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

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

cite somewhere (Allen et al., 2012; Débarre, 2017)

When strategy transmission is purely genetic, it makes sense to assume that mutation is relatively weak. A social strategy can however also be culturally transmitted from parent to offspring, in which case "rebellion" (as in Frank's Rebellious Child Model (Frank, 1997)) can be frequent. For simplicity though, we will keep using the word "mutation", keeping in mind that strategy transmission does not have to be genetic.

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

2 Model and methods

2.1 Assumptions

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

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

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

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

{eq:defE}

[margin note: attention, maybe rather $1/(n-1)$]

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

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

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

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

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

{eq:defD}

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

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

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

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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.

2.2 Methods

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.

Check results with regular results

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 ev-
129 ery 10^3 generations and computing the average frequency of altruists.

Code
availability

3 Results

3.1 Expected proportion of altruists

We want to compute the expected proportion of altruists in the population. Some steps can be done without specifying the life-cycle. We represent the state of the population at a given time t using indicator variables $X_i(t)$, $1 \le i \le N$, 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 $\overline{X}(t) = \sum_{i=1}^N X_i(t)$. We denote by $B_{ji}(X(t), \omega)$, written B_{ji} for simplicity, the probability that the individual at site j at time $t+1$ is the newly established offspring of the individual living at site i at time t. We denote by $D_i(X(t), \omega)$ (D_i for simplicity) the probability that the individual living at site i at time t has been replaced (*i.e.*, died) at time $t+1$. Both quantities depend on the chosen life-cycle. Since a dead individual is immediately replaced by one new individual,

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

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

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

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. (4a) 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

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

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

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¹⁶⁰ Given that there is no absorbing population state (a lost strategy can always
¹⁶¹ be recreated by mutation), there is a stationary distribution of population states,
¹⁶² and the expected frequency of altruists does not change anymore; we denote by
¹⁶³ $\xi(\mathbf{X}, \omega, \mu)$ the probability that the population is in state $\mathbf{X}$, given the strength of
¹⁶⁴ selection ω and the mutation probability μ. Taking the expectation of eq. (5a)
¹⁶⁵ ($\mathbb{E}[\overline{X}] = \sum_{X \in \Omega} \overline{X} \xi(\mathbf{X}, \omega, \mu)$), we obtain, after reorganizing:

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

¹⁶⁶ Now, we use the assumption of weak selection ($\omega \ll 1$) and consider the first-
¹⁶⁷ order expansion of eq. (6) for ω close to 0. First, we note that in the absence
¹⁶⁸ of selection ($\omega = 0$), the population is at a mutation-drift balance, and the ex-
¹⁶⁹ pected state of every site i is then $\mathbb{E}_0[X_i] = \sum_{X \in \Omega} X_i \xi(X, 0, \mu) = p$, the mutation
¹⁷⁰ bias. Secondly, we further expand derivatives of B_{ji} and D_i using the chain rule,
¹⁷¹ using the variables f_k ($1 \le k \le N$), corresponding to individual fecundities (also,
¹⁷² recall that $f_k = 1$ when $\omega = 0$). Finally, we use the shorthand notation ∂_x to de-
¹⁷³ note $\left. \frac{\partial}{\partial x} \right|_{x=0}$. Thirdly, we note that for all the life-cycles that we consider, the
¹⁷⁴ number of deaths in the population during one time step does not depend on
¹⁷⁵ population composition (exactly 1 death for the Moran life-cycles, and exactly
¹⁷⁶ N for the Wright-Fisher life-cycle), so that $\partial_\omega \sum_{i,j=1}^{N} B_{ij}$ does not depend on ω.
¹⁷⁷ After simplification and reorganization, the first order expansion of eq. (6) yields
¹⁷⁸

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

¹⁷⁹ 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
¹⁸⁰ the expected state of the pair of sites (i, j), evaluated in the absence of selection
¹⁸¹ ($\omega = 0$). We can also replace these terms by

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

¹⁸² recursions on P_{ij} will reveal that Q_{ij} can be interpreted as a probability of iden-
¹⁸³ tity by descent, *i.e.*, the probability that the individuals at sites i and j have a

common ancestor and that no mutation has occurred on either lineage since the ancestor.

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

$$\mathbb{E}\left[\overline{X}\right] = p + \omega\,\partial_\omega\mathbb{E}\left[\overline{X}\right] + O\left(\omega^2\right), \qquad (9) \quad \texttt{\{eq:EXgeneric\}}$$

where $\partial_\omega\mathbb{E}\left[\overline{X}\right]$ is a shorthand notation for $\left.\dfrac{\partial\mathbb{E}\left[\overline{X}\right]}{\partial\omega}\right|_{\omega=0}$, which is given by eq. (7).

3.2 Identity by descent

We need to find equations for the expected state of pairs of sites (P_{ij}) and probabilities of identity by descent (Q_{ij}), quantities that are evaluated in the absence of selection (*i.e.*, for $\omega = 0$). To do so, we follow the same steps as in the previous section: we first write expectations at the next time step given a current state, and we then take the expectation of this. Here we focus on identity by descent Q_{ij}, but expectations of the state of pairs of sites P_{ij} are simply recovered using eq. (8).

Because of the structure of the population, there are only three different values of Q_{ij}:

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

3.2.1 Moran updating

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

$$Q_{ij}^{\text{M}} = \frac{1-\mu}{2} \sum_{k=1}^{N} \left(d_{kj} Q_{ki}^{\text{M}} + d_{ki} Q_{kj}^{\text{M}} \right). \qquad (11)$$

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

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{eq:QM}

$$Q_{\text{in}}^{\text{M}} = \frac{(1-\mu)\big(m+\mu(d(1-m)-1)\big)}{(1-\mu)\,m(d\mu(n-1)+1)+(d-1)\mu(\mu(n-1)+1)},\qquad(12a)$$

$$Q_{\text{out}}^{\text{M}} = \frac{(1-\mu)\,m}{(1-\mu)\,m(d\mu(n-1)+1)+(d-1)\mu(\mu(n-1)+1)}.\qquad(12b)$$

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

210   We confirm that Q_{in}^{M} and $Q_{\text{out}}^{\text{M}}$ are equal to 1 when the mutation probabil-
211 ity μ tends to 0; in the absence of mutation indeed, the population ends up
212 fixed for one of the two types, and all individuals are identical by descent. How-
213 ever, trouble arises if we also want to consider infinite population (when the
214 number of demes $N_D \to \infty$), because the order of limits matters. For instance,
215 $\lim_{d\to\infty} Q_{\text{out}}^{M} = 0$.

216   **3.2.2 Wright-Fisher updating**

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

$$Q_{ij}^{\text{WF}} = (1-\mu)^2 \sum_{k,\ell=1}^{N} d_{ki} d_{\ell j} Q_{kl}^{\text{WF}}.\qquad(13)$$

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

223   We then obtain {eq:QWF}

$$Q_{\text{in}}^{\text{WF}} = \frac{-d + M_1 + M_2}{(n-1)d + M_1 + M_2},\qquad(14a)$$

$$Q_{\text{out}}^{\text{WF}} = \frac{-\frac{1}{d-1}M_1 + M2}{(n-1)d + M_1 + M_2},\qquad(14b)$$

224 with

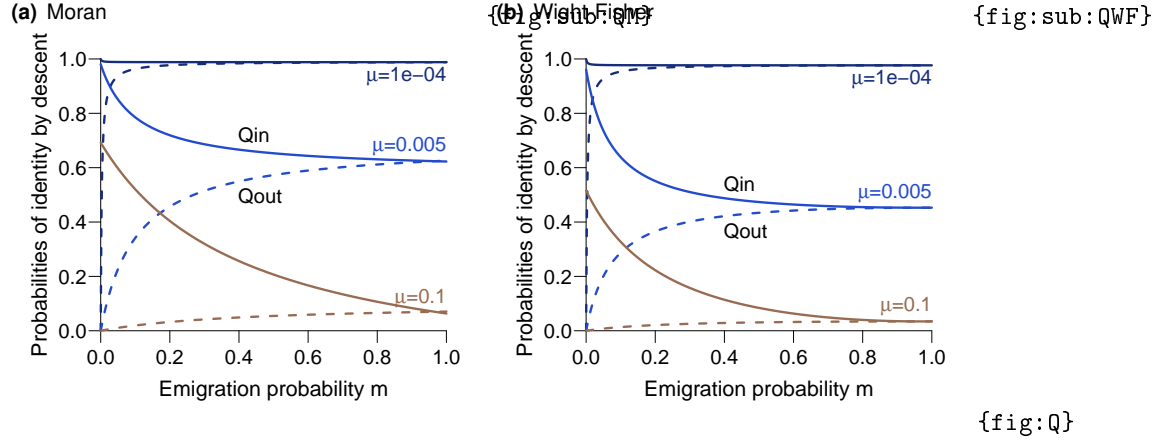$$M_1 = \frac{d-1}{1-\frac{(1-\mu)^2(d(1-m)-1)^2}{(d-1)^2}} \text{ and } M_2 = \frac{1}{1-(1-\mu)^2}.$$

(a) Moran   {Fig:sub:QM}   **(b)** Wight-Fisher   {fig:sub:QWF}

{fig:Q}

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

Here, $Q_{\mathrm{in}}^{\mathrm{WF}}$ 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 $\mu \to 1$. When the number of demes is very large ($d \to \infty$) 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 $\partial_\omega \mathbb{E}\left[\overline{X}\right]$ as follows:

$$\partial_\omega \mathbb{E}\left[\overline{X}\right] = \frac{p(1-p)}{\mu} \left[\mathsf{b}\left(\beta_{\mathrm{D}} - \beta_{\mathrm{I}}\right) - \mathsf{c}\left(\gamma_{\mathrm{D}} - \gamma_{\mathrm{I}}\right)\right], \qquad (15) \quad \{\mathtt{eq:dEXgeneric}\}$$

where the subscript $_{\mathrm{D}}$ refers to "direct" effects, and the subscript $_{\mathrm{I}}$ to "indirect" effects. These indirect effects correspond to (kin) competition: by providing a

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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}

$$\beta_D^{BD} = \beta_D^{DB} = (1 - \mu) Q_{in}^M, \tag{16a}$$ {eq:bBDD}

$$\beta_D^{WF} = (1 - \mu) Q_{in}^{WF}; \tag{16b}$$ {eq:bWFD}

$$\gamma_D^{BD} = \gamma_D^{BD} = \gamma_D^{WF} = 1 - \mu. \tag{16c}$$ {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. (16a) and eq. (16b). The direct effect of the fecundity cost c however does not depend on the type of interactant.

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

3.3.2 Indirect effects

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

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

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₂₆₇ identical-by-descent to it; we obtain

$$\beta_I^{BD} = (1-m)\left(\frac{n-1}{n}Q_{in}^M + \frac{1}{n}\right) + m\,Q_{out}^M - \mu\frac{1+(n-1)Q_{in}^M + n(d-1)Q_{out}^M}{nd} \qquad (17a) \quad \{eq:bBDI\}$$

$$= \gamma_D^{BD}.$$

₂₆₈ The formulas are the same for the indirect effects associated to b and to c; in
₂₆₉ other words, the balance between the two indirect effects remains the same
₂₇₀ when the emigration probability changes. The term $\left(\frac{n-1}{n}Q_{in}^M + \frac{1}{n}\right)$, which we will
₂₇₁ see appear again later, corresponds to the probability that two individuals sam-
₂₇₂ pled with replacement from the same deme are identical by descent. Indirect
₂₇₃ effects are indeed also felt by the focal individual itself (*e.g.*, increasing the fe-
₂₇₄ cundity of another individual implies decreasing one's own relative fecundity).
₂₇₅   Replacing Q_{in} and Q_{out} by their formula for the Moran life-cycle (eq. (12)),
₂₇₆ we see that both are decreasing functions of the emigration probability m.

3.3.3 Moran Death-Birth

₂₇₈ With this life-cycle, death comes first and every individual in the population has
₂₇₉ the same survival probability $(1/N)$. The indirect consequences of changing a
₂₈₀ focal individual's fecundity affect all individuals who can send their offspring to
₂₈₁ the same locations are the focal, and are identical by descent to it. We obtain

$$\beta_I^{DB} = (1-\mu)\left[\left(\frac{1}{n} + \frac{(n-1)Q_{in}^M}{n}\right)\left((1-m)^2 + \frac{m^2}{(d-1)}\right)\right.$$
$$\left. + m\left(2(1-m) + (d-2)\frac{m}{(d-1)}\right)Q_{out}^M\right] \qquad (17b) \quad \{eq:bDBI\}$$

$$= \gamma_I^{DB}$$

₂₈₂ The first term within the brackets in eq. (17b) corresponds individuals from the
₂₈₃ same deme whose offspring either does not emigrate, or emigrate to the same
₂₈₄ deme, and the second term, to individuals from different demes who end up in
₂₈₅ the same location (either one of their demes, or a third deme).
₂₈₆   Here again, $\beta_I = \gamma_I$, so the balance between the two does not change when
₂₈₇ the emigration probability m increases.
₂₈₈   Replacing Q_{in} and Q_{out} by their formulas given in eq. (12), we can see that
₂₈₉ $\beta_I = \gamma_I$ first decreases with the emigration probability m, and increases again
₂₉₀ after a threshold value m_c' (given in the appendix; $m_c' < (d-1)/d$).   name

₂₉₁ ### 3.3.4 Wright-Fisher

₂₉₂ Generations are synchronous, and all individuals again all have the same sur-
₂₉₃ vival probability (now equal to 0). As a result, the formulas for β_I^{WF} and γ_I^{WF} are
₂₉₄ the same as β_I^{DB} and γ_I^{WF}, except that instead of Q_{in}^M and Q_{out}^M, we need to use
₂₉₅ Q_{in}^{WF} and Q_{out}^{WF} (given in eq. (14)). Once this is done, we see that $\beta_I^{WF} = \gamma_I^{WF} =$
₂₉₆ first decreases with the emigration probability m, and increases again after the
₂₉₇ threshold value $m_c = (d-1)/d$ (which was identified previously as the emigra-
₂₉₈ tion probability such that offspring have an equal chance of landing in their na-
₂₉₉ tal deme or in any other deme).

₃₀₀ ## 3.4 Identifying threshold values of the mutation probability μ

₃₀₁ In the previous section, we investigated the impact of changes in the emigra-
₃₀₂ tion probability m on each of the terms that make up the expected frequency of
₃₀₃ altruists $\mathbb{E}[\overline{X}]$. Now we need to combine these different terms to focus on the
₃₀₄ quantity we are eventually interested in, $\mathbb{E}[\overline{X}]$. The rather lengthy formulas that
₃₀₅ we obtain are relegated to the <mark>appendix</mark>, and we concentrate here on the results.

₃₀₆ ### 3.4.1 Moran Birth-Death

₃₀₇ For this life-cycle, we find that the expected frequency of altruists $\mathbb{E}[\overline{X}]$ is a mono-
₃₀₈ tonic function of the emigration probability m; the direction of the change de-
₃₀₉ pends on the value of the mutation probability μ compared to a threshold value
₃₁₀ μ_c^{BD}. When $\mu < \mu_c^{BD}$, $\mathbb{E}[\overline{X}]$ decreases with m, while when $\mu > \mu_c^{BD}$, $\mathbb{E}[\overline{X}]$ increases
₃₁₁ with m; μ_c^{BD} is given by

$$\mu_c^{BD} = 1 - \frac{b - c + \sqrt{(b-c)\left(4b(nd)^2 + b - c\right)}}{2bnd} \qquad (18) \quad \{\text{eq:mucBD}\}$$

₃₁₂ This result is illustrated in figure 2(b).

donner la valeur

₃₁₃ ### 3.4.2 Moran Death-Birth

₃₁₄ The relationship between $\mathbb{E}[\overline{X}]$ and m is a bit more complicated for this life-
₃₁₅ cycle. For simplicity, we concentrate on what happens starting from low em-
₃₁₆ igration probabilities. If the benefits b provided by altruists are relatively low
₃₁₇ (b $<$ c$(n+1)$), $\mathbb{E}[\overline{X}]$ initially increases with m provided the mutation probability
₃₁₈ μ is greater than a threshold value μ_c^{DB} given in eq. (19) below; otherwise, when
₃₁₉ the benefits are high enough, $\mathbb{E}[\overline{X}]$ initially increases with m for any value of μ.

₁₃

320 Combining these results, we write

$$\mu_c^{\mathrm{DB}} = \begin{cases} \dfrac{\mathsf{b}-(n+1)\mathsf{c}}{(n-1)\mathsf{c}-(2n-1)\mathsf{b}} & \text{if } \mathsf{b} < \mathsf{c}(n+1), \\ 0 & \text{otherwise.} \end{cases} \qquad (19) \quad \texttt{\{eq:mucDB\}}$$

321 The expected frequency of altruists $\mathbb{E}\big[\overline{X}\big]$ reaches a maximum for an emigration
322 probability m_c^{DB} (whose complicatedequation is in the appendix), as can be seen
323 in figure 2(a). The limit of this critical emigration probability m_c^{DB} when $\mu \to 0$ is
324 0: we recover the result that more emigration is detrimental to the evolution of
325 altruism when the mutation probability is either null or vanishingly small.

> do

> attention order of limits

> appendix

3.4.3 Wright-Fisher

327 The expected frequency of altruists in the population reaches an extremum when
328 $m = m_c^{\mathrm{WF}} = \frac{d-1}{d}$. This extremum is a maximum when the mutation probability
329 is higher than a threshold value μ_c^{WF} given by

$$\mu_c^{\mathrm{WF}} = 1 - \sqrt{1 - \frac{\mathsf{c}}{\mathsf{b}}}, \qquad (20)$$

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

3.5 Relaxing key assumptions

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

> le pb c'est ptet simplement que 1 individu ca pose probleme!

> todo

14

(a) Death-Birth {(b).EXDB}sher {(c).EXBD}sher {fig:

(b) Birth-Death {fig:EXDB}
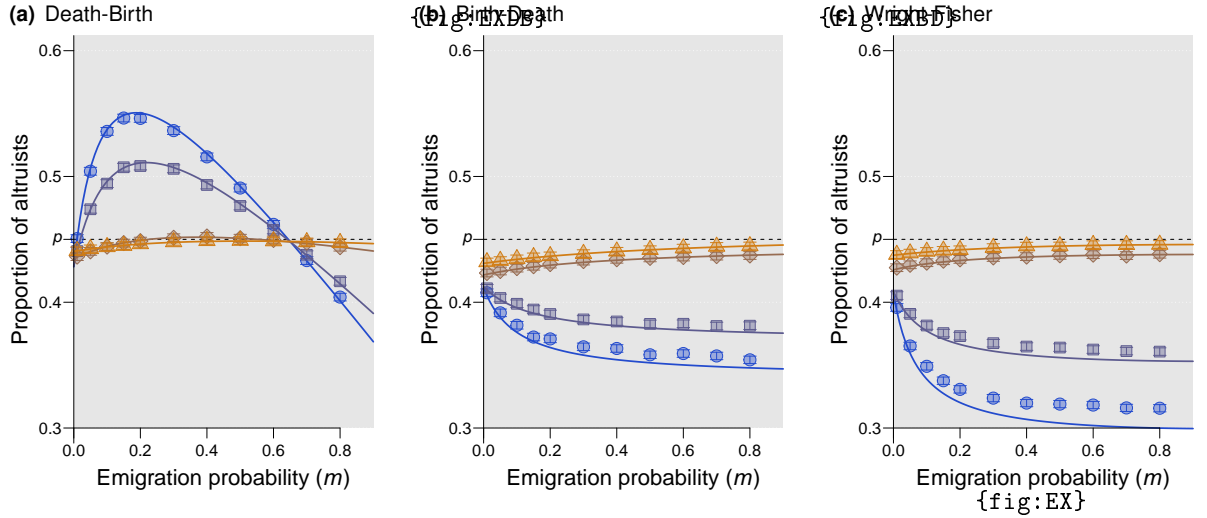
(c) Wright-Fisher {fig:EXBD}

{fig:EX}

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.

We used a quantitative measure, $\mathbb{E}[\overline{X}]$, 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 $\mathbb{E}[\overline{X}] > p$. 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 $\mathbb{E}[\overline{X}]$ 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 $d \to \infty$ and $\mu \to 0$. Need to

15

361 specify how small the mutation probability is compared to the size of the popu-
362 lation.

363   Our model bears resemblance to the Rebellious Child Model by Frank (1997),
364 who studied the evolution of a vertically transmitted cultural trait in an asexu-
365 ally reproducing population. In his analysis however, and as acknowledged in
366 the legend of his Figure 7, the model is not fully dynamic because relatedness
367 r is treated as a fixed parameter, which does not depend on mutation. In our
368 mechanistic treatment, r does depend on the mutation probability μ because
369 probabilities of identity by descent do. Mutation was also previously included
370 in models investigating the maintenance of cooperative microorganisms in the
371 presence of cheaters (Brockhurst et al., 2007; Frank, 2010). In both of these mod-
372 els however, only loss-of-function mutation was considered (in our model, this
373 is obtained by setting the mutation biais at $p = 0$). This means that the all-
374 cheaters state is absorbing, and that no matter how favored cooperators may
375 otherwise be, in the long run a finite population will only consist of cheaters.
376   Voter model

References

Alizon, S. & Taylor, P. 2008: Empty sites can promote altruistic behavior. Evolution 62(6):1335–1344.

Allen, B.; Lippner, G.; Chen, Y.-T.; Fotouhi, B.; Momeni, N.; Yau, S.-T. & Nowak, M. A. 2017: Evolutionary dynamics on any population structure. Nature 544(7649):227–230.

Allen, B.; Traulsen, A.; Tarnita, C. E. & Nowak, M. A. 2012: How mutation affects evolutionary games on graphs. Journal of Theoretical Biology 299:97 – 105. Evolution of Cooperation.

Brockhurst, M. A.; Buckling, A. & Gardner, A. 2007: Cooperation peaks at intermediate disturbance. Current Biology 17(9):761–765.

Débarre, F. 2017: Fidelity of parent-offspring transmission and the evolution of social behavior in structured populations. Journal of Theoretical Biology 420:26 – 35.

Fletcher, J. A. & Doebeli, M. 2009: A simple and general explanation for the evolution of altruism. Proceedings of the Royal Society B: Biological Sciences 276(1654):13–19.

Frank, S. A. 1997: The price equation, fisher's fundamental theorem, kin selection, and causal analysis. Evolution 51(6):1712–1729.

Frank, S. A. 2010: Microbial secretor–cheater dynamics. Philosophical Transactions of the Royal Society of London B: Biological Sciences 365(1552):2515–2522.

Hamilton, W. 1964: The genetical evolution of social behaviour. i. Journal of Theoretical Biology 7(1):1 – 16.

Hamilton, W. D. 1975: Innate social aptitudes of man: an approach from evolutionary genetics. Biosocial anthropology 53:133–55.

Lehmann, L.; Keller, L. & Sumpter, D. J. T. 2007: The evolution of helping and harming on graphs: the return of the inclusive fitness effect. Journal of Evolutionary Biology 20(6):2284–2295.

Lion, S. 2016: Moment equations in spatial evolutionary ecology. Journal of theoretical biology 405:46–57.

17

Ohtsuki, H.; Hauert, C.; Lieberman, E. & Nowak, M. A. 2006: A simple rule for the evolution of cooperation on graphs and social networks. Nature 441(7092):502–505.

Rodrigues, A. M. M. & Gardner, A. 2012: Evolution of helping and harming in heterogeneous populations. Evolution 66(7):2065–2079.

Tarnita, C. E. & Taylor, P. D. 2014: Measures of relative fitness of social behaviors in finite structured population models. The American Naturalist 184(4):477–488.

Taylor, P. 1992: Altruism in viscous populations—an inclusive fitness model. Evolutionary ecology 6(4):352–356.

Taylor, P.; Lillicrap, T. & Cownden, D. 2011: Inclusive fitness analysis on mathematical groups. Evolution 65(3):849–859.

Taylor, P. D.; Day, T. & Wild, G. 2007: Evolution of cooperation in a finite homogeneous graph. Nature 447(7143):469–472.

Taylor, P. D. & Irwin, A. J. 2000: Overlapping generations can promote altruistic behavior. Evolution 54(4):1135–1141.

Wilson, D. S.; Pollock, G. B. & Dugatkin, L. A. 1992: Can altruism evolve in purely viscous populations? Evolutionary Ecology 6(4):331–341.

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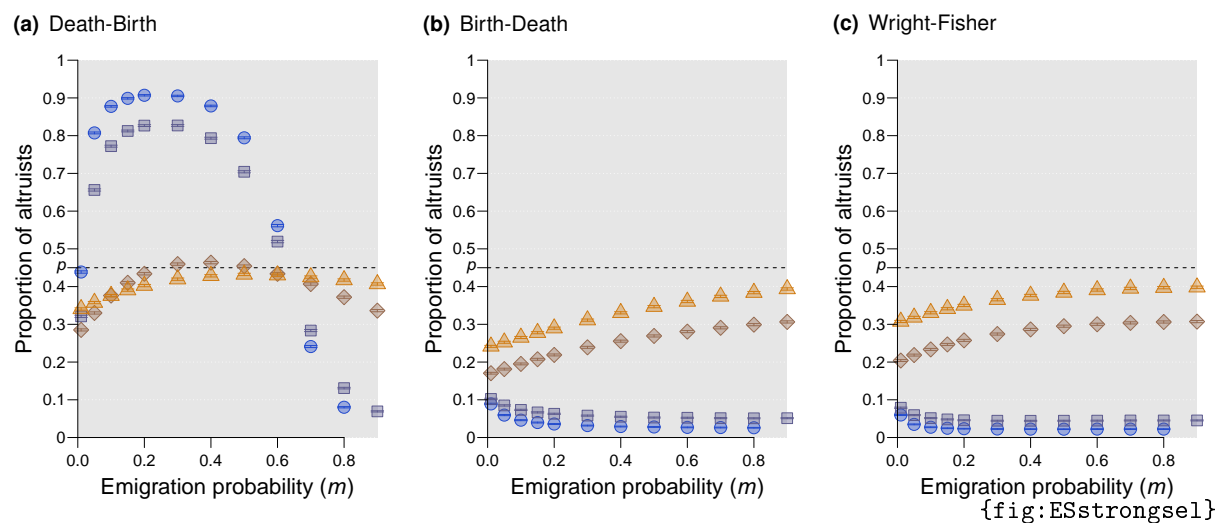
Figure S1: Equivalent of figure 2 but with strong selection ($\omega = 0.1$); all other parameters and legend are identical to those of figure 2.

(a) Death-Birth

(b) Birth-Death

(c) Wright-Fisher

Figure S2: Equivalent of figure 2 but with a heterogeneous population structure: deme sizes range form 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.
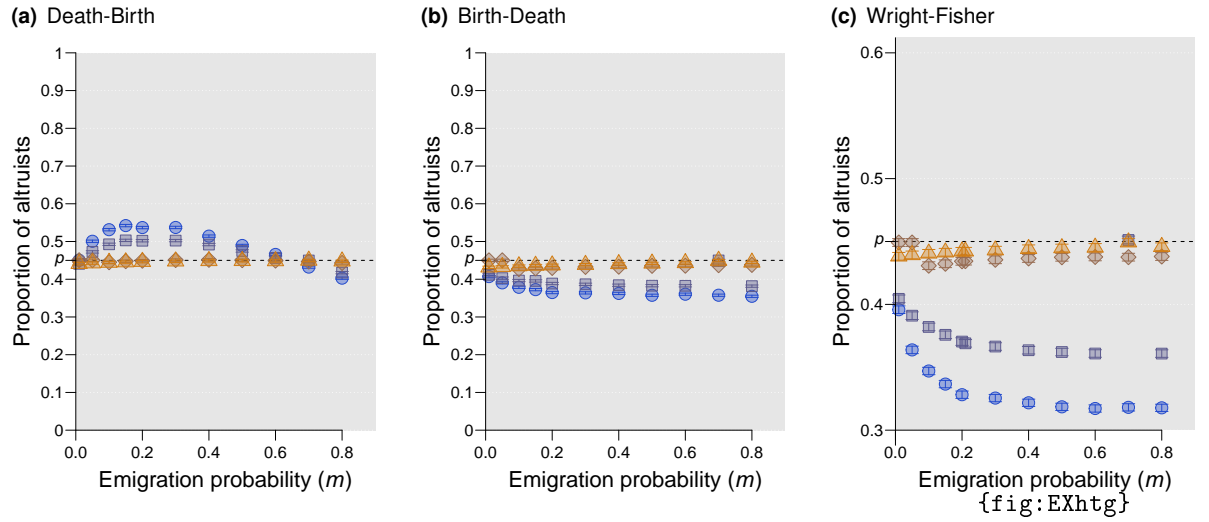
(a) Death-Birth   **(b)** Birth-Death   **(c)** Wright-Fisher

{fig:island_htgpop}
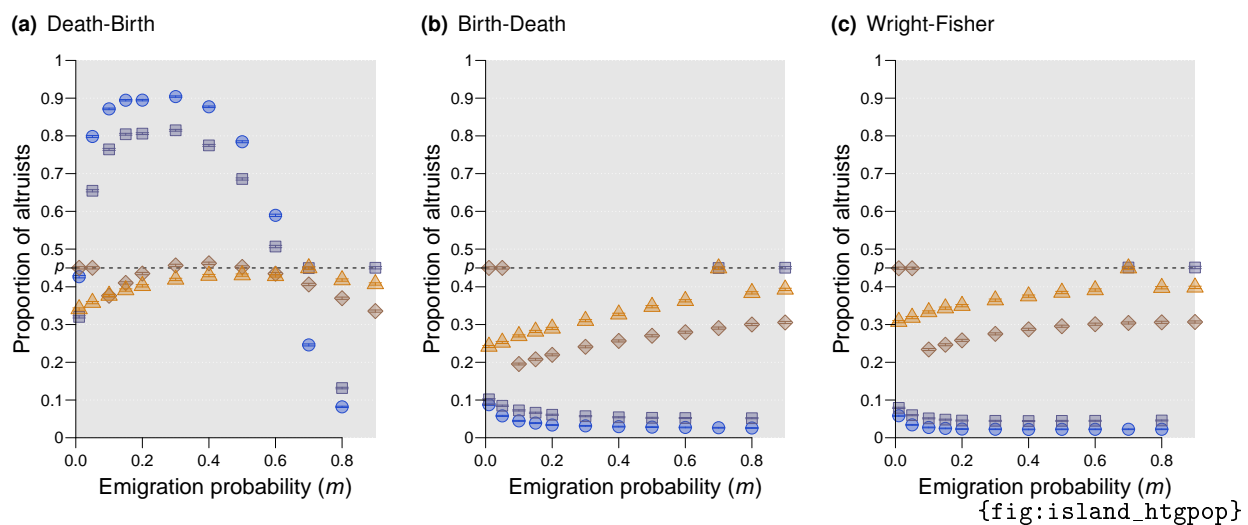
Figure S3: Strong selection, heterogeneous population

₄₂₇   Adaptation of my equations to a subdivided population. Notation, for a
₄₂₈ quantity Y that depends on two sites ($Y = e, d, Q$):

$$Y_{\text{self}} := Y_{i,i} \tag{.1a}$$

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

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

₄₂₉ For a site i, G_i denotes the deme the site belongs to, and notation $j \in G_i$ means
₄₃₀ that sites i and j are in the same deme.
₄₃₁   The expected frequency of altruists in the population is given by

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

Moran, Birth-Death

$$
\begin{aligned}
\beta^D_{\text{BD}} &= \sum_{k,\ell=1}^{N} \frac{1-\mu}{N} e_{kl} Q_{lk} \\
&= \sum_{k=1}^{N} \frac{1-\mu}{N} \Big(e_{\text{self}} + (n-1)\,e_{\text{in}}\,Q_{\text{in}} + (N-n)\,e_{\text{out}}\,Q_{\text{out}}\Big) \\
&= (1-\mu)\Big(e_{\text{self}} + (n-1)\,e_{\text{in}}\,Q_{\text{in}} + (N-n)\,e_{\text{out}}\,Q_{\text{out}}\Big). \tag{.3a}
\end{aligned}
$$

$$\beta_{\text{BD}}^I = \sum_{j,k,l=1}^{N} \left(\frac{d_{lj}}{N} - \frac{\mu}{N^2} \right) e_{kl} Q_{jk}$$

$$= \frac{1}{N} \sum_{j=1}^{N} \left[\left(\sum_{l=1}^{N} d_{lj} e_{jl} \right) + \sum_{\substack{k \in G_j \\ k \neq j}} \left(\sum_{l=1}^{N} d_{lj} e_{kl} Q_{\text{in}} Q_{\text{in}} \right) + \sum_{k \notin G_j} \sum_{l=1}^{N} d_{lj} \left(e_{kl} Q_{\text{out}} Q_{\text{out}} \right) \right]$$

$$+ \frac{\mu}{N^2} \sum_{j=1}^{N} \left(\sum_{l=1}^{N} e_{kl} \right) \left(\sum_{k=1}^{N} Q_{jk} \right)$$

$$= \frac{1}{N} \sum_{j=1}^{N} \left[d_{\text{self}} e_{\text{self}} + (n-1) d_{\text{in}} e_{\text{in}} + (N-n) d_{\text{out}} e_{\text{out}} \right.$$

$$+ \sum_{\substack{k \in G_j \\ k \neq j}} (d_{\text{in}} e_{\text{self}} + d_{\text{self}} e_{\text{in}} + (n-2) d_{\text{in}} e_{\text{in}} + (N-n) d_{\text{out}} e_{\text{out}}) Q_{\text{in}}$$

$$\left. + \sum_{k \notin G_j} (d_{\text{self}} e_{\text{out}} + (n-1) d_{\text{in}} e_{\text{out}} + d_{\text{out}} e_{\text{self}} + (n-1) d_{\text{out}} e_{\text{in}} + (N-2n) d_{\text{out}} e_{\text{out}}) Q_{\text{out}} \right]$$

$$- \frac{\mu}{N} (1 + (n-1) Q_{\text{in}} + (N-n) Q_{\text{out}}) (e_{\text{self}} + (n-1) e_{\text{in}} + (N-n) e_{\text{out}})$$

$$= d_{\text{self}} e_{\text{self}} + (n-1) d_{\text{in}} e_{\text{in}} + (N-n) d_{\text{out}} e_{\text{out}}$$

$$+ (n-1) (d_{\text{in}} e_{\text{self}} + d_{\text{self}} e_{\text{in}} + (n-2) d_{\text{in}} e_{\text{in}} + (N-n) d_{\text{out}} e_{\text{out}}) Q_{\text{in}}$$

$$+ (N-n) (d_{\text{self}} e_{\text{out}} + (n-1) d_{\text{in}} e_{\text{out}} + d_{\text{out}} e_{\text{self}} + (n-1) d_{\text{out}} e_{\text{in}} + (N-2n) d_{\text{out}} e_{\text{out}}) Q_{\text{out}}$$

$$- \frac{\mu}{N} (1 + (n-1) Q_{\text{in}} + (N-n) Q_{\text{out}}) (e_{\text{self}} + (n-1) e_{\text{in}} + (N-n) e_{\text{out}}). \quad \text{(.3b)}$$

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

$$\gamma_{\text{BD}}^I = \frac{1}{N} \sum_{j,k=1}^{N} \left(d_{kj} - \frac{\mu}{N} \right) Q_{jk}$$

$$= \frac{1}{N} \sum_{j=1}^{N} \left[d_{\text{self}} - \frac{\mu}{N} + (n-1) \left(d_{\text{in}} - \frac{\mu}{N} \right) Q_{\text{in}} + (N-n) \left(d_{\text{out}} - \frac{\mu}{N} \right) Q_{\text{out}} \right]$$

$$= d_{\text{self}} + (n-1) d_{\text{in}} Q_{\text{in}} + (N-n) d_{\text{out}} Q_{\text{out}}$$

$$- \frac{\mu}{N} (1 + (n-1) Q_{\text{in}} + (N-n) Q_{\text{out}}) \quad \text{(.3d)}$$

Moran, Death-Birth

$$\beta_{\text{DB}}^D = \frac{1-\mu}{N} \sum_{j,k=1}^{N} Q_{jk} e_{jk} = \beta_{\text{BD}}^D$$

$$= (1-\mu)\Big(e_{\text{self}} + (n-1)e_{\text{in}} Q_{\text{in}} + (N-n)e_{\text{out}} Q_{\text{out}}\Big). \tag{.4a}$$

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

432 Presented in the table in the appendix.

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

$$\gamma_{\text{DB}}^I = (1-\mu) \sum_{i,j,k=1}^{N} \frac{d_{ji} d_{ki}}{N} Q_{jk}$$

$$= \frac{1-\mu}{N} \sum_{j=1}^{N} \sum_{i=1}^{N} \Big(d_{ji} d_{ji} + \sum_{\substack{k\neq j \\ k\in G_j}} d_{ji} d_{ki} Q_{\text{in}} + \sum_{k\notin G_j} d_{ji} d_{ki} Q_{\text{out}}\Big)$$

$$= \frac{1-\mu}{N} \sum_{j=1}^{N} \Bigg[d_{\text{self}} d_{\text{self}} + (n-1) d_{\text{in}} d_{\text{in}} + (N-n) d_{\text{out}} d_{\text{out}}$$

$$+ (n-1)\Big(d_{\text{self}} d_{\text{in}} + d_{\text{in}} d_{\text{self}} + (n-2) d_{\text{in}} d_{\text{in}} + (N-n) d_{\text{out}} d_{\text{out}}\Big) Q_{\text{in}}$$

$$+ (N-n)\Big(d_{\text{self}} d_{\text{out}} + (n-1) d_{\text{in}} d_{\text{out}} + d_{\text{out}} d_{\text{self}} + (n-1) d_{\text{out}} d_{\text{in}} + (N-2n) d_{\text{out}} d_{\text{out}}\Big) Q_{\text{out}} \Bigg]$$

$$\tag{.4d}$$

433 **Probabilities of identity by descent**

434 <mark>WF est faux. Il faut utiliser les formules Fourier...!</mark>

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

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

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

$$Q_{\text{in}} = \frac{1-\mu}{2}\Big((d_{\text{in}} + d_{\text{self}}Q_{\text{in}}) + (d_{\text{self}}Q_{\text{in}} + d_{\text{in}})$$
$$+ (n-2)(d_{\text{in}}Q_{\text{in}} + d_{\text{in}}Q_{\text{in}}) + (N-n)(d_{\text{out}}Q_{\text{out}} + d_{\text{out}}Q_{\text{out}})\Big)$$
$$= (1-\mu)\Big(d_{\text{in}} + d_{\text{self}}Q_{\text{in}} + (n-2)d_{\text{in}}Q_{\text{in}} + (N-n)d_{\text{out}}Q_{\text{out}}\Big). \qquad (.5\text{b})$$

And for $j \notin G_i$,

$$Q_{\text{out}} = \frac{1-\mu}{2}\Big((d_{\text{out}} + d_{\text{self}}Q_{\text{out}}) + (n-1)(d_{\text{out}}Q_{\text{in}} + d_{\text{in}}Q_{\text{out}})$$
$$+ (d_{\text{self}}Q_{\text{out}} + d_{\text{out}}) + (n-1)(d_{\text{in}}Q_{\text{out}} + d_{\text{out}}Q_{\text{in}})$$
$$+ (N-2n)(d_{\text{out}}Q_{\text{out}} + d_{\text{out}}Q_{\text{out}})\Big)$$
$$= (1-\mu)\Big(d_{\text{out}} + d_{\text{self}}Q_{\text{out}} + (n-1)(d_{\text{out}}Q_{\text{in}} + d_{\text{in}}Q_{\text{out}}) + (N-2n)d_{\text{out}}Q_{\text{out}}\Big)$$
$$(.5\text{c})$$

Wright-Fisher For $j \neq i$,

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

25

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

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

And when $j \notin G_i$, we have

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

$$(.6c)$$

<mark>PAS FINI</mark>

Appendix

All combinations for i, j, k, l. Notation: (i, j) means that i and j are in the same deme, but are different; G_i refers to the deme containing site i.

	j	k	l	Notation	Count	d_{ji}	d_{li}	e_{kl}	Q_{jk}
1	$j=i$	$k=i$	$l=i$	$(i=j=k=l)$	1	d_{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	$j=i$	$k=i$	$l\not\in G_i$	$(i=j=k),(l)$	$N-n$	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	$j=i$	$k\neq i; k\in G_i$	$l\not\in G_i$	$(i=j,k),(l)$	$(n-1)(N-n)$	d_{self}	d_{out}	e_{out}	Q_{in}
8	$j=i$	$k\not\in G_i$	$l=i=j$	$(i=j=l),(k)$	$(N-n)$	d_{self}	d_{self}	e_{out}	Q_{out}
9	$j=i$	$k\not\in G_i$	$l\neq i, l\in G_i$	$(i=j,l),(k)$	$(N-n)(n-1)$	d_{self}	d_{in}	e_{out}	Q_{out}
10	$j=i$	$k\not\in G_i$	$l=k$	$(i=j),(k=l)$	$(N-n)$	d_{self}	d_{out}	e_{self}	Q_{out}
11	$j=i$	$k\not\in G_i$	$l\neq k; l\in G_k$	$(i=j),(k,l)$	$(N-n)(n-1)$	d_{self}	d_{out}	e_{in}	Q_{out}
12	$j=i$	$k\not\in G_i$	$l\not\in G_i, G_k$	$(i=j),(k),(l)$	$(N-n)(N-2n)$	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	$j\neq i, j\in G_i$	$k=i$	$l\not\in G_i$	$(i=k,j),(l)$	$(n-1)(N-n)$	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	$j\neq i, j\in G_i$	$k=j$	$l\not\in G_i$	$(i,j=k),(l)$	$(n-1)(N-n)$	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	$j\neq i, j\in G_i$	$k\neq i,j; k\in G_i$	$l\not\in G_i$	$(i,j,k),(l)$	$(n-1)(n-2)(N-n)$	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

A Island model

With self replacement

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

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

Without self-replacement

$$d_{\text{self}} = 0, \tag{A.8a}$$

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

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

B IDB

B.1 Moran

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

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

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

We have

$$\tilde{\mathcal{D}}_{\substack{q_1 \\ q_2}} = d_{\text{self}} + \sum_{l_2=1}^{N_2-1} d_{\text{in}} \exp\left(-\iota \frac{2\pi q_2 l_2}{N_2}\right) + \sum_{l_1=1}^{N_1-1} \sum_{l_2=0}^{N_2-1} d_{\text{out}} \exp\left(-\iota \frac{2\pi q_1 l_1}{N_1}\right) \exp\left(-\iota \frac{2\pi q_2 l_2}{N_2}\right)$$

$$= d_{\text{self}} + \left(\delta_{q_2}(N_2-1) + (1-\delta_{q_2})(-1)\right) d_{\text{in}} + \left(\delta_{q_1}(N_1-1) + (1-\delta_{q_1})(-1)\right)\left(\delta_{q_2} N_2\right) d_{\text{out}}$$

$$= d_{\text{self}} + \left(\delta_{q_2} N_2 - 1\right) d_{\text{in}} + \left(\delta_{q_1} N_1 - 1\right) \delta_{q_2} N_2 d_{\text{out}}. \tag{B.10a}$$

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

$$\tilde{\mathcal{D}}_{\substack{0 \\ 0}} = 1, \tag{B.11a}$$

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

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

So for $\tilde{\mathcal{Q}}$,

$$\tilde{\mathcal{Q}}_{\substack{r_1 \\ r_2}} = \frac{\mu \lambda_M'}{N} \left[\frac{1}{1-(1-\mu)\tilde{\mathcal{D}}_{\substack{0 \\ 0}}} + \sum_{q_2=1}^{N_2-1} \frac{1}{1-(1-\mu)\tilde{\mathcal{D}}_{\substack{0 \\ q_2}}} \exp\left(-\iota \frac{2\pi q_2 r_2}{N_2}\right) + \sum_{q_1=1}^{N_1-1} \frac{1}{1-(1-\mu)\tilde{\mathcal{D}}_{\substack{q_1 \\ 0}}} \exp\left(-\iota \frac{2\pi q_1 r_1}{N_1}\right) \right.$$

$$\left. + \sum_{q_1=1}^{N_1-1}\sum_{q_2=1}^{N_2-1} \frac{1}{1-(1-\mu)\tilde{\mathcal{D}}_{\substack{q_1 \\ q_2}}} \exp\left(-\iota \frac{2\pi q_1 r_1}{N_1}\right) \exp\left(-\iota \frac{2\pi q_2 r_2}{N_2}\right) \right]$$

$$= \frac{\mu \lambda_M'}{N} \left[\frac{1}{1-(1-\mu)} + \frac{1}{1-(1-\mu)(d_{\text{self}}-d_{\text{in}})}(\delta_{r_2} N_2 - 1) + \frac{1}{1-(1-\mu)(1-m-\frac{m}{d-1})}(\delta_{r_1} N_1 - 1) \right.$$

$$\left. + \frac{1}{1-(1-\mu)(d_{\text{self}}-d_{\text{in}})}(\delta_{r_1} N_1 - 1)(\delta_{r_2} N_2 - 1) \right]. \tag{B.12a}$$

In particular,

$$\tilde{\mathcal{Q}}_{\substack{0 \\ 0}} = \frac{\mu \lambda_M'}{N} \left[\frac{1}{\mu} + \frac{1}{1-(1-\mu)(d_{\text{self}}-d_{\text{in}})}(n-1) + \frac{1}{1-(1-\mu)(1-m-\frac{m}{d-1})}(D-1) \right.$$

$$\left. + \frac{1}{1-(1-\mu)(d_{\text{self}}-d_{\text{in}})}(D-1)(n-1) \right]$$

$$= 1. \tag{B.12b}$$

We find λ_M' using the above equation. When $r_1 = 0$, the two individuals are in the same deme. They are different when $r_2 \not\equiv 0$:

$$Q_{\text{in}} = \frac{\mu \lambda_M'}{N} \left[\frac{1}{\mu} + \frac{1}{1-(1-\mu)(d_{\text{self}}-d_{\text{in}})}(-1) + \frac{1}{1-(1-\mu)(1-m-\frac{m}{d-1})}(D-1) \right.$$

$$\left. + \frac{1}{1-(1-\mu)(d_{\text{self}}-d_{\text{in}})}(D-1)(-1) \right]. \tag{B.12c}$$

And when $r_1 \not\equiv 0$, the two individuals are in different demes:

$$Q_{\text{out}} = \frac{\mu \lambda_M'}{N} \left[\frac{1}{\mu} + \frac{1}{1-(1-\mu)(d_{\text{self}}-d_{\text{in}})}(-1) + \frac{1}{1-(1-\mu)(1-m-\frac{m}{d-1})}(-1) \right.$$

$$\left. + \frac{1}{1-(1-\mu)(d_{\text{self}}-d_{\text{in}})} \right]. \tag{B.12d}$$

B.2 Wright-Fisher

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

$$= \frac{1}{N}\left[\frac{\mu \lambda'_{WF}}{1-(1-\mu)^2(\tilde{\mathcal{D}}_{\substack{0 \\ 0}})^2} + \sum_{q_2=1}^{N_2-1} \frac{\mu \lambda'_{WF}}{1-(1-\mu)^2(\tilde{\mathcal{D}}_{\substack{0 \\ q_2}})^2} \exp\left(-\iota \frac{2\pi q_2 r_2}{N_2}\right) \right.$$

$$+ \sum_{q_1=1}^{N_1-1} \frac{\mu \lambda'_{WF}}{1-(1-\mu)^2(\tilde{\mathcal{D}}_{\substack{q_1 \\ 0}})^2} \exp\left(-\iota \frac{2\pi q_1 r_1}{N_1}\right)$$

$$\left. + \sum_{q_1=1}^{N_1-1} \sum_{q_2=1}^{N_2-1} \frac{\mu \lambda'_{WF}}{1-(1-\mu)^2(\tilde{\mathcal{D}}_{\substack{q_1 \\ q_2}})^2} \exp\left(-\iota \frac{2\pi q_1 r_1}{N_1}\right) \exp\left(-\iota \frac{2\pi q_2 r_2}{N_2}\right) \right] \quad \text{(B.13)}$$

$$= \frac{\mu \lambda'_{WF}}{N}\left[\frac{1}{1-(1-\mu)^2} + \frac{1}{1-(1-\mu)^2(d_{\text{self}}-d_{\text{in}})^2}(\delta_{q_2} N_2 - 1) \right.$$

$$+ \frac{1}{1-(1-\mu)^2(1-m-\frac{m}{d-1})^2}(\delta_{q_1} N_1 - 1)$$

$$\left. + \frac{1}{1-(1-\mu)^2(d_{\text{self}}-d_{\text{in}})^2}(\delta_{q_1} N_1 - 1)(\delta_{q_2} N_2 - 1) \right]$$

$$= \frac{\mu \lambda'_{WF}}{N}\left[\frac{1}{1-(1-\mu)^2} + \frac{1}{1-(1-\mu)^2(d_{\text{self}}-d_{\text{in}})^2}(\delta_{q_2} N_2 - 1)\delta_{q_1} N_1 \right.$$

$$\left. + \frac{1}{1-(1-\mu)^2(1-m-\frac{m}{d-1})^2}(\delta_{q_1} N_1 - 1) \right]. \quad \text{(B.14)}$$

459 To find λ'_{WF}, we solve

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

460 Then,

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

461 and

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