Article Title: Imperfect strategy transmission can reverse the role of population viscosity on the evolution of altruism .

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1 Abstract

2 Population viscosity, *i.e.*, low emigration out of the natal deme, leads to high

3 within-deme relatedness, which is beneficial to the evolution of altruistic behav-

4 ior when social interactions take place among deme-mates. At the same time

5 however, it increases competition among related individuals. The evolution of

6 altruism depends on the balance between these opposite effects. This balance

7 is already known to be affected by details of the life-cycle; we show here that

8 it further depends on the fidelity of strategy transmission from parents to their

9 offspring. We consider different life-cycles (Wright-Fisher, with synchronous

10 non-overlapping generations, Moran Death-Birth and Moran Birth-Death, both

11 with exactly one individual dying and reproducing at each time step) and we

12 identify thresholds of parent-offspring strategy transmission inaccuracy, above

13 which the effect of population viscosity on the frequency of altruists maintained

14 in the population qualitatively changes. Analytical predictions are first obtained

15 analytically under weak selection and equal deme sizes, then confirmed with

16 stochastic simulations relaxing these assumptions. This result challenges the

17 notion that the evolution of altruism requires limited dispersal.

Impact Summary

The evolution of altruistic behavior has fascinated and puzzled evolutionary biologists for a long time: how can a strategy whereby individuals help others at their own cost be maintained in a population? One answer is the fact that altruists may interact with other altruists more often than non-altruists do, a situation made possible by spatial structure and low emigration. Low emigration indeed means that an individual is mostly surrounded by related individuals; when social strategies are faithfully transmitted from parents to offspring, and social interactions are local as well, then altruists interact mainly with other altruists. However, this also means that related individuals have to compete against each other. Whether altruism eventually evolves depends on the balance between these beneficial and detrimental consequences of low emigration. Previous work has shown that the balance depends on the life-cycle that the population undergoes; under nearly perfect strategy transmission, low emigration goes from being neutral to the evolution of altruism (when generations are synchronous and non-overlapping) to favorable. In this work, we show that this conclusion qualitatively changes when offspring do not necessarily adopt their parent's strategy, that is, when strategy transmission is imperfect. This can be due to mutation when transmission is genetic, but also to imperfect vertical cultural transmission. We identify thresholds of strategy transmission infidelity, above which higher emigration is more conducive to the evolution of altruism than low emigration. The predictions are first obtained mathematically under the restrictive assumptions that selection is weak and that all demes have the same size, but are then confirmed with computer simulations relaxing these assumptions. This work shows that the evolution of altruism does not require – and even can be hampered by – low emigration.

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., 2007a; 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 (West et al., 2002). 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 (1992a) in a model with synchronous generations (*i.e.*, Wright-Fisher model) and a subdivided population of constant, infinite size. The cancellation result was later extended to heterogeneous populations (Rodrigues & Gardner, 2012, with synchronous generations and infinite population size), and other life-cycles, with generic 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. In this study, we will

consider three different life-cycles: Wright-Fisher, where the whole population is renewed at each time step, and two Moran life-cycles (Birth-Death and Death-Birth), where a single individual dies and is replaced at each time step.

A large number of studies on the evolution of social behavior consider simple population structures (typically, homogeneous populations *sensu* Taylor et al. (2007a)) and often also infinite population sizes (but see Allen et al., 2017, for results on any structure). These studies also make use of weak selection approximations, and commonly assume rare (*e.g.*, Leturque & Rousset, 2002; Taylor et al., 2007b; Tarnita & Taylor, 2014) or absent mutation (for models assuming infinite population sizes, or models concentrating on fixation probabilities Lehmann & Rousset, 2014; Van Cleve, 2015, for recent reviews). Often, these simplifying assumptions are a necessary step towards obtaining explicit analytical results. Although artificial, simple population structures (*e.g.*, regular graphs, or subdivided populations with demes of equal sizes) help reduce the dimensionality of the system under study, in particular when the structure of the population displays symmetries such that all sites behave the same way in expectation. Weak selection approximations are crucial for disentangling spatial moments (Lion, 2016), that is, changes in global *vs.* local frequencies (though they can in some cases be relaxed, as in Mullon & Lehmann, 2014). Mutation, however, is usually ignored by classical models of inclusive fitness because these models assume infinite population sizes, so that there is no need to add mechanisms that restore genetic diversity (Tarnita & Taylor, 2014). In populations of finite size, this diversifying effect can be obtained thanks to mutation.

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)) does not have to be rare. Imperfect strategy transmission can alter evolutionary dynamics, in particular in spatially struc-

tured populations (see *e.g.*, Allen et al., 2012; Débarre, 2017, for graph-structured populations). Here, we want to explore the consequences of imperfect strategy transmission from parents to their offspring on the evolution of altruistic behavior in subdivided populations. For the sake of concision, we use the word "mutation" throughout the paper, keeping in mind that strategy transmission does not have to be genetic.

For each of the three life-cycles that we consider, we compute the expected (*i.e.*, long-term) frequency of altruists maintained in a subdivided population, and investigate how it is affected by mutation and emigration. We find that, contrary to what happens with perfect strategy transmission, higher emigration can increase 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.*, each deme contains 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. The type of the individual living at site i ($1 \leq i \leq N$) is given by an indicator variable X_i, equal to 1 if the individual is an altruist, and to 0 if it is a defector. The state of the entire population is given by a N-long vector $\mathbf{X}$. For a given population state $\mathbf{X}$, the proportion of altruists is $\overline{X} = \sum_{i=1}^{N} X_i$. All symbols are summarized in table S1.

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

125 parent but instead get one randomly: with probability v, they become altruists,

126 with probability $1 - v$ they become defectors. We call the parameter v the muta-

127 tion bias.

128 An individual of type X_k expresses a social phenotype $\phi_k = \delta X_k$, where δ is

129 assumed to be small ($\delta \ll 1$). Social interactions take place within each deme;

130 each individual interacts with the $n - 1$ other deme members. Denoting by e_{ij}

131 the interaction probability between individuals living at sites i and j, we have

132 $e_{ij} = 1/(n-1)$ if i and j are two different sites in the same deme, and $e_{ij} = 0$

133 otherwise. We assume that social interactions affect individual fecundity; f_k de-

134 notes the fecundity of the individual at site k. The baseline fecundity, *i.e.* indi-

135 vidual fecundity when no altruists are present in the population, is set equal to 1.

136 We denote by b the marginal effect of a deme-mate's phenotype on the fecundity

137 of a focal individual, and by $-c$ the marginal effect of a focal individual's pheno-

138 type on its own fecundity ($c \le b$). With these assumptions are notation, at the

139 first order in δ, the fecundity of the individual living at site k is given by ____ remove?

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

140 Offspring remain in the parental deme with probability $1 - m$; when they

141 do, they land on any site of the deme with equal probability (including the very

142 site of their parent). With probability m, offspring emigrate to a different deme,

143 chosen uniformly at random among the other demes. Denoting by d_{ij} the prob-

144 ability of moving from site i to site j, we have

$$d_{ij} = \begin{cases} d_{\text{in}} = \frac{1-m}{n} & \text{if both sites are in the same deme;} \\[2ex] d_{\text{out}} = \frac{m}{(N_D-1)n} & \text{if the two sites are in different demes,} \end{cases} \qquad (2) \quad \{\text{eq:defD}\}$$

145 with $0 < m < 1 - \frac{1}{N_D}$ (the upper bound implies $d_{\text{in}} > d_{\text{out}}$).

146 We denote by $B_i = B_i(\mathbf{X}, \delta)$ the expected number of successful offspring of the

individual living at site i (successful means alive at the next time step), and by $D_i = D_i(\mathbf{X}, \delta)$ the probability that the individual living at site i dies. Both depend on the state of the population $\mathbf{X}$, but also on the way the population is updated from one time step to the next, *i.e.*, on the chosen life-cycle (also called updating rule). We will specifically explore three different 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.

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

2.2 Methods

2.2.1 Analytical part

The calculation steps to obtain the expected (*i.e.*, long-term) proportion of altruists are given in Appendix A. They go as follows: first, we write an equation for the expected frequency of altruists in the population at time $t + 1$, conditional on the composition of the population at time t; we then take the expectation of this quantity and consider large times t. After this, we write a first order expansion for phenotypic differences δ close to 0 (this corresponds to weak selection approximation).

The formula involves quantities that can be identified as neutral probabilities of identity by descent Q_{ij}, *i.e.*, the probability that individuals living at site i and j share a common ancestor and that no mutation occurred on either lineage since that ancestor, in a model with no selection ($\omega = 0$; this is the "mutation definition" of identity by descent (Rousset & Billiard, 2000).)

These neutral probabilities of identity by descent depend on the chosen life-cycle, and are also computed by taking the long-term expectation of conditional expectations after one time step (see Appendix A.2 and B.2).

All the results obtained analytically were checked numerically using specific population structures (see supplementary Mathematica file (Wolfram Research, Inc., 2017).)

2.2.2 Stochastic simulations

We also ran stochastic simulations (coded in C). The simulations were run for 10^8 generations (one generation is one time step for the Wright-Fisher life-cycle, and N time steps for the Moran life-cycles). For each set of parameters and life-cycle, using R (R Core Team, 2015), we estimated the long-term frequency of altruists by sampling the population every 10^3 generations and computing the average frequency of altruists.

All scripts are available at

https://github.com/flodebarre/SocEvolSubdivPop/tree/master/Programs

3 Results

3.1 Probabilities of identity by descent

As we will see later, the expected frequencies of altruists in the population depend on probabilities of identity by descent of pairs of sites, Q_{ij}. Two individuals are said to be identical by descent if there has not been any mutation on either lineage since their common ancestor. Because of the structure of the population, there are only three types of pairs of individuals, and hence three different values of the probabilities of identity by descent of pairs of sites Q_{ij}:

$$Q_{ij} = \begin{cases} 1 & \text{when } i = j; \\ Q_{\text{in}} & \text{when } i \neq j \text{ and both sites are in the same deme;} \\ Q_{\text{out}} & \text{when sites } i \text{ and } j \text{ are in different demes.} \end{cases} \quad (3)$$

The values of Q_{in} and Q_{out} depend on the type of life-cycle that we consider.

3.1.1 Moran updating

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

$$Q_{ij}^{\text{M}} = \frac{1-\mu}{2} \sum_{k=1}^{N} \left(d_{kj} Q_{ki}^{\text{M}} + d_{ki} Q_{kj}^{\text{M}} \right). \quad (4)$$

Given the law of total probabilities, we first consider the site that was last updated ($1/2$ chance that it was j rather than i); then we consider each potential parent k, weighted by the dispersal probabilities d_{kj}. Then the individuals at sites i and j are identical by descent (IBD) if i and j's parent were IBD (Q_{ki}^{M}) and if no mutation occurred ($1-\mu$). Replacing the dispersal probabilities d_{ij} by their values (given in eq. (2)), we eventually obtain (see Appendix A.2 for calculation

$$Q_{\text{in}}^{\text{M}} = \frac{(1-\mu)\left(m + \mu(N_D(1-m)-1)\right)}{(1-\mu)m(N_D\mu(n-1)+1) + (N_D-1)\mu(\mu(n-1)+1)}, \qquad (5a)$$

$$Q_{\text{out}}^{\text{M}} = \frac{(1-\mu)m}{(1-\mu)m(N_D\mu(n-1)+1) + (N_D-1)\mu(\mu(n-1)+1)}. \qquad (5b)$$

212 The probability that two different deme-mates are identical by descent, Q_{in}^{M}, de-

213 creases monotonically with the emigration probability m, while $Q_{\text{out}}^{\text{M}}$ monoton-

214 ically increases with m (see figure 1(a)).

215   When the mutation probability μ is vanishingly small ($\mu \to 0$), both Q_{in}^{M} and

216 $Q_{\text{out}}^{\text{M}}$ are equal to 1: in the absence of mutation indeed, the population ends up

217 fixed for one of the two types, and all individuals are identical by descent. Note

218 that we obtain a different result if we first assumed that the size of the popu-

219 lation is infinite ($N_D \to \infty$), because the order of limits matters; for instance,

220 $\lim_{d\to\infty} Q_{\text{out}}^{M} = 0$.

3.1.2   Wright-Fisher updating

222 Under a Wright-Fisher life-cycle, generations are synchronous: all individuals

223 are replaced at each time step. Probabilities of identity by descent satisfy, for any

224 pair of sites i and $j \neq i$

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

225 The sum is over all possible parents k and ℓ of i and j, weighted by the disper-

226 sal probabilities to sites i and j; the individuals at sites i and j are identical by

227 descent if their parents were ($Q_{k\ell}$) and if neither mutated ($(1-\mu)^2$).

228   Replacing the dispersal probabilities d_{ij} by their values (given in eq. (2)) and

`{eq:QWF}`

$$Q_{\text{in}}^{\text{WF}} = \frac{-N_D + M_1 + M_2}{(n-1)N_D + M_1 + M_2}, \tag{7a}$$

$$Q_{\text{out}}^{\text{WF}} = \frac{-\frac{1}{N_D-1}M_1 + M2}{(n-1)N_D + M_1 + M_2}, \tag{7b}$$

with

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

(These formulas are compatible with, *e.g.*, results presented by Cockerham & Weir (1987), adapted for haploid individuals).

In the Wright-Fisher life-cycle, $Q_{\text{in}}^{\text{WF}}$ decreases until $m = m_c^{\text{WF}} = \frac{d-1}{d}$, then increases again, while Q_{out}^{WF} follows the opposite pattern. The threshold value m_c^{WF} 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 (*i.e.*, $d_{\text{in}} = d_{\text{out}}$).

The two probabilities of identity by descent go to 1 when the mutation probability μ is very small ($\mu \to 0$), except if we first assume that the number of demes is very large ($N_D \to \infty$); for instance, with this life-cycle as well, $\lim_{N_D \to \infty} Q_{\text{out}}^{\text{WF}} = 0$.

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 (compare figure 1(a) and 1(b)).

3.2 Expected frequencies of altruists for each life-cycle

For each of the life-cycles that we consider, the expected frequency of altruists in the population, $\mathbb{E}[\overline{X}]$, can be approximated as

$$\mathbb{E}[\overline{X}] \approx \nu + \omega \frac{\nu(1-\nu)}{\mu} \left[\mathsf{b}\left(\beta_{\mathrm{D}} - \beta_{\mathrm{I}}\right) - \mathsf{c}\left(\gamma_{\mathrm{D}} - \gamma_{\mathrm{I}}\right) \right]. \qquad (8) \quad \texttt{\{eq:EXapprox\}}$$

(Calculations leading to eq. (8) are presented in Appendix A.)

The mutation bias ν corresponds to the expected proportion of altruists in the population in the absence of selection (*i.e.*, when $\omega = 0$); ω is the parameter that scales the effects of interactions between individuals, which is assumed to be small. The subscript $_{\mathrm{D}}$ refers to "direct" effects, and the subscript $_{\mathrm{I}}$ to "indirect" effects. "Direct" effects involve effects on primary beneficiaries of the benefits (b) and costs (c) of social interactions (West & Gardner, 2010), *i.e.*, social interactants (for the benefits b) and the focal individuals themselves (for the costs c). "Indirect" effects corresponds to effects on secondary interactants, *i.e.*, to (kin) competition. By providing a benefit to a deme-mate and thereby increasing its fecundity, a focal altruist indirectly harms others by reducing their relative fecundity (β_{I} term in eq. (8)); by having a reduced fecundity due to the cost of altruism, a focal altruist indirectly favors others by increasing their relative fecundity (γ_{I} term).

We now present the values of these different terms for the three life-cycles under study.

3.2.1 Direct effects

Direct (/primary) effects are similar for the three life-cycles; the only difference is the value of probabilities of identity by descent Q (as seen in the previous sec-

266 tion, they differ between Moran and Wright-Fisher life-cycles): {eq:directeffects}

$$\beta_{\mathrm{D}}^{\mathrm{BD}} = \beta_{\mathrm{D}}^{\mathrm{DB}} = \left(1 - \mu\right) Q_{\mathrm{in}}^{\mathrm{M}}, \tag{9a} \quad \texttt{\{eq:bBDD\}}$$

$$\beta_{\mathrm{D}}^{\mathrm{WF}} = \left(1 - \mu\right) Q_{\mathrm{in}}^{\mathrm{WF}}; \tag{9b} \quad \texttt{\{eq:bWFD\}}$$

$$\gamma_{\mathrm{D}}^{\mathrm{BD}} = \gamma_{\mathrm{D}}^{\mathrm{BD}} = \gamma_{\mathrm{D}}^{\mathrm{WF}} = 1 - \mu. \tag{9c} \quad \texttt{\{eq:cBDD\}}$$

267 For both benefits and costs, direct effects only count when there is no mutation
268 (hence the $(1 - \mu)$ factors). Direct effects of benefits b (eq. (9a) and eq. (9b)) only
269 count if the interaction takes place with an individual who is identical by de-
270 scent. With the population structure that we consider, social interactions only
271 occur within demes, so only Q_{in} is present in eq. (9a) and eq. (9b). On the other
272 hand, the direct effect of the fecundity cost c (eq. (9c)) does not depend on the
273 type of interactant, since the same cost c is paid by altruists irrespective of the
274 interactant's identity.

275   As seen in the previous section, $Q_{\mathrm{in}}^{\mathrm{M}}$ and $Q_{\mathrm{in}}^{\mathrm{WF}}$ decrease with the emigration
276 probability m (actually only until $m = \frac{d-1}{d}$ for the latter). Consequently, the mag-
277 nitude of the direct (beneficial) effects of benefits b provided by altruists (β_{D})
278 decreases when the emigration probability m increases, while the direct (detri-
279 mental) effects (γ_{D}) due to the direct cost of altruism c are constant. As a result,
280 if we only considered direct effects, we would conclude that more emigration m
281 is detrimental to the evolution of altruistic behaviour. However, there are also
282 indirect effects at play.

283 ### 3.2.2 Indirect effects

284 Indirect (/secondary) effects are collateral effects on other individuals; they de-
285 pend on the type of life-cycle, and always involve individuals who are identical
286 by descent.

Moran Birth-Death Changing the fecundity of a focal individual has two kinds of indirect effects on others: *i*) it changes 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 changes 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 identical-by-descent to it. For this life-cycle, the indirect effects are:

$$
\begin{aligned}
\beta_{\mathrm{I}}^{\mathrm{BD}} &= (1-m)\left(\frac{n-1}{n}Q_{\mathrm{in}}^{\mathrm{M}} + \frac{1}{n}\right) + m\,Q_{\mathrm{out}}^{\mathrm{M}} - \mu\frac{1 + (n-1)Q_{\mathrm{in}}^{\mathrm{M}} + n(d-1)Q_{\mathrm{out}}^{\mathrm{M}}}{nd} \\
&= \gamma_{\mathrm{I}}^{\mathrm{BD}}.
\end{aligned}
\tag{10a}
$$
{eq:bBDI}

(Calculation details are presented in Appendix A.)

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

Replacing Q_{in} and Q_{out} by their formula for the Moran life-cycle (eq. (5)), we conclude that $\beta_{\mathrm{I}}^{\mathrm{BD}} = \gamma_{\mathrm{I}}^{\mathrm{BD}}$ are decreasing functions of the emigration probability m (calculations in the supplementary Mathematica file).

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

descent to it. We obtain

$$\beta_{\mathrm{I}}^{\mathrm{DB}} = (1-\mu)\left[\left(\frac{1}{n} + \frac{(n-1)Q_{\mathrm{in}}^{\mathrm{M}}}{n}\right)\left((1-m)^2 + \frac{m^2}{(d-1)}\right) \right.$$
$$\left. + Q_{\mathrm{out}}^{\mathrm{M}}\left(2m(1-m) + (d-2)\frac{m^2}{(d-1)}\right)\right] \qquad \text{(10b)} \quad \texttt{\{eq:bDBI\}}$$
$$= \gamma_{\mathrm{I}}^{\mathrm{DB}}$$

The brackets in eq. (10b) contain a sum of two terms. The first term corresponds two individuals from the same deme (with replacement) whose offspring either do not emigrate, or emigrate together to the same deme. The second term corresponds to individuals initially from different demes who end up in the same deme (either one of their home demes, or a third deme).

Here again, $\beta_{\mathrm{I}} = \gamma_{\mathrm{I}}$, so the balance between indirect benefits and indirect costs does not change when the emigration probability m increases.

Replacing Q_{in} and Q_{out} by their formulas given in eq. (5), we can conclude that $\beta_{\mathrm{I}}^{\mathrm{DB}} = \gamma_{\mathrm{I}}^{\mathrm{DB}}$ first decreases with the emigration probability m, and increases again after a threshold value m_c', which is smaller than $m_c^{\mathrm{WF}} = (d-1)/d$) (calculation details are presented in the supplementary Mathematica file).

Wright-Fisher   With this life-cycle, generations are synchronous and all individuals again all have the same survival probability (now equal to 0 at all sites). As a result, the formulas for $\beta_{\mathrm{I}}^{\mathrm{WF}}$ and $\gamma_{\mathrm{I}}^{\mathrm{WF}}$ are the same as $\beta_{\mathrm{I}}^{\mathrm{DB}}$ and $\gamma_{\mathrm{I}}^{\mathrm{WF}}$, except that instead of $Q_{\mathrm{in}}^{\mathrm{M}}$ and $Q_{\mathrm{out}}^{\mathrm{M}}$, we need to use $Q_{\mathrm{in}}^{\mathrm{WF}}$ and $Q_{\mathrm{out}}^{\mathrm{WF}}$ (given in eq. (7)). Once this is done, we see that $\beta_{\mathrm{I}}^{\mathrm{WF}} = \gamma_{\mathrm{I}}^{\mathrm{WF}}$ first decreases with the emigration probability m, and increases again after the threshold value $m_c^{\mathrm{WF}} = (d-1)/d$. This emigration threshold was identified above as the emigration probability such that offspring have an equal chance of landing in their natal deme or in any other deme, *i.e.*, $d_{\mathrm{in}} = d_{\mathrm{out}}$ (calculation details are presented in the supplementary Mathematica file.)

3.3 Identifying threshold values of the mutation probability μ

In the previous section, we investigated the impact of changes in the emigration probability m on each of the terms that make up the expected frequency of altruists $\mathbb{E}[\overline{X}]$. Now we need to combine these different terms to focus on the quantity we are eventually interested in, $\mathbb{E}[\overline{X}]$. The rather lengthy formulas that we obtain are relegated to the Appendixand supplementary Mathematica file, and we concentrate here on the results.

3.3.1 Moran Birth-Death

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

$$\mu_c^{\text{BD}} = 1 - \frac{\text{b} - \text{c} + \sqrt{(\text{b} - \text{c})\left(4\text{b}(nd)^2 + \text{b} - \text{c}\right)}}{2\text{b}nd} \tag{11} \quad \{\text{eq:mucBD}\}$$

This result is illustrated in figure 2(b); with the parameters of the figure, $\mu_c^{\text{BD}} \approx 0.026$.

3.3.2 Moran Death-Birth

The relationship between $\mathbb{E}[\overline{X}]$ and m is a bit more complicated for this life-cycle. For simplicity, we concentrate on what happens starting from low emigration probabilities (*i.e.*, the sign of the slope of $\mathbb{E}[\overline{X}]$ as a function of m when $m \to 0$). If the benefits b provided by altruists are relatively low (b $< \text{c}(n + 1)$), $\mathbb{E}[\overline{X}]$ initially increases with m provided the mutation probability μ is greater than a threshold value μ_c^{DB} given in eq. (12) below; otherwise, when the benefits are high enough, $\mathbb{E}[\overline{X}]$ initially increases with m for any value of μ. Combining

³⁵⁴ these results, we write

$$\mu_c^{\mathrm{DB}} = \begin{cases} \dfrac{(n+1)\mathsf{c} - \mathsf{b}}{(2n-1)\mathsf{b} - (n-1)\mathsf{c}} & \text{if } \mathsf{b} < \mathsf{c}(n+1), \\ 0 & \text{otherwise.} \end{cases} \qquad (12) \quad \{\mathrm{eq:mucDB}\}$$

³⁵⁵ In figure 2(a), the parameters are such that $\mu_c^{\mathrm{DB}} = 0$.

³⁵⁶   The expected frequency of altruists $\mathbb{E}\big[\overline{X}\big]$ then reaches a maximum at an em-
³⁵⁷ igration probability m_c^{DB} (whose complicated equation is given in the supple-
³⁵⁸ mentary Mathematica file), as can be seen in figure 2(a). When the mutation
³⁵⁹ probability gets close to 0 ($\mu \to 0$), m_c^{DB} also gets close to 0,

³⁶⁰ 3.3.3 Wright-Fisher

³⁶¹ The expected frequency of altruists in the population reaches an extremum when
³⁶² $m = m_c^{\mathrm{WF}} = \frac{d-1}{d}$. This extremum is a maximum when the mutation probability
³⁶³ is higher than a threshold value μ_c^{WF} given by

$$\mu_c^{\mathrm{WF}} = 1 - \sqrt{1 - \frac{\mathsf{c}}{\mathsf{b}}}, \qquad (13)$$

³⁶⁴ and it is a minimum otherwise. With the parameters of figure 2(c), $\mu_c^{\mathrm{WF}} = 0.034$.

³⁶⁵ 3.4 Relaxing key assumptions

³⁶⁶ To derive our analytical results, we had to make a number of simplifying assump-
³⁶⁷ tions, such as the fact that selection is weak ($\omega \ll 1$), and the fact that the struc-
³⁶⁸ ture of the population is regular (all demes have the same size n). We explored
³⁶⁹ with numerical simulations the effect of relaxing these key assumptions. When
³⁷⁰ selection is strong, the patterns that we identified not only still hold but are even
³⁷¹ more marked, as shown on figure S1.

³⁷²   To relax the assumption of equal deme sizes, we randomly drew deme sizes
³⁷³ at the beginning of simulations, with sizes ranging from 2 to 6 individuals and

374 on average $\overline{n} = 4$ individuals per deme as previously. As shown in figure S2, the
375 patterns initially obtained with a homogeneous population structure are robust
376 when the structure is heterogeneous.

377   For the Moran model, it may seem odd that an offspring can replace its own
378 parent (which can occur since $d_{ii} \neq 0$). Figure S3, plotted with dispersal prob-
379 abilities preventing immediate replacement of one's own parent (for all sites i,
380 $d_{ii} = d_{\text{self}} = 0$; $d_{\text{in}} = (1 - m)/(n - 1)$ for two different sites in the same deme, d_{out}
381 remaining unchanged), confirms that this does affect our conclusions.

382   4   Discussion

383 The expected frequency of altruists in a subdivided population can in-
384 crease with the probability of emigration

385 Assuming that the transmission of a social strategy (being an altruist or a defec-
386 tor) from a parent to its offspring could be imperfect, we found that the expected
387 frequency of altruists maintained in a population could increase with the prob-
388 ability m of emigration out of the parental deme, a parameter tuning population
389 viscosity. This result can seem surprising, because it contradicts the conclusions
390 obtained under the assumption of nearly perfect strategy transmission (*i.e.*, in
391 the case of genetic transmission, when mutation is very weak or absent). Under
392 nearly perfect strategy transmission indeed, increased population viscosity (*i.e.*,
393 decreased emigration probability) is either neutral (Taylor, 1992a, and dashed
394 lines in figures 2(b)–(c)) or favorable (Taylor et al., 2007a, and dashed lines in
395 figure 2(a)) to the evolution of altruistic behavior.

396 Quantitative vs. qualitative measures

397 We used a quantitative measure, the expected frequency of altruists in the popu-
398 lation ($\mathbb{E}[\overline{X}]$), to explore how non-zero mutation probabilities altered the impact

of population viscosity. Often however, evolutionary success is measured quali-
tatively, 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 model, this amounts to saying that altruism is favored whenever
$\mathbb{E}\left[\overline{X}\right] > \nu$ (ν is plotted as a horizontal dashed line in figure 2). Some of our con-
clusions change if we switch to this qualitative measure of evolutionary success:
Under the Moran Birth-Death and Wright-Fisher life-cycles, population viscosity
does not promote the evolution of altruism – actually, these two life-cycles can-
not 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 favored only at interme-
diate emigration probabilities (figure 2(a)): increased emigration can still favor
the evolution of altruism under this qualitative criterion.

The result is due to indirect (/secondary) effects

To explain how the frequency of altruists can increase with the emigration prob-
ability m, let us go back to the decomposition of the expected frequency of al-
truists in the population $\mathbb{E}\left[\overline{X}\right]$ into different terms (eq. (8)). For all the life-cycles
that we consider, the direct effect of helping others (β_{D}) decreases with emigra-
tion m, while the direct effect of the cost of helping (γ_{D}) does not change with
m. If we (erroneously) considered only direct effects, we would conclude that
the expected proportion of altruists decreases with the emigration probability
m, because an increase in m reduces the probability that two interactants (two
deme-mates in this model) are identical by descent. But this explanation ignores
indirect, competitive, effects. In the three life-cycles that we considered, $\beta_{\mathrm{I}} = \gamma_{\mathrm{I}}$,
so the overall indirect effects are given by $(-(\mathrm{b} - \mathrm{c})\beta_{\mathrm{I}})$. Hence, any increase of
$\mathbb{E}\left[\overline{X}\right]$ with m is driven by β_{I}. Indirect effects correspond to competition: helping
another individual indirectly harms others – even the individual who is provid-

ing help is indirectly harmed. This competition can be diluted by increasing the emigration probability m. The overall effect of m on the expected frequency of altruists depends on the balance between direct and indirect effects. This balance depends on the fidelity of parent-offspring transmission (μ), in particular because probabilities of identity by descent depend on μ.

Indirect (secondary) effects are less straightforward to understand than direct (/primary) effects, yet they play a crucial role for social evolution in spatially structured populations. Competition among relatives is for instance behind Taylor (1992b)'s cancellation result; similarly, the qualitative differences between the Moran Birth-Death and Moran Death-Birth life-cycles is explained by the different scales of competition that the two life-cycle produce (Grafen & Archetti, 2008; Débarre et al., 2014). Secondary effects are also behind the evolution of social behaviors such as spite (West & Gardner, 2010).

How small is small and how large is large?

Our results were derived under the assumption of weak selection, assuming that the phenotypic difference between altruists and defectors is small ($\delta \ll 0$). We considered any fidelity of transmission (any μ between 0 and 1) and population size. However, most models considering subdivided populations assume nearly perfect strategy transmission ($\mu \to 0$) and infinite population sizes (number of demes $N_D \to \infty$). The order in which these limits are taken matters, *i.e.*, one needs to specify how small μ, but also ω, are compared to the inverse size of the population. This remark complements findings by Sample & Allen (2017), who highlighted the quantitative differences between different orders of weak selection and large population limits.

Imperfect transmission and Rebellious Children

Our model bears resemblance to the Rebellious Child Model by Frank (1997), who studied the evolution of a vertically transmitted cultural trait in an asexually reproducing population. In Frank's model, however, relatedness r is treated as a fixed parameter (as acknowledged in the legend of Figure 7 in Frank (1997)). Our model is mechanistic; relatedness r necessarily depends on the mutation probability μ, because probabilities of identity by descent do.

Mutation was also previously included in models investigating the maintenance of cooperative microorganisms in the presence of cheaters (Brockhurst et al., 2007; Frank, 2010). In both of these models however, only loss-of-function mutation was considered, which corresponds to setting the mutation bias at $\nu = 0$ in our model. This means that the all-cheaters state is absorbing; no matter how favored cooperators may otherwise be, in the long run, a finite population will only consist of cheaters.

Interactions and dispersal graphs

Compared to graphs classically used in evolutionary graph theory (*e.g.*, regular random graphs, grids), the island model is particular because the interaction graph and the dispersal graph are different: interactions take place only within demes ($e_{\text{out}} = 0$), while offspring can disperse out of their natal deme ($d_{\text{out}} > 0$). One may wonder whether our result depends on this difference between the two graphs. Figure S4 shows that the result still holds when the dispersal and interaction graphs are the same. In this figure indeed, we let a proportion m (equal to the dispersal probability) of interactions occur outside of the deme where the individuals live, and set d_{self}, the probability of self replacement, equal to 0, so that the dispersal and interactions graphs are the same.

Coevolution of dispersal and social behavior

This work also raises the question of what would happen if dispersal (*e.g.,* the emigration probability m) could evolve as well. Recent work on the topic has shown that under some conditions disruptive selection could take place, leading to a polymorphism between sessile altruists and mobile defectors (Parvinen, 2013; Mullon et al., 2017). The assumptions of these studies however differ from ours in important ways, in that they consider continuous traits and use an adaptive dynamics framework, where, notably, mutations are assumed to be very rare. It remains to be investigated how non-rare and potentially large mutations would affect their result.

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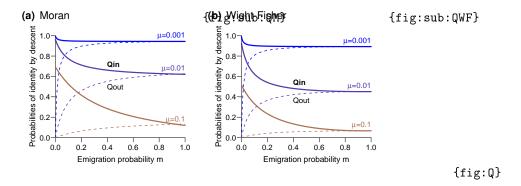Wolfram Research, Inc. 2017: Mathematica, Version 11.1. Champaign, IL, 2017.

Figures

{fig:sub:QMF}

{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), as a function of the emigration probability m, for different values of the mutation probability μ (0.001, 0.01, 0.1), and for the two types of life-cycles ((a): Moran, (b): Wright-Fisher). Other parameters: $n = 4$ individuals per deme, $N_D = 15$ demes.
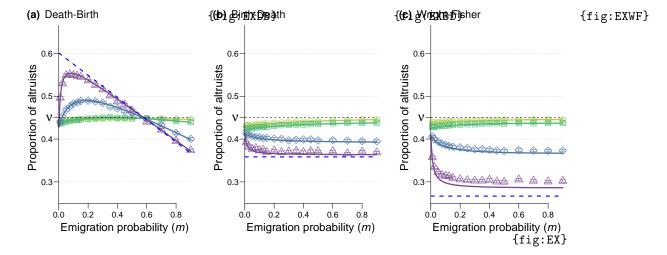
Figure 2: Expected proportion of altruists under weak selection, as a function of the emigration probability m, for different mutation values ($\mu = 0.001$ (blue, dots), 0.01 (purple, squares), 0.1 (brown, diamonds), 0.25 (orange, triangles); the dashed blue lines correspond to $\mu = 0$) and different life-cycles ((a) Moran Death-Birth, (b) Moran Birth Death, (c) Wright-Fisher). The curves are the analytical results, the points are the output of numerical simulations. Parameters: $\omega = 0.005$, $\nu = 0.45$, $b = 15$, $c = 1$, $n = 4$ individuals per deme, $N_D = 15$ demes.

Supplementary figures

(a) Death-Birth **(b)** Birth-Death **(c)** Wright-Fisher
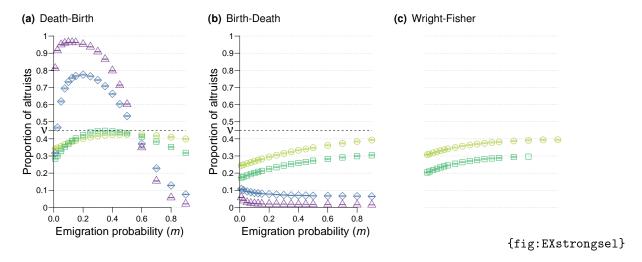
{fig:EXstrongsel}

Figure S1: Equivalent of figure 2 (simulations only) but with strong selection ($\omega =$ 0.1); please note the change of scale on the vertical axis. All other parameters and legends are identical to those of figure 2 (increasing mutation probabilities from blue dots to orange triangles).
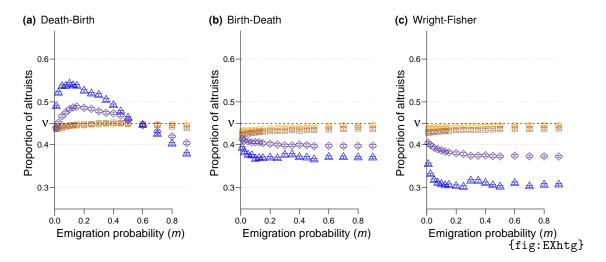
(a) Death-Birth **(b)** Birth-Death **(c)** Wright-Fisher

{fig:EXhtg}

Figure S2: Equivalent of figure 2 (simulations only) 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.
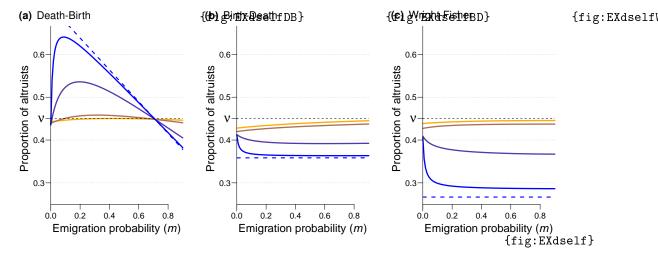

(a) Death-Birth {fig:EXdselfDB} **(b)** Birth-Death {fig:EXdselfBD} **(c)** Wright-Fisher {fig:EXdselfW

{fig:EXdself}

Figure S3: Equivalent of figure 2 (analysis only), with no self-replacement ($d_{ii} = d_{\mathrm{self}} = 0$ for all sites).

2017-09-01

(a) Death-Birth   {(b) Birth-DeathDEDB}   {(c) Wright-FisherEBD}   {fig:EXsameDE
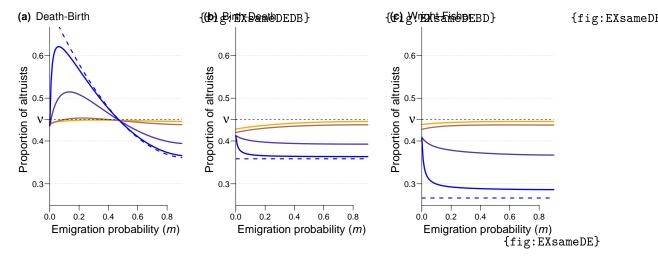
{fig:EXsameDE}

Figure S4: Equivalent of figure 2 (analysis only), with equal dispersal and interaction graphs (*i.e.*, no self-replacement [$d_{ii} = d_{\text{self}} = 0$ for all sites], and a proportion m of the interactions occurring outside of the home deme).

Supplementary Table

b	Fecundity benefit given by altruists to social interactants
c	Fecundity cost paid by altruists
d_{ij}	Dispersal probability from site i to site j
e_{ij}	Interaction probability from site i to site j
n	Deme size
N_D	Number of demes
N	Total population size ($N = N_D n$)
m	Emigration probability
Q_{ij}	(Long-term) Probability of identity by descent of individuals at sites i and j
X_i	Indicator variable, equal to 1 if site i is occupied by an altruist, to 0 otherwise (r.v.)
$\overline{X}$	Frequency of altruists in the population (r.v.)
β	Term associated to the benefits b
γ	Term associated to the costs c
μ	Mutation probability
ν	Mutation bias: probability that mutant is altruist
ω	Parameter scaling the relative effect of social interactions on fecundity
D	Subscript corresponding to direct/primary effects
I	Subscript corresponding to indirect/secondary effects
in	Subscript used when $i \neq j$ and the two sites are in the same deme
out	Subscript used when the two sites i and j are in different demes
self	Subscript used when $i = j$
BD	Superscript corresponding to the Moran Birth-Death model
DB	Superscript corresponding to the Moran Death-Birth model
M	Superscript corresponding to a Moran model
WF	Superscript corresponding to the Wright-Fisher model

{tab:symbols}

Table S1: List of symbols. "r.v." means *random variable*.

Appendix

A Expected frequency of altruists

A.1 For a generic life-cycle

We want to compute the expected proportion of altruists in the population. 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 $\overline{X}(t) = \sum_{i=1}^{N} X_i(t)$. We denote by $B_{ji}(X(t),\delta)$, 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. The expected number of successful offspring produced by the individual living at site i at time t is given by $B_i = \sum_{j=1}^{N} B_{ji}$. We denote by $D_i(X(t),\delta)$ (D_i for simplicity) the probability that the individual living at site i at time t has been replaced (*i.e.*, died) at time $t+1$. These quantities depend on the chosen life-cycle and on the state of the population; they are given in table S2 for each of the life-cycles that we consider.

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

Table S2: Formulas of B_{ij} and D_i for each of the life-cycles that we consider; f_i (shorthand notation for $f_i(X,\delta)$) is the fecundity of the individual living at site i, as defined in eq. (1), and d_{ji} is a dispersal probability, given in eq. (2).

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

$$D_i = \sum_{j=1}^{N} B_{ij} \tag{A.1a}$$

holds for all sites i. The structure of the population is also such that in the absence of selection ($\delta = 0$, 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 off-spring (*i.e.*, of having offspring that become adults at the next time step), so that

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

where the ^{0} subscript means that the quantities are evaluated for $\delta = 0$. This also implies that B_{ij}^0 and D_i^0 do not depend on the state **X** of the population. For the Moran life-cycles, $B^* = 1/N$, while for the Wright-Fisher life-cycle, $B^* = 1$. (The difference between eq. (A.1b) and 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

$$\mathbb{E}\big[\overline{X}(t+1)|\mathbf{X}(t)\big] = \frac{1}{N} \sum_{i=1}^{N} \big[B_i(1-\mu)X_i + (1-D_i)X_i + B_i\mu\nu\big]. \tag{A.2a} \quad \{\text{eq:conditionalchange}\}$$

The first term within the brackets corresponds to births of unmutated offspring from parents who are altruists (X_i). The second term corresponds to the survival of altruists. The third term corresponds to the births of mutants who became altruists (which occurs with probability ν), which ever the type of the parent.

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; the expected frequency of altruists does not change anymore for large times t (realized frequencies of course keep changing). We denote by $\xi(\mathbf{X}, \delta, \mu)$ the prob-ability that the population is in state **X**, given the strength of selection δ and the mutation probability μ. Taking the expectation of eq. (A.2a) ($\mathbb{E}\big[\overline{X}\big] = \sum_{X \in \Omega} \overline{X}\xi(\mathbf{X}, \delta, \mu)$), we obtain, after reorganizing:

$$0 = \frac{1}{N} \sum_{X \in \Omega} \left[\sum_{i=1}^{N} \big(B_i(1-\mu)X_i - D_iX_i\big) + \sum_{i=1}^{N} B_i\mu\nu \right] \xi(\mathbf{X}, \delta, \mu). \tag{A.3} \quad \{\text{eq:statdist}\}$$

Now, we use the assumption of weak selection ($\delta \ll 1$) and consider the first-order expansion of eq. (A.3) for δ close to 0. First, we note that in the absence of selection ($\delta = 0$), the population is at a mutation-drift balance; the expected state of every site i is then $\mathbb{E}_0\big[X_i\big] = \sum_{X \in \Omega} X_i\xi(X, 0, \mu) = \nu$ (recall that ν is the mutation bias parameter). Secondly, we note that for all the life-cycles that we consider, the total number of deaths in the population during one time step does not depend on population composition (it is exactly 1 death for the Moran life-cycles, and exactly N for the Wright-Fisher life-cycle), so that $\sum_{i,j=1}^{N} B_{ij}$ does not depend on δ. Consequently, the last term of eq. (A.3) vanishes when we take its derivative with respect to δ, for the life-cycles that we consider.

The first order expansion of eq. (A.3) yields

$$0 = \frac{\delta}{N} \sum_{i=1}^{N} \left[\sum_{X \in \Omega} \left(\frac{\partial B_i}{\partial \delta}(1-\mu) - \frac{\partial D_i}{\partial \delta} \right) X_i\xi(\mathbf{X}, 0, \mu) - \sum_{X \in \Omega} \mu B^* X_i \frac{\partial \xi}{\partial \delta} \right] + O\big(\delta^2\big), \tag{A.4} \quad \{\text{eq:weaksel0}\}$$

631 where the derivatives are evaluated at $\delta = 0$, and where we used eq. (A.1b) to
632 simplify the second term. For conciseness, we define

$$W_i = (1 - \mu)B_i + (1 - D_i), \qquad\qquad (A.5) \quad \{\texttt{eq:app:defW}\}$$

633 a measure of fitness counting offspring only when they are unmutated. With
634 this, using the expectation notation, and denoting by $\mathbb{E}_0[\,]$ expectations under
635 $\delta = 0$, we can rewrite and reorganize eq. (A.4) as

$$\delta \mu B^* \frac{\partial \mathbb{E}[\overline{X}]}{\partial \delta} = \frac{\delta}{N} \sum_{i=1}^{N} \mathbb{E}_0 \Big[\frac{\partial W_i}{\partial \delta} X_i \Big] + O(\delta^2). \qquad (A.6) \quad \{\texttt{eq:weaksel0reorg}\}$$

636 Now, we use a first time the law of total probabilities, taking individual pheno-
637 types ϕ_k are intermediate variables:

$$\begin{aligned}
\frac{\partial W_i}{\partial \delta} &= \sum_{k=1}^{N} \frac{\partial W_i}{\partial \phi_k} \frac{\partial \phi_k}{\partial \delta} \\
&= \sum_{k=1}^{N} \frac{\partial W_i}{\partial \phi_k} X_k, \qquad\qquad (A.7) \quad \{\texttt{eq:totalproba1}\}
\end{aligned}$$

638 by definition of ϕ_k, and where the first derivative is evaluated for all $\phi_i = 0$. With
639 the notation $P_{ij} = \mathbb{E}_0[X_i X_j]$, eq. (A.6) becomes

$$\delta \mu B^* \frac{\partial \mathbb{E}[\overline{X}]}{\partial \delta} = \frac{\delta}{N} \sum_{i=1}^{N} \sum_{k=1}^{N} \frac{\partial W_i}{\partial \phi_k} P_{ik} + O(\delta^2). \qquad (A.8) \quad \{\texttt{eq:weaksel1}\}$$

640 So far, we have not used the specificities of the population structure that we con-
641 sider. Once we have fixed a focal individual i, in expectation there are only three
642 types of individuals: the focal itself, $n - 1$ other individuals in the focal's deme
643 (denoted by in), and $N - n$ individuals in other demes (denoted by out). We note
644 that since the size of the population is fixed ($\sum_{i=1}^{N}(B_i - D_i) = 0$), and since the
645 total number of births does not depend on population composition in the life-
646 cycles that we consider,

$$\sum_{i=1}^{N} \frac{\partial W_i}{\partial \delta} = 0,$$

647 which we can rewrite as (Rousset & Billiard, 2000)

$$\frac{\partial W_i}{\partial \phi_i} + (n - 1) \frac{\partial W_i}{\partial \phi_{\text{in}}} + (N - n) \frac{\partial W_i}{\partial \phi_{\text{out}}} = 0. \qquad (A.9) \quad \{\texttt{eq:derivsumW}\}$$

648 With this, eq. (A.8) becomes

$$\delta \mu B^* \frac{\partial \mathbb{E}[\overline{X}]}{\partial \delta} = \frac{\delta}{N} \sum_{i=1}^{N} \left(\frac{\partial W_i}{\partial \phi_i} + (n - 1) \frac{\partial W_i}{\partial \phi_{\text{in}}} \frac{P_{\text{in}} - P_{\text{out}}}{P_{ii} - P_{\text{out}}} \right) (P_{ii} - P_{\text{out}}). \qquad (A.10) \quad \{\texttt{eq:weaksel1CBRP}\}$$

649 We can also replace the P terms by

$$P_{ij} = \nu^2 + \nu(1-\nu)Q_{ij}. \qquad (A.11) \quad \{\text{eq:QP}\}$$

650 In Appendix A.2, we will see that recursions on P_{ij} reveal that Q_{ij} can be inter-
651 preted as a probability of identity by descent, *i.e.*, the probability that the individ-
652 uals at sites i and j have a common ancestor and that no mutation has occurred
653 on either lineage since the ancestor. Eq. (A.10) becomes

$$\delta \mu B^* \frac{\partial \mathbb{E}[\overline{X}]}{\partial \delta} = \frac{\delta}{N} \sum_{i=1}^{N} \left(\underbrace{\frac{\partial W_i}{\partial \phi_i}}_{-\mathcal{C}} + \underbrace{(n-1)\frac{\partial W_i}{\partial \phi_{\text{in}}}}_{\mathcal{B}} \underbrace{\frac{Q_{\text{in}} - Q_{\text{out}}}{1 - Q_{\text{out}}}}_{R} \right)(1 - Q_{\text{out}})\nu(1-\nu). \quad (A.12) \quad \{\text{eq:weaksel1CBR}\}$$

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

$$\mathbb{E}[\overline{X}] = \nu + \omega \left. \frac{\partial \mathbb{E}[\overline{X}]}{\partial \omega} \right|_{\omega=0} + O(\omega^2), \qquad (A.13) \quad \{\text{eq:EXgeneric}\}$$

656 where $\left. \dfrac{\partial \mathbb{E}[\overline{X}]}{\partial \omega} \right|_{\omega=0}$ is obtained from eq. (A.8). We then need to replace the B_{ij} and
657 D_j terms by their formulas for each life-cycle (given in table S2), and the d_{ij} and
658 e_{ij} terms by their formulas (given in eq. (2)) and eq. (??), respectively. For each
659 life-cycle we can group terms as

$$\left. \frac{\partial \mathbb{E}[\overline{X}]}{\partial \omega} \right|_{\omega=0} \approx \frac{\nu(1-\nu)}{\mu} \left[\mathsf{b}\left(\beta_D - \beta_I\right) - \mathsf{c}\left(\gamma_D - \gamma_I\right) \right], \qquad (A.14)$$

660 where D terms come from the numerators of B_{ij} and D_i, and I terms come from
661 the denominator of B_{ij} and D_i; replacing B_{ij} and D_i by their formulas given in
662 table S2, we obtain the following sets of equations for each life-cycle:

$$\{\text{eq:EXBDsums}\}$$

Moran Birth-Death

$$\beta_D^{\text{BD}} = \sum_{k,\ell=1}^{N} \frac{1-\mu}{N} e_{k\ell} Q_{\ell k}^{\text{M}}, \qquad (A.15a)$$

$$\beta_I^{\text{BD}} = \sum_{j,k,\ell=1}^{N} \left(\frac{d_{\ell j}}{N} - \frac{\mu}{N^2} \right) e_{k\ell} Q_{jk}^{\text{M}}, \qquad (A.15b)$$

$$\gamma_D^{\text{BD}} = 1 - \mu, \qquad (A.15c)$$

$$\gamma_I^{\text{BD}} = \sum_{j,k=1}^{N} \left(\frac{d_{kj}}{N} - \frac{\mu}{N^2} \right) Q_{jk}^{\text{M}}. \qquad (A.15d)$$

Moran Death-Birth

$$\beta_D^{DB} = \sum_{k,\ell=1}^{N} \frac{1-\mu}{N} e_{k\ell} Q_{\ell k}^M, \tag{A.16a}$$

$$\beta_I^{DB} = (1-\mu) \sum_{i,j,k,\ell=1}^{N} \frac{d_{ji} d_{\ell i}}{N} e_{k\ell} Q_{jk}^M, \tag{A.16b}$$

$$\gamma_D^{DB} = 1 - \mu, \tag{A.16c}$$

$$\gamma_I^{DB} = (1-\mu) \sum_{i,j,k=1}^{N} \frac{d_{ji} d_{ki}}{N} Q_{jk}^M. \tag{A.16d}$$

Wright-Fisher

$$\beta_D^{WF} = \sum_{k,\ell=1}^{N} \frac{1-\mu}{N} e_{k\ell} Q_{\ell k}^{WF}, \tag{A.17a}$$

$$\beta_I^{WF} = (1-\mu) \sum_{i,j,k,\ell=1}^{N} \frac{d_{ji} d_{\ell i}}{N} e_{k\ell} Q_{jk}^{WF}, \tag{A.17b}$$

$$\gamma_D^{WF} = 1 - \mu, \tag{A.17c}$$

$$\gamma_I^{WF} = (1-\mu) \sum_{i,j,k=1}^{N} \frac{d_{ji} d_{ki}}{N} Q_{jk}^{WF}. \tag{A.17d}$$

663 System (A.17)s the same set of equations as for the Moran Death-Birth model
664 (system (A.1)), except for the values of probabilities of identity by descent... that
665 we now need to compute.

A.2 Probabilities of identity by descent

667 Here we show the link between the expected state of a pair of sites P_{ij} and prob-
668 abilities of identity by descent Q_{ij}. In our derivation of $\mathbb{E}[\overline{X}]$, P_{ij} is the quantity
669 that appears, but most studies use Q_{ij}. Both are evaluated in the absence of
670 selection ($\omega = 0$).

A.2.1 Moran model

672 In a Moran model, exactly one individual dies and one individual reproduces
673 during one time step. Given a state **X** at time t, at time $t+1$ both sites i and
674 $j \neq i$ are occupied by altruists, if *i)* it was the case at time t and neither site was
675 replaced by a non-altruist (first term in eq. (A.18)), or *ii)* if exactly one of the two
676 sites was occupied by a non-altruist at time t, but the site was replaced by an

altruist (second and third terms of eq. (A.18)):

$$\mathbb{E}\big[X_i X_j(t+1)|X(t) = \mathbf{X}\big] = X_i X_j \left(1 - \sum_{k=1}^{N} \frac{1}{N}\big(d_{ki} + d_{kj}\big)\big((1-X_k)(1-\mu) + \mu(1-v)\big)\right)$$
$$+ X_i(1-X_j) \sum_{k=1}^{N} \frac{1}{N} d_{kj}\big(X_k(1-\mu) + \mu v\big) \qquad \text{(A.18)} \quad \texttt{\{eq:app:PijM1\}}$$
$$+ X_j(1-X_i) \sum_{k=1}^{N} \frac{1}{N} d_{ki}\big(X_k(1-\mu) + \mu v\big).$$

We take the expectation of this quantity, and consider that the stationary distribution is reached ($t \to \infty$); then $\mathbb{E}\big[X_i X_j(t+1)\big] = \mathbb{E}\big[X_i X_j(t)\big]$, and we obtain

$$P_{ij} = \frac{1}{2}\left(\sum_{k=1}^{N}(1-\mu)\big(d_{kj}P_{ki} + d_{ki}P_{kj}\big)\right) + \mu v^2 \qquad (i \neq j), \qquad \text{(A.19)} \quad \texttt{\{eq:app:PijM\}}$$

while $P_{ii} = v$.

Now we substitute $P_{ij} = v^2 + v(1-v)Q_{ij}$ in eq. (A.19), we obtain

$$Q_{ij} = \frac{1}{2} \sum_{k=1}^{N}(1-\mu)\big(d_{ki}Q_{kj} + d_{kj}Q_{ki}\big), \qquad \text{(A.20)} \quad \texttt{\{eq:app:QijM\}}$$

and we realize that Q_{ij} is the probability that the individuals at sites i and $j \neq i$ are identical by descent. To compute it indeed, we need to pick which site was last updated (equal probabilities), then who was the parent (k); the other individual needs to be identical by descent to the parent, and no mutation should have occurred $(1-\mu)$.

A.2.2 Wright-Fisher model

In a Wright-Fisher model, all individuals are replaced at each time step, so we directly consider the state of the parents:

$$\mathbb{E}\big[X_i X_j(t+1)|X(t) = \mathbf{X}\big] = \sum_{k,\ell=1}^{N} d_{ki}d_{\ell j}\bigg(X_k X_\ell(1-\mu+\mu v)^2$$
$$+ (X_k(1-X_\ell) + (1-X_k)X_\ell)(1-\mu+\mu v)(\mu v)$$
$$+ (1-X_k)(1-X_\ell)(\mu v)^2\bigg) \qquad \text{(A.21)} \quad \texttt{\{eq:app:PijWF1\}}$$

The first term of eq. (A.21) corresponds to both parents being altruists, and having altruist offspring; the second line corresponds to exactly one parent being altruist, and the third line to both parents being non-altruists (in this latter case, the two offspring have to be both mutants to be altruists).
Taking the expectation and simplifying, we obtain

$$P_{ij} = \sum_{k,\ell=1}^{N}\big(P_{kl}(1-\mu)^2\big) + (2-\mu)\mu v^2. \qquad \text{(A.22)} \quad \texttt{\{eq:app:PijWF\}}$$

Replacing P_{ij} by $v^2 + v(1-v)Q_{ij}$, eq. (A.22) becomes

$$Q_{ij} = \sum_{k,\ell=1}^{N} d_{ki} d_{\ell j} Q_{k\ell} (1-\mu)^2. \qquad \text{(A.23)} \quad \texttt{\{eq:app:QijWF\}}$$

Again, Q_{ij} corresponds to a probability of identity by descent: the individuals at sites i and j are identical by descent if their parents were and if neither mutated $((1-\mu)^2)$.

B In a subdivided population

B.1 β and γ

Now, we need to adapt the results presented in Appendix A to our structure of interest, a subdivided population, with dispersal and interaction probabilities given by eq. (2) and eq. (**??**). For the β and γ terms, we use a brute-force approach, replacing d_{ij} and e_{ij} by their values in a subdivided population, and simplifying the equations (for instance, there are 60 different cases to consider for the four sums that appear in $\beta_{\mathrm{I}}^{\mathrm{DB}}$, shown in the table in section B.4 below). The calculations and subsequent simplifications are detailed in the supplementary Mathematica file, and the results are presented in the main text (system (9), eq. (10a), and eq. (10b)).

B.2 Probabilities of identity by descent

For the probabilities of identity by descent, we could also use a brute-force approach, but calculations are faster if we use formulas derived in Débarre (2017) for "two-dimensional population structures". The name comes from the fact that we only need two types of transformations to go from any site to any other site in the population: permutations on the deme index, and permutations on the within-deme index.

We rewrite site labels ($1 \leq i \leq N$) as (ℓ_1, ℓ_2), where ℓ_1 is the index of the deme ($1 \leq \ell_1 \leq N_D$) and ℓ_2 the position of the site within the deme ($1 \leq \ell_2 \leq n$). Then, we introduce notations $\tilde{d}_{\substack{i_1 \\ i_2}}$ and $\tilde{Q}_{\substack{i_1 \\ i_2}}$, that correspond to the dispersal probability and probability of identity by descent to a site at distances i_1 and i_2 in the among-demes and within-deme dimensions (*e.g.*, $\tilde{d}_{\substack{i_1 \\ i_2}} = d_{\substack{j_1\ j_1+i_1 \\ j_2, j_2+i_2}}$.)

Also, in this section, we distinguish between $d_{\mathrm{self}} = d_{ii}$ and d_{in} (in the main text, $d_{\mathrm{self}} = d_{\mathrm{in}}$).

B.2.1 Moran model

In Débarre (2017), it was shown that

$$\tilde{Q}_{\substack{r_1 \\ r_2}} = \frac{1}{N} \sum_{q_1=0}^{N_1-1} \sum_{q_2=0}^{N_2-1} \frac{\mu \lambda'_M}{1 - (1-\mu)\tilde{\mathcal{D}}_{\substack{q_1 \\ q_2}}} \exp\left(\iota \frac{2\pi q_1 r_1}{N_1}\right) \exp\left(\iota \frac{2\pi q_2 r_2}{N_2}\right) \qquad \text{(B.24a)}$$

with

$$\tilde{\mathcal{D}}_{\substack{q_1 \\ q_2}} = \sum_{\ell_1=0}^{N_1-1} \sum_{\ell_2=0}^{N_2-1} \tilde{d}_{\substack{\ell_1 \\ \ell_2}} \exp\left(-\iota \frac{2\pi q_1 \ell_1}{N_1}\right) \exp\left(-\iota \frac{2\pi q_2 \ell_2}{N_2}\right), \qquad \text{(B.24b)}$$

727 and λ'_M such that $\tilde{\mathcal{Q}}_0 = 1$. Let us first compute $\tilde{\mathcal{D}}_{\substack{q_1 \\ q_2}}$ in the case of a subdivided
728 population, with $N_1 = N_D$ and $N_2 = n$:

$$
\begin{aligned}
\tilde{\mathcal{D}}_{\substack{q_1 \\ q_2}} &= d_{\text{self}} + \sum_{\ell_2=1}^{N_2-1} d_{\text{in}} \exp\left(-\imath \frac{2\pi q_2 \ell_2}{N_2}\right) + \sum_{\ell_1=1}^{N_1-1} \sum_{\ell_2=0}^{N_2-1} d_{\text{out}} \exp\left(-\imath \frac{2\pi q_1 \ell_1}{N_1}\right) \exp\left(-\imath \frac{2\pi q_2 \ell_2}{N_2}\right) \\
&= d_{\text{self}} + \left(\delta_{q_2}(N_2-1) + (1-\delta_{q_2})(-1)\right) d_{\text{in}} + \left(\delta_{q_1}(N_1-1) + (1-\delta_{q_1})(-1)\right)\left(\delta_{q_2} N_2\right) d_{\text{out}} \\
&= d_{\text{self}} + \left(\delta_{q_2} N_2 - 1\right) d_{\text{in}} + \left(\delta_{q_1} N_1 - 1\right) \delta_{q_2} N_2 d_{\text{out}}.
\end{aligned}
\tag{B.25a}
$$

729 (δ_q is equal to 1 when q is equal to 0 modulo the relevant dimension, and to 0
730 otherwise). So for the three types of distances that we need to consider (distance
731 0, distance to another deme-mate, distance to individual in another deme), and
732 with $N_1 = N_D$ and $N_2 = n$, we obtain   {eq:app:Dsystem}

$$
\tilde{\mathcal{D}}_0 = 1, \tag{B.26a}
$$

$$
\tilde{\mathcal{D}}_{\substack{q_1 \\ 0}} = 1 - m - \frac{m}{d-1} \quad (q_1 \not\equiv 0 \pmod{N_1}), \tag{B.26b}
$$

$$
\tilde{\mathcal{D}}_{\substack{q_1 \\ q_2}} = d_{\text{self}} - d_{\text{in}} \quad (q_2 \not\equiv 0 \pmod{N_2}). \tag{B.26c}
$$

733 So for $\tilde{\mathcal{Q}}$, using system (B.26) in eq. (B.24a),

$$
\begin{aligned}
\tilde{\mathcal{Q}}_{\substack{r_1 \\ r_2}} &= \frac{\mu \lambda'_M}{N} \left[\frac{1}{1-(1-\mu)\tilde{\mathcal{D}}_0} + \sum_{q_2=1}^{N_2-1} \frac{1}{1-(1-\mu)\tilde{\mathcal{D}}_{\substack{0 \\ q_2}}} \exp\left(-\imath \frac{2\pi q_2 r_2}{N_2}\right) \right. \\
&\quad + \sum_{q_1=1}^{N_1-1} \frac{1}{1-(1-\mu)\tilde{\mathcal{D}}_{\substack{q_1 \\ 0}}} \exp\left(-\imath \frac{2\pi q_1 r_1}{N_1}\right) \\
&\quad \left. + \sum_{q_1=1}^{N_1-1} \sum_{q_2=1}^{N_2-1} \frac{1}{1-(1-\mu)\tilde{\mathcal{D}}_{\substack{q_1 \\ q_2}}} \exp\left(-\imath \frac{2\pi q_1 r_1}{N_1}\right) \exp\left(-\imath \frac{2\pi q_2 r_2}{N_2}\right) \right] \\
&= \frac{\mu \lambda'_M}{N} \left[\frac{1}{1-(1-\mu)} + \frac{1}{1-(1-\mu)(d_{\text{self}}-d_{\text{in}})}(\delta_{r_2} N_2 - 1) \right. \\
&\quad + \frac{1}{1-(1-\mu)(1-m-\frac{m}{d-1})}(\delta_{r_1} N_1 - 1) \\
&\quad \left. + \frac{1}{1-(1-\mu)(d_{\text{self}}-d_{\text{in}})}(\delta_{r_1} N_1 - 1)(\delta_{r_2} N_2 - 1) \right]. \tag{B.27} \quad \{eq:app:Q2DMsol\}
\end{aligned}
$$

734 In particular,

$$
\begin{aligned}
\tilde{\mathcal{Q}}_0 &= \frac{\mu \lambda'_M}{N} \left[\frac{1}{\mu} + \frac{1}{1-(1-\mu)(d_{\text{self}}-d_{\text{in}})}(n-1) + \frac{1}{1-(1-\mu)(1-m-\frac{m}{d-1})}(D-1) \right. \\
&\quad \left. + \frac{1}{1-(1-\mu)(d_{\text{self}}-d_{\text{in}})}(D-1)(n-1) \right] \\
&= 1. \tag{B.28a} \quad \{eq:app:Q2D1\}
\end{aligned}
$$

We find λ'_M using the eq. (B.28a). Going back to eq. (B.27), when $r_1 = 0$, the two individuals are in the same deme. They are different when $r_2 \not\equiv 0$, and so:

$$Q_{\text{in}} = \frac{\mu \lambda'_M}{N} \left[\frac{1}{\mu} + \frac{1}{1 - (1-\mu)(d_{\text{self}} - d_{\text{in}})}(-1) + \frac{1}{1 - (1-\mu)(1 - m - \frac{m}{d-1})}(D-1) \right.$$
$$\left. + \frac{1}{1 - (1-\mu)(d_{\text{self}} - d_{\text{in}})}(D-1)(-1) \right]. \tag{B.28b}$$

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

$$Q_{\text{out}} = \frac{\mu \lambda'_M}{N} \left[\frac{1}{\mu} + \frac{1}{1 - (1-\mu)(d_{\text{self}} - d_{\text{in}})}(-1) + \frac{1}{1 - (1-\mu)(1 - m - \frac{m}{d-1})}(-1) \right.$$
$$\left. + \frac{1}{1 - (1-\mu)(d_{\text{self}} - d_{\text{in}})} \right]. \tag{B.28c}$$

With $d_{\text{self}} = d_{\text{in}} = (1-m)/n$, we recover the equations given in the main text (system (5)).

B.3 Wright-Fisher

For the Wright-Fisher updating, the equation for $\tilde{Q}$ is different:

$$\tilde{Q}^{r_1}_{r_2} = \frac{1}{N} \sum_{q_1=0}^{N_1-1} \sum_{q_2=0}^{N_2-1} \frac{\mu \lambda'_{WF}}{1 - (1-\mu)^2 (\tilde{\mathcal{D}}^{q_1}_{q_2})^2} \exp\left(-\iota \frac{2\pi q_1 r_1}{N_1}\right) \exp\left(-\iota \frac{2\pi q_2 r_2}{N_2}\right), \tag{B.29}$$

with $\tilde{\mathcal{D}}$ given in eq. (B.24b). In a subdivided population, with $N_1 = N_D$ and $N_2 = n$, this becomes

$$
\begin{aligned}
\tilde{\mathcal{Q}}_{r_2}^{r_1} &= \frac{1}{N}\left[\frac{\mu \lambda'_{WF}}{1-(1-\mu)^2(\tilde{\mathcal{D}}_0)^2} + \sum_{q_2=1}^{N_2-1} \frac{\mu \lambda'_{WF}}{1-(1-\mu)^2(\tilde{\mathcal{D}}_{0}_{q_2})^2} \exp\left(-\iota \frac{2\pi q_2 r_2}{N_2}\right) \right. \\
&\quad + \sum_{q_1=1}^{N_1-1} \frac{\mu \lambda'_{WF}}{1-(1-\mu)^2(\tilde{\mathcal{D}}_{q_1}_{0})^2} \exp\left(-\iota \frac{2\pi q_1 r_1}{N_1}\right) \\
&\quad \left. + \sum_{q_1=1}^{N_1-1}\sum_{q_2=1}^{N_2-1} \frac{\mu \lambda'_{WF}}{1-(1-\mu)^2(\tilde{\mathcal{D}}_{q_1}_{q_2})^2} \exp\left(-\iota \frac{2\pi q_1 r_1}{N_1}\right)\exp\left(-\iota \frac{2\pi q_2 r_2}{N_2}\right)\right] \\
&= \frac{\mu \lambda'_{WF}}{N}\left[\frac{1}{1-(1-\mu)^2} + \frac{1}{1-(1-\mu)^2(d_{\text{self}}-d_{\text{in}})^2}(\delta_{q_2} N_2 - 1) \right. \\
&\quad + \frac{1}{1-(1-\mu)^2(1-m-\frac{m}{d-1})^2}(\delta_{q_1} N_1 - 1) \\
&\quad \left. + \frac{1}{1-(1-\mu)^2(d_{\text{self}}-d_{\text{in}})^2}(\delta_{q_1} N_1 - 1)(\delta_{q_2} N_2 - 1)\right] \\
&= \frac{\mu \lambda'_{WF}}{N}\left[\frac{1}{1-(1-\mu)^2} + \frac{1}{1-(1-\mu)^2(d_{\text{self}}-d_{\text{in}})^2}(\delta_{q_2} N_2 - 1)\delta_{q_1} N_1 \right. \\
&\quad \left. + \frac{1}{1-(1-\mu)^2(1-m-\frac{m}{d-1})^2}(\delta_{q_1} N_1 - 1)\right]. \qquad\qquad \text{(B.30)} \quad \texttt{\{eq:app:Q2DWFsol\}}
\end{aligned}
$$

To find λ'_{WF}, we solve $\tilde{\mathcal{Q}}_0^0 = 1$, *i.e.*,

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

(B.31a)

Then from eq. (B.30) we deduce

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

(B.31b)

and

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

(B.31c)

With $d_{\text{self}} = d_{\text{in}} = (1-m)/n$, we recover the equations given in the main text (system (7)).

B.4 Unpacking β_I^{DB}

{sec:app:betaI}

The table below contains all combinations for i, j, k, l involved in the four sums. (i, j): means that i and j are different sites in the same deme; G_i: 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}
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
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}