag{A.10d}$$

Moran, Death-Birth

$$\begin{aligned}\beta_{\text{DB}}^D &= \frac{1-\mu}{N} \sum_{j,k=1}^N Q_{jk} e_{jk} = \beta_{\text{BD}}^D \\ &= (1-\mu) \left(e_{\text{self}} + (n-1) e_{\text{in}} Q_{\text{in}} + (N-n) e_{\text{out}} Q_{\text{out}} \right).\end{aligned}\quad (\text{A.11a})$$

$$\beta_{\text{DB}}^I = \frac{1-\mu}{N} \sum_{i,j,k,l=1}^N d_{ji} d_{li} e_{kl} Q_{jk} \quad (\text{A.11b})$$

444 Presented in the table in the appendix.

$$\gamma_{\text{DB}}^D = 1 - \mu = \gamma_{\text{BD}}^D. \quad (\text{A.11c})$$

$$\begin{aligned}\gamma_{\text{DB}}^I &= (1-\mu) \sum_{i,j,k=1}^N \frac{d_{ji} d_{ki}}{N} Q_{jk} \\ &= \frac{1-\mu}{N} \sum_{j=1}^N \sum_{i=1}^N \left(d_{ji} d_{ji} + \sum_{\substack{k \neq j \\ k \in G_j}} d_{ji} d_{ki} Q_{\text{in}} + \sum_{k \notin G_j} d_{ji} d_{ki} Q_{\text{out}} \right) \\ &= \frac{1-\mu}{N} \sum_{j=1}^N \left[d_{\text{self}} d_{\text{self}} + (n-1) d_{\text{in}} d_{\text{in}} + (N-n) d_{\text{out}} d_{\text{out}} \right. \\ &\quad \left. + (n-1) \left(d_{\text{self}} d_{\text{in}} + d_{\text{in}} d_{\text{self}} + (n-2) d_{\text{in}} d_{\text{in}} + (N-n) d_{\text{out}} d_{\text{out}} \right) Q_{\text{in}} \right. \\ &\quad \left. + (N-n) \left(d_{\text{self}} d_{\text{out}} + (n-1) d_{\text{in}} d_{\text{out}} + d_{\text{out}} d_{\text{self}} + (n-1) d_{\text{out}} d_{\text{in}} + (N-2n) d_{\text{out}} d_{\text{out}} \right) Q_{\text{out}} \right] \\ &\quad (\text{A.11d})\end{aligned}$$

445 Probabilities of identity by descent

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

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

$$Q_{ij} = \frac{1-\mu}{2} \sum_{k=1}^N (d_{kj} Q_{ki} + d_{ki} Q_{kj}). \quad (\text{A.12a})$$

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

$$\begin{aligned}
Q_{\text{in}} &= \frac{1-\mu}{2} \left((d_{\text{in}} + d_{\text{self}} Q_{\text{in}}) + (d_{\text{self}} Q_{\text{in}} + d_{\text{in}}) \right. \\
&\quad \left. + (n-2)(d_{\text{in}} Q_{\text{in}} + d_{\text{in}} Q_{\text{in}}) + (N-n)(d_{\text{out}} Q_{\text{out}} + d_{\text{out}} Q_{\text{out}}) \right) \\
&= (1-\mu) \left(d_{\text{in}} + d_{\text{self}} Q_{\text{in}} + (n-2)d_{\text{in}} Q_{\text{in}} + (N-n)d_{\text{out}} Q_{\text{out}} \right). \tag{A.12b}
\end{aligned}$$

449 And for $j \notin G_i$,

$$\begin{aligned}
Q_{\text{out}} &= \frac{1-\mu}{2} \left((d_{\text{out}} + d_{\text{self}} Q_{\text{out}}) + (n-1)(d_{\text{out}} Q_{\text{in}} + d_{\text{in}} Q_{\text{out}}) \right. \\
&\quad \left. + (d_{\text{self}} Q_{\text{out}} + d_{\text{out}}) + (n-1)(d_{\text{in}} Q_{\text{out}} + d_{\text{out}} Q_{\text{in}}) \right. \\
&\quad \left. + (N-2n)(d_{\text{out}} Q_{\text{out}} + d_{\text{out}} Q_{\text{out}}) \right) \\
&= (1-\mu) \left(d_{\text{out}} + d_{\text{self}} Q_{\text{out}} + (n-1)(d_{\text{out}} Q_{\text{in}} + d_{\text{in}} Q_{\text{out}}) + (N-2n)d_{\text{out}} Q_{\text{out}} \right) \tag{A.12c}
\end{aligned}$$

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

$$Q_{ij} = (1-\mu)^2 \sum_{k,l=1}^N d_{ki} d_{lj} Q_{kl}. \tag{A.13a}$$

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

$$\begin{aligned}
Q_{\text{in}} &= (1 - \mu)^2 \left[\left(d_{\text{self}} d_{\text{in}} + d_{\text{in}} d_{\text{self}} + (n - 2) d_{\text{in}} d_{\text{in}} + (N - n) d_{\text{out}} d_{\text{out}} \right) \right. \\
&\quad + \left(d_{\text{self}} d_{\text{self}} + (n - 2) d_{\text{self}} d_{\text{in}} \right. \\
&\quad \quad + (n - 1) d_{\text{in}} d_{\text{in}} + (n - 2) d_{\text{in}} d_{\text{self}} \\
&\quad \quad \left. + (n - 2)(n - 2) d_{\text{in}} d_{\text{in}} + (N - n)(n - 1) d_{\text{out}} d_{\text{out}} \right) Q_{\text{in}} \\
&\quad + \left((N - n) d_{\text{self}} d_{\text{out}} + (N - n)(n - 1) d_{\text{in}} d_{\text{out}} \right. \\
&\quad \quad + (N - n) d_{\text{out}} d_{\text{self}} + (N - n)(n - 1) d_{\text{out}} d_{\text{in}} \\
&\quad \quad \left. + (N - n)(N - 2n) d_{\text{out}} d_{\text{out}} \right) Q_{\text{out}} \Big] \\
&= (1 - \mu)^2 \left[\left(2 d_{\text{in}} d_{\text{self}} + (n - 2) d_{\text{in}}^2 + (N - n) d_{\text{out}}^2 \right) \right. \\
&\quad + \left(d_{\text{self}}^2 + 2(n - 2) d_{\text{self}} d_{\text{in}} + (n^2 - 3n + 3) d_{\text{in}}^2 + (N - n)(n - 1) d_{\text{out}}^2 \right) Q_{\text{in}} \\
&\quad + \left(2(N - n) d_{\text{self}} d_{\text{out}} + 2(N - n)(n - 1) d_{\text{in}} d_{\text{out}} \right. \\
&\quad \quad \left. + (N - n)(N - 2n) d_{\text{out}} d_{\text{out}} \right) Q_{\text{out}} \Big] \tag{A.13b}
\end{aligned}$$

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

$$\begin{aligned}
Q_{\text{out}} &= (1 - \mu)^2 \left[\left(2 d_{\text{self}} d_{\text{out}} + 2(n - 1) d_{\text{in}} d_{\text{out}} + (N - 2n) d_{\text{out}}^2 \right) \right. \\
&\quad + \left(2(n - 1) d_{\text{self}} d_{\text{out}} + 2(n - 1)^2 d_{\text{in}} d_{\text{out}} + (N - 2n)(n - 1) d_{\text{out}}^2 \right) Q_{\text{in}} \\
&\quad + \left(d_{\text{self}} d_{\text{self}} + (n - 1) d_{\text{self}} d_{\text{in}} + (N - 2n) d_{\text{self}} d_{\text{out}} \right. \\
&\quad \quad + (n - 1) d_{\text{in}} d_{\text{self}} + (n - 1)^2 d_{\text{in}}^2 + (n - 1)(N - 2n) d_{\text{in}} d_{\text{out}} \\
&\quad \quad \left. + (N - n) d_{\text{out}} d_{\text{self}} + (N - n)(n - 1) d_{\text{out}} d_{\text{in}} + (N - n)(N - 2n) d_{\text{out}} d_{\text{out}} \right) Q_{\text{out}} \Big]. \tag{A.13c}
\end{aligned}$$

453 **PAS FINI**

454 **Appendix**

455 All combinations for i, j, k, l . Notation: (i, j) means that i and j are in the same
456 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} |

457 **A Island model**

458 With self replacement

$$d_{\text{self}} = d_{\text{in}} = \frac{1-m}{n}, \quad (\text{A.14a})$$

$$d_{\text{out}} = \frac{m}{N-n}. \quad (\text{A.14b})$$

459 Without self-replacement

$$d_{\text{self}} = 0, \quad (\text{A.15a})$$

$$d_{\text{in}} = \frac{1-m}{n-1}, \quad (\text{A.15b})$$

$$d_{\text{out}} = \frac{m}{N-n}. \quad (\text{A.15c})$$

460 **B IDB**

461 **B.1 Moran**

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

$$\tilde{\mathcal{D}}_{q_1}^{q_2} = \sum_{l_1=0}^{N_1-1} \sum_{l_2=0}^{N_2-1} \tilde{d}_{l_1} \exp\left(-i \frac{2\pi q_1 l_1}{N_1}\right) \exp\left(-i \frac{2\pi q_2 l_2}{N_2}\right) \quad (\text{B.16a})$$

$$\tilde{\mathcal{Q}}_{r_1}^{r_2} = \frac{1}{N} \sum_{q_1=0}^{N_1-1} \sum_{q_2=0}^{N_2-1} \frac{\mu \lambda'_M}{1 - (1-\mu) \tilde{\mathcal{D}}_{q_1}^{q_2}} \exp\left(i \frac{2\pi q_1 r_1}{N_1}\right) \exp\left(i \frac{2\pi q_2 r_2}{N_2}\right) \quad (\text{B.16b})$$

463 We have

$$\begin{aligned} \tilde{\mathcal{D}}_{q_1}^{q_2} &= d_{\text{self}} + \sum_{l_2=1}^{N_2-1} d_{\text{in}} \exp\left(-i \frac{2\pi q_2 l_2}{N_2}\right) + \sum_{l_1=1}^{N_1-1} \sum_{l_2=0}^{N_2-1} d_{\text{out}} \exp\left(-i \frac{2\pi q_1 l_1}{N_1}\right) \exp\left(-i \frac{2\pi q_2 l_2}{N_2}\right) \\ &= d_{\text{self}} + (\delta_{q_2}(N_2-1) + (1-\delta_{q_2})(-1)) d_{\text{in}} + (\delta_{q_1}(N_1-1) + (1-\delta_{q_1})(-1)) (\delta_{q_2} N_2) d_{\text{out}} \\ &= d_{\text{self}} + (\delta_{q_2} N_2 - 1) d_{\text{in}} + (\delta_{q_1} N_1 - 1) \delta_{q_2} N_2 d_{\text{out}}. \end{aligned} \quad (\text{B.17a})$$

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

$$\tilde{\mathcal{D}}_0^0 = 1, \quad (\text{B.18a})$$

$$\tilde{\mathcal{D}}_{q_1}^0 = 1 - m - \frac{m}{d-1} \quad (q_1 \not\equiv 0 \pmod{N_1}), \quad (\text{B.18b})$$

$$\tilde{\mathcal{D}}_{q_1}^{q_2} = d_{\text{self}} - d_{\text{in}} \quad (q_2 \not\equiv 0 \pmod{N_2}). \quad (\text{B.18c})$$

465 So for \tilde{Q} ,

$$\begin{aligned}
\tilde{Q}_{r_1} &= \frac{\mu\lambda'_M}{N} \left[\frac{1}{1-(1-\mu)\tilde{D}_0} + \sum_{q_2=1}^{N_2-1} \frac{1}{1-(1-\mu)\tilde{D}_{q_2}} \exp\left(-i\frac{2\pi q_2 r_2}{N_2}\right) + \sum_{q_1=1}^{N_1-1} \frac{1}{1-(1-\mu)\tilde{D}_{q_1}} \exp\left(-i\frac{2\pi q_1 r_1}{N_1}\right) \right. \\
&\quad \left. + \sum_{q_1=1}^{N_1-1} \sum_{q_2=1}^{N_2-1} \frac{1}{1-(1-\mu)\tilde{D}_{q_1}} \exp\left(-i\frac{2\pi q_1 r_1}{N_1}\right) \exp\left(-i\frac{2\pi q_2 r_2}{N_2}\right) \right] \\
&= \frac{\mu\lambda'_M}{N} \left[\frac{1}{1-(1-\mu)} + \frac{1}{1-(1-\mu)(d_{\text{self}}-d_{\text{in}})} (\delta_{r_2} N_2 - 1) + \frac{1}{1-(1-\mu)(1-m-\frac{m}{d-1})} (\delta_{r_1} N_1 - 1) \right. \\
&\quad \left. + \frac{1}{1-(1-\mu)(d_{\text{self}}-d_{\text{in}})} (\delta_{r_1} N_1 - 1)(\delta_{r_2} N_2 - 1) \right]. \tag{B.19a}
\end{aligned}$$

466 In particular,

$$\begin{aligned}
\tilde{Q}_0 &= \frac{\mu\lambda'_M}{N} \left[\frac{1}{\mu} + \frac{1}{1-(1-\mu)(d_{\text{self}}-d_{\text{in}})} (n-1) + \frac{1}{1-(1-\mu)(1-m-\frac{m}{d-1})} (D-1) \right. \\
&\quad \left. + \frac{1}{1-(1-\mu)(d_{\text{self}}-d_{\text{in}})} (D-1)(n-1) \right] \\
&= 1. \tag{B.19b}
\end{aligned}$$

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

$$\begin{aligned}
Q_{\text{in}} &= \frac{\mu\lambda'_M}{N} \left[\frac{1}{\mu} + \frac{1}{1-(1-\mu)(d_{\text{self}}-d_{\text{in}})} (-1) + \frac{1}{1-(1-\mu)(1-m-\frac{m}{d-1})} (D-1) \right. \\
&\quad \left. + \frac{1}{1-(1-\mu)(d_{\text{self}}-d_{\text{in}})} (D-1)(-1) \right]. \tag{B.19c}
\end{aligned}$$

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

$$\begin{aligned}
Q_{\text{out}} &= \frac{\mu\lambda'_M}{N} \left[\frac{1}{\mu} + \frac{1}{1-(1-\mu)(d_{\text{self}}-d_{\text{in}})} (-1) + \frac{1}{1-(1-\mu)(1-m-\frac{m}{d-1})} (-1) \right. \\
&\quad \left. + \frac{1}{1-(1-\mu)(d_{\text{self}}-d_{\text{in}})} \right]. \tag{B.19d}
\end{aligned}$$

B.2 Wright-Fisher

$$\begin{aligned}
\tilde{Q}_{r_1 r_2} &= \frac{1}{N} \sum_{q_1=0}^{N_1-1} \sum_{q_2=0}^{N_2-1} \frac{\mu \lambda'_{WF}}{1 - (1-\mu)^2 (\tilde{D}_{q_1})^2} \exp\left(-i \frac{2\pi q_1 r_1}{N_1}\right) \exp\left(-i \frac{2\pi q_2 r_2}{N_2}\right) \\
&= \frac{1}{N} \left[\frac{\mu \lambda'_{WF}}{1 - (1-\mu)^2 (\tilde{D}_0)^2} + \sum_{q_2=1}^{N_2-1} \frac{\mu \lambda'_{WF}}{1 - (1-\mu)^2 (\tilde{D}_0)^2} \exp\left(-i \frac{2\pi q_2 r_2}{N_2}\right) \right. \\
&\quad + \sum_{q_1=1}^{N_1-1} \frac{\mu \lambda'_{WF}}{1 - (1-\mu)^2 (\tilde{D}_0)^2} \exp\left(-i \frac{2\pi q_1 r_1}{N_1}\right) \\
&\quad \left. + \sum_{q_1=1}^{N_1-1} \sum_{q_2=1}^{N_2-1} \frac{\mu \lambda'_{WF}}{1 - (1-\mu)^2 (\tilde{D}_{q_1})^2} \exp\left(-i \frac{2\pi q_1 r_1}{N_1}\right) \exp\left(-i \frac{2\pi q_2 r_2}{N_2}\right) \right] \quad (\text{B.20})
\end{aligned}$$

$$\begin{aligned}
&= \frac{\mu \lambda'_{WF}}{N} \left[\frac{1}{1 - (1-\mu)^2} + \frac{1}{1 - (1-\mu)^2 (d_{\text{self}} - d_{\text{in}})^2} (\delta_{q_2} N_2 - 1) \right. \\
&\quad + \frac{1}{1 - (1-\mu)^2 (1 - m - \frac{m}{d-1})^2} (\delta_{q_1} N_1 - 1) \\
&\quad \left. + \frac{1}{1 - (1-\mu)^2 (d_{\text{self}} - d_{\text{in}})^2} (\delta_{q_1} N_1 - 1) (\delta_{q_2} N_2 - 1) \right] \\
&= \frac{\mu \lambda'_{WF}}{N} \left[\frac{1}{1 - (1-\mu)^2} + \frac{1}{1 - (1-\mu)^2 (d_{\text{self}} - d_{\text{in}})^2} (\delta_{q_2} N_2 - 1) \delta_{q_1} N_1 \right. \\
&\quad \left. + \frac{1}{1 - (1-\mu)^2 (1 - m - \frac{m}{d-1})^2} (\delta_{q_1} N_1 - 1) \right]. \quad (\text{B.21})
\end{aligned}$$

471 To find λ'_{WF} , we solve

$$1 = \frac{\mu \lambda'_{WF}}{N} \left[\frac{1}{1 - (1-\mu)^2} + \frac{1}{1 - (1-\mu)^2 (d_{\text{self}} - d_{\text{in}})^2} (N_2 - 1) N_1 + \frac{1}{1 - (1-\mu)^2 (1 - m - \frac{m}{d-1})^2} (N_1 - 1) \right]. \quad (\text{B.22a})$$

472 Then,

$$Q_{\text{in}} = \frac{\mu \lambda'_{WF}}{N} \left[\frac{1}{1 - (1-\mu)^2} - \frac{1}{1 - (1-\mu)^2 (d_{\text{self}} - d_{\text{in}})^2} N_1 + \frac{1}{1 - (1-\mu)^2 (1 - m - \frac{m}{d-1})^2} (N_1 - 1) \right]. \quad (\text{B.22b})$$

473 and

$$Q_{\text{out}} = \frac{\mu \lambda'_{WF}}{N} \left[\frac{1}{1 - (1-\mu)^2} - \frac{1}{1 - (1-\mu)^2 (1 - m - \frac{m}{d-1})^2} \right]. \quad (\text{B.22c})$$