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

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Abstract

Population viscosity, *i.e.*, low emigration out of the natal deme, leads to high within-deme relatedness, which is beneficial to the evolution of altruistic behavior when social interactions take place among deme-mates. At the same time however, it increases competition among related individuals. The evolution of altruism depends on the balance between these opposite effects. This balance is already known to be affected by details of the life-cycle; we show here that it further depends on the fidelity of strategy transmission from parents to their offspring. We consider different life-cycles (Wright-Fisher, with synchronous non-overlapping generations, Moran Death-Birth and Moran Birth-Death, both with exactly one individual dying and reproducing at each time step) and we identify thresholds of parent-offspring strategy transmission inaccuracy, above which the effect of population viscosity on the frequency of altruists maintained in the population qualitatively changes. Analytical predictions are first obtained analytically under weak selection and equal deme sizes, then confirmed with stochastic simulations relaxing these assumptions. This result challenges the 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.

Titre!!!

Abstract!!!

Fin discussion qui est encore en notes

Voter model, faire figure et discuter de la deconnexion entre d et e

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 (1992) 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 Mullan & 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 structured 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.*, 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. 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 $\bar{X} = \sum_{i=1}^N X_i$. 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 parent but instead get one randomly: with probability ν , they become altruists, with probability $1 - \nu$ they become defectors. We call the parameter ν 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 ($\omega \ll 1$). Denoting by e_{ij} the interaction probability between individuals living at sites i and j , we have

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

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

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

Although our assumptions may seem restrictive: we assume that fecundity benefits are unconditional, *i.e.*, the same which ever the type of the recipient, and the fecundity effects are additive, *i.e.*, the effect of interacting with k altruists is k times the effect of interacting with one altruist. And yet, the same fecundities are obtained with a generic fecundity function, after linearization, under the assumption that altruists and defectors are phenotypically close (see Appendix A 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 probability of moving from site i to site j , we have

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

The way the population is updated from one time step to the next depends 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.

121 2.2 Methods

122 2.2.1 Analytical part

123 To derive the expected (*i.e.*, long-term) proportion of altruists in the population,
124 we use the toolbox presented in Débarre (2017), which is valid for any regular
125 population and any life-cycle. Calculation details are given in Appendix B; they
126 go as follows. First, we write an equation for the expected frequency of altruists
127 in the population at time $t + 1$, conditional on the composition of the population
128 at time t ; we then take the expectation of this quantity, for large times t . After
129 this, we use the assumption that selection is weak ($\omega \ll 1$) and write a first order
130 expansion of the expression that we have obtained. By doing so, we let appear
131 quantities that can be identified as neutral probabilities of identity by descent
132 Q_{ij} , *i.e.*, the probability that individuals living at site i and j share a common
133 ancestor and that no mutation occurred on either lineage since that ancestor, in
134 a model with no selection ($\omega = 0$) – this is the “mutation definition of identity by
135 descent (Rousset & Billiard, 2000).

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

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

142 2.2.2 Stochastic simulations

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

149 All scripts are available at

150 <https://github.com/flodebarre/SocEvolSubdivPop/tree/master/Programs>

151 3 Results

152 3.1 Probabilities of identity by descent

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

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

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

160 3.1.1 Moran updating

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

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

163 Given the law of total probabilities, we first consider the site that was last up-
 164 dated (1/2 chance that it was j rather than i); then we consider each potential
 165 parent k , weighted by the dispersal probabilities d_{kj} . Then the individuals at
 166 sites i and j are identical by descent (IBD) if i and j 's parent were IBD (Q_{ki}^M) and
 167 if no mutation occurred ($1-\mu$). Replacing the dispersal probabilities d_{ij} by their
 168 values (given in eq. (3)), we eventually obtain (see Appendix B.2 for calculation
 169 steps):

{eq:QM}

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

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

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

173 When the mutation probability μ is vanishingly small ($\mu \rightarrow 0$), both Q_{in}^M and
 174 Q_{out}^M are equal to 1: in the absence of mutation indeed, the population ends up
 175 fixed for one of the two types, and all individuals are identical by descent. Note
 176 that we obtain a different result if we first assumed that the size of the popu-
 177 lation is infinite ($N_D \rightarrow \infty$), because the order of limits matters; for instance,
 178 $\lim_{d \rightarrow \infty} Q_{\text{out}}^M = 0$.

179 3.1.2 Wright-Fisher updating

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

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

183 The sum is over all possible parents k and ℓ of i and j , weighted by the disper-
 184 sal probabilities to sites i and j ; the individuals at sites i and j are identical by
 185 descent if their parents were $(Q_{k\ell})$ and if neither mutated $((1 - \mu)^2)$.

186 Replacing the dispersal probabilities d_{ij} by their values (given in eq. (3)) and
 187 skipping calculation steps (but see Appendix B.2 for details), we obtain: {eq: QWF}

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

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

188 with

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

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

191 In the Wright-Fisher life-cycle, $Q_{\text{in}}^{\text{WF}}$ decreases until $m = m_c^{\text{WF}} = \frac{d-1}{d}$, then in-
 192 creases again, while $Q_{\text{out}}^{\text{WF}}$ follows the opposite pattern. The threshold value m_c^{WF}
 193 corresponds to an emigration probability so high that an individual's offspring is
 194 as likely to land in its parent's deme as in any other deme (*i.e.*, $d_{\text{in}} = d_{\text{out}}$).

195 The two probabilities of identity by descent go to 1 when the mutation prob-
 196 ability μ is very small ($\mu \rightarrow 0$), except if we first assume that the number of demes
 197 is very large ($N_D \rightarrow \infty$); for instance, with this life-cycle as well, $\lim_{N_D \rightarrow \infty} Q_{\text{out}}^{\text{WF}} =$
 198 0.

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

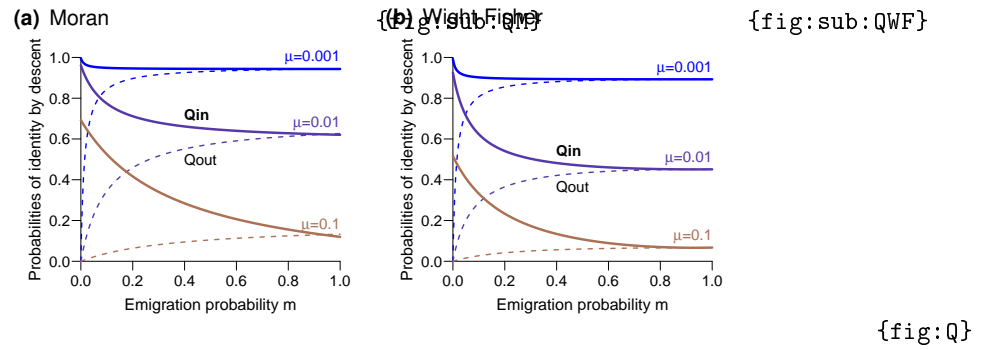


Figure 1: Probabilities of identity by descent, for two different individuals within the same deme (Q_{in} , full curves) and two individuals in different demes (Q_{out} , dashed curves), as a function of the emigration probability m , for different values of the mutation probability μ (0.001, 0.01, 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.

202 3.2 Expected frequencies of altruists for each life-cycle

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

$$\mathbb{E}[\bar{X}] \approx v + \omega \frac{v(1-v)}{\mu} [b(\beta_D - \beta_I) - c(\gamma_D - \gamma_I)]. \quad (9) \quad \{\text{eq:EXapprox}\}$$

205 (Calculations leading to eq. (9) are presented in Appendix B.)

206 The mutation bias v corresponds to the expected proportion of altruists in the
207 population in the absence of selection (*i.e.*, when $\omega = 0$); ω is the parameter
208 that scales the effects of interactions between individuals, which is assumed to
209 be small. The subscript $_D$ refers to “direct” effects, and the subscript $_I$ to “in-
210 direct” effects. “Direct” effects involve effects on primary beneficiaries of the
211 benefits (b) and costs (c) of social interactions (West & Gardner, 2010), *i.e.*, so-
212 cial interactants (for the benefits b) and the focal individuals themselves (for the
213 costs c). “Indirect” effects corresponds to effects on secondary interactants, *i.e.*,
214 to (kin) competition. By providing a benefit to a deme-mate and thereby in-
215 creasing its fecundity, a focal altruist indirectly harms others by reducing their
216 relative fecundity (β_I term in eq. (9)); by having a reduced fecundity due to the
217 cost of altruism, a focal altruist indirectly favors others by increasing their rela-
218 tive fecundity (γ_I term).

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

221 3.2.1 Direct effects

222 Direct (/primary) effects are similar for the three life-cycles; the only difference
223 is the value of probabilities of identity by descent Q (as seen in the previous sec-
224 tion, they differ between Moran and Wright-Fisher life-cycles):

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

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

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

225 For both benefits and costs, direct effects only count when there is no mutation
226 (hence the $(1 - \mu)$ factors). Direct effects of benefits b (eq. (10a) and eq. (10b))
227 only count if the interaction takes place with an individual who is identical by
228 descent. With the population structure that we consider, social interactions only
229 occur within demes, so only Q_{in} is present in eq. (10a) and eq. (10b). On the other
230 hand, the direct effect of the fecundity cost c (eq. (10c)) does not depend on the
231 type of interactant, since the same cost c is paid by altruists irrespective of the
232 interactant’s identity.

233 As seen in the previous section, Q_{in}^M and Q_{in}^{WF} decrease with the emigration
234 probability m (actually only until $m = \frac{d-1}{d}$ for the latter). Consequently, the mag-
235 nitude of the direct (beneficial) effects of benefits b provided by altruists (β_D)
236 decreases when the emigration probability m increases, while the direct (detrimental)
237 effects (γ_D) due to the direct cost of altruism c are constant. As a result,

if we only considered direct effects, we would conclude that more emigration m is detrimental to the evolution of altruistic behaviour. However, there are also indirect effects at play.

3.2.2 Indirect effects

Indirect (/secondary) effects are collateral effects on other individuals; they depend on the type of life-cycle, and always involve individuals who are identical 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:

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

(Calculation details are presented in Appendix B.)

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 $\left(\frac{n-1}{n} Q_{\text{in}}^{\text{M}} + \frac{1}{n} \right)$, 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. (6)), we conclude that $\beta_I^{\text{BD}} = \gamma_I^{\text{BD}}$ 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

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

268 The brackets in eq. (11b) contain a sum of two terms. The first term corresponds
 269 two individuals from the same deme (with replacement) whose offspring either
 270 do not emigrate, or emigrate together to the same deme. The second term cor-
 271 responds to individuals initially from different demes who end up in the same
 272 deme (either one of their home demes, or a third deme).

273 Here again, $\beta_I = \gamma_I$, so the balance between indirect benefits and indirect
 274 costs does not change when the emigration probability m increases.

275 Replacing Q_{in} and Q_{out} by their formulas given in eq. (6), we can conclude
 276 that $\beta_I^{DB} = \gamma_I^{DB}$ first decreases with the emigration probability m , and increases
 277 again after a threshold value m'_c , which is smaller than $m_c^{WF} = (d-1)/d$ (calcu-
 278 lation details are presented in the supplementary Mathematica file).

279 **Wright-Fisher** With this life-cycle, generations are synchronous and all indi-
 280 viduals again all have the same survival probability (now equal to 0 at all sites).
 281 As a result, the formulas for β_I^{WF} and γ_I^{WF} are the same as β_I^{DB} and γ_I^{WF} , except
 282 that instead of Q_{in}^M and Q_{out}^M , we need to use Q_{in}^{WF} and Q_{out}^{WF} (given in eq. (8)). Once
 283 this is done, we see that $\beta_I^{WF} = \gamma_I^{WF}$ first decreases with the emigration probabili-
 284 ty m , and increases again after the threshold value $m_c^{WF} = (d-1)/d$. This emi-
 285 gration threshold was identified above as the emigration probability such that
 286 offspring have an equal chance of landing in their natal deme or in any other
 287 deme, *i.e.*, $d_{in} = d_{out}$ (calculation details are presented in the supplementary
 288 Mathematica file.)

289 3.3 Identifying threshold values of the mutation probability μ

290 In the previous section, we investigated the impact of changes in the emigration
 291 probability m on each of the terms that make up the expected frequency of altru-
 292 ists $\mathbb{E}[\bar{X}]$. Now we need to combine these different terms to focus on the quantity
 293 we are eventually interested in, $\mathbb{E}[\bar{X}]$. The rather lengthy formulas that we ob-
 294 tain are relegated to the Appendix and supplementary Mathematica file, and we
 295 concentrate here on the results.

296 3.3.1 Moran Birth-Death

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

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

302 This result is illustrated in figure 2(b); with the parameters of the figure, $\mu_c^{BD} \approx$
 303 0.026.

3.3.2 Moran Death-Birth

The relationship between $\mathbb{E}[\bar{X}]$ 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 $\mathbb{E}[\bar{X}]$ as a function of m when $m \rightarrow 0$). If the benefits b provided by altruists are relatively low ($b < c(n+1)$), $\mathbb{E}[\bar{X}]$ initially increases with m provided the mutation probability μ is greater than a threshold value μ_c^{DB} given in eq. (13) below; otherwise, when the benefits are high enough, $\mathbb{E}[\bar{X}]$ initially increases with m for any value of μ . Combining these results, we write

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

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

The expected frequency of altruists $\mathbb{E}[\bar{X}]$ then reaches a maximum at an emigration probability m_c^{DB} (whose complicated equation is given in the supplementary Mathematica file), as can be seen in figure 2(a). When the mutation probability gets close to 0 ($\mu \rightarrow 0$), m_c^{DB} also gets close to 0,

3.3.3 Wright-Fisher

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

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

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

3.4 Relaxing key assumptions

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

To relax the assumption of equal deme sizes, we randomly drew deme sizes at the beginning of simulations, with sizes ranging from 2 to 6 individuals and on average $\bar{n} = 4$ individuals per deme as previously. As shown in figure S2, the patterns initially obtained with a homogeneous population structure are robust when the structure is heterogeneous.

For the Moran model, it may seem odd that an offspring can replace its own parent (which can occur since $d_{ii} \neq 0$). Figure S3, plotted with dispersal probabilities preventing immediate replacement of one's own parent (for all sites i ,

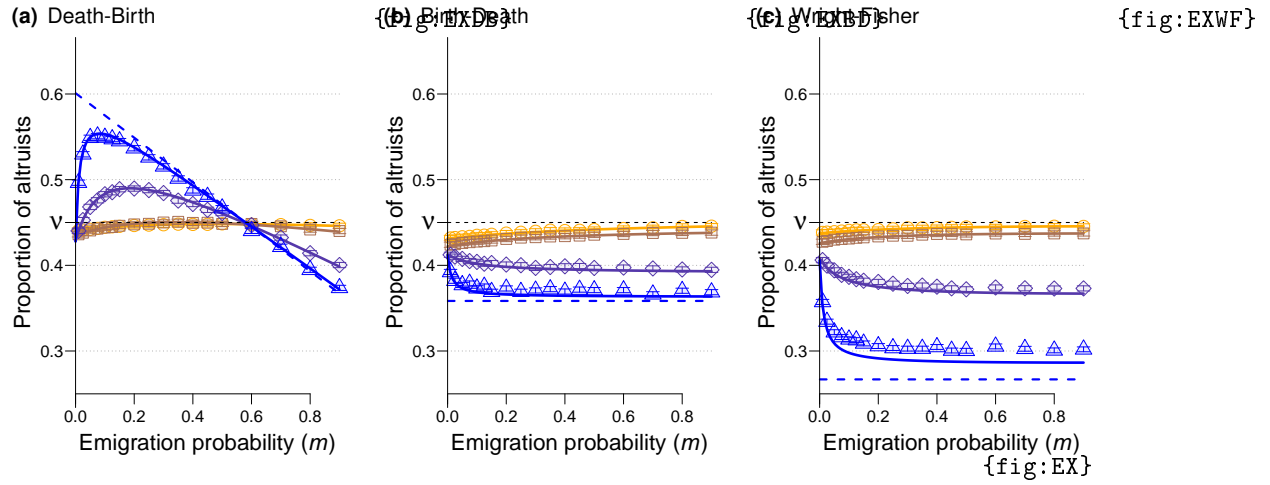


Figure 2: Expected proportion of altruists under weak selection, as a function of the emigration probability m , for different mutation values ($\mu = 0.001$ (blue, dots), 0.01 (purple, squares), 0.1 (brown, diamonds), 0.25 (orange, triangles); the dashed blue lines correspond to $\mu = 0$ and different 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.

338 $d_{ii} = d_{\text{self}} = 0$; $d_{\text{in}} = (1 - m)/(n - 1)$ for two different sites in the same deme, d_{out}
 339 remaining unchanged), confirms that this does affect our conclusions.

340 4 Discussion

341 The expected frequency of altruists in a subdivided population can in- 342 crease with the probability of emigration

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

354 Quantitative vs. qualitative measures

355 We used a quantitative measure, the expected frequency of altruists in the popu-
 356 lation ($\mathbb{E}[\bar{X}]$), to explore how non-zero mutation probabilities altered the impact
 357 of population viscosity. Often however, evolutionary success is measured quali-
 358 tatively, by comparing a quantity (an expected frequency, or, in models with no
 359 mutation, a probability of fixation) to the value it would have in the absence of
 360 selection. In our model, this amounts to saying that altruism is favored whenever
 361 $\mathbb{E}[\bar{X}] > v$ (v is plotted as a horizontal dashed line in figure 2). Some of our con-
 362 clusions change if we switch to this qualitative measure of evolutionary success:
 363 Under the Moran Birth-Death and Wright-Fisher life-cycles, population viscosity
 364 does not promote the evolution of altruism – actually, these two life-cycles can-
 365 not ever promote altruistic behavior for any regular population structure (Taylor
 366 et al., 2011), whichever the probability of mutation (Débarre, 2017). However,
 367 under a Moran Death-Birth life-cycle, altruism can be favored only at interme-
 368 diate emigration probabilities (figure 2(a)): increased emigration can still favor
 369 the evolution of altruism under this qualitative criterion.

370 The result is due to indirect (/secondary) effects

371 To explain how the frequency of altruists can increase with the emigration prob-
 372 ability m , let us go back to the decomposition of the expected frequency of al-
 373 truists in the population $\mathbb{E}[\bar{X}]$ into different terms (eq. (9)). For all the life-cycles
 374 that we consider, the direct effect of helping others (β_D) decreases with emigra-
 375 tion m , while the direct effect of the cost of helping (γ_D) does not change with
 376 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, $\beta_I = \gamma_I$, so the overall indirect effects are given by $-(b - c)\beta_I$. Hence, any increase of $\mathbb{E}[\bar{X}]$ with m is driven by β_I . Indirect effects correspond to competition: helping another individual indirectly harms others – even the individual who is providing 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 .

Westetal2002 for review on competition. Indirect effects and cancellation result Taylor1992 + (Queller, 1994) (Ohtsuki, 2010, with n player games) Indirect effects scale of competition explain why BD DB differences (Grafen & Archetti, 2008). Can explain the evolution of social behaviors such as spite (West & Gardner, 2010)WG10. Mitigate the effects of fecundity costs associated to a beneficial trait (Débarre, 2015).

Primary and secondary recipients West and Gardner 2010.

Competitive effects are less straightforward to explain than direct

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 ($\mu \rightarrow 0$) and infinite population sizes (number of demes $N_D \rightarrow \infty$). 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

419 $v = 0$ in our model. This means that the all-cheaters state is absorbing; no matter
420 how favored cooperators may otherwise be, in the long run, a finite population
421 will only consist of cheaters.
422

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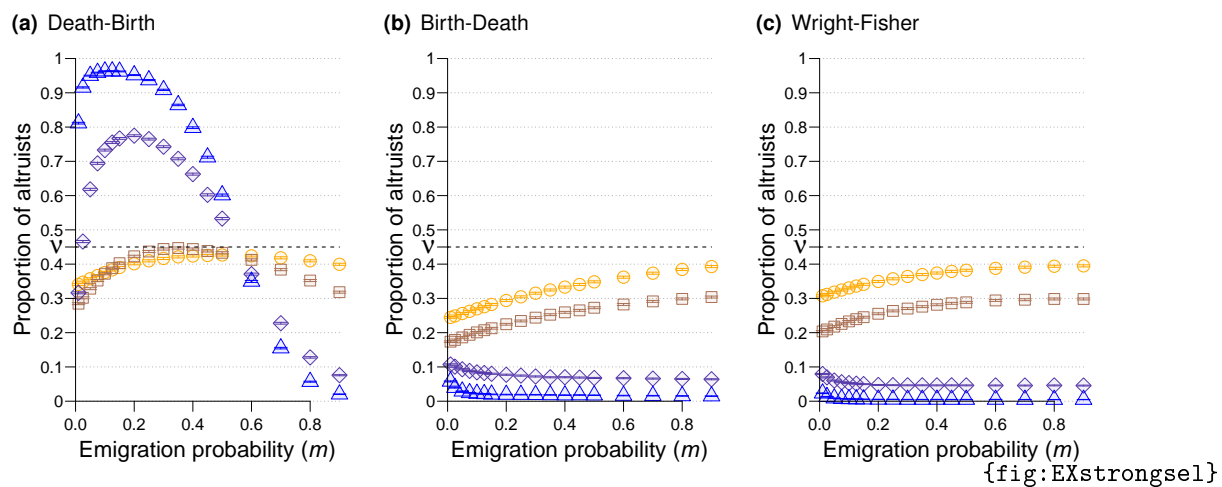


Figure S1: Equivalent of figure 2 (simulations only) but with strong selection ($\omega = 0.1$); please note the change of scale on the vertical axis. All other parameters and legends are identical to those of figure 2 (increasing mutation probabilities from blue dots to orange triangles).

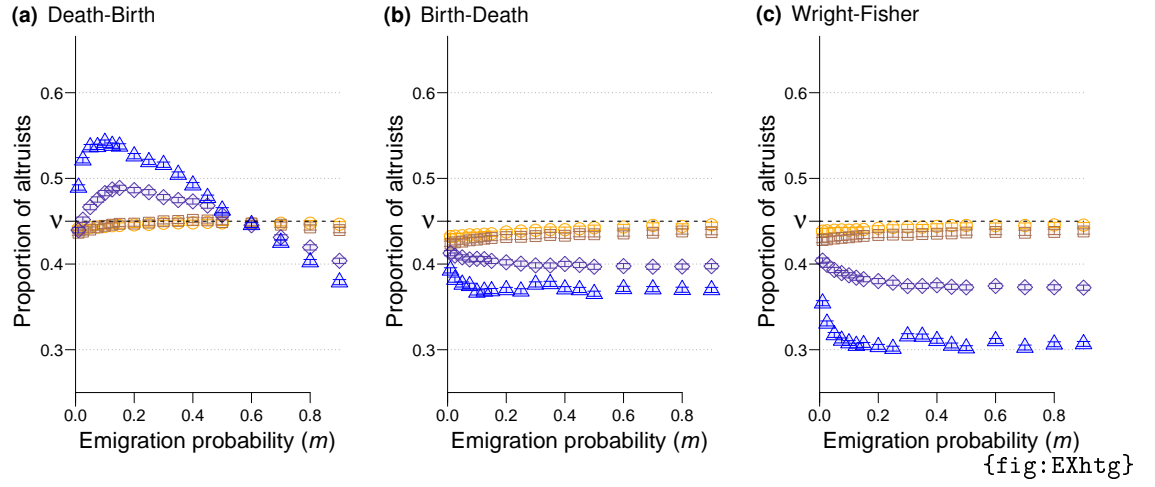


Figure S2: Equivalent of figure 2 (simulations only) but with a heterogeneous population structure: deme sizes range from 1 to 5 individuals per deme, the average deme size is 4 as in figure 2; all other parameters and legend are identical to those of figure 2.

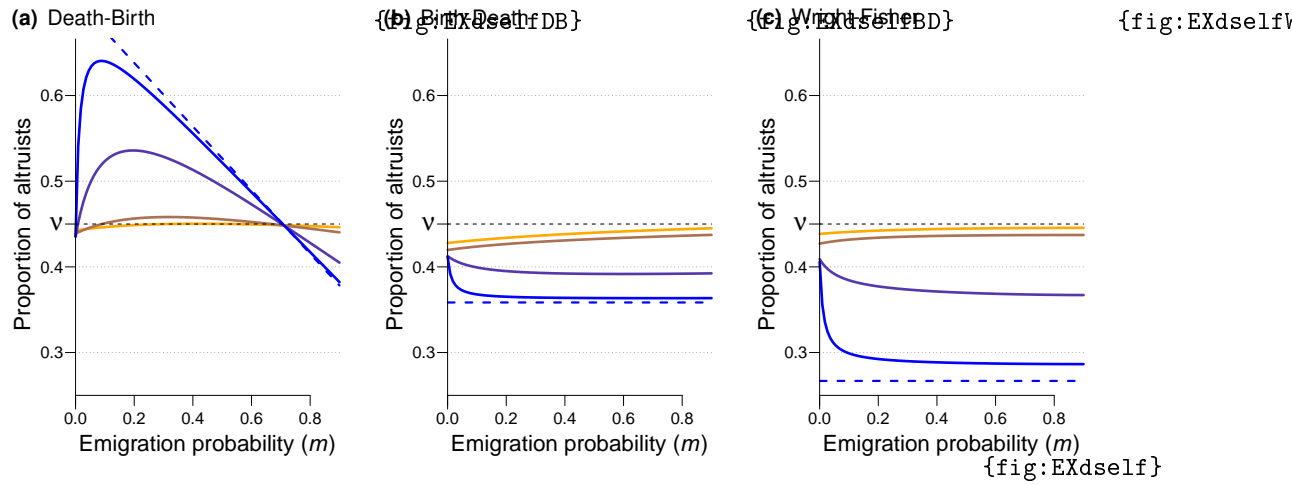


Figure S3: Equivalent of figure 2 (analysis only), with no self-replacement ($d_{ii} = d_{\text{self}} = 0$ for all sites).

511 **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.) |
| \bar{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 Fecundity and weak selection approximation

{sec:app:F}

Here we show that the fecundity function presented in eq. (2) can be obtained from a generic fecundity function, under the assumption of small phenotypic differences between altruists and defectors.

Let us denote by ϕ_i the phenotype of the individual living at site i , and assume that the phenotypic value of altruists and defectors differs by $\omega \ll 1$, so that

$$\phi_i = \phi^{(0)} + \omega X_i, \quad (\text{A.1}) \quad \{\text{eq:app:phidef}\}$$

where $\phi^{(0)}$ is the phenotype of defectors (and $\phi_0 + \omega$ the phenotype of altruists).

We consider a generic fecundity function, that depends on the focal individual's phenotype, and on the phenotype of all the individuals that it interacts with, weighted by the probability of interaction (e_{ki} for an individual at site k , $1 \leq k \leq N$). For instance, the fecundity of an individual at site i is given by a function with $N + 1$ arguments

$$F_i = \mathcal{F}(e_{1,i}\phi_1, \dots, e_{N,i}\phi_N; \phi_i),$$

which, using eq. (A.1), becomes

$$F_i = \mathcal{F}(e_{1,i}(\phi^{(0)} + \omega X_1), \dots, e_{N,i}(\phi^{(0)} + \omega X_N); \phi^{(0)} + \omega X_i). \quad (\text{A.2}) \quad \{\text{eq:app:Fi}\}$$

We then write a first-order expansion of eq. (A.2) for $\omega \ll 1$:

$$F_i = \mathcal{F}(e_{1,i}\phi^{(0)}, \dots, e_{N,i}\phi^{(0)}; \phi^{(0)}) + \omega \left[\sum_{k=1}^N (e_{ki} X_k \partial_{(k)} \mathcal{F}|_{\omega=0}) + X_i \partial_{(N+1)} \mathcal{F}|_{\omega=0} \right] + O(\omega^2), \quad (\text{A.3}) \quad \{\text{eq:app:DLF}\}$$

where $\partial_{(k)} \mathcal{F}|_{\omega=0}$ is the derivative of \mathcal{F} with respect to its k^{th} argument, evaluated at $\omega = 0$. The first term in eq. (A.3) is the fecundity of individual i when there is not a single altruist in the population.

Given the chosen structure of the population, all individuals have the same number of social interactions, so they end up having the same fecundity when the population is fixed for the defector type. Without loss of generality, we set this baseline fecundity equal to 1. If we now consider that it does not matter where the benefits of social interactions come from, only that they are received by the focal individual, then $\partial_{(k)} \mathcal{F}$ is the same for all k , $1 \leq k \leq N$; let us denote it by b . If we denote by $-c$ the marginal effect of the focal individual's phenotype on its own fecundity (i.e., $-c = \partial_{N+1} \mathcal{F}|_{\omega=0}$), then we obtain

$$F_i = 1 + \omega \left(b \sum_{k=1}^N e_{ki} X_k - c X_i \right) + O(\omega^2), \quad (\text{A.4})$$

which is equal to f_i as defined in eq. (2), neglecting terms in ω^2 and higher.

B Expected frequency of altruists

{sec:app:EX}

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

In this section, we work with a generic regular population structure (with symmetries such that all individuals behave the same way in expectation), of which the island model is a particular case.

B.1 For a generic life-cycle

{sec:app:generic}

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 $\bar{X}(t) = \sum_{i=1}^N X_i(t)$. We denote by $B_{ji}(X(t), \omega)$, written B_{ji} for simplicity, the probability that the individual at site j at time $t+1$ is the newly established offspring of the individual living at site i at time t . We denote by $D_i(X(t), \omega)$ (D_i for simplicity) the probability that the individual living at site i at time t has been replaced (*i.e.*, died) at time $t+1$. Both quantities depend on the chosen life-cycle and on the state of the population; they are given in table S2 for each of the life-cycles that we consider.

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

{tab:BD}

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

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

$$D_i = \sum_{j=1}^N B_{ij} \quad (\text{B.5a}) \quad \{\text{eq:DBequiv}\}$$

holds for all sites i . The structure of the population is also such that in the absence of selection ($\omega = 0$, so that $f_i = 1$ for all sites $1 \leq i \leq N$), all individuals have

563 the same probability of dying and the same probability of having successful off-
 564 spring (*i.e.*, of having offspring that become adults at the next time step), so that
 565

$$D_i^0 = \sum_{j=1}^N B_{ji}^0 = B^*, \quad (\text{B.5b}) \quad \{\text{eq:DBRV}\}$$

566 where the ⁰ subscript means that the quantities are evaluated for $\omega = 0$. This
 567 also implies that B_{ij}^0 and D_i^0 do not depend on the state \mathbf{X} of the population. For
 568 the Moran life-cycles, $B^* = 1/N$, while for the Wright-Fisher life-cycle, $B^* = 1$.
 569 (The difference between eq. (B.5b) and eq. (B.5a) is that we are now considering
 570 offspring produced by i landing on j).

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

$$\mathbb{E}[\bar{X}(t+1)|\mathbf{X}(t)] = \frac{1}{N} \sum_{i=1}^N \left[\sum_{j=1}^N B_{ij} (X_j(1-\mu) + \mu v) + (1-D_i)X_i \right]. \quad (\text{B.6a}) \quad \{\text{eq:conditionalchange}\}$$

573 The first term within the brackets corresponds to births: the type of the individ-
 574 ual living at i at time $t + 1$ depends on the type of its parent (living at site j), and
 575 on whether mutation occurred. The second term in the brackets of eq. (B.6a)
 576 corresponds to the survival of the individual living at site i .

577 Given that there is no absorbing population state (a lost strategy can always
 578 be recreated by mutation), there is a stationary distribution of population states;
 579 the expected frequency of altruists does not change anymore for large times t
 580 (realized frequencies of course keep changing). We denote by $\xi(\mathbf{X}, \omega, \mu)$ the prob-
 581 ability that the population is in state \mathbf{X} , given the strength of selection ω and the
 582 mutation probability μ . Taking the expectation of eq. (B.6a) ($\mathbb{E}[\bar{X}] = \sum_{\mathbf{X} \in \Omega} \bar{X} \xi(\mathbf{X}, \omega, \mu)$),
 583 we obtain, after reorganizing:

$$0 = \frac{1}{N} \sum_{\mathbf{X} \in \Omega} \sum_{i=1}^N \left[\sum_{j=1}^N B_{ij} (X_j(1-\mu) + \mu v) - D_i X_i \right] \xi(\mathbf{X}, \omega, \mu). \quad (\text{B.7}) \quad \{\text{eq:statdist}\}$$

584 Now, we use the assumption of weak selection ($\omega \ll 1$) and consider the first-
 585 order expansion of eq. (B.7) for ω close to 0. First, we note that in the absence
 586 of selection ($\omega = 0$), the population is at a mutation-drift balance; the expected
 587 state of every site i is then $\mathbb{E}_0[X_i] = \sum_{\mathbf{X} \in \Omega} X_i \xi(\mathbf{X}, 0, \mu) = v$ (recall that v is the mu-
 588 tation bias parameter). Secondly, we further expand derivatives of B_{ji} and D_i
 589 thanks to the chain rule, using the variables f_k ($1 \leq k \leq N$), corresponding to in-
 590 dividual fecundities (also, recall that $f_k = 1$ when $\omega = 0$). Thirdly, we note that for
 591 all the life-cycles that we consider, the total number of deaths in the population
 592 during one time step does not depend on population composition (it is exactly
 593 1 death for the Moran life-cycles, and exactly N for the Wright-Fisher life-cycle),
 594 so that $\sum_{i,j=1}^N B_{ij}$ does not depend on ω . After simplification and reorganization,

595 the first order expansion of eq. (B.7) yields

$$\begin{aligned}
0 = & \frac{1}{N} \sum_{i,k=1}^N \left[\frac{\partial \left(\sum_{j=1}^N (1-\mu) B_{ji} - D_i \right)}{\partial f_k} \right]_{f_k=1} \\
& \times \left(\sum_{\ell=1}^N e_{\ell k} b \sum_{X \in \Omega} X_{\ell} X_i \xi(\mathbf{X}, 0, \mu) - c \sum_{X \in \Omega} X_k X_i \xi(\mathbf{X}, 0, \mu) \right) \\
& - B^* \mu \frac{\partial \mathbb{E}[\bar{X}]}{\partial \omega} \Big|_{\omega=0} + O(\omega^2). \tag{B.8} \quad \text{\texttt{eq:weaksel1}}
\end{aligned}$$

596 The terms $\sum_{X \in \Omega} X_i X_j \xi(\mathbf{X}, 0, \mu)$, that we will denote by P_{ij} , correspond to the
597 expected state of the pair of sites (i, j) , evaluated in the absence of selection
598 ($\omega = 0$). We can also replace these terms by

$$P_{ij} = v^2 + v(1-v)Q_{ij}. \tag{B.9} \quad \text{\texttt{eq:QP}}$$

599 In Appendix B.2, we will see that recursions on P_{ij} reveal that Q_{ij} can be inter-
600 preted as a probability of identity by descent, *i.e.*, the probability that the individ-
601 uals at sites i and j have a common ancestor and that no mutation has occurred
602 on either lineage since the ancestor.

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

$$\mathbb{E}[\bar{X}] = v + \omega \frac{\partial \mathbb{E}[\bar{X}]}{\partial \omega} \Big|_{\omega=0} + O(\omega^2), \tag{B.10} \quad \text{\texttt{eq:EXgeneric}}$$

605 where $\frac{\partial \mathbb{E}[\bar{X}]}{\partial \omega} \Big|_{\omega=0}$ is obtained from eq. (B.8). We then need to replace the B_{ij} and
606 D_j terms by their formulas for each life-cycle (given in table S2), and the d_{ij} and
607 e_{ij} terms by their formulas (given in eq. (3)) and eq. (1), respectively). For each
608 life-cycle we can group terms as

$$\frac{\partial \mathbb{E}[\bar{X}]}{\partial \omega} \Big|_{\omega=0} \approx \frac{v(1-v)}{\mu} [b(\beta_D - \beta_I) - c(\gamma_D - \gamma_I)], \tag{B.11}$$

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

\text{\texttt{eq:EXBDsums}}

Moran Birth-Death

$$\beta_D^{\text{BD}} = \sum_{k,\ell=1}^N \frac{1-\mu}{N} e_{k\ell} Q_{\ell k}^{\text{M}}, \tag{B.12a}$$

$$\beta_I^{\text{BD}} = \sum_{j,k,\ell=1}^N \left(\frac{d_{\ell j}}{N} - \frac{\mu}{N^2} \right) e_{k\ell} Q_{jk}^{\text{M}}, \tag{B.12b}$$

$$\gamma_D^{\text{BD}} = 1 - \mu, \tag{B.12c}$$

$$\gamma_I^{\text{BD}} = \sum_{j,k=1}^N \left(\frac{d_{kj}}{N} - \frac{\mu}{N^2} \right) Q_{jk}^{\text{M}}. \tag{B.12d}$$

{eq:EXDBsums}

Moran Death-Birth

$$\beta_D^{DB} = \sum_{k,\ell=1}^N \frac{1-\mu}{N} e_{k\ell} Q_{\ell k}^M, \quad (B.13a)$$

$$\beta_I^{DB} = (1-\mu) \sum_{i,j,k,\ell=1}^N \frac{d_{ji}d_{\ell i}}{N} e_{k\ell} Q_{jk}^M, \quad (B.13b)$$

$$\gamma_D^{DB} = 1-\mu, \quad (B.13c)$$

$$\gamma_I^{DB} = (1-\mu) \sum_{i,j,k=1}^N \frac{d_{ji}d_{ki}}{N} Q_{jk}^M. \quad (B.13d)$$

{eq:EXWFsums}

Wright-Fisher

$$\beta_D^{WF} = \sum_{k,\ell=1}^N \frac{1-\mu}{N} e_{k\ell} Q_{\ell k}^{WF}, \quad (B.14a)$$

$$\beta_I^{WF} = (1-\mu) \sum_{i,j,k,\ell=1}^N \frac{d_{ji}d_{\ell i}}{N} e_{k\ell} Q_{jk}^{WF}, \quad (B.14b)$$

$$\gamma_D^{WF} = 1-\mu, \quad (B.14c)$$

$$\gamma_I^{WF} = (1-\mu) \sum_{i,j,k=1}^N \frac{d_{ji}d_{ki}}{N} Q_{jk}^{WF}. \quad (B.14d)$$

612 System (B.14)s the same set of equations as for the Moran Death-Birth model
 613 (system (B.1)), except for the values of probabilities of identity by descent... that
 614 we now need to compute.

B.2 Probabilities of identity by descent

{sec:app:IBD}

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

B.2.1 Moran model

621 In a Moran model, exactly one individual dies and one individual reproduces
 622 during one time step. Given a state \mathbf{X} at time t , at time $t+1$ both sites i and
 623 $j \neq i$ are occupied by altruists, if i) it was the case at time t and neither site was
 624 replaced by a non-altruist (first term in eq. (B.15)), or ii) if exactly one of the two
 625 sites was occupied by a non-altruist at time t , but the site was replaced by an

626 altruist (second and third terms of eq. (B.15)):

$$\begin{aligned}\mathbb{E}[X_i X_j(t+1)|X(t) = \mathbf{X}] &= X_i X_j \left(1 - \sum_{k=1}^N \frac{1}{N} (d_{ki} + d_{kj}) ((1 - X_k)(1 - \mu) + \mu(1 - \nu)) \right) \\ &\quad + X_i(1 - X_j) \sum_{k=1}^N \frac{1}{N} d_{kj} (X_k(1 - \mu) + \mu\nu) \\ &\quad + X_j(1 - X_i) \sum_{k=1}^N \frac{1}{N} d_{ki} (X_k(1 - \mu) + \mu\nu).\end{aligned}\tag{B.15} \quad \{\text{eq:app:PijM1}\}$$

627 We take the expectation of this quantity, and consider that the stationary dis-
628 tribution is reached ($t \rightarrow \infty$); then $\mathbb{E}[X_i X_j(t+1)] = \mathbb{E}[X_i X_j(t)]$, and we obtain

$$P_{ij} = \frac{1}{2} \left(\sum_{k=1}^N (1 - \mu) (d_{kj} P_{ki} + d_{ki} P_{kj}) \right) + \mu\nu^2 \quad (i \neq j), \tag{B.16} \quad \{\text{eq:app:PijM}\}$$

629 while $P_{ii} = \nu$.

630 Now we substitute $P_{ij} = \nu^2 + \nu(1 - \nu)Q_{ij}$ in eq. (B.16), we obtain

$$Q_{ij} = \frac{1}{2} \sum_{k=1}^N (1 - \mu) (d_{ki} Q_{kj} + d_{kj} Q_{ki}), \tag{B.17} \quad \{\text{eq:app:QijM}\}$$

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

636 B.2.2 Wright-Fisher model

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

$$\begin{aligned}\mathbb{E}[X_i X_j(t+1)|X(t) = \mathbf{X}] &= \sum_{k,\ell=1}^N d_{ki} d_{\ell j} \left(X_k X_\ell (1 - \mu + \mu\nu)^2 \right. \\ &\quad + (X_k(1 - X_\ell) + (1 - X_k) X_\ell) (1 - \mu + \mu\nu)(\mu\nu) \\ &\quad \left. + (1 - X_k)(1 - X_\ell)(\mu\nu)^2 \right)\end{aligned}\tag{B.18} \quad \{\text{eq:app:PijWF1}\}$$

639 The first term of eq. (B.18) corresponds to both parents being altruists, and hav-
640 ing altruist offspring; the second line corresponds to exactly one parent being
641 altruist, and the third line to both parents being non-altruists (in this latter case,
642 the two offspring have to be both mutants to be altruists).

643 Taking the expectation and simplifying, we obtain

$$P_{ij} = \sum_{k,\ell=1}^N (P_{kl}(1 - \mu)^2) + (2 - \mu)\mu\nu^2. \tag{B.19} \quad \{\text{eq:app:PijWF}\}$$

644 Replacing P_{ij} by $v^2 + v(1-v)Q_{ij}$, eq. (B.19) becomes

$$Q_{ij} = \sum_{k,\ell=1}^N d_{ki}d_{\ell j}Q_{k\ell}(1-\mu)^2. \quad (\text{B.20})$$

645 Again, Q_{ij} corresponds to a probability of identity by descent: the individuals at
 646 sites i and j are identical by descent if their parents were and if neither mutated
 647 $((1-\mu)^2)$.

C In a subdivided population

{sec:app:subdiv}

C.1 β and γ

{sec:app:bcsubdiv}

Now, we need to adapt the results presented in Appendix B to our structure of interest, a subdivided population, with dispersal and interaction probabilities given by eq. (3) and eq. (1). 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 β_1^{DB} , shown in the table in section C.4 below). The calculations and subsequent simplifications are detailed in the supplementary Mathematica file, and the results are presented in the main text (system (10), eq. (11a), and eq. (11b)).

C.2 Probabilities of identity by descent

{sec:app:Qsubdiv}

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}_{i_1} and \tilde{Q}_{i_1} , 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., $\tilde{d}_{i_1} = d_{j_1 j_1 + i_1}$).

Also, in this section, we distinguish between $d_{\text{self}} = d_{i_1 i_2}$ and d_{in} (in the main text, $d_{\text{self}} = d_{\text{in}}$).

C.2.1 Moran model

In Débarre (2017), it was shown that

$$\tilde{Q}_{r_1} = \frac{1}{N} \sum_{q_1=0}^{N_1-1} \sum_{q_2=0}^{N_2-1} \frac{\mu \lambda'_M}{1 - (1 - \mu) \tilde{D}_{q_1}} \exp\left(i \frac{2\pi q_1 r_1}{N_1}\right) \exp\left(i \frac{2\pi q_2 r_2}{N_2}\right) \quad (\text{C.21a}) \quad \{\text{eq:app:Q2DM}\}$$

with

$$\tilde{D}_{q_1} = \sum_{\ell_1=0}^{N_1-1} \sum_{\ell_2=0}^{N_2-1} \tilde{d}_{\ell_1} \exp\left(-i \frac{2\pi q_1 \ell_1}{N_1}\right) \exp\left(-i \frac{2\pi q_2 \ell_2}{N_2}\right), \quad (\text{C.21b}) \quad \{\text{eq:app:D2D}\}$$

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

$$\begin{aligned}\tilde{D}_{q_1} &= d_{\text{self}} + \sum_{\ell_2=1}^{N_2-1} d_{\text{in}} \exp\left(-i \frac{2\pi q_2 \ell_2}{N_2}\right) + \sum_{\ell_1=1}^{N_1-1} \sum_{\ell_2=0}^{N_2-1} d_{\text{out}} \exp\left(-i \frac{2\pi q_1 \ell_1}{N_1}\right) \exp\left(-i \frac{2\pi q_2 \ell_2}{N_2}\right) \\ &= d_{\text{self}} + (\delta_{q_2}(N_2 - 1) + (1 - \delta_{q_2})(-1)) d_{\text{in}} + (\delta_{q_1}(N_1 - 1) + (1 - \delta_{q_1})(-1)) (\delta_{q_2} N_2) d_{\text{out}} \\ &= d_{\text{self}} + (\delta_{q_2} N_2 - 1) d_{\text{in}} + (\delta_{q_1} N_1 - 1) \delta_{q_2} N_2 d_{\text{out}}.\end{aligned}\quad (\text{C.22a})$$

678 (δ_q is equal to 1 when q is equal to 0 modulo the relevant dimension, and to 0
 679 otherwise). So for the three types of distances that we need to consider (distance
 680 0, distance to another deme-mate, distance to individual in another deme), and
 681 with $N_1 = N_D$ and $N_2 = n$, we obtain {eq:app:Dsystem}

$$\tilde{D}_0 = 1, \quad (\text{C.23a})$$

$$\tilde{D}_{q_1} = 1 - m - \frac{m}{d-1} \quad (q_1 \not\equiv 0 \pmod{N_1}), \quad (\text{C.23b})$$

$$\tilde{D}_{q_1} = d_{\text{self}} - d_{\text{in}} \quad (q_2 \not\equiv 0 \pmod{N_2}). \quad (\text{C.23c})$$

682 So for \tilde{Q} , using system (C.23) in eq. (C.21a),

$$\begin{aligned}\tilde{Q}_{r_1} &= \frac{\mu \lambda'_M}{N} \left[\frac{1}{1 - (1 - \mu) \tilde{D}_0} + \sum_{q_2=1}^{N_2-1} \frac{1}{1 - (1 - \mu) \tilde{D}_{q_2}} \exp\left(-i \frac{2\pi q_2 r_2}{N_2}\right) + \sum_{q_1=1}^{N_1-1} \frac{1}{1 - (1 - \mu) \tilde{D}_{q_1}} \exp\left(-i \frac{2\pi q_1 r_1}{N_1}\right) \right. \\ &\quad \left. + \sum_{q_1=1}^{N_1-1} \sum_{q_2=1}^{N_2-1} \frac{1}{1 - (1 - \mu) \tilde{D}_{q_1}} \exp\left(-i \frac{2\pi q_1 r_1}{N_1}\right) \exp\left(-i \frac{2\pi q_2 r_2}{N_2}\right) \right] \\ &= \frac{\mu \lambda'_M}{N} \left[\frac{1}{1 - (1 - \mu)} + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})} (\delta_{r_2} N_2 - 1) + \frac{1}{1 - (1 - \mu)(1 - m - \frac{m}{d-1})} (\delta_{r_1} N_1 - 1) \right. \\ &\quad \left. + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})} (\delta_{r_1} N_1 - 1) (\delta_{r_2} N_2 - 1) \right].\end{aligned}\quad (\text{C.24}) \quad \{\text{eq:app:Q2DMsol}\}$$

683 In particular,

$$\begin{aligned}\tilde{Q}_0 &= \frac{\mu \lambda'_M}{N} \left[\frac{1}{\mu} + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})} (n - 1) + \frac{1}{1 - (1 - \mu)(1 - m - \frac{m}{d-1})} (D - 1) \right. \\ &\quad \left. + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})} (D - 1)(n - 1) \right] \\ &= 1.\end{aligned}\quad (\text{C.25a}) \quad \{\text{eq:app:Q2D1}\}$$

684 We find λ'_M using the eq. (C.25a). Going back to eq. (C.24), when $r_1 = 0$, the two
 685 individuals are in the same deme. They are different when $r_2 \neq 0$, and so:

$$\begin{aligned}Q_{\text{in}} &= \frac{\mu \lambda'_M}{N} \left[\frac{1}{\mu} + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})} (-1) + \frac{1}{1 - (1 - \mu)(1 - m - \frac{m}{d-1})} (D - 1) \right. \\ &\quad \left. + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})} (D - 1)(-1) \right].\end{aligned}\quad (\text{C.25b})$$

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

$$Q_{\text{out}} = \frac{\mu \lambda'_M}{N} \left[\frac{1}{\mu} + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})} (-1) + \frac{1}{1 - (1 - \mu)(1 - m - \frac{m}{d-1})} (-1) + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})} \right]. \quad (\text{C.25c})$$

With $d_{\text{self}} = d_{\text{in}} = (1 - m)/n$, we recover the equations given in the main text (system (6)).

C.3 Wright-Fisher

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

$$\tilde{Q}_{r_1 r_2} = \frac{1}{N} \sum_{q_1=0}^{N_1-1} \sum_{q_2=0}^{N_2-1} \frac{\mu \lambda'_{WF}}{1 - (1 - \mu)^2 (\tilde{D}_{q_1})^2} \exp\left(-i \frac{2\pi q_1 r_1}{N_1}\right) \exp\left(-i \frac{2\pi q_2 r_2}{N_2}\right), \quad (\text{C.26})$$

with \tilde{D} given in eq. (C.21b). In a subdivided population, with $N_1 = N_D$ and $N_2 = n$, this becomes

$$\begin{aligned} \tilde{Q}_{r_1 r_2} &= \frac{1}{N} \left[\frac{\mu \lambda'_{WF}}{1 - (1 - \mu)^2 (\tilde{D}_0)^2} + \sum_{q_2=1}^{N_2-1} \frac{\mu \lambda'_{WF}}{1 - (1 - \mu)^2 (\tilde{D}_0)^2} \exp\left(-i \frac{2\pi q_2 r_2}{N_2}\right) \right. \\ &\quad + \sum_{q_1=1}^{N_1-1} \frac{\mu \lambda'_{WF}}{1 - (1 - \mu)^2 (\tilde{D}_{q_1})^2} \exp\left(-i \frac{2\pi q_1 r_1}{N_1}\right) \\ &\quad \left. + \sum_{q_1=1}^{N_1-1} \sum_{q_2=1}^{N_2-1} \frac{\mu \lambda'_{WF}}{1 - (1 - \mu)^2 (\tilde{D}_{q_1})^2} \exp\left(-i \frac{2\pi q_1 r_1}{N_1}\right) \exp\left(-i \frac{2\pi q_2 r_2}{N_2}\right) \right] \\ &= \frac{\mu \lambda'_{WF}}{N} \left[\frac{1}{1 - (1 - \mu)^2} + \frac{1}{1 - (1 - \mu)^2 (d_{\text{self}} - d_{\text{in}})^2} (\delta_{q_2} N_2 - 1) \right. \\ &\quad + \frac{1}{1 - (1 - \mu)^2 (1 - m - \frac{m}{d-1})^2} (\delta_{q_1} N_1 - 1) \\ &\quad \left. + \frac{1}{1 - (1 - \mu)^2 (d_{\text{self}} - d_{\text{in}})^2} (\delta_{q_1} N_1 - 1) (\delta_{q_2} N_2 - 1) \right] \\ &= \frac{\mu \lambda'_{WF}}{N} \left[\frac{1}{1 - (1 - \mu)^2} + \frac{1}{1 - (1 - \mu)^2 (d_{\text{self}} - d_{\text{in}})^2} (\delta_{q_2} N_2 - 1) \delta_{q_1} N_1 \right. \\ &\quad \left. + \frac{1}{1 - (1 - \mu)^2 (1 - m - \frac{m}{d-1})^2} (\delta_{q_1} N_1 - 1) \right]. \quad (\text{C.27}) \quad \{\text{eq:app:Q2DWFsol}\} \end{aligned}$$

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

$$1 = \frac{\mu \lambda'_{WF}}{N} \left[\frac{1}{1 - (1 - \mu)^2} + \frac{1}{1 - (1 - \mu)^2 (d_{\text{self}} - d_{\text{in}})^2} (N_2 - 1) N_1 + \frac{1}{1 - (1 - \mu)^2 (1 - m - \frac{m}{d-1})^2} (N_1 - 1) \right]. \quad (\text{C.28a})$$

694 Then from eq. (C.27) we deduce

$$Q_{\text{in}} = \frac{\mu\lambda'_{WF}}{N} \left[\frac{1}{1 - (1 - \mu)^2} - \frac{1}{1 - (1 - \mu)^2 (d_{\text{self}} - d_{\text{in}})^2} N_1 + \frac{1}{1 - (1 - \mu)^2 (1 - m - \frac{m}{d-1})^2} (N_1 - 1) \right]. \quad (\text{C.28b})$$

695 and

$$Q_{\text{out}} = \frac{\mu\lambda'_{WF}}{N} \left[\frac{1}{1 - (1 - \mu)^2} - \frac{1}{1 - (1 - \mu)^2 (1 - m - \frac{m}{d-1})^2} \right]. \quad (\text{C.28c})$$

696 With $d_{\text{self}} = d_{\text{in}} = (1 - m)/n$, we recover the equations given in the main text (sys-
697 tem (8)).

699 The table below contains all combinations for i, j, k, l involved in the four sums. (i, j) : means
700 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} |