

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. However, a detri-
5 mental side-effect of low emigration is the increase in competition among re-
6 lated individuals. The evolution of altruism depends on the balance between
7 these opposite effects. This balance is already known to be affected by details
8 of the life-cycle; we show here that it further depends on the fidelity of strategy
9 transmission from parents to their offspring. We consider different life-cycles
10 and identify thresholds of parent-offspring strategy transmission inaccuracy, above
11 which higher emigration can increase the frequency of altruists maintained in
12 the population. **EXPLAIN RESULT** Predictions were first obtained analytically
13 assuming weak selection and equal deme sizes, then confirmed with stochastic
14 simulations relaxing these assumptions. This result challenges the notion that
15 the evolution of altruism **REMOVE REQUIRE** requires limited dispersal.

16 **Introduction**

17 In his pioneering work on the evolution of social behavior, Hamilton suggested
18 that altruistic behavior would be associated to limited dispersal (Hamilton, 1964,
19 p. 10). This notion, that tighter links between individuals are beneficial to the
20 evolution of altruism, has been shown to hold in a number of population struc-
21 tures (see *e.g.* Allen et al., 2017; Lehmann et al., 2007; Ohtsuki et al., 2006; Taylor
22 et al., 2007a). The rationale is that altruism is favored when altruists interact
23 more with altruists than defectors do (Hamilton, 1975, p. 141; Fletcher & Doe-
24 beli, 2009), a condition that is met in viscous populations, *i.e.*, populations with
25 limited dispersal.

26 Yet, living next to your kin also implies competing against them (West et al.,
27 2002), which is detrimental to the evolution of altruism. The evolution of so-
28 cial traits hence depends on the balance between the positive effects of inter-
29 actions with related individuals and the detrimental consequences of kin com-
30 petition. Under specific conditions, the two effects can even compensate each
31 other, thereby annihilating the impact of population viscosity on the evolution
32 of altruism. First identified with computer simulations (Wilson et al., 1992), this
33 cancellation result was analyzed by Taylor (1992a) in a model with synchronous
34 generations (*i.e.*, Wright-Fisher model) and a subdivided population of constant,
35 infinite size. The cancellation result was later extended to heterogeneous pop-
36 ulations (Rodrigues & Gardner, 2012, with synchronous generations and infinite
37 population size), and other life-cycles, with generic regular population struc-
38 tures (Taylor et al., 2011, with synchronous generations but also with continuous
39 generations and Birth-Death updating). However, small changes in the model's
40 assumptions, such as overlapping generations (Taylor & Irwin, 2000) or the pres-
41 ence of empty sites (Alizon & Taylor, 2008) can tip the balance back in the favor
42 of altruism. This high dependence on life-cycle specificities highlights the dif-
43 ficulty of making general statements about the role of spatial structure on the

44 evolution of altruism. In this study, we will consider three different life-cycles:
45 Wright-Fisher, where the whole population is renewed at each time step, and
46 two Moran life-cycles (Birth-Death and Death-Birth), where a single individual
47 dies and is replaced at each time step. These life-cycles are classically used in
48 studies on altruism in structured populations. Even though they differ by seem-
49 ingly minor details, they are known to have very different outcomes in models
50 with perfect parent-offspring transmission (*e.g.*, Lehmann et al., 2007; Ohtsuki
51 et al., 2006; Rousset, 2004; Taylor, 1992a, 2010).

52 A large number of studies on the evolution of social behavior consider simple
53 population structures (typically, homogeneous populations *sensu* Taylor et al.
54 (2007a)) and often also infinite population sizes (but see Allen et al., 2017, for
55 results on any structure). These studies also make use of weak selection approx-
56 imations, and commonly assume rare (*e.g.*, Leturque & Rousset, 2002; Tarnita
57 & Taylor, 2014; Taylor et al., 2007b) or absent mutation (for models assuming
58 infinite population sizes, or models concentrating on fixation probabilities; see
59 Lehmann & Rousset, 2014; Van Cleve, 2015, for recent reviews). Often, these sim-
60 plifying assumptions are a necessary step towards obtaining explicit analytical
61 results. Although artificial, simple population structures (*e.g.*, regular graphs, or
62 subdivided populations with demes of equal sizes) help reduce the dimension-
63 ality of the system under study, in particular when the structure of the popula-
64 tion displays symmetries such that all sites behave the same way in expectation.
65 Weak selection approximations are crucial for disentangling spatial moments
66 (Lion, 2016), that is, changes in global *vs.* local frequencies (though they can in
67 some cases be relaxed, as in Mullan & Lehmann, 2014). Mutation, however, is
68 usually ignored by classical models of inclusive fitness because these models as-
69 sume infinite population sizes, so that there is no need to add mechanisms that
70 restore genetic diversity (Tarnita & Taylor, 2014). In populations of finite size,
71 this diversifying effect can be obtained thanks to mutation.

72 When strategy transmission is purely genetic, it makes sense to assume that
73 mutation is relatively infrequent. A social strategy can however also be culturally
74 transmitted from parent to offspring, in which case “rebellion” (as in Frank’s Re-
75 bellious Child Model (Frank, 1997)) does not have to be rare. Imperfect strategy
76 transmission can alter evolutionary dynamics, in particular in spatially struc-
77 tured populations (see *e.g.*, Allen et al., 2012; Débarre, 2017, for graph-structured
78 populations).

79 Here, we want to explore the consequences of imperfect strategy transmis-
80 sion from parents to their offspring on the evolution of altruistic behavior in sub-
81 divided populations¹. The question was tackled by Frank (1997), but with a “non
82 fully” dynamic model. His method, done “in the spirit of comparative statics”
83 (Frank, 1997, p.1721)², precluded the exploration of the effects of population vis-
84 cosity on the evolution altruism. reformuler

85 For each of the three life-cycles that we consider, we compute the expected
86 (*i.e.*, long-term) frequency of altruists maintained in a subdivided population,
87 and investigate how this frequency is affected by mutation and emigration. We
88 find that, contrary to what happens with perfect strategy transmission, higher
89 emigration can increase the expected frequency of altruists in the population.

90 **Model and methods**

91 **Assumptions**

92 We consider a population of size N , subdivided into N_D demes connected by
93 dispersal, each deme hosting exactly n individuals (*i.e.*, each deme contains n
94 sites, each of which is occupied by exactly one individual; we have $nN_D = N$).
95 Each site has a unique label i , $1 \leq i \leq N$. There are two types of individuals in
96 the population, altruists and defectors. The type of the individual living at site i

¹Note that 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.

²Terms with quotes are citations from Frank’s article.

97 $(1 \leq i \leq N)$ is given by an indicator variable X_i , equal to 1 if the individual is an
 98 altruist, and to 0 if it is a defector. The state of the entire population is given by
 99 a N -long vector \mathbf{X} . For a given population state \mathbf{X} , the proportion of altruists is
 100 $\bar{X} = \sum_{i=1}^N X_i$. All symbols are summarized in table A1.

101 Reproduction is asexual. The offspring of altruists are altruists themselves
 102 with probability $1 - \mu_{1 \rightarrow 0}$, and are defectors otherwise ($0 < \mu_{1 \rightarrow 0} \leq 1/2$). Similarly,
 103 the offspring of defectors are defectors with probability $1 - \mu_{0 \rightarrow 1}$, and are altruists
 104 otherwise ($0 < \mu_{0 \rightarrow 1} \leq 1/2$). Our calculations will be simpler if we introduce the
 105 following change of parameters:

$$\nu = \frac{\mu_{0 \rightarrow 1}}{\mu_{1 \rightarrow 0} + \mu_{0 \rightarrow 1}} \quad (0 < \nu < 1), \text{ and} \quad (1a)$$

$$\mu = \mu_{1 \rightarrow 0} + \mu_{0 \rightarrow 1} \quad (0 < \mu \leq 1). \quad (1b)$$

106 The composite parameter ν corresponds to the expected frequency of altruists
 107 in the population at the mutation-drift balance (*i.e.*, in the absence of selection;
 108 see Appendix A for details). We call ν the “mutation bias” parameter. Parameter
 109 μ is the sum of the two mutation probabilities. In the absence of selection, at the
 110 mutation-drift equilibrium, the correlation between the types of offspring and
 111 the type of their parents is $1 - \mu$ (see Appendix A for details for the calculation).
 112 We call μ the mutation parameter.

113 An individual of type X_k expresses a social phenotype $\phi_k = \delta X_k$, where δ is
 114 assumed to be small ($\delta \ll 1$). Social interactions take place within each deme,
 115 benefits are shared with the $n - 1$ other deme-mates. We assume that social in-
 116 teractions affect individual fecundity; f_k denotes the fecundity of the individual
 117 at site k . We denote by b the sum of the marginal effects of deme-mates’ phe-
 118 notypes on the fecundity of a focal individual, and by $-c$ the marginal effect of
 119 a focal individual’s phenotype on its own fecundity ($c \leq b$; see system (A22) for
 120 formal definitions).

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

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

126 with $0 < m < 1 - \frac{1}{N_D}$. (This upper bound is here to ensure that within-deme
 127 relatedness R , which will be defined later in the article, remains positive.)

128 We denote by $B_i = B_i(\mathbf{X}, \delta)$ the expected number of successful offspring of the
 129 individual living at site i (successful means alive at the next time step), and by
 130 $D_i = D_i(\mathbf{X}, \delta)$ the probability that the individual living at site i dies. Both depend
 131 on the state of the population \mathbf{X} , but also on the way the population is updated
 132 from one time step to the next, *i.e.*, on the chosen life-cycle (also called updating
 133 rule). We also define

$$W_i := (1 - \mu)B_i + 1 - D_i, \quad (3) \quad \{\text{eq: defW}\}$$

134 a particular definition of fitness, where the number of offspring produced (B_i) is
 135 scaled by the parent-offspring type correlation $(1 - \mu)$.

136 We will specifically explore three different life-cycles. At the beginning of
 137 each step of each life-cycle, all individuals produce offspring, that can be mu-
 138 tated; then these juveniles move, within the parental deme or outside of it, and
 139 land on a site. The next events occurring during the time step depend on the
 140 life-cycle:

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

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

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

149 **Methods**

150 **Analytical part**

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

158 The formula involves quantities that can be identified as neutral probabili-
 159 ties of identity by descent Q_{ij} , *i.e.*, the probability that individuals living at site
 160 i and j share a common ancestor and that no mutation occurred on either lin-
 161 eage since that ancestor, in a model with no selection ($\delta = 0$; this is the “muta-
 162 tion definition” of identity by descent (Rousset & Billiard, 2000).) In a subdivided
 163 population like ours, there are three possible values of Q_{ij} :

$$Q_{ij} = \begin{cases} 1 & \text{when } i = j, \\ Q_{\text{in}} & \text{when } i \neq j \text{ and both sites are in the same deme,} \\ Q_{\text{out}} & \text{when both sites are in different demes.} \end{cases} \quad (4) \quad \{\text{eq:Q3}\}$$

164 These neutral probabilities of identity by descent depend on the chosen life-
 165 cycle, and are also computed by taking the long-term expectation of conditional

166 expectations after one time step (see Appendix C.1 and C.2 and supplementary
 167 Mathematica file (Wolfram Research, Inc., 2017).)

168 **Stochastic simulations**

169 We also ran stochastic simulations (coded in C). The simulations were run for 10^8
 170 generations (one generation is one time step for the Wright-Fisher life-cycle, and
 171 N time steps for the Moran life-cycles). For each set of parameters and life-cycle,
 172 using R (R Core Team, 2015), we estimated the long-term frequency of altruists
 173 by sampling the population every 10^3 generations and computing the average
 174 frequency of altruists. All scripts are available at
 175 <https://flodebarre.github.io/SocEvolSubdivPop/>

176 **Results**

177 **Expected frequencies of altruists for each life-cycle**

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

$$\mathbb{E}[\bar{X}] \approx v + \frac{\delta}{\mu B^*} v(1-v)(1-Q_{\text{out}}) \times \left[\underbrace{\frac{\partial W}{\partial f_{\bullet}}(-c) + \frac{\partial W}{\partial f_{\text{in}}}b}_{-C} + \underbrace{\left(\frac{\partial W}{\partial f_{\bullet}}b + (n-1)\frac{\partial W}{\partial f_{\text{in}}}(-c) + (n-2)\frac{\partial W}{\partial f_{\text{in}}}b \right)}_{\mathcal{B}} \underbrace{\frac{Q_{\text{in}} - Q_{\text{out}}}{1 - Q_{\text{out}}}}_R \right], \quad (5) \quad \{\text{eq:EXapprox}\}$$

180 with W as defined in eq. (3). (Calculations leading to eq. (5) are presented in Ap-
 181 pendix B; notations are recapitulated in table A1)

182 The mutation bias v corresponds to the expected proportion of altruists in the
 183 population in the absence of selection (*i.e.*, when $\delta = 0$); δ is the parameter that
 184 scales the strength of selection ($\delta \ll 1$). The $-C$ term groups the effects corre-
 185 sponding to the effects of a change of a focal individual's phenotype on its own
 186 fitness (with the fitness definition given in eq. (3).) The \mathcal{B} term corresponds to

187 the sum of the effects on an individual's fitness of the change of deme-mates'
 188 phenotypes. It is multiplied by R , which is relatedness. Also note the overall
 189 $(1 - Q_{\text{out}})$ factor. All of these terms depend on the chosen life-cycle, and on pa-
 190 rameters such as the mutation probability μ and the emigration probability m .

191 **comment on decoupling nu and mu**

192 We now present the values of these different terms for the three life-cycles
 193 under study. The equations are obtained by replacing the derivatives of W by
 194 their specific formulas for each life-cycle, which are presented in Appendix B.2.
 195 The formulas of probabilities of identity by descent are more complicated, so not
 196 substituted, but they can be found in eq. (A40) and eq. (A44). The additional su-
 197 perscripts correspond to the life-cycles (WF: Wright-Fisher, M: Moran (either),
 198 DB: Moran Death-Birth, BD: Moran Birth-Death.) Finally, for each life-cycle,
 199 we further decompose the $-C$ and B terms into primary (subscript P) and sec-
 200 ondary (subscript S) effects (West & Gardner, 2010). Primary effects correspond
 201 to unmediated consequences of interactions (they are included in $\frac{\partial W}{\partial f}$), while
 202 secondary effects correspond to consequences of interactions mediated by other
 203 individuals, including competition. Primary and secondary effects correspond
 204 to what was called “direct” and “indirect” effects, respectively, in Débarre (2017);
 205 Débarre et al. (2014), but the terminology was updated for more consistency with
 206 other authors. All equations are of the form

$$\mathbb{E}[\bar{X}] \approx \nu + \frac{\delta}{\mu} \nu(1 - \nu)(1 - Q_{\text{out}}) \left[\underbrace{\begin{pmatrix} -C_P \\ -C_S \end{pmatrix}}_{-C} + \underbrace{\begin{pmatrix} B_P \\ +B_S \end{pmatrix}}_B \underbrace{\frac{Q_{\text{in}} - Q_{\text{out}}}{1 - Q_{\text{out}}}}_R \right]. \quad (6) \quad \{\text{eq:EXgeneric}\}$$

207 virer les EXBD etc, se focaliser sur primary et secondary pour etre plus
 compact. Commencer par R pour decrire l'effet de la mutation

208 **Moran Birth-Death** With the Birth-Death life-cycle, eq. (5) becomes

$$\mathbb{E}[\bar{X}] \approx v + \frac{\delta}{\mu} v(1-v)(1-Q_{\text{out}}^M) \times \left[\underbrace{\left(\frac{(1-\mu)(-c)}{+(b-c)\left(\frac{\mu}{N} - \frac{1-m}{n}\right)} \right)}_{-\mathcal{C}^{\text{BD}}} + \underbrace{\left(\frac{(1-\mu)b}{+(b-c)(n-1)\left(\frac{\mu}{N} - \frac{1-m}{n}\right)} \right)}_{\mathcal{B}^{\text{BD}}} \underbrace{\left(\frac{Q_{\text{in}}^M - Q_{\text{out}}^M}{1 - Q_{\text{out}}^M} \right)}_{R^M} \right], \quad (7) \quad \{\text{eq:EXBD}\}$$

209 The secondary effects (second line in the parentheses) include competitive ef-
 210 fects on the probability of reproducing, and consequences of social interactions
 211 on the probability that a given individual dies. Note that the secondary effects
 212 remain negative for the realistic range of emigration values that we consider (*i.e.*,
 213 $m < 1 - 1/N_D$).

214 **Moran Death-Birth** With the Death-Birth life-cycle, eq. (5) becomes

$$\mathbb{E}[\bar{X}] \approx v + \frac{\delta}{\mu} v(1-v)(1-Q_{\text{out}}^M) \times \left[\underbrace{\left(\frac{(1-\mu)(-c)}{-(b-c)(1-\mu)\left(\frac{(1-m)^2}{n} + \frac{m^2}{N-n}\right)} \right)}_{-\mathcal{C}^{\text{DB}}} + \underbrace{\left(\frac{(1-\mu)b}{-(b-c)(n-1)(1-\mu)\left(\frac{(1-m)^2}{n} + \frac{m^2}{N-n}\right)} \right)}_{\mathcal{B}^{\text{DB}}} \underbrace{\left(\frac{Q_{\text{in}}^M - Q_{\text{out}}^M}{1 - Q_{\text{out}}^M} \right)}_{R^M} \right], \quad (8) \quad \{\text{eq:EXDB}\}$$

215 With this life-cycle, Death occurs first, and the probability of dying is indepen-
 216 dent from the state of the population (since we assume that social interactions
 217 affect fecundity. We can therefore factor $(1-\mu)$ in all terms. The primary ef-
 218 fects (first lines in the parentheses) remain the same as with the Birth-Death
 219 life-cycle. However, the Death-Birth life-cycle leads to different secondary ef-
 220 fects compared to the Birth-Death life-cycle: competition occurs at a different
 221 scale (Grafen & Archetti, 2008). Finally, with this life-cycle as we defined it, the
 222 probabilities of identity by descent are the same as with the Birth-Death model.

Wright-Fisher

$$\mathbb{E}[\bar{X}] \approx v + \frac{\delta}{\mu} v(1-v)(1-Q_{\text{out}}^{\text{WF}}) \times \left[\underbrace{\left(\frac{(1-\mu)(-c)}{-(b-c)(1-\mu)\left(\frac{(1-m)^2}{n} + \frac{m^2}{N-n}\right)} \right)}_{-C^{\text{WF}}} + \underbrace{\left(\frac{(1-\mu)b}{-(b-c)(n-1)(1-\mu)\left(\frac{(1-m)^2}{n} + \frac{m^2}{N-n}\right)} \right)}_{B^{\text{WF}}} \underbrace{\left(\frac{Q_{\text{in}}^{\text{WF}} - Q_{\text{out}}^{\text{WF}}}{1 - Q_{\text{out}}^{\text{WF}}} \right)}_{R^{\text{WF}}} \right], \quad (9) \quad \{\text{eq:EXWF}\}$$

223 The only – but important – different between eq. (9) and eq. (8) is the value of the
 224 probabilities of identity by descent, because the number of individuals that are
 225 updated at each time step differs.

226 Primary effects

227 Let us first focus on primary effects, shown on the first lines in the parentheses
 228 in eq. (7)–eq. (9). They are the same for the three life-cycles that we consider,
 229 and they do not depend on the emigration probability m . At the same time, as
 230 shown on figure 1, the relatedness terms R^{M} and R^{WF} decrease with m (keeping
 231 $m < 1 - \frac{1}{N_D}$; see figure 1) Consequently, if we ignored secondary effects, we would
 232 conclude that even with imperfect strategy transmission ($\mu > 0$), increasing the
 233 emigration probability m decreases the expected frequency of altruists in the
 234 population (as our intuition may suggest already.) However, secondary effects
 235 play a role as well.

236 Changes with the emigration probability m

237 For the three life-cycles, the secondary effects are negative (with $0 < m < 1 - \frac{1}{N_D}$)
 238 and they increase with the emigration probability m . In other words, these detri-
 239 mental secondary effects weaken when the emigration probability increases. This
 240 effect goes against the reduction of relatedness R as m increases. Hence, we
 241 need to consider the entire equations to know the overall effect of the emigra-

tion probability m on the expected frequency of altruists $\mathbb{E}[\bar{X}]$ and on how it is affected by the (in)fidelity of parent-offspring transmission μ (see Figure 2).

The rather lengthy formulas that we obtain are relegated to the Appendix and supplementary Mathematica file, and we concentrate here on the results.

Moran Birth-Death

For the Moran Birth-Death life-cycle, we find that the expected frequency of altruists $\mathbb{E}[\bar{X}]$ 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 $\mu < \mu_c^{\text{BD}}$, $\mathbb{E}[\bar{X}]$ decreases with m , while when $\mu > \mu_c^{\text{BD}}$, $\mathbb{E}[\bar{X}]$ increases with m . The critical value μ_c^{BD} is given by

$$\mu_c^{\text{BD}} = 1 - \frac{b - c + \sqrt{(b - c)(4bN^2 + b - c)}}{2bN} \quad (10) \quad \{\text{eq:mucBD}\}$$

(recall that N is the total size of the population, $N = nN_D$.) This result is illustrated in figure 2(b); with the parameters of the figure, $\mu_c^{\text{BD}} \approx 0.026$. The threshold value increases with both deme size n and number of demes N_D , up to a maximum value $1 - \sqrt{1 - c/b}$ (equal to 0.034 with our parameters.)

With this life-cycle however, the expected frequency of altruists $\mathbb{E}[\bar{X}]$ remains lower than v , its value in the absence of selection (*i.e.*, when $\delta = 0$).

Moran Death-Birth

The relationship between $\mathbb{E}[\bar{X}]$ and m is a bit more complicated for the Moran Death-Birth life-cycle. For simplicity, we concentrate on what happens starting from low emigration probabilities (*i.e.*, on 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. (11) below; otherwise, when the benefits are high enough, $\mathbb{E}[\bar{X}]$ initially increases with m for any value of μ .

266 Combining these results, we write

$$\mu_c^{\text{DB}} = \begin{cases} \frac{(n+1)c - b}{(2n-1)b - (n-1)c} & \text{if } b < c(n+1), \\ 0 & \text{otherwise.} \end{cases} \quad (11) \quad \{\text{eq:mucDB}\}$$

267 When $b < c(n+1)$, the mutation threshold does not depend on the number of
 268 demes N_D , but increases when the size of the demes n increases. In figure 2(a),
 269 the parameters are such that $\mu_c^{\text{DB}} = 0$.

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

274 With the Death-Birth life-cycle, the expected frequency of altruists is higher
 275 than its neutral value v for intermediate values of the emigration probability m
 276 (unless $\mu \rightarrow 0$, in which case the lower bound tends to 0).

277 **Wright-Fisher**

278 Under a Wright-Fisher updating, the expected frequency of altruists in the pop-
 279 ulation reaches an extremum at the highest admissible emigration value $m =$
 280 $1 - \frac{1}{N_D}$. This extremum is a maximum when the mutation probability is higher
 281 than a threshold value μ_c^{WF} given by

$$\mu_c^{\text{WF}} = 1 - \sqrt{1 - \frac{c}{b}}, \quad (12)$$

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

283 With the Wright-Fisher life-cycle however, the expected frequency of altruists
 284 remains below its value in the absence of selection, v .

285 Interpreting the effect of m on $\mathbb{E}[\bar{X}]$

286 The result, that higher emigration probabilities can actually favor altruistic be-
 287 havior, may seem surprising, even though it is confirmed by simulations. The
 288 result may appear counterintuitive because explanations for the effect of popu-
 289 lation viscosity on the evolution of altruism often focus on primary effects. The
 290 role played by secondary effects is harder to grasp. To better understand the role
 291 played by the mutation probability μ , we now focus on a qualitative condition
 292 for the evolution of altruism and on the Death-Birth life-cycle:

$$\mathbb{E}[\bar{X}] > v \Leftrightarrow R^M > \frac{\mathcal{C}^{DB}}{\mathcal{B}^{DB}}. \quad (13) \quad \{\text{eq:BCcond}\}$$

293 (having made sure that $\mathcal{B}^{DB} > 0$, as shown in the supplementary Mathemati-
 294 cal file). With this life-cycle, the $\mathcal{C}^{DB}/\mathcal{B}^{DB}$ ratio does not change with the muta-
 295 tion probability μ , but it decreases with the emigration probability m ($0 < m <$
 296 $1 - 1/N_D$). This decrease of the $\mathcal{C}^{DB}/\mathcal{B}^{DB}$ ratio is due to secondary effects (com-
 297 petition) diminishing as emigration increases. Relatedness, on the other hand,
 298 decreases with both μ and m (see figure 3(a)).

299 When the emigration probability m is vanishingly small, $\lim_{m \rightarrow 0} R^M \leq \lim_{m \rightarrow 0} \frac{\mathcal{C}^{DB}}{\mathcal{B}^{DB}}$,
 300 the two only being equal when $\mu = 0$. Hence, it is only when strategy transmis-
 301 sion is perfect that condition (13) is satisfied for vanishingly low m . Then, as m
 302 increases, the $\frac{\mathcal{C}^{DB}}{\mathcal{B}^{DB}}$ ratio and relatedness R do not decrease with the same slope.
 303 Provided the mutation probability μ is not too high, *i.e.*, that R initially is not too
 304 low already, there can be a range of emigration values m such that condition (13)
 305 is satisfied (*i.e.*, the R curve is higher than the \mathcal{C}/\mathcal{B} curve in figure 3(a)).

306 Relaxing key assumptions

307 To derive our analytical results, we had to make a number of simplifying assump-
 308 tions, such as the fact that selection is weak ($\delta \ll 1$), and the fact that the struc-

309 ture of the population is regular (all demes have the same size n). We explored
310 with numerical simulations the effect of relaxing these key assumptions.

311 When selection is strong, the patterns that we identified not only still hold
312 but are even more marked, as shown on figure A1.

313 To relax the assumption of equal deme sizes, we randomly drew deme sizes
314 at the beginning of simulations, with sizes ranging from 2 to 6 individuals and
315 on average $\bar{n} = 4$ individuals per deme as previously. As shown in figure A2, the
316 patterns initially obtained with a homogeneous population structure are robust
317 when the structure is heterogeneous.

318 For the Moran model, it may seem odd that an offspring can replace its own
319 parent (which can occur since $d_{ii} \neq 0$). Figure A3, plotted with dispersal prob-
320 abilities preventing immediate replacement of one's own parent (for all sites i ,
321 $d_{ii} = d_{\text{self}} = 0$; $d_{\text{in}} = (1 - m)/(n - 1)$ for two different sites in the same deme, d_{out}
322 remaining unchanged), confirms that this does affect our conclusions.

323 The results are obtained in a population of finite size (the figures are done
324 with $N_D = 15$ demes), but still hold when the size of the population is larger (see
325 *e.g.*, figure 3(b), showing the range of emigration and mutation values such that
326 altruism is favored, plotted also for $N_D \rightarrow \infty$).

327 Compared to graphs classically used in evolutionary graph theory (*e.g.*, regu-
328 lar random graphs, grids), the island model is particular because the interaction
329 graph and the dispersal graph are different: interactions take place only within
330 demes ($e_{\text{out}} = 0$), while offspring can disperse out of their natal deme ($d_{\text{out}} > 0$).
331 One may wonder whether our result depends on this difference between the two
332 graphs. Figure A4 shows that the result still holds when the dispersal and inter-
333 action graphs are the same. In this figure indeed, we let a proportion m (equal
334 to the dispersal probability) of interactions occur outside of the deme where the
335 individuals live, and set d_{self} , the probability of self replacement, equal to 0, so
336 that the dispersal and interactions graphs are the same. Our conclusions remain

337 unchanged.

338 **Discussion**

339 **The expected frequency of altruists in a subdivided population can in-** 340 **crease with the probability of emigration**

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

352 **Quantitative vs. qualitative measures**

353 Often, evolutionary success is measured qualitatively, by comparing a quantity
354 (an expected frequency, or, in models with no mutation, a probability of fixation)
355 to the value it would have in the absence of selection. In our model, this amounts
356 to saying that altruism is favored whenever $\mathbb{E}[\bar{X}] > v$ (v is plotted as a horizon-
357 tal dashed line in figure 2). Some of our conclusions change if we switch to this
358 qualitative measure of evolutionary success: Under the Moran Birth-Death and
359 Wright-Fisher life-cycles, population viscosity does not promote the evolution of
360 altruism – actually, these two life-cycles cannot ever promote altruistic behavior
361 for any regular population structure (Taylor et al., 2011), whichever the probabil-

ity of mutation (Débarre, 2017). However, under a Moran Death-Birth life-cycle (figure 2(a)), altruism can be favored only at intermediate emigration probabilities. Starting for initially low values of m , increasing the emigration probability can still favor the evolution of altruism under this qualitative criterion (see figure 3(b).)

The result is due to secondary effects

The result, that frequency of altruists can increase with the emigration probability m , may seem counterintuitive. It is the case because verbal explanations for the evolution of altruism often rely on primary effects only. Relatedness R decreases with m , so it may be tempting to conclude that increases in the emigration probability m are necessarily detrimental to the evolution of altruism. However, secondary effects play an opposite role, as competition decreases with m . To further explain the relative weight of the detrimental and beneficial consequences of increases in the emigration probability m , let us focus on the Death-Birth life-cycle and consider the qualitative criterion for evolutionary success ($\mathbb{E}[\bar{X}] > v$, i.e. $R > C/B$; figure 3.)

When parent-offspring strategy transmission is nearly perfect ($\mu \rightarrow 0$), for vanishingly small emigration probabilities ($m \rightarrow 0$), both R and the C/B ratio tend to 1. An increase in the mutation probability μ reduces R while leaving C/B unchanged. In other words, for vanishingly small emigration probabilities, altruism is favored by selection only when transmission fidelity is nearly perfect. Let us now consider that benefits b of social interactions are high enough for altruism to be favored at low m when $\mu \rightarrow 0$ (as in figure 3(a)). Starting from low values of m , small increases in m have a stronger effect on the C/B ratio than on relatedness R : local competition is initially so strong that the beneficial reduction in competition caused by an increase in m initially predominates over the detrimental reduction in relatedness R . The opposite holds for much higher

389 values of m : competition is already small enough that reducing it further does
390 not outweigh the reduction in relatedness R .

391 Secondary effects are less straightforward to understand than primary ef-
392 fects, and yet they play a crucial role for social evolution in spatially structured
393 populations. Competition among relatives is for instance the reason for Taylor
394 (1992b)’s cancellation result. Similarly, the qualitative differences between the
395 Moran Birth-Death and Moran Death-Birth life-cycles is explained by the differ-
396 ent scales of competition that the two life-cycle produce (Débarre et al., 2014;
397 Grafen & Archetti, 2008). Secondary effects are also behind the evolution of so-
398 cial behaviors such as spite (West & Gardner, 2010).

399 **How small is small and how large is large?**

400 Our results were derived under the assumption of weak selection, assuming that
401 the phenotypic difference between altruists and defectors is small ($\delta \ll 1$). We
402 considered any fidelity of transmission (any μ between 0 and 1) and population
403 size. However, most models considering subdivided populations assume nearly
404 perfect strategy transmission ($\mu \rightarrow 0$) and infinite population sizes (number of
405 demes $N_D \rightarrow \infty$). The point is technical, but it is important to know that the or-
406 der in which these limits are taken matters, *i.e.*, one needs to specify how small
407 μ and δ are compared to the inverse size of the population. This remark com-
408 plements findings by Sample & Allen (2017), who highlighted the quantitative
409 differences between different orders of weak selection and large population lim-
410 its.

411 **Imperfect transmission and Rebellious Children**

412 Our model bears resemblance to the Rebellious Child Model by Frank (1997),
413 who studied the evolution of a vertically transmitted cultural trait in an asexually
414 reproducing population. In Frank’s model, however, relatedness r is treated as

415 a fixed parameter (as acknowledged in the legend of Figure 7 in Frank (1997)).
416 Our model is mechanistic; relatedness r necessarily depends on the mutation
417 probability μ , because probabilities of identity by descent do.

418 Mutation was also previously included in models investigating the mainte-
419 nance of cooperative microorganisms in the presence of cheaters (Brockhurst
420 et al., 2007; Frank, 2010). In both of these models however, only loss-of-function
421 mutation was considered, which corresponds to setting the mutation bias at
422 $\nu = 0$ in our model. This means that the all-cheaters state is absorbing; no matter
423 how favored cooperators may otherwise be, in the long run, a finite population
424 will only consist of cheaters.

425 **Cultural transmission**

426 Strategy transmission does not have to be genetic: it can be cultural. In our
427 model, strategy transmission occurs upon reproduction, so this is a case of ver-
428 tical cultural transmission.

429 The model could nevertheless be interpreted as a representation of horizon-
430 tal transmission, if we described reproduction as an instance of an individual
431 convincing another one to update its strategy. The Moran Death-Birth model
432 can be interpreted as a modified imitation scheme (Boyd & Richerson, 2002; Oht-
433 suki et al., 2006) – with a specific function specifying who is imitated –, with mu-
434 tation (Kandori et al., 1993). First, we choose uniformly at random an individual
435 who may change its strategy; with probability μ the individual chooses a random
436 strategy (altruistic with probability ν), and with probability $1 - \mu$ it imitates an-
437 other individual. Who is imitated depends on the distance to the focal individual
438 (with probability m it is a random individual in another deme) and on the “fe-
439 cundities” of those individuals (as shown in table A2). With this interpretation of
440 the updating rule however, there is not reproduction nor death anymore.

441 It remains to be investigated how imperfect strategy transmission would af-

fect the effect of population viscosity on the evolution of altruism in a model im-
plementing both reproduction and horizontal cultural transmission (as in Lehmann
et al., 2008). Such a model could then contrast the effects of imperfect genetic
transmission and imperfect horizontal cultural transmission.

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, lead-
ing to a polymorphism between sessile altruists and mobile defectors (Mullon
et al., 2017; Parvinen, 2013). 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 mu-
tations would affect their result.

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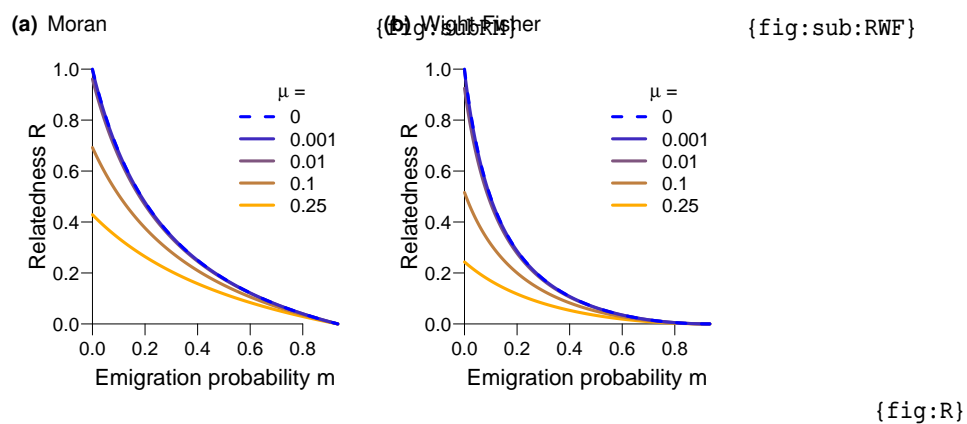


Figure 1: Within-deme relatedness of pairs of individuals, as a function of the emigration probability m , for different values of the mutation probability μ (from 0 [blue] to 0.25 [orange]), and for the two types of life-cycles ((a): Moran, (b): Wright-Fisher). Other parameters: $n = 4$ individuals per deme, $N_D = 15$ demes.

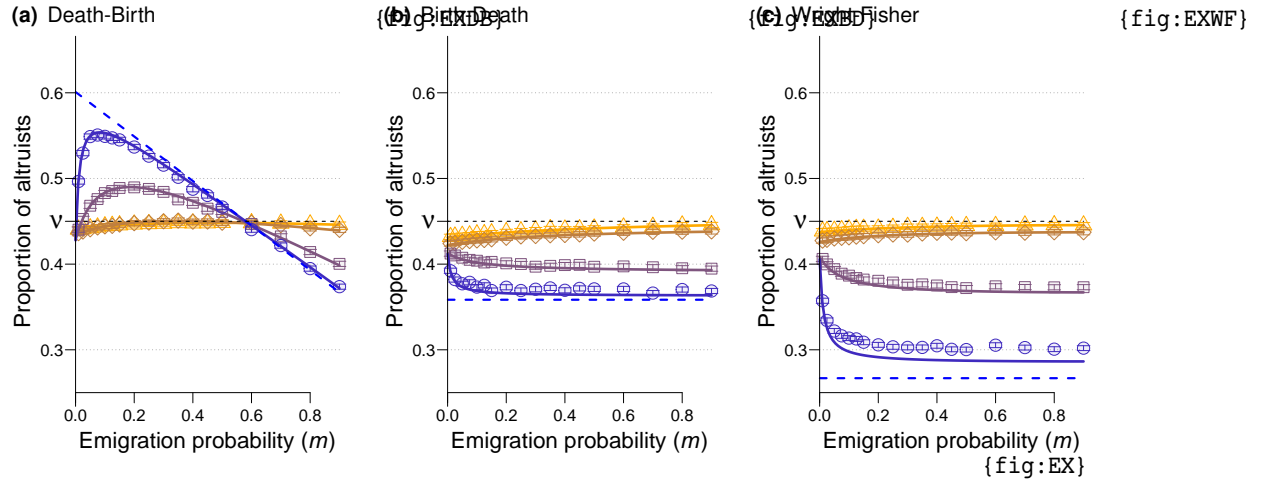


Figure 2: Expected proportion of altruists under weak selection, as a function of the emigration probability m , for different mutation values ($\mu = 0.001$ (blue, dots), 0.01 (purple, squares), 0.1 (brown, diamonds), 0.25 (orange, triangles); the dashed blue lines correspond to $\mu = 0$) and different 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: $\delta = 0.005$, $v = 0.45$, $b = 15$, $c = 1$, $n = 4$ individuals per deme, $N_D = 15$ demes.

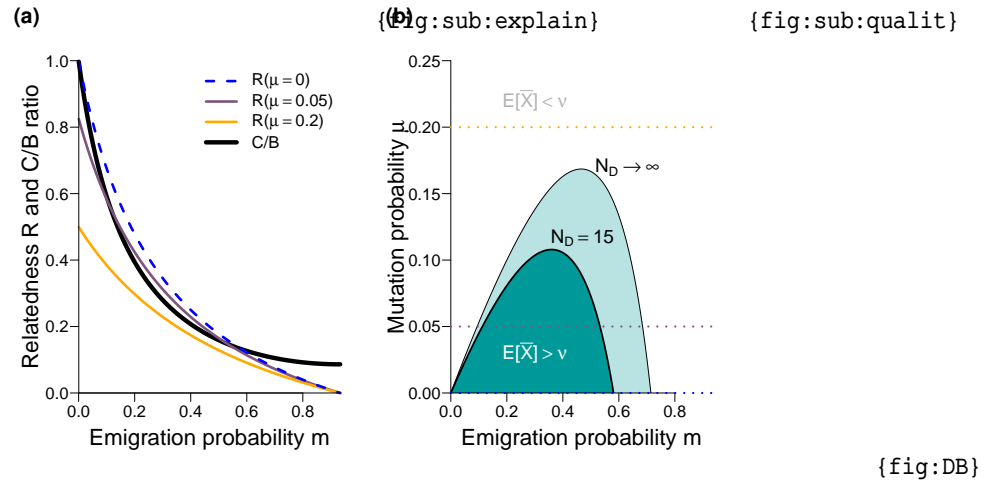


Figure 3: Understanding the effect of emigration m on whether altruism is favored in the Death-Birth life-cycle. (a) Comparison of the C/B ratio (thick black curve) and relatedness R (thin curves) for different values of the mutation probability μ (same color code as previously). (b) (m, μ) combinations for which $E[\bar{X}] > v$. The dotted horizontal lines correspond to the mutation values used in panel (a). Unless specified, all other parameters are the same as in figure 2.

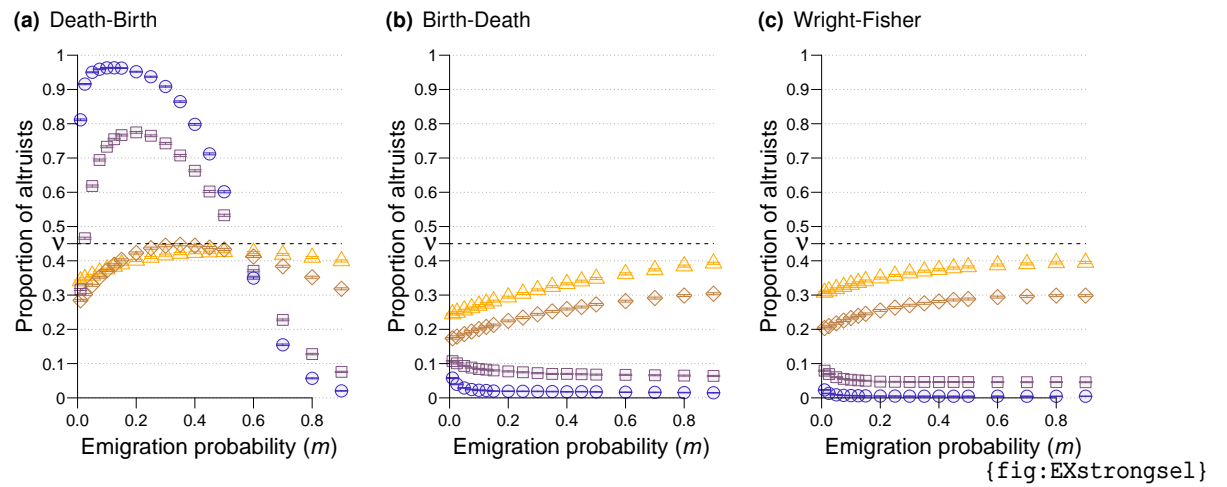


Figure A1: Equivalent of figure 2 (simulations only) but with strong selection ($\delta = 0.1$); please note the change of scale on the vertical axis. All other parameters and legends are identical to those of figure 2 (increasing mutation probabilities from blue dots to orange triangles).

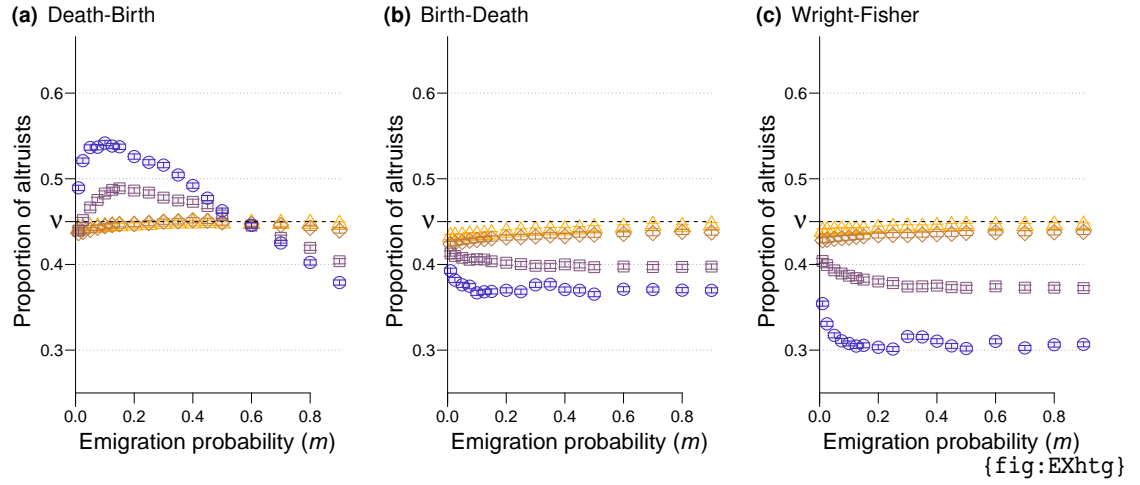


Figure A2: Equivalent of figure 2 (simulations only) but with a heterogeneous population structure: deme sizes range from 1 to 5 individuals per deme, the average deme size is 4 as in figure 2; all other parameters and legend are identical to those of figure 2.

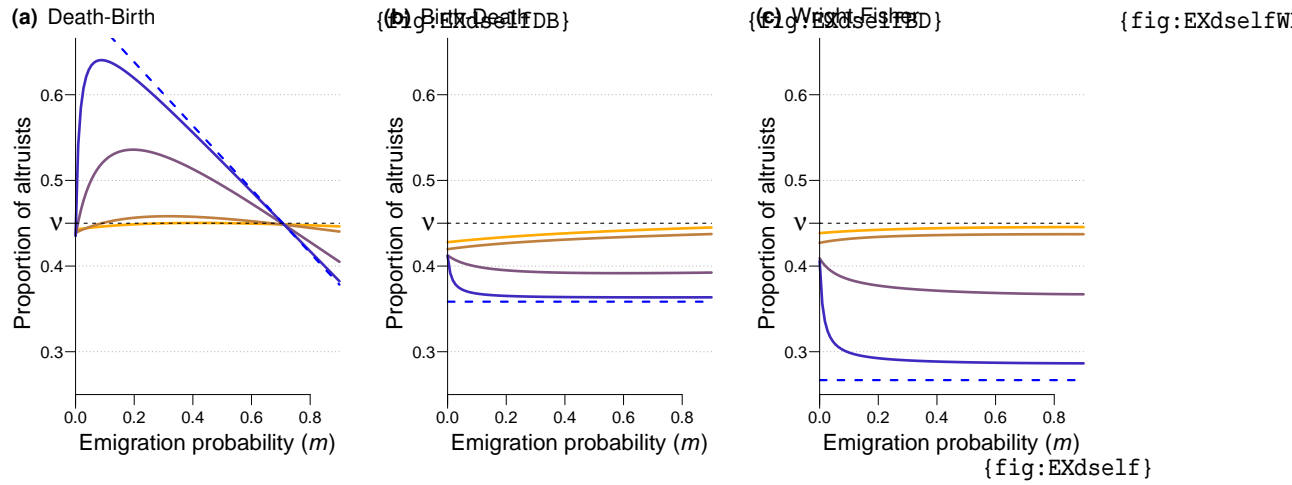


Figure A3: Equivalent of figure 2 (analysis only), with no self-replacement ($d_{ii} = d_{\text{self}} = 0$ for all sites).

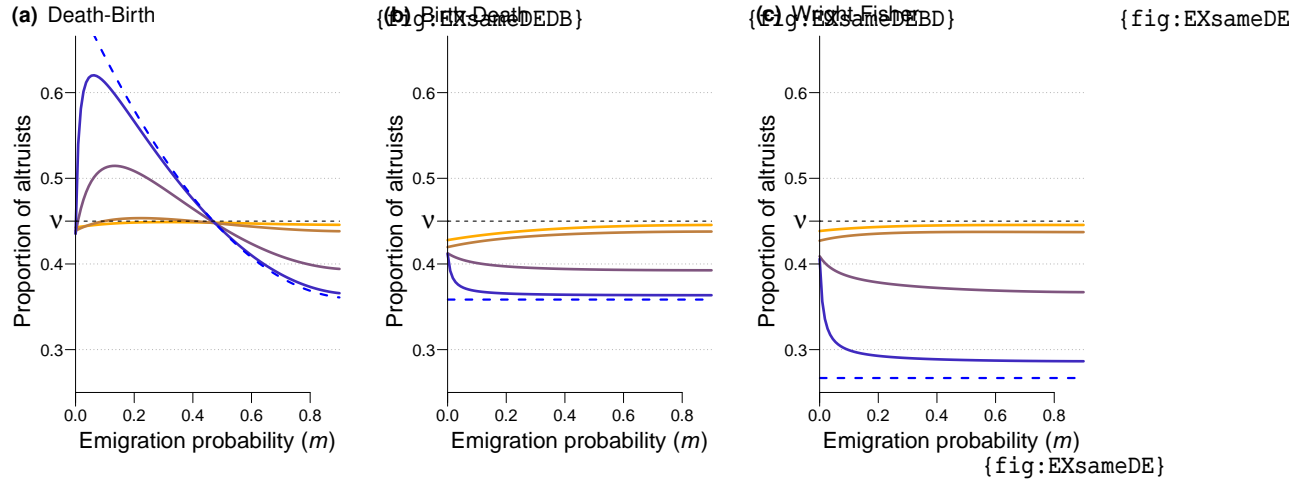


Figure A4: Equivalent of figure 2 (analysis only), with equal dispersal and interaction graphs (*i.e.*, no self-replacement [$d_{ii} = d_{\text{self}} = 0$ for all sites], and a proportion m of the interactions occurring outside of the home deme).

Supplementary Table

b	Sum of the marginal effects of deme-mates' phenotypes on focal individual's fecundity (benefit)
\mathcal{B}	Sum of the marginal effects of deme-mates' phenotypes on the fitness W of a focal individual
B_i	Expected number of successful offspring of the individual living at site i (r.v.)
B^*	Value of B_i for all sites, in the absence of selection ($\delta = 0$)
c	Marginal effect of a focal individual's phenotype on its own fecundity (cost)
\mathcal{C}	Marginal effect of an individual's phenotype on its own fitness W
d_{ij}	Dispersal probability from site i to site j
D_i	Probability that the individual currently living at site i is dead at the end of the time step (r.v.)
e_{ij}	Interaction probability from site i to site j
f_i	Fecundity of the individual currently living at site i (r.v.)
n	Deme size
N_D	Number of demes
N	Total population size ($N = N_D n$)
m	Emigration probability
P_{ij}	(Long-term) Expected state of the pair of sites (i, j)
Q_{ij}	(Long-term) Probability of identity by descent of individuals at sites i and j
R	Pairwise within-deme relatedness (see eq. (5))
W_i	Measure of fitness, counting offspring only when unmutated (see eq. (3))
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.)
δ	Phenotypic distance between altruists and defectors; strength of selection
ϕ_i	Phenotype of the individual living at site i ; $\phi_i = \delta X_i$ (r.v.)
μ	Mutation probability
ν	Mutation bias: probability that mutant is altruist
P	Subscript corresponding to primary effects
S	Subscript corresponding to secondary effects
•	Subscript used to denote a focal individual
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 $i = j$
0	Sub- or superscript meaning that a quantity is evaluated at $\delta = 0$
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 A1: List of symbols. "r.v." means *random variable*.

Appendix

567 A Mutation parameters

{sec:app:mutation}

568 In the main text, we first introduce effective mutation parameters: $\mu_{1 \rightarrow 0}$, the
569 probability that an altruist has defector offspring, and $\mu_{0 \rightarrow 1}$, the probability that
570 a defector has altruist offspring.

571 A.1 Expected frequency of altruists at the mutation drift balance

572 Let Y be the type of a randomly chosen individual in the population, and let
573 Y' be the type of a randomly chosen individual at the next time step. Given a
574 frequency v of altruists in the population, we have

$$\mathbb{E}[Y] = v, \quad (\text{A1a})$$

$$\mathbb{E}[Y'] = v(1 - \mu_{1 \rightarrow 0}) + (1 - v)\mu_{0 \rightarrow 1}. \quad (\text{A1b})$$

575 The expected frequency of altruists is found by solving $\mathbb{E}[Y] = \mathbb{E}[Y']$, and we
576 obtain

$$v = \frac{\mu_{0 \rightarrow 1}}{\mu_{1 \rightarrow 0} + \mu_{0 \rightarrow 1}}. \quad (\text{A2}) \quad \{\text{eq:app:nuformula}\}$$

577 A.2 Parent-offspring correlation at the mutation drift balance

578 We can then compute the parent-offspring type correlation at the mutation-drift
579 balance. First, let us compute the parent-offspring covariance:

$$\begin{aligned} \text{Cov}[Y Y'] &= \mathbb{E}[Y Y'] - \mathbb{E}[Y']\mathbb{E}[Y] \\ &= v(1 - \mu_{1 \rightarrow 0}) - (v(1 - \mu_{1 \rightarrow 0}) + (1 - v)\mu_{0 \rightarrow 1})v \\ &= v(1 - v)(1 - \mu_{1 \rightarrow 0} - \mu_{0 \rightarrow 1}). \end{aligned} \quad (\text{A3}) \quad \{\text{eq:app:Cov}\}$$

580 Then, the standard deviations are given by

$$\begin{aligned} \sigma_Y &= \sqrt{\mathbb{E}[Y^2] - \mathbb{E}[Y]^2} = \sqrt{\mathbb{E}[Y] - \mathbb{E}[Y]^2} \\ &= \sqrt{v(1 - v)}, \end{aligned} \quad (\text{A4}) \quad \{\text{eq:app:SD1}\}$$

581 and

$$\begin{aligned} \sigma_{Y'} &= \sqrt{\mathbb{E}[Y'^2] - \mathbb{E}[Y']^2} = \sqrt{\mathbb{E}[Y'] - \mathbb{E}[Y']^2} \\ &= \sqrt{v(1 - v)(1 - \mu_{1 \rightarrow 0} - \mu_{0 \rightarrow 1}) - (v(1 - v)(1 - \mu_{1 \rightarrow 0} - \mu_{0 \rightarrow 1}))^2}. \end{aligned} \quad (\text{A5}) \quad \{\text{eq:app:SD2}\}$$

582 The parent-offspring correlation is given by

$$\text{Corr}[Y Y'] = \frac{\text{Cov}[Y Y']}{\sigma_Y \sigma_{Y'}};$$

583 using the formulas eq. (A3)–(A5), and replacing v by its value (mutation-drift
584 equilibrium, eq. (A2)), we obtain

$$\text{Corr}[Y Y'] = 1 - (\mu_{1 \rightarrow 0} + \mu_{0 \rightarrow 1}) = 1 - \mu. \quad (\text{A6})$$

585 **A.3 Redefining the mutation scheme**

{sec:app:mutnew}

586 If we denote by X_i the type of a given parent, then the expected type of one of its
587 offspring is

$$\mathbb{E}[X'_i|X_i] = X_i(1 - \mu_{1 \rightarrow 0}) + (1 - X_i)\mu_{0 \rightarrow 1}. \quad (\text{A7a}) \quad \{\text{eq:app:expoff}\}$$

588 Replacing $\mu_{1 \rightarrow 0}$ and $\mu_{0 \rightarrow 1}$ by equivalent combinations of μ and ν , *i.e.*,

$$\mu_{1 \rightarrow 0} = \mu(1 - \nu) \text{ and } \mu_{0 \rightarrow 1} = \mu\nu, \quad (\text{A7b})$$

589 then eq. (A7a) becomes

$$\mathbb{E}[X'_i|X_i] = X_i(1 - \mu) + \mu\nu. \quad (\text{A7c}) \quad \{\text{eq:app:expoff2}\}$$

590 We can redefine the mutation scheme and interpret eq. (A7c) as follows. Parents
591 transmit their strategy to their offspring with probability $1 - \mu$; with probability
592 μ , offspring do not inherit their strategy from their parent but instead get one
593 randomly: with probability ν , they become altruists, with probability $1 - \nu$ they
594 become defectors. With this alternative description, we can call “mutants” indi-
595 viduals who have the same type as their parent.

B Expected frequency of altruists

{sec:app:EX}

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 $B_{ji}(X(t), \delta)$, 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 A2 for each of the life-cycles that we consider.

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

{tab:BD}

Table A2: Formulas of B_{ji} 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 , and d_{ji} is a dispersal probability, given in eq. (2).

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

$$D_i = \sum_{j=1}^N B_{ji} \quad (\text{A8a}) \quad \{\text{eq:DBequiv}\}$$

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 offspring (*i.e.*, of having offspring that become adults at the next time step), so that

$$D_i^0 = \sum_{j=1}^N B_{ji}^0 = B_i^0 =: B^*, \quad (\text{A8b}) \quad \{\text{eq:DBRV}\}$$

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 \mathbf{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. (A8b) and eq. (A8a) is that we are now considering offspring produced by i landing on j).

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

$$\mathbb{E}[\bar{X}(t+1)|\mathbf{X}(t)] = \frac{1}{N} \sum_{i=1}^N [B_i(1-\mu)X_i + (1-D_i)X_i + B_i\mu\nu]. \quad (\text{A9a}) \quad \{\text{eq:conditionalchange}\}$$

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), whichever 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 probability that the population is in state \mathbf{X} , given the strength of selection δ and the mutation probability μ . Taking the expectation of eq. (A9a) ($\mathbb{E}[\bar{X}] = \sum_{\mathbf{X} \in \Omega} \bar{X} \xi(\mathbf{X}, \delta, \mu)$), we obtain, after reorganizing:

$$0 = \frac{1}{N} \sum_{\mathbf{X} \in \Omega} \left[\sum_{i=1}^N (B_i(1-\mu)X_i - D_i X_i) + \sum_{i=1}^N B_i \mu \nu \right] \xi(\mathbf{X}, \delta, \mu). \quad (\text{A10}) \quad \{\text{eq:statdist}\}$$

Now, we use the assumption of weak selection ($\delta \ll 1$) and consider the first-order expansion of eq. (A10) for δ close to 0.

$$\begin{aligned} 0 = & \frac{1}{N} \sum_{\mathbf{X} \in \Omega} \left[\sum_{i=1}^N (B_i^0(1-\mu)X_i - D_i^0 X_i) + \sum_{i=1}^N B_i^0 \mu \nu \right] \xi(\mathbf{X}, 0, \mu) \\ & + \frac{1}{N} \sum_{\mathbf{X} \in \Omega} \left[\sum_{i=1}^N \left(\frac{\partial B_i(1-\mu) - D_i}{\partial \delta} X_i \right) + \sum_{i=1}^N \frac{\partial B_i}{\partial \delta} \mu \nu \right] \xi(\mathbf{X}, 0, \mu) \\ & + \frac{1}{N} \sum_{\mathbf{X} \in \Omega} \left[\sum_{i=1}^N (B_i^0(1-\mu)X_i - D_i^0 X_i) + \sum_{i=1}^N B_i^0 \mu \nu \right] \frac{\partial \xi(\mathbf{X}, \delta, \mu)}{\partial \delta}, \end{aligned} \quad (\text{A11}) \quad \{\text{eq:app:TaylorDetail}\}$$

where all the derivatives are evaluated for $\delta = 0$. The first line of eq. (A11) is equal to zero, because $B_i^0 = D_i^0 = B^*$ (eq. (A8b)), and because in the absence of selection ($\delta = 0$), the expected state of every site i is $\mathbb{E}_0[X_i] = \sum_{\mathbf{X} \in \Omega} X_i \xi(\mathbf{X}, 0, \mu) = \nu$ (recall that ν is the mutation bias parameter). The second terms of the second and third lines are both zero, because for all the life-cycles that we consider, the total number of births in the population during one time step ($\sum_{i=1}^N B_i$) does not depend on population phenotypic composition (it is exactly 1 death for the Moran life-cycles, and exactly N for the Wright-Fisher life-cycle). Eq. (A11) then

645 becomes

$$0 = \frac{\delta}{N} \sum_{i=1}^N \left[\sum_{X \in \Omega} \left(\frac{\partial B_i}{\partial \delta} (1 - \mu) - \frac{\partial D_i}{\partial \delta} \right) X_i \xi(\mathbf{X}, 0, \mu) - \sum_{X \in \Omega} \mu B^* X_i \frac{\partial \xi}{\partial \delta} \right] + O(\delta^2), \quad (\text{A12}) \quad \{\text{eq:weaksel0}\}$$

646 where the derivatives are evaluated at $\delta = 0$. For conciseness, we define

$$W_i = (1 - \mu) B_i + (1 - D_i), \quad (\text{A13}) \quad \{\text{eq:app:defW}\}$$

647 a measure of fitness counting offspring only when they are unmutated (in the
648 sense of the alternate mutation scheme described in Appendix A.3). With this,
649 using the expectation notation, and denoting by $\mathbb{E}_0[\cdot]$ expectations under $\delta = 0$,
650 we can rewrite and reorganize eq. (A12) as

$$\delta \mu B^* \frac{\partial \mathbb{E}[\bar{X}]}{\partial \delta} = \frac{\delta}{N} \sum_{i=1}^N \mathbb{E}_0 \left[\frac{\partial W_i}{\partial \delta} X_i \right] + O(\delta^2). \quad (\text{A14}) \quad \{\text{eq:weaksel0reorg}\}$$

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

$$\begin{aligned} \frac{\partial W_i}{\partial \delta} &= \sum_{k=1}^N \frac{\partial W_i}{\partial \phi_k} \frac{\partial \phi_k}{\partial \delta} \\ &= \sum_{k=1}^N \frac{\partial W_i}{\partial \phi_k} X_k, \end{aligned} \quad (\text{A15}) \quad \{\text{eq:totalprobal}\}$$

653 by definition of ϕ_k ($\phi_k = \delta X_k$), and where the derivatives are evaluated for all
654 $\phi_i = 0$. Introducing the notation $P_{ij} = \mathbb{E}_0[X_i X_j]$ (expected state of a pair of sites),
655 eq. (A14) becomes

$$\delta \mu B^* \frac{\partial \mathbb{E}[\bar{X}]}{\partial \delta} = \frac{\delta}{N} \sum_{i=1}^N \sum_{k=1}^N \frac{\partial W_i}{\partial \phi_k} P_{ik} + O(\delta^2). \quad (\text{A16}) \quad \{\text{eq:weaksel1}\}$$

656 So far, we have not used the specificities of the population structure that we
657 consider. Once we have fixed a focal individual i , in expectation there are only
658 three types of individuals: the focal itself (denoted by “•”), $n - 1$ other individu-
659 als in the focal’s deme (denoted by “in”), and $N - n$ individuals in other demes
660 (denoted by “out”). We note that given that the size of the population is fixed
661 ($\sum_{i=1}^N (B_i - D_i) = 0$), and given that the total number of births does not depend
662 on population composition in the life-cycles that we consider,

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

663 which we can rewrite as (Rousset & Billiard, 2000, p.817–818)

$$\frac{\partial W_i}{\partial \phi_i} + (n - 1) \frac{\partial W_i}{\partial \phi_{\text{in}}} + (N - n) \frac{\partial W_i}{\partial \phi_{\text{out}}} = 0. \quad (\text{A17}) \quad \{\text{eq:derivsumW}\}$$

664 With this, eq. (A16) becomes

$$\delta\mu B^* \frac{\partial \mathbb{E}[\bar{X}]}{\partial \delta} = \frac{\delta}{N} \sum_{i=1}^N \left(\frac{\partial W_i}{\partial \phi_i} + (n-1) \frac{\partial W_i}{\partial \phi_{in}} \frac{P_{in} - P_{out}}{P_{ii} - P_{out}} \right) (P_{ii} - P_{out}) + O(\delta^2). \quad (\text{A18}) \quad \{\text{eq:weaksel1CBRP}\}$$

665 We can also replace the P terms by

$$\begin{aligned} P_{ij} &= Q_{ij}v + (1 - Q_{ij})v^2 \\ &= v^2 + v(1 - v)Q_{ij}. \end{aligned} \quad (\text{A19}) \quad \{\text{eq:QP}\}$$

666 In Appendix C.1, using recursions on P_{ij} , we will see that Q_{ij} can be interpreted
667 as a probability of identity by descent, *i.e.*, the probability that the individuals at
668 sites i and j have a common ancestor and that no mutation (using the alterna-
669 tive mutation scheme described in Appendix A.3) has occurred on either lineage
670 since the ancestor. Eq. (A18) becomes

$$\delta\mu B^* \frac{\partial \mathbb{E}[\bar{X}]}{\partial \delta} = \frac{\delta}{N} \sum_{i=1}^N \underbrace{\left(\frac{\partial W_i}{\partial \phi_i} \right)}_{-C} + \underbrace{(n-1) \frac{\partial W_i}{\partial \phi_{in}}}_{B} \underbrace{\frac{Q_{in} - Q_{out}}{1 - Q_{out}}}_{R} (1 - Q_{out})v(1 - v) + O(\delta^2). \quad (\text{A20}) \quad \{\text{eq:weaksel1CBRP}\}$$

671 We can further decompose the derivatives, now using the fecundities f_ℓ as
672 intermediate variables, *i.e.*,

$$\frac{\partial W_i}{\partial \phi_k} = \sum_{\ell=1}^N \frac{\partial W_i}{\partial f_\ell} \frac{\partial f_\ell}{\partial \phi_k}. \quad (\text{A21})$$

673 With our notation, and given that social interactions take place within demes
674 and affect fecundity, we have \{\text{eq:derivf}\}

$$\left. \frac{\partial f_\ell}{\partial \phi_\ell} \right|_{\delta=0} = -c, \quad (\text{A22a})$$

$$\left. \frac{\partial f_\ell}{\partial \phi_{in}} \right|_{\delta=0} = \frac{b}{n-1}, \quad (\text{A22b})$$

$$\left. \frac{\partial f_\ell}{\partial \phi_{out}} \right|_{\delta=0} = 0. \quad (\text{A22c})$$

675 Eq. (A20) then becomes (using notation \bullet to refer to the focal individual itself,
676 and where $W = W_i$, since the derivatives are the same for all i):

$$\begin{aligned} \delta\mu B^* \frac{\partial \mathbb{E}[\bar{X}]}{\partial \delta} &= \delta v(1 - v)(1 - Q_{out}) \times \\ &\quad \left(\underbrace{\left(\frac{\partial W}{\partial f_\bullet} (-c) + \frac{\partial W}{\partial f_{in}} b \right)}_{-C} + \underbrace{\left(\frac{\partial W}{\partial f_\bullet} b + (n-1) \frac{\partial W}{\partial f_{in}} (-c) + (n-2) \frac{\partial W}{\partial f_{in}} b \right)}_{B} \underbrace{\frac{Q_{in} - Q_{out}}{1 - Q_{out}}}_{R} \right) + O(\delta^2). \end{aligned} \quad (\text{A23}) \quad \{\text{eq:weaksel2}\}$$

677 (As previously, all derivatives are evaluated at $\delta = 0$.)

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

$$\mathbb{E}[\bar{X}] = \nu + \delta \left. \frac{\partial \mathbb{E}[\bar{X}]}{\partial \delta} \right|_{\delta=0} + O(\delta^2), \quad (\text{A24}) \quad \{\text{eq:app:EXgeneric}\}$$

680 where $\nu = \mathbb{E}_0[\bar{X}]$ (expected frequency in the absence of selection), and where
681 $\left. \frac{\partial \mathbb{E}[\bar{X}]}{\partial \delta} \right|_{\delta=0}$ is obtained from eq. (A23). We then need to replace the B_i and D_i
682 terms by their formulas for each life-cycle; they are given in table A2.

683 B.2 Derivatives for the specific life-cycles {\sec:app:dW}

684 Using the formulas presented in table A2, and the definition of $W = W_i$ given in
685 eq. (A13), we obtain the following equations:

{\eq:dWBD}

Moran Birth-Death

$$\left. \frac{\partial W^{\text{BD}}}{\partial f_{\bullet}} \right|_{\delta=0} = (1 - \mu) \left(\frac{1}{N} - \frac{1}{N^2} \right) - \left(\frac{1 - m}{nN} - \frac{1}{N^2} \right) = \frac{1 - \mu}{N} + \frac{\mu}{N^2} - \frac{1 - m}{nN}, \quad (\text{A25a})$$

$$\left. \frac{\partial W^{\text{BD}}}{\partial f_{\text{in}}} \right|_{\delta=0} = (1 - \mu) \left(-\frac{1}{N^2} \right) - \left(\frac{1 - m}{nN} - \frac{1}{N^2} \right) = \frac{\mu}{N^2} - \frac{1 - m}{nN}. \quad (\text{A25b})$$

{\eq:dWDB}

Moran Death-Birth

$$\left. \frac{\partial W^{\text{DB}}}{\partial f_{\bullet}} \right|_{\delta=0} = \frac{1 - \mu}{N} \left[1 - \left(\frac{(1 - m)^2}{n} + \frac{m^2}{N - n} \right) \right], \quad (\text{A26a})$$

$$\left. \frac{\partial W^{\text{DB}}}{\partial f_{\text{in}}} \right|_{\delta=0} = -\frac{1 - \mu}{N} \left(\frac{(1 - m)^2}{n} + \frac{m^2}{N - n} \right). \quad (\text{A26b})$$

686 In addition, for both Moran life-cycles, we have $B_{\text{M}}^* = 1/N$.

{\eq:dWWF}

Wright-Fisher

$$\left. \frac{\partial W^{\text{WF}}}{\partial f_{\bullet}} \right|_{\delta=0} = (1 - \mu) \left[1 - \left(\frac{(1 - m)^2}{n} + \frac{m^2}{N - n} \right) \right], \quad (\text{A27a})$$

$$\left. \frac{\partial W^{\text{WF}}}{\partial f_{\text{in}}} \right|_{\delta=0} = -(1 - \mu) \left(\frac{(1 - m)^2}{n} + \frac{m^2}{N - n} \right). \quad (\text{A27b})$$

687 For the Wright-Fisher life-cycle, we have $B_{\text{WF}}^* = 1$.

688 Combining these equations with eq. (A24) and eq. (A23) given eqs. (7)–(9) in
689 the main text.

690 C Probabilities of identity by descent

691 C.1 Expected state of pairs of sites and probabilities of identity by de- 692 scent

{sec:app:IBD}

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

697 C.1.1 Moran model

698 In a Moran model, exactly one individual dies and one individual reproduces
699 during one time step. Given a state \mathbf{X} at time t , at time $t + 1$ both sites i and
700 $j \neq i$ are occupied by altruists, if i it was the case at time t and neither site was
701 replaced by a non-altruist (first term in eq. (A28)), or ii if exactly one of the two
702 sites was occupied by a non-altruist at time t , but the site was replaced by an
703 altruist (second and third terms of eq. (A28)):

$$\begin{aligned} \mathbb{E}[X_i X_j(t+1) | X(t) = \mathbf{X}] = & X_i X_j \left(1 - \sum_{k=1}^N \frac{1}{N} (d_{ki} + d_{kj}) ((1 - X_k)(1 - \mu) + \mu(1 - \nu)) \right) \\ & + X_i(1 - X_j) \sum_{k=1}^N \frac{1}{N} d_{kj} (X_k(1 - \mu) + \mu\nu) \\ & + X_j(1 - X_i) \sum_{k=1}^N \frac{1}{N} d_{ki} (X_k(1 - \mu) + \mu\nu). \end{aligned} \quad (\text{A28}) \quad \{\text{eq:app:Pi jM1}\}$$

704 We take the expectation of this quantity, and consider that the stationary dis-
705 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

$$P_{ij} = \frac{1}{2} \left(\sum_{k=1}^N (1 - \mu) (d_{kj} P_{ki} + d_{ki} P_{kj}) \right) + \mu\nu^2 \quad (i \neq j), \quad (\text{A29}) \quad \{\text{eq:app:Pi jM}\}$$

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

707 Now we substitute $P_{ij} = \nu^2 + \nu(1 - \nu)Q_{ij}$ in eq. (A29), we obtain

$$Q_{ij} = \frac{1}{2} \sum_{k=1}^N (1 - \mu) (d_{ki} Q_{kj} + d_{kj} Q_{ki}), \quad (\text{A30}) \quad \{\text{eq:app:Qi jM}\}$$

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

713 **C.1.2 Wright-Fisher model**

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

$$\begin{aligned} \mathbb{E}[X_i X_j(t+1) | X(t) = \mathbf{X}] = & \sum_{k, \ell=1}^N d_{ki} d_{\ell j} \left(X_k X_\ell (1 - \mu + \mu v)^2 \right. \\ & + (X_k(1 - X_\ell) + (1 - X_k)X_\ell) (1 - \mu + \mu v)(\mu v) \\ & \left. + (1 - X_k)(1 - X_\ell)(\mu v)^2 \right) \end{aligned} \quad (A31) \quad \{\text{eq:app:Pi jWF1}\}$$

716 The first term of eq. (A31) corresponds to both parents being altruists, and hav-
717 ing altruist offspring; the second line corresponds to exactly one parent being
718 altruist, and the third line to both parents being non-altruists (in this latter case,
719 the two offspring have to be both mutants to be altruists).

720 Taking the expectation and simplifying, we obtain

$$P_{ij} = \sum_{k, \ell=1}^N (P_{kl}(1 - \mu)^2) + (2 - \mu)\mu v^2. \quad (A32) \quad \{\text{eq:app:Pi jWF}\}$$

721 Replacing P_{ij} by $v^2 + v(1 - v)Q_{ij}$, eq. (A32) becomes

$$Q_{ij} = \sum_{k, \ell=1}^N d_{ki} d_{\ell j} Q_{k\ell} (1 - \mu)^2. \quad (A33) \quad \{\text{eq:app:QijWF}\}$$

722 Again, Q_{ij} corresponds to a probability of identity by descent: the individuals at
723 sites i and j are identical by descent if their parents were and if neither mutated
724 $((1 - \mu)^2)$.

725 C.2 Probabilities of identity by descent in a subdivided population {sec:app:Qsubdiv}

726 Two individuals are said to be identical by descent if there has not been any mu-
 727 tation on either lineage since their common ancestor. Because of the structure
 728 of the population, there are only three types of pairs of individuals, and hence
 729 three different values of the probabilities of identity by descent of pairs of sites
 730 Q_{ij} :

$$Q_{ij} = \begin{cases} 1 & \text{when } i = j; \\ Q_{\text{in}} & \text{when } i \neq j \text{ and both sites are in the same deme;} \\ Q_{\text{out}} & \text{when sites } i \text{ and } j \text{ are in different demes.} \end{cases} \quad (\text{A34})$$

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

732 Here, we will use formulas derived in Débarre (2017) for “two-dimensional
 733 population structures”. The name comes from the fact that we only need two
 734 types of transformations to go from any site to any other site in the population:
 735 permutations on the deme index, and permutations on the within-deme index.
 736 We rewrite site labels ($1 \leq i \leq N$) as (ℓ_1, ℓ_2) , where ℓ_1 is the index of the deme ($1 \leq$
 737 $\ell_1 \leq N_D$) and ℓ_2 the position of the site within the deme ($1 \leq \ell_2 \leq n$). Then, we
 738 introduce notations \tilde{d}_{i_1, i_2} and \tilde{Q}_{i_1, i_2} , that correspond to the dispersal probability and
 739 probability of identity by descent to a site at distances i_1 and i_2 in the among-
 740 demes and within-deme dimensions (e.g., $\tilde{d}_{i_1, i_2} = d_{j_1, j_2}$ where $j_1 = \ell_1 + i_1$ and $j_2 = \ell_2 + i_2$).

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

743 C.2.1 Moran model

744 In Débarre (2017), it was shown that

$$\tilde{Q}_{r_1, r_2} = \frac{1}{N} \sum_{q_1=0}^{N_1-1} \sum_{q_2=0}^{N_2-1} \frac{\mu \lambda'_M}{1 - (1 - \mu) \tilde{D}_{q_1, q_2}} \exp\left(i \frac{2\pi q_1 r_1}{N_1}\right) \exp\left(i \frac{2\pi q_2 r_2}{N_2}\right) \quad (\text{A35a}) \quad \{\text{eq:app:Q2DM}\}$$

745 with

$$\tilde{D}_{q_1, q_2} = \sum_{\ell_1=0}^{N_1-1} \sum_{\ell_2=0}^{N_2-1} \tilde{d}_{\ell_1, \ell_2} \exp\left(-i \frac{2\pi q_1 \ell_1}{N_1}\right) \exp\left(-i \frac{2\pi q_2 \ell_2}{N_2}\right), \quad (\text{A35b}) \quad \{\text{eq:app:D2D}\}$$

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

$$\begin{aligned} \tilde{D}_{q_1, q_2} &= d_{\text{self}} + \sum_{\ell_2=1}^{N_2-1} d_{\text{in}} \exp\left(-i \frac{2\pi q_2 \ell_2}{N_2}\right) + \sum_{\ell_1=1}^{N_1-1} \sum_{\ell_2=0}^{N_2-1} d_{\text{out}} \exp\left(-i \frac{2\pi q_1 \ell_1}{N_1}\right) \exp\left(-i \frac{2\pi q_2 \ell_2}{N_2}\right) \\ &= d_{\text{self}} + (\delta_{q_2} (N_2 - 1) + (1 - \delta_{q_2}) (-1)) d_{\text{in}} + (\delta_{q_1} (N_1 - 1) + (1 - \delta_{q_1}) (-1)) (\delta_{q_2} N_2) d_{\text{out}} \\ &= d_{\text{self}} + (\delta_{q_2} N_2 - 1) d_{\text{in}} + (\delta_{q_1} N_1 - 1) \delta_{q_2} N_2 d_{\text{out}}. \end{aligned} \quad (\text{A36a})$$

748 (δ_q is equal to 1 when q is equal to 0 modulo the relevant dimension, and to 0
 749 otherwise). So for the three types of distances that we need to consider (distance
 750 0, distance to another deme-mate, distance to individual in another deme), and
 751 with $N_1 = N_D$ and $N_2 = n$, we obtain

{eq:app:Dsystem}

$$\tilde{D}_0 = 1, \quad (\text{A37a})$$

$$\tilde{D}_{q_1} = 1 - m - \frac{m}{N_D - 1} \quad (q_1 \not\equiv 0 \pmod{N_1}), \quad (\text{A37b})$$

$$\tilde{D}_{q_1} = d_{\text{self}} - d_{\text{in}} \quad (q_2 \not\equiv 0 \pmod{N_2}). \quad (\text{A37c})$$

752 So for \tilde{Q} , using system (A37) in eq. (A35a),

$$\begin{aligned} \tilde{Q}_{r_1} &= \frac{\mu \lambda'_M}{N} \left[\frac{1}{1 - (1 - \mu) \tilde{D}_0} + \sum_{q_2=1}^{N_2-1} \frac{1}{1 - (1 - \mu) \tilde{D}_{q_2}} \exp\left(-\iota \frac{2\pi q_2 r_2}{N_2}\right) \right. \\ &\quad + \sum_{q_1=1}^{N_1-1} \frac{1}{1 - (1 - \mu) \tilde{D}_{q_1}} \exp\left(-\iota \frac{2\pi q_1 r_1}{N_1}\right) \\ &\quad \left. + \sum_{q_1=1}^{N_1-1} \sum_{q_2=1}^{N_2-1} \frac{1}{1 - (1 - \mu) \tilde{D}_{q_1}} \exp\left(-\iota \frac{2\pi q_1 r_1}{N_1}\right) \exp\left(-\iota \frac{2\pi q_2 r_2}{N_2}\right) \right] \\ &= \frac{\mu \lambda'_M}{N} \left[\frac{1}{1 - (1 - \mu)} + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})} (\delta_{r_2} N_2 - 1) \right. \\ &\quad + \frac{1}{1 - (1 - \mu)(1 - m - \frac{m}{N_D - 1})} (\delta_{r_1} N_1 - 1) \\ &\quad \left. + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})} (\delta_{r_1} N_1 - 1)(\delta_{r_2} N_2 - 1) \right]. \quad (\text{A38}) \quad \{\text{eq:app:Q2DMsol}\} \end{aligned}$$

753 In particular,

$$\begin{aligned} \tilde{Q}_0 &= \frac{\mu \lambda'_M}{N} \left[\frac{1}{\mu} + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})} (n - 1) + \frac{1}{1 - (1 - \mu)(1 - m - \frac{m}{N_D - 1})} (N_D - 1) \right. \\ &\quad \left. + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})} (N_D - 1)(n - 1) \right] \\ &= 1. \quad (\text{A39a}) \quad \{\text{eq:app:Q2D1}\} \end{aligned}$$

754 We find λ'_M using eq. (A39a). Let's now go back to eq. (A38): when $r_1 = 0$, the two
 755 individuals are in the same deme. They are different when $r_2 \neq 0$, and so:

$$\begin{aligned} Q_{\text{in}} &= \frac{\mu \lambda'_M}{N} \left[\frac{1}{\mu} + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})} (-1) + \frac{1}{1 - (1 - \mu)(1 - m - \frac{m}{N_D - 1})} (D - 1) \right. \\ &\quad \left. + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})} (D - 1)(-1) \right]. \quad (\text{A39b}) \end{aligned}$$

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

$$Q_{\text{out}} = \frac{\mu \lambda'_M}{N} \left[\frac{1}{\mu} + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})}(-1) + \frac{1}{1 - (1 - \mu)(1 - m - \frac{m}{N_D - 1})}(-1) + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})} \right]. \quad (\text{A39c})$$

757 With $d_{\text{self}} = d_{\text{in}} = (1 - m)/n$, we eventually obtain:

{eq:QM}

$$Q_{\text{in}}^M = \frac{(1 - \mu)(m + \mu(N_D(1 - m) - 1))}{(1 - \mu)m(N_D\mu(n - 1) + 1) + (N_D - 1)\mu(\mu(n - 1) + 1)}, \quad (\text{A40a})$$

$$Q_{\text{out}}^M = \frac{(1 - \mu)m}{(1 - \mu)m(N_D\mu(n - 1) + 1) + (N_D - 1)\mu(\mu(n - 1) + 1)}. \quad (\text{A40b})$$

758 The probability that two different deme-mates are identical by descent, Q_{in}^M , de-
759 creases monotonically with the emigration probability m , while Q_{out}^M monoton-
760 ically increases with m (see figure A5(a)).

761 When the mutation probability μ is vanishingly small ($\mu \rightarrow 0$), both Q_{in}^M and
762 Q_{out}^M are equal to 1: in the absence of mutation indeed, the population ends up
763 fixed for one of the two types, and all individuals are identical by descent. Note
764 that we obtain a different result if we first assumed that the size of the popu-
765 lation is infinite ($N_D \rightarrow \infty$), because the order of limits matters; for instance,
766 $\lim_{d \rightarrow \infty} Q_{\text{out}}^M = 0$.

767 C.2.2 Wright-Fisher

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

$$\tilde{Q}_{r_1 r_2} = \frac{1}{N} \sum_{q_1=0}^{N_1-1} \sum_{q_2=0}^{N_2-1} \frac{\mu \lambda'_{WF}}{1 - (1 - \mu)^2 (\tilde{D}_{q_1})^2} \exp\left(-i \frac{2\pi q_1 r_1}{N_1}\right) \exp\left(-i \frac{2\pi q_2 r_2}{N_2}\right), \quad (\text{A41})$$

769 with $\tilde{\mathcal{D}}$ given in eq. (A35b). In a subdivided population, with $N_1 = N_D$ and $N_2 = n$,
 770 this becomes

$$\begin{aligned}
 \tilde{Q}_{r_1 r_2} &= \frac{1}{N} \left[\frac{\mu \lambda'_{WF}}{1 - (1 - \mu)^2 (\tilde{\mathcal{D}}_0)^2} + \sum_{q_2=1}^{N_2-1} \frac{\mu \lambda'_{WF}}{1 - (1 - \mu)^2 (\tilde{\mathcal{D}}_{q_2})^2} \exp\left(-i \frac{2\pi q_2 r_2}{N_2}\right) \right. \\
 &\quad + \sum_{q_1=1}^{N_1-1} \frac{\mu \lambda'_{WF}}{1 - (1 - \mu)^2 (\tilde{\mathcal{D}}_{q_1})^2} \exp\left(-i \frac{2\pi q_1 r_1}{N_1}\right) \\
 &\quad \left. + \sum_{q_1=1}^{N_1-1} \sum_{q_2=1}^{N_2-1} \frac{\mu \lambda'_{WF}}{1 - (1 - \mu)^2 (\tilde{\mathcal{D}}_{q_1})^2} \exp\left(-i \frac{2\pi q_1 r_1}{N_1}\right) \exp\left(-i \frac{2\pi q_2 r_2}{N_2}\right) \right] \\
 &= \frac{\mu \lambda'_{WF}}{N} \left[\frac{1}{1 - (1 - \mu)^2} + \frac{1}{1 - (1 - \mu)^2 (d_{\text{self}} - d_{\text{in}})^2} (\delta_{q_2} N_2 - 1) \right. \\
 &\quad + \frac{1}{1 - (1 - \mu)^2 (1 - m - \frac{m}{N_D-1})^2} (\delta_{q_1} N_1 - 1) \\
 &\quad \left. + \frac{1}{1 - (1 - \mu)^2 (d_{\text{self}} - d_{\text{in}})^2} (\delta_{q_1} N_1 - 1) (\delta_{q_2} N_2 - 1) \right] \\
 &= \frac{\mu \lambda'_{WF}}{N} \left[\frac{1}{1 - (1 - \mu)^2} + \frac{1}{1 - (1 - \mu)^2 (d_{\text{self}} - d_{\text{in}})^2} (\delta_{q_2} N_2 - 1) \delta_{q_1} N_1 \right. \\
 &\quad \left. + \frac{1}{1 - (1 - \mu)^2 (1 - m - \frac{m}{N_D-1})^2} (\delta_{q_1} N_1 - 1) \right]. \tag{A42} \quad \{\text{eq:app:Q2DWFsol}\}
 \end{aligned}$$

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

$$1 = \frac{\mu \lambda'_{WF}}{N} \left[\frac{1}{1 - (1 - \mu)^2} + \frac{1}{1 - (1 - \mu)^2 (d_{\text{self}} - d_{\text{in}})^2} (N_2 - 1) N_1 + \frac{1}{1 - (1 - \mu)^2 (1 - m - \frac{m}{N_D-1})^2} (N_1 - 1) \right]. \tag{A43a}$$

772 Then from eq. (A42) we deduce

$$Q_{\text{in}} = \frac{\mu \lambda'_{WF}}{N} \left[\frac{1}{1 - (1 - \mu)^2} - \frac{1}{1 - (1 - \mu)^2 (d_{\text{self}} - d_{\text{in}})^2} N_1 + \frac{1}{1 - (1 - \mu)^2 (1 - m - \frac{m}{N_D-1})^2} (N_1 - 1) \right]. \tag{A43b}$$

773 and

$$Q_{\text{out}} = \frac{\mu \lambda'_{WF}}{N} \left[\frac{1}{1 - (1 - \mu)^2} - \frac{1}{1 - (1 - \mu)^2 (1 - m - \frac{m}{d-1})^2} \right]. \tag{A43c}$$

774 With $d_{\text{self}} = d_{\text{in}} = (1 - m)/n$, we obtain: {\text{eq:QWF}}

$$Q_{\text{in}}^{\text{WF}} = \frac{-N_D + M_1 + M_2}{(n - 1)N_D + M_1 + M_2}, \tag{A44a}$$

$$Q_{\text{out}}^{\text{WF}} = \frac{-\frac{1}{N_D-1} M_1 + M_2}{(n - 1)N_D + M_1 + M_2}, \tag{A44b}$$

775 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 $m = m_c^{\text{WF}} = \frac{N_D - 1}{N_D}$, while $Q_{\text{out}}^{\text{WF}}$ follows the opposite pattern. The threshold value m_c^{WF} corresponds to an emigration probability so high that $d_{\text{in}} = d_{\text{out}}$.

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

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 A5(a) and A5(b)).

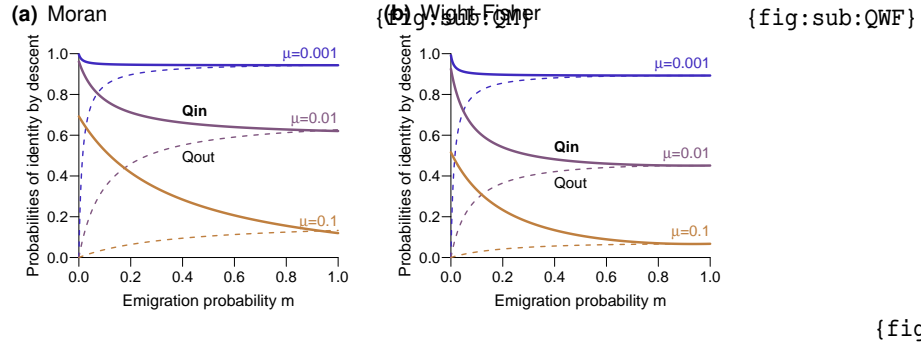


Figure A5: Probabilities of identity by descent, for two different individuals within the same deme (Q_{in} , full curves) and two individuals in different demes (Q_{out} , dashed curves), as a function of the emigration probability m , for different values of the mutation probability μ (0.001, 0.01, 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.