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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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**Short Running Title:** Mutation and altruism in subdivided populations.

**Keywords:** Altruism, Subdivided population, Mutation, Migration, Cooperation, Island model.

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Check  $\omega$  removes entirely + explain delta in table

## 1 Abstract

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

16 stochastic simulations relaxing these assumptions. This result challenges the  
17 notion that the evolution of altruism requires limited dispersal.

## 18 **Impact Summary**

19 The evolution of altruistic behavior has fascinated and puzzled evolutionary bi-  
20 ologists for a long time: how can a strategy whereby individuals help others at  
21 their own cost be maintained in a population? One answer is the fact that altru-  
22 ists may interact with other altruists more often than non-altruists do, a situa-  
23 tion made possible by spatial structure and low emigration. Low emigration in-  
24 deed means that an individual is mostly surrounded by related individuals; when  
25 social strategies are faithfully transmitted from parents to offspring, and social  
26 interactions are local as well, then altruists interact mainly with other altruists.  
27 However, this also means that related individuals have to compete against each  
28 other. Whether altruism eventually evolves depends on the balance between  
29 these beneficial and detrimental consequences of low emigration. Previous work  
30 has shown that the balance depends on the life-cycle that the population under-  
31 goes; under nearly perfect strategy transmission, low emigration goes from be-  
32 ing neutral to the evolution of altruism (when generations are synchronous and  
33 non-overlapping) to favorable. In this work, we show that this conclusion qual-  
34 itatively changes when offspring do not necessarily adopt their parent's strat-  
35 egy, that is, when strategy transmission is imperfect. This can be due to muta-  
36 tion when transmission is genetic, but also to imperfect vertical cultural trans-  
37 mission. We identify thresholds of strategy transmission infidelity, above which  
38 higher emigration is more conducive to the evolution of altruism than low em-  
39 igration. The predictions are first obtained mathematically under the restric-  
40 tive assumptions that selection is weak and that all demes have the same size,  
41 but are then confirmed with computer simulations relaxing these assumptions.  
42 This work shows that the evolution of altruism does not require – and even can  
43 be hampered by – low emigration.

## 44 1 Introduction

45 In his pioneering work on the evolution of social behavior, Hamilton suggested  
46 that altruistic behavior would be associated to limited dispersal (Hamilton, 1964,  
47 p. 10). This notion, that tighter links between individuals favor the evolution of  
48 altruism, has been shown to hold in a number of population structures (see *e.g.*  
49 Ohtsuki et al., 2006; Taylor et al., 2007a; Lehmann et al., 2007). The rationale that  
50 altruism is favored when altruists interact more with altruists than defectors do  
51 (Hamilton, 1975, p. 141; Fletcher & Doebeli, 2009), a condition that is met in  
52 viscous populations, *i.e.*, populations with limited dispersal.

53 Yet, living next to your kin also implies competing against them (West et al.,  
54 2002). The evolution of social traits hence depends on the balance between the  
55 positive effects of interactions with related individuals and the detrimental con-  
56 sequences of kin competition. Under specific conditions, the two effects can  
57 even compensate each other, thereby annihilating the impact of population vis-  
58 cosity on the evolution of altruism. First identified with computer simulations  
59 (Wilson et al., 1992), this cancellation result was analyzed by Taylor (1992a) in  
60 a model with synchronous generations (*i.e.*, Wright-Fisher model) and a sub-  
61 divided population of constant, infinite size. The cancellation result was later  
62 extended to heterogeneous populations (Rodrigues & Gardner, 2012, with syn-  
63 chronous generations and infinite population size), and other life-cycles, with  
64 generic regular population structures (Taylor et al., 2011, with synchronous gen-  
65 erations but also with continuous generations and Birth-Death updating). How-  
66 ever, small changes in the model's assumptions, such as overlapping generations  
67 (Taylor & Irwin, 2000) or the presence of empty sites (Alizon & Taylor, 2008) can  
68 tip the balance back in the favor of altruism. This high dependence on life-  
69 cycle specificities highlights the difficulty of making general statements about  
70 the role of spatial structure on the evolution of altruism. In this study, we will

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

74 A large number of studies on the evolution of social behavior consider simple  
75 population structures (typically, homogeneous populations *sensu* Taylor et al.  
76 (2007a)) and often also infinite population sizes (but see Allen et al., 2017, for  
77 results on any structure). These studies also make use of weak selection ap-  
78 proximations, and commonly assume rare (*e.g.*, Leturque & Rousset, 2002; Tay-  
79 lor et al., 2007b; Tarnita & Taylor, 2014) or absent mutation (for models assum-  
80 ing infinite population sizes, or models concentrating on fixation probabilities  
81 Lehmann & Rousset, 2014; Van Cleve, 2015, for recent reviews). Often, these sim-  
82 plifying assumptions are a necessary step towards obtaining explicit analytical  
83 results. Although artificial, simple population structures (*e.g.*, regular graphs, or  
84 subdivided populations with demes of equal sizes) help reduce the dimension-  
85 ality of the system under study, in particular when the structure of the popula-  
86 tion displays symmetries such that all sites behave the same way in expectation.  
87 Weak selection approximations are crucial for disentangling spatial moments  
88 (Lion, 2016), that is, changes in global *vs.* local frequencies (though they can in  
89 some cases be relaxed, as in Mullon & Lehmann, 2014). Mutation, however, is  
90 usually ignored by classical models of inclusive fitness because these models as-  
91 sume infinite population sizes, so that there is no need to add mechanisms that  
92 restore genetic diversity (Tarnita & Taylor, 2014). In populations of finite size,  
93 this diversifying effect can be obtained thanks to mutation.

94 When strategy transmission is purely genetic, it makes sense to assume that  
95 mutation is relatively weak. A social strategy can however also be culturally  
96 transmitted from parent to offspring, in which case “rebellion” (as in Frank’s Re-  
97 bellious Child Model (Frank, 1997)) does not have to be rare. Imperfect strategy  
98 transmission can alter evolutionary dynamics, in particular in spatially struc-

99 tured populations (see *e.g.*, Allen et al., 2012; Débarre, 2017, for graph-structured  
100 populations). Here, we want to explore the consequences of imperfect strategy  
101 transmission from parents to their offspring on the evolution of altruistic behav-  
102 ior in subdivided populations. For the sake of concision, we use the word “mu-  
103 tation” throughout the paper, keeping in mind that strategy transmission does  
104 not have to be genetic.

105 For each of the three life-cycles that we consider, we compute the expected  
106 (*i.e.*, long-term) frequency of altruists maintained in a subdivided population,  
107 and investigate how it is affected by mutation and emigration. We find that, con-  
108 trary to what happens with perfect strategy transmission, higher emigration can  
109 increase the expected frequency of altruists in the population.

## 110 2 Model and methods

### 111 2.1 Assumptions

112 We consider a population of size  $N$ , subdivided into  $N_D$  demes, each hosting  
113 exactly  $n$  individuals (*i.e.*, each deme contains  $n$  sites, each of which is occupied  
114 by exactly one individual; we have  $nN_D = N$ ). Each site has a unique label  $i$ ,  
115  $1 \leq i \leq N$ . There are two types of individuals in the population, altruists and  
116 defectors. The type of the individual living at site  $i$  ( $1 \leq i \leq N$ ) is given by an  
117 indicator variable  $X_i$ , equal to 1 if the individual is an altruist, and to 0 if it is a  
118 defector. The state of the entire population is given by a  $N$ -long vector  $\mathbf{X}$ . For a  
119 given population state  $\mathbf{X}$ , the proportion of altruists is  $\bar{X} = \sum_{i=1}^N X_i$ . All symbols  
120 are summarized in table S1.

121 Reproduction is asexual. Parents transmit their strategy to their offspring  
122 with probability  $1 - \mu$ ; this transmission can be genetic or cultural (vertical cul-  
123 tural transmission), but for simplicity, we refer to the parameter  $\mu$  as a mutation  
124 probability. With probability  $\mu$ , offspring do not inherit their strategy from their

parent but instead get one randomly: with probability  $\nu$ , they become altruists, with probability  $1 - \nu$  they become defectors. We call the parameter  $\nu$  the mutation bias.

An individual of type  $X_k$  expresses a social phenotype  $\phi_k = \delta X_k$ , where  $\delta$  is assumed to be small ( $\delta \ll 1$ ). Social interactions take place within each deme, benefits are shared with the  $n - 1$  other deme-mates. We assume that social interactions affect individual fecundity;  $f_k$  denotes the fecundity of the individual at site  $k$ . We denote by  $b$  the marginal effect of a deme-mate's phenotype on the fecundity of a focal individual, and by  $-c$  the marginal effect of a focal individual's phenotype on its own fecundity ( $c \leq b$ ).

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

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

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

We denote by  $B_i = B_i(\mathbf{X}, \delta)$  the expected number of successful offspring of the individual living at site  $i$  (successful means alive at the next time step), and by  $D_i = D_i(\mathbf{X}, \delta)$  the probability that the individual living at site  $i$  dies. Both depend on the state of the population  $\mathbf{X}$ , but also on the way the population is updated from one time step to the next, *i.e.*, on the chosen life-cycle (also called updating rule). We will specifically explore three different life-cycles. At the beginning of each step of each life-cycle, all individuals produce offspring, that can be mutated; then these juveniles move, within the parental deme or outside of it, and land on a site. The next events occurring during the time step depend on the

150 life-cycle:

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

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

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

## 159 2.2 Methods

### 160 2.2.1 Analytical part

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

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

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



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

### 179 2.2.2 Stochastic simulations

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

186 All scripts are available at

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

## 188 3 Results

### 189 3.1 Probabilities of identity by descent

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

$$Q_{ij} = \begin{cases} 1 & \text{when } i = j; \\ Q_{\text{in}} & \text{when } i \neq j \text{ and both sites are in the same deme;} \\ Q_{\text{out}} & \text{when sites } i \text{ and } j \text{ are in different demes.} \end{cases} \quad (2)$$

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

### 197 3.1.1 Moran updating

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

$$Q_{ij}^M = \frac{1-\mu}{2} \sum_{k=1}^N (d_{kj} Q_{ki}^M + d_{ki} Q_{kj}^M). \quad (3)$$

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

$$Q_{\text{in}}^M = \frac{(1-\mu)(m + \mu(N_D(1-m) - 1))}{(1-\mu)m(N_D\mu(n-1) + 1) + (N_D - 1)\mu(\mu(n-1) + 1)}, \quad (4a)$$

$$Q_{\text{out}}^M = \frac{(1-\mu)m}{(1-\mu)m(N_D\mu(n-1) + 1) + (N_D - 1)\mu(\mu(n-1) + 1)}. \quad (4b)$$

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

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

### 216 3.1.2 Wright-Fisher updating

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

$$Q_{ij}^{\text{WF}} = (1 - \mu)^2 \sum_{k, \ell=1}^N d_{ki} d_{\ell j} Q_{kl}^{\text{WF}}. \quad (5)$$

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

223 Replacing the dispersal probabilities  $d_{ij}$  by their values (given in eq. (1)) and  
 224 skipping calculation steps (but see Appendix A.2 for details), we obtain: {eq: QWF}

$$Q_{\text{in}}^{\text{WF}} = \frac{-N_D + M_1 + M_2}{(n-1)N_D + M_1 + M_2}, \quad (6a)$$

$$Q_{\text{out}}^{\text{WF}} = \frac{-\frac{1}{N_D-1}M_1 + M_2}{(n-1)N_D + M_1 + M_2}, \quad (6b)$$

225 with

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

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

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

232 The two probabilities of identity by descent go to 1 when the mutation prob-  
 233 ability  $\mu$  is very small ( $\mu \rightarrow 0$ ), except if we first assume that the number of demes  
 234 is very large ( $N_D \rightarrow \infty$ ); for instance, with this life-cycle as well,  $\lim_{N_D \rightarrow \infty} Q_{\text{out}}^{\text{WF}} =$   
 235 0.

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

## 239 3.2 Expected frequencies of altruists for each life-cycle

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

$$\mathbb{E}[\bar{X}] \approx v + \omega \frac{v(1-v)}{\mu} [b(\beta_D - \beta_I) - c(\gamma_D - \gamma_I)]. \quad (7) \quad \{\text{eq:EXapprox}\}$$

242 (Calculations leading to eq. (7) are presented in Appendix A.)

243 The mutation bias  $v$  corresponds to the expected proportion of altruists in the  
244 population in the absence of selection (*i.e.*, when  $\omega = 0$ );  $\omega$  is the parameter  
245 that scales the effects of interactions between individuals, which is assumed to  
246 be small. The subscript <sub>D</sub> refers to “direct” effects, and the subscript <sub>I</sub> to “in-  
247 direct” effects. “Direct” effects involve effects on primary beneficiaries of the  
248 benefits ( $b$ ) and costs ( $c$ ) of social interactions (West & Gardner, 2010), *i.e.*, so-  
249 cial interactants (for the benefits  $b$ ) and the focal individuals themselves (for the  
250 costs  $c$ ). “Indirect” effects corresponds to effects on secondary interactants, *i.e.*,  
251 to (kin) competition. By providing a benefit to a deme-mate and thereby in-  
252 creasing its fecundity, a focal altruist indirectly harms others by reducing their  
253 relative fecundity ( $\beta_I$  term in eq. (7)); by having a reduced fecundity due to the  
254 cost of altruism, a focal altruist indirectly favors others by increasing their rela-  
255 tive fecundity ( $\gamma_I$  term).

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

### 258 3.2.1 Direct effects

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

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

$$\beta_D^{BD} = \beta_D^{DB} = (1 - \mu) Q_{in}^M, \quad (8a) \quad \{eq:bBDD\}$$

$$\beta_D^{WF} = (1 - \mu) Q_{in}^{WF}; \quad (8b) \quad \{eq:bWFD\}$$

$$\gamma_D^{BD} = \gamma_D^{DB} = \gamma_D^{WF} = 1 - \mu. \quad (8c) \quad \{eq:cBDD\}$$

262 For both benefits and costs, direct effects only count when there is no mutation  
 263 (hence the  $(1 - \mu)$  factors). Direct effects of benefits  $b$  (eq. (8a) and eq. (8b)) only  
 264 count if the interaction takes place with an individual who is identical by de-  
 265 scent. With the population structure that we consider, social interactions only  
 266 occur within demes, so only  $Q_{in}$  is present in eq. (8a) and eq. (8b). On the other  
 267 hand, the direct effect of the fecundity cost  $c$  (eq. (8c)) does not depend on the  
 268 type of interactant, since the same cost  $c$  is paid by altruists irrespective of the  
 269 interactant's identity.

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

### 278 3.2.2 Indirect effects

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

282 **Moran Birth-Death** Changing the fecundity of a focal individual has two kinds  
 283 of indirect effects on others: *i*) it changes their probability of being the one cho-  
 284 sen to reproduce – this affects all individuals in the population who are identical  
 285 by descent to the focal, and *ii*) it changes their probability of dying because the  
 286 number of offspring landing in their site changes – this affects individuals in the  
 287 population who can send offspring at the same locations as the focal and are  
 288 identical-by-descent to it. For this life-cycle, the indirect effects are:

$$\begin{aligned}\beta_I^{\text{BD}} &= (1 - m) \left( \frac{n-1}{n} Q_{\text{in}}^{\text{M}} + \frac{1}{n} \right) + m Q_{\text{out}}^{\text{M}} - \mu \frac{1 + (n-1)Q_{\text{in}}^{\text{M}} + n(d-1)Q_{\text{out}}^{\text{M}}}{nd} \\ &= \gamma_I^{\text{BD}}.\end{aligned}\tag{9a} \quad \{\text{eq:bBDI}\}$$

289 (Calculation details are presented in Appendix A.)

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

297 Replacing  $Q_{\text{in}}$  and  $Q_{\text{out}}$  by their formula for the Moran life-cycle (eq. (4)), we  
 298 conclude that  $\beta_I^{\text{BD}} = \gamma_I^{\text{BD}}$  are decreasing functions of the emigration probabil-  
 299 ity  $m$  (calculations in the supplementary Mathematica file).

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

304 descent to it. We obtain

$$\begin{aligned}\beta_I^{\text{DB}} &= (1 - \mu) \left[ \left( \frac{1}{n} + \frac{(n-1)Q_{\text{in}}^{\text{M}}}{n} \right) \left( (1-m)^2 + \frac{m^2}{(d-1)} \right) \right. \\ &\quad \left. + Q_{\text{out}}^{\text{M}} \left( 2m(1-m) + (d-2) \frac{m^2}{(d-1)} \right) \right] \\ &= \gamma_I^{\text{DB}}\end{aligned}\tag{9b} \quad \{\text{eq: bDBI}\}$$

305 The brackets in eq. (9b) contain a sum of two terms. The first term corresponds  
306 two individuals from the same deme (with replacement) whose offspring either  
307 do not emigrate, or emigrate together to the same deme. The second term cor-  
308 responds to individuals initially from different demes who end up in the same  
309 deme (either one of their home demes, or a third deme).

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

312 Replacing  $Q_{\text{in}}$  and  $Q_{\text{out}}$  by their formulas given in eq. (4), we can conclude  
313 that  $\beta_I^{\text{DB}} = \gamma_I^{\text{DB}}$  first decreases with the emigration probability  $m$ , and increases  
314 again after a threshold value  $m'_c$ , which is smaller than  $m_c^{\text{WF}} = (d-1)/d$  (calcu-  
315 lation details are presented in the supplementary Mathematica file).

316 **Wright-Fisher** With this life-cycle, generations are synchronous and all indi-  
317 viduals again all have the same survival probability (now equal to 0 at all sites).  
318 As a result, the formulas for  $\beta_I^{\text{WF}}$  and  $\gamma_I^{\text{WF}}$  are the same as  $\beta_I^{\text{DB}}$  and  $\gamma_I^{\text{WF}}$ , except  
319 that instead of  $Q_{\text{in}}^{\text{M}}$  and  $Q_{\text{out}}^{\text{M}}$ , we need to use  $Q_{\text{in}}^{\text{WF}}$  and  $Q_{\text{out}}^{\text{WF}}$  (given in eq. (6)). Once  
320 this is done, we see that  $\beta_I^{\text{WF}} = \gamma_I^{\text{WF}}$  first decreases with the emigration probab-  
321 ity  $m$ , and increases again after the threshold value  $m_c^{\text{WF}} = (d-1)/d$ . This em-  
322 igration threshold was identified above as the emigration probability such that  
323 offspring have an equal chance of landing in their natal deme or in any other  
324 deme, *i.e.*,  $d_{\text{in}} = d_{\text{out}}$  (calculation details are presented in the supplementary  
325 Mathematica file.)



### 3.3 Identifying threshold values of the mutation probability $\mu$

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

#### 3.3.1 Moran Birth-Death

For this life-cycle, we find that the expected frequency of altruists  $\mathbb{E}[\bar{X}]$  is a monotonic function of the emigration probability  $m$ ; the direction of the change depends on the value of the mutation probability  $\mu$  compared to a threshold value  $\mu_c^{\text{BD}}$ . 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  $\mu_c^{\text{BD}}$  is given by

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

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

#### 3.3.2 Moran Death-Birth

The relationship between  $\mathbb{E}[\bar{X}]$  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  $\mu$  is greater than a threshold value  $\mu_c^{\text{DB}}$  given in eq. (11) below; otherwise, when the benefits are high enough,  $\mathbb{E}[\bar{X}]$  initially increases with  $m$  for any value of  $\mu$ . Combining

349 these results, we write

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

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

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

### 355 3.3.3 Wright-Fisher

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

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

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

## 360 3.4 Relaxing key assumptions

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

367 To relax the assumption of equal deme sizes, we randomly drew deme sizes  
 368 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  $i$ ,  $d_{ii} = d_{\text{self}} = 0$ ;  $d_{\text{in}} = (1 - m)/(n - 1)$  for two different sites in the same deme,  $d_{\text{out}}$  remaining unchanged), confirms that this does affect our conclusions.

## 4 Discussion

### The expected frequency of altruists in a subdivided population can increase with the probability of emigration

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

### Quantitative vs. qualitative measures

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

394 of population viscosity. Often however, evolutionary success is measured quali-  
 395 tatively, by comparing a quantity (an expected frequency, or, in models with no  
 396 mutation, a probability of fixation) to the value it would have in the absence of  
 397 selection. In our model, this amounts to saying that altruism is favored whenever  
 398  $\mathbb{E}[\bar{X}] > \nu$  ( $\nu$  is plotted as a horizontal dashed line in figure 2). Some of our con-  
 399 clusions change if we switch to this qualitative measure of evolutionary success:  
 400 Under the Moran Birth-Death and Wright-Fisher life-cycles, population viscosity  
 401 does not promote the evolution of altruism – actually, these two life-cycles can-  
 402 not ever promote altruistic behavior for any regular population structure (Taylor  
 403 et al., 2011), whichever the probability of mutation (Débarre, 2017). However,  
 404 under a Moran Death-Birth life-cycle, altruism can be favored only at interme-  
 405 diate emigration probabilities (figure 2(a)): increased emigration can still favor  
 406 the evolution of altruism under this qualitative criterion.

#### 407 **The result is due to indirect (/secondary) effects**

408 To explain how the frequency of altruists can increase with the emigration prob-  
 409 ability  $m$ , let us go back to the decomposition of the expected frequency of al-  
 410 truists in the population  $\mathbb{E}[\bar{X}]$  into different terms (eq. (7)). For all the life-cycles  
 411 that we consider, the direct effect of helping others ( $\beta_D$ ) decreases with emigra-  
 412 tion  $m$ , while the direct effect of the cost of helping ( $\gamma_D$ ) does not change with  
 413  $m$ . If we (erroneously) considered only direct effects, we would conclude that  
 414 the expected proportion of altruists decreases with the emigration probability  
 415  $m$ , because an increase in  $m$  reduces the probability that two interactants (two  
 416 deme-mates in this model) are identical by descent. But this explanation ignores  
 417 indirect, competitive, effects. In the three life-cycles that we considered,  $\beta_I = \gamma_I$ ,  
 418 so the overall indirect effects are given by  $-(b - c)\beta_I$ . Hence, any increase of  
 419  $\mathbb{E}[\bar{X}]$  with  $m$  is driven by  $\beta_I$ . Indirect effects correspond to competition: helping  
 420 another individual indirectly harms others – even the individual who is provid-

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

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

#### How small is small and how large is large?

Our results were derived under the assumption of weak selection, assuming that the phenotypic difference between altruists and defectors is small ( $\delta \ll 0$ ). We considered any fidelity of transmission (any  $\mu$  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  $\mu$ , but also  $\omega$ , 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.

## 445 **Imperfect transmission and Rebellious Children**

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

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

## 459 **Interactions and dispersal graphs**

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

## 470   **Coevolution of dispersal and social behavior**

471   This work also raises the question of what would happen if dispersal (*e.g.*, the  
472   emigration probability  $m$ ) could evolve as well. Recent work on the topic has  
473   shown that under some conditions disruptive selection could take place, lead-  
474   ing to a polymorphism between sessile altruists and mobile defectors (Parvinen,  
475   2013; Mullan et al., 2017). The assumptions of these studies however differ from  
476   ours in important ways, in that they consider continuous traits and use an adap-  
477   tive dynamics framework, where, notably, mutations are assumed to be very  
478   rare. It remains to be investigated how non-rare and potentially large mutations  
479   would affect their result.

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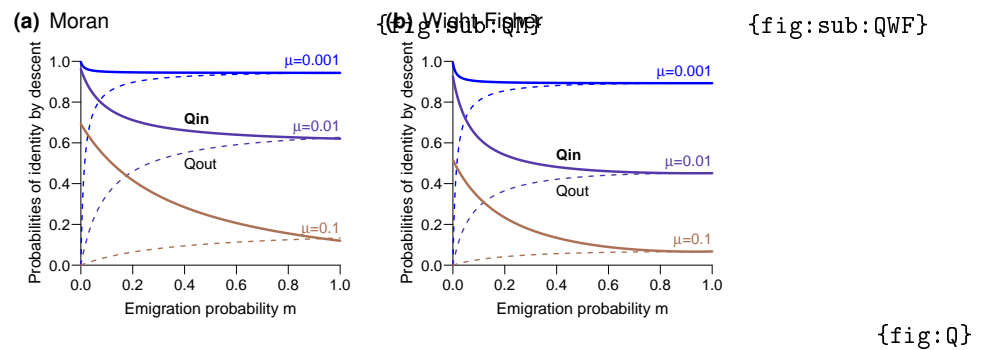
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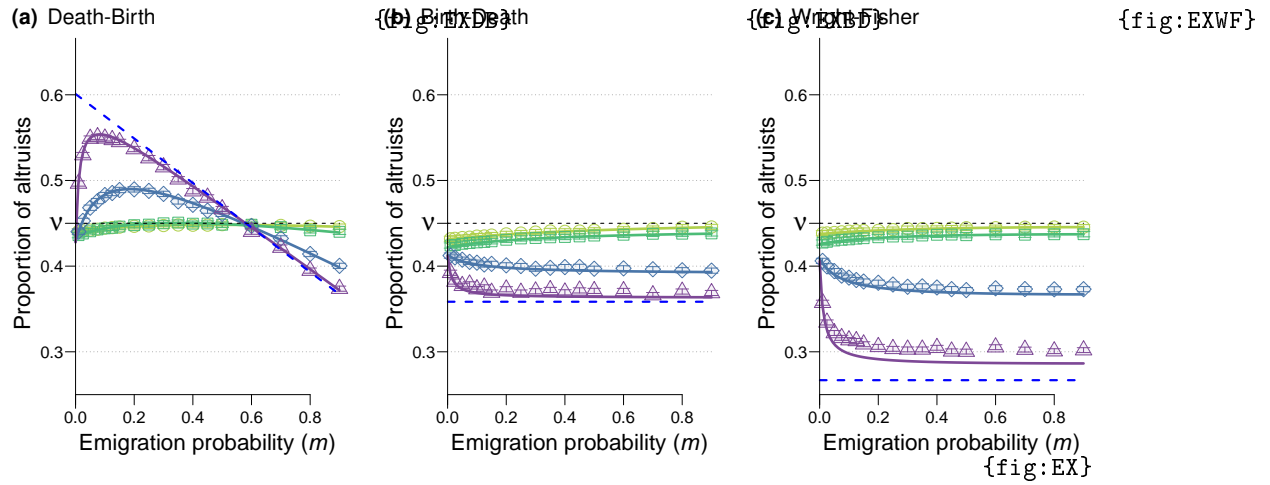
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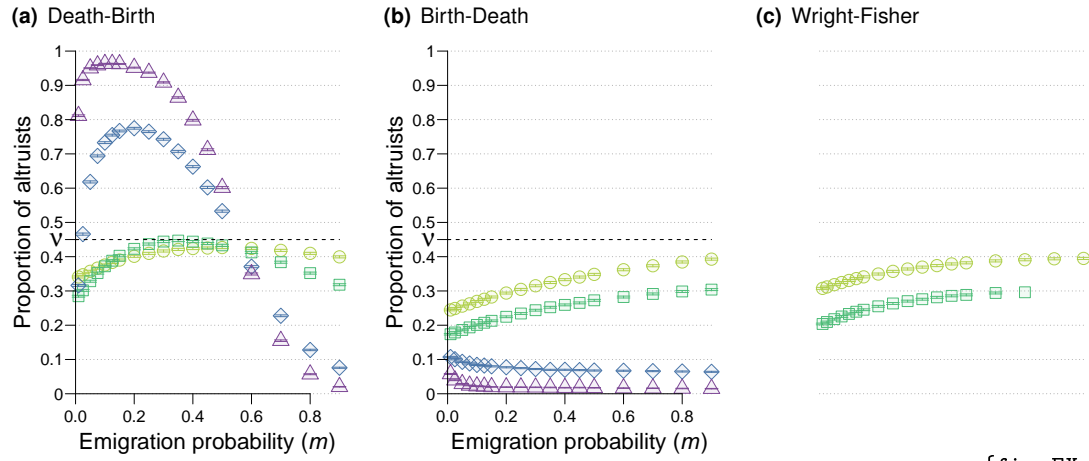
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**Figure 1:** Probabilities of identity by descent, for two different individuals within the same deme ( $Q_{in}$ , full curves) and two individuals in different demes ( $Q_{out}$ , dashed curves), as a function of the emigration probability  $m$ , for different values of the mutation probability  $\mu$  (0.001, 0.01, 0.1), and for the two types of life-cycles ((a): Moran, (b): Wright-Fisher). Other parameters:  $n = 4$  individuals per deme,  $N_D = 15$  demes.

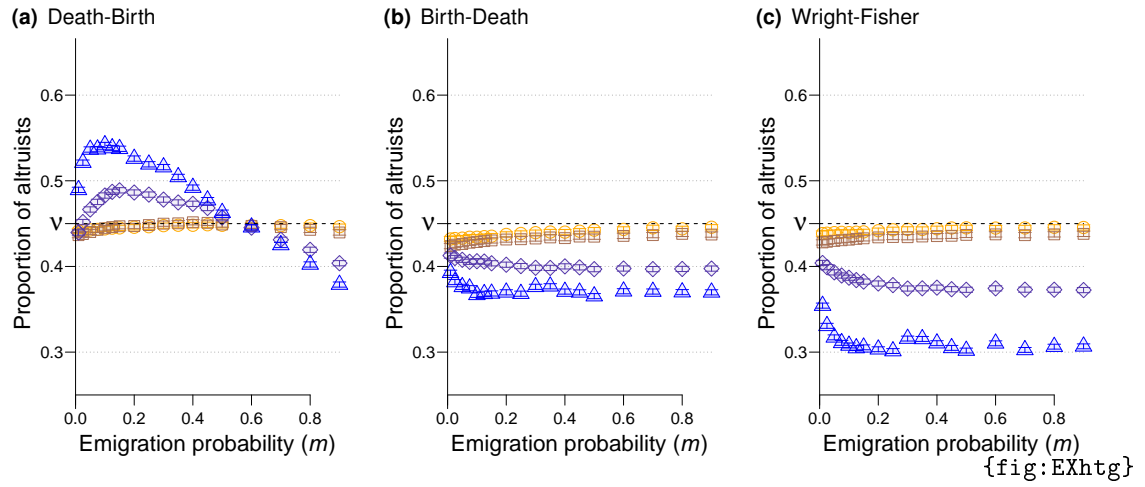


**Figure 2:** Expected proportion of altruists under weak selection, as a function of the emigration probability  $m$ , for different mutation values ( $\mu = 0.001$  (blue, dots),  $0.01$  (purple, squares),  $0.1$  (brown, diamonds),  $0.25$  (orange, triangles); the dashed blue lines correspond to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

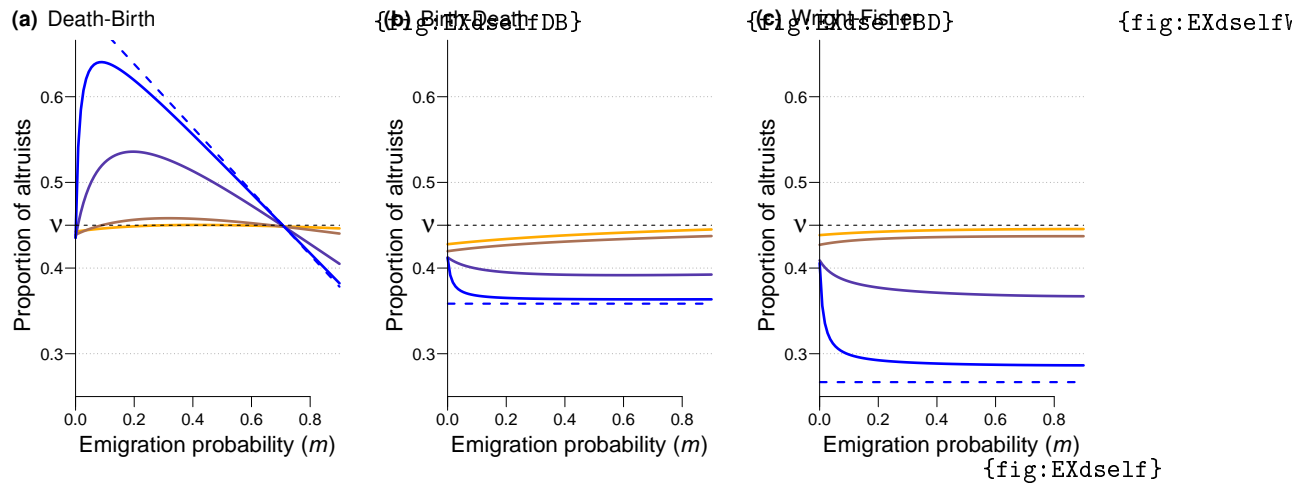


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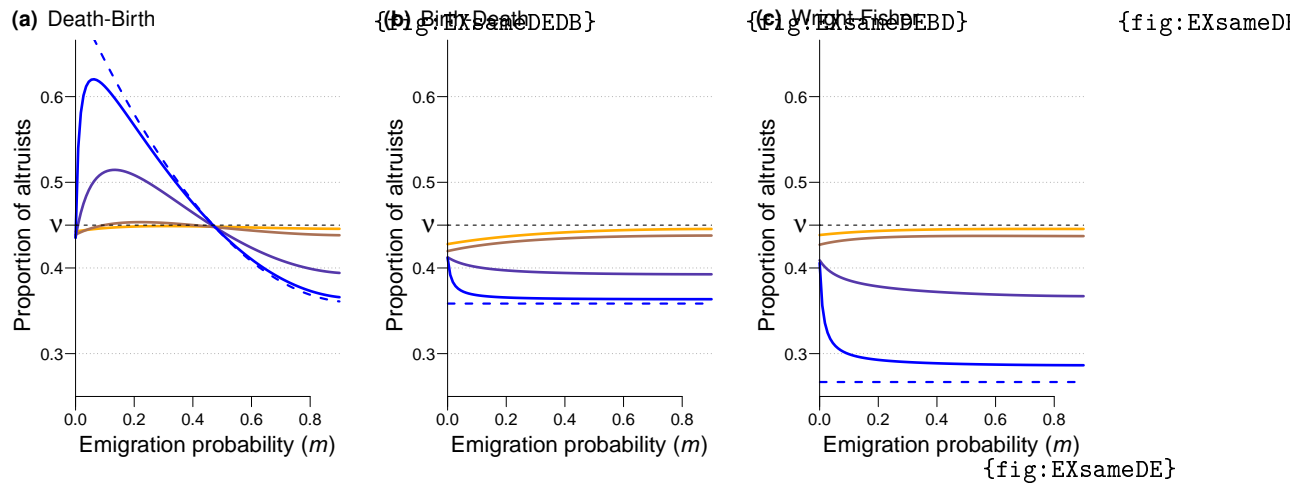
**Figure S1:** Equivalent of figure 2 (simulations only) but with strong selection ( $\omega = 0.1$ ); please note the change of scale on the vertical axis. All other parameters and legends are identical to those of figure 2 (increasing mutation probabilities from blue dots to orange triangles).



**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).



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

$b$	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.)
$\beta$	Term associated to the benefits $b$
$\gamma$	Term associated to the costs $c$
$\mu$	Mutation probability
$\nu$	Mutation bias: probability that mutant is altruist
$\omega$	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*.



574

## Appendix

### A Expected frequency of altruists

{sec:app:EX}

#### A.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 S2 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 S2:** 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. (1).

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

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

holds for all sites  $i$ . The structure of the population is also such that in the absence of selection ( $\delta = 0$ , 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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Now, we use a first time the law of total probabilities, taking individual phenotypes  $\phi_k$  are intermediate variables:

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

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

$$\delta \mu B^* \frac{\partial \mathbb{E}[\bar{X}]}{\partial \delta} = \frac{\delta}{N} \sum_{i=1}^N \sum_{k=1}^N \frac{\partial W_i}{\partial \phi_k} P_{ik} + O(\delta^2). \quad (\text{A.8}) \quad \{\text{eq:weaksel11}\}$$

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

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

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

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

With this, eq. (A.8) becomes

$$\delta \mu B^* \frac{\partial \mathbb{E}[\bar{X}]}{\partial \delta} = \frac{\delta}{N} \sum_{i=1}^N \left( \frac{\partial W_i}{\partial \phi_i} + (n - 1) \frac{\partial W_i}{\partial \phi_{\text{in}}} \frac{P_{\text{in}} - P_{\text{out}}}{P_{ii} - P_{\text{out}}} \right) (P_{ii} - P_{\text{out}}) + O(\delta^2). \quad (\text{A.10}) \quad \{\text{eq:weaksel11CBRP}\}$$

644 We can also replace the  $P$  terms by

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

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

$$\delta\mu B^* \frac{\partial \mathbb{E}[\bar{X}]}{\partial \delta} = \frac{\delta}{N} \sum_{i=1}^N \left( \underbrace{\frac{\partial W_i}{\partial \phi_i}}_{-C} + \underbrace{(n-1) \frac{\partial W_i}{\partial \phi_{\text{in}}}}_B \underbrace{\frac{Q_{\text{in}} - Q_{\text{out}}}{1 - Q_{\text{out}}}}_R \right) (1 - Q_{\text{out}}) \nu (1 - \nu) + O(\delta^2). \quad (\text{A.12}) \quad \{\text{eq:weaksel1CBR}\}$$

649 We can further decompose the derivatives, now using the fecundities  $f_\ell$  as  
 650 intermediate variables, *i.e.*,

$$\frac{\partial W_i}{\partial \phi_k} = \sum_{\ell=1}^N \frac{\partial W_i}{\partial f_\ell} \frac{\partial f_\ell}{\partial \phi_k}. \quad (\text{A.13})$$

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

$$\left. \frac{\partial f_\ell}{\partial \phi_\ell} \right|_{\delta=0} = -c, \quad (\text{A.14a})$$

$$\left. \frac{\partial f_\ell}{\partial \phi_{\text{in}}} \right|_{\delta=0} = \frac{b}{n-1}, \quad (\text{A.14b})$$

$$\left. \frac{\partial f_\ell}{\partial \phi_{\text{out}}} \right|_{\delta=0} = 0. \quad (\text{A.14c})$$

653 Eq. (A.12) then becomes (using notation  $\bullet$  to refer to the focal individual itself,  
 654 and where  $W = W_i$ , since the derivatives are the same for all  $i$ ):

$$\delta\mu B^* \frac{\partial \mathbb{E}[\bar{X}]}{\partial \delta} = \delta \nu (1 - \nu) (1 - Q_{\text{out}}) \times \left( \underbrace{\left( \frac{\partial W}{\partial f_\bullet} (-c) + \frac{\partial W}{\partial f_{\text{in}}} b \right)}_{-C} + \underbrace{\left( \frac{\partial W}{\partial f_\bullet} b + \frac{\partial W}{\partial f_{\text{in}}} (-c) + (n-2) \frac{\partial W}{\partial f_{\text{in}}} b \right)}_B \underbrace{\frac{Q_{\text{in}} - Q_{\text{out}}}{1 - Q_{\text{out}}}}_R \right) + O(\delta^2). \quad (\text{A.15}) \quad \{\text{eq:weaksel2}\}$$

655 Finally, we obtain a first-order approximation of the expected frequency of altru-  
 656 ists in the population with

$$\mathbb{E}[\bar{X}] = \nu + \delta \left. \frac{\partial \mathbb{E}[\bar{X}]}{\partial \delta} \right|_{\delta=0} + O(\delta^2), \quad (\text{A.16}) \quad \{\text{eq:EXgeneric}\}$$

657 where  $\left. \frac{\partial \mathbb{E}[\bar{X}]}{\partial \delta} \right|_{\delta=0}$  is obtained from eq. (A.15). We then need to replace the  $B_i$  and  
 658  $D_i$  terms by their formulas for each life-cycle (given in table S2).

## 659 A.2 Probabilities of identity by descent

{sec:app:IBD}

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

### 664 A.2.1 Moran model

665 In a Moran model, exactly one individual dies and one individual reproduces  
666 during one time step. Given a state  $\mathbf{X}$  at time  $t$ , at time  $t + 1$  both sites  $i$  and  
667  $j \neq i$  are occupied by altruists, if  $i)$  it was the case at time  $t$  and neither site was  
668 replaced by a non-altruist (first term in eq. (A.17)), or  $ii)$  if exactly one of the two  
669 sites was occupied by a non-altruist at time  $t$ , but the site was replaced by an  
670 altruist (second and third terms of eq. (A.17)):

$$\begin{aligned} \mathbb{E}[X_i X_j(t+1) | X(t) = \mathbf{X}] = & X_i X_j \left( 1 - \sum_{k=1}^N \frac{1}{N} (d_{ki} + d_{kj}) ((1 - X_k)(1 - \mu) + \mu(1 - \nu)) \right) \\ & + X_i(1 - X_j) \sum_{k=1}^N \frac{1}{N} d_{kj} (X_k(1 - \mu) + \mu\nu) \\ & + X_j(1 - X_i) \sum_{k=1}^N \frac{1}{N} d_{ki} (X_k(1 - \mu) + \mu\nu). \end{aligned} \quad (\text{A.17}) \quad \{\text{eq:app:Pi j M1}\}$$

671 We take the expectation of this quantity, and consider that the stationary dis-  
672 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

$$P_{ij} = \frac{1}{2} \left( \sum_{k=1}^N (1 - \mu) (d_{kj} P_{ki} + d_{ki} P_{kj}) \right) + \mu\nu^2 \quad (i \neq j), \quad (\text{A.18}) \quad \{\text{eq:app:Pi j M}\}$$

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

674 Now we substitute  $P_{ij} = \nu^2 + \nu(1 - \nu)Q_{ij}$  in eq. (A.18), we obtain

$$Q_{ij} = \frac{1}{2} \sum_{k=1}^N (1 - \mu) (d_{ki} Q_{kj} + d_{kj} Q_{ki}), \quad (\text{A.19}) \quad \{\text{eq:app:Qi j M}\}$$

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

### 680 A.2.2 Wright-Fisher model

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

$$\begin{aligned} \mathbb{E}[X_i X_j(t+1) | X(t) = \mathbf{X}] = & \sum_{k, \ell=1}^N d_{ki} d_{\ell j} \left( X_k X_\ell (1 - \mu + \mu v)^2 \right. \\ & + (X_k(1 - X_\ell) + (1 - X_k)X_\ell) (1 - \mu + \mu v)(\mu v) \\ & \left. + (1 - X_k)(1 - X_\ell)(\mu v)^2 \right) \end{aligned} \quad (A.20) \quad \{\text{eq:app:PijWF1}\}$$

683 The first term of eq. (A.20) corresponds to both parents being altruists, and hav-  
684 ing altruist offspring; the second line corresponds to exactly one parent being  
685 altruist, and the third line to both parents being non-altruists (in this latter case,  
686 the two offspring have to be both mutants to be altruists).

687 Taking the expectation and simplifying, we obtain

$$P_{ij} = \sum_{k, \ell=1}^N (P_{kl}(1 - \mu)^2) + (2 - \mu)\mu v^2. \quad (A.21) \quad \{\text{eq:app:PijWF}\}$$

688 Replacing  $P_{ij}$  by  $v^2 + v(1 - v)Q_{ij}$ , eq. (A.21) becomes

$$Q_{ij} = \sum_{k, \ell=1}^N d_{ki} d_{\ell j} Q_{k\ell} (1 - \mu)^2. \quad (A.22) \quad \{\text{eq:app:QijWF}\}$$

689 Again,  $Q_{ij}$  corresponds to a probability of identity by descent: the individuals at  
690 sites  $i$  and  $j$  are identical by descent if their parents were and if neither mutated  
691  $((1 - \mu)^2)$ .

## B In a subdivided population

{sec:app:subdiv}

### B.1 $\beta$ and $\gamma$

{sec:app:bcsubdiv}

Now, we need to adapt the results presented in Appendix A to our structure of interest, a subdivided population, with dispersal and interaction probabilities given by eq. (1) and eq. (??). For the  $\beta$  and  $\gamma$  terms, we use a brute-force approach, replacing  $d_{ij}$  and  $e_{ij}$  by their values in a subdivided population, and simplifying the equations (for instance, there are 60 different cases to consider for the four sums that appear in  $\beta_1^{\text{DB}}$ , shown in the table in section B.4 below). The calculations and subsequent simplifications are detailed in the supplementary Mathematica file, and the results are presented in the main text (system (8), eq. (9a), and eq. (9b)).

### B.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  $(\ell_1, \ell_2)$ , where  $\ell_1$  is the index of the deme ( $1 \leq \ell_1 \leq N_D$ ) and  $\ell_2$  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  $d_{\text{in}}$  (in the main text,  $d_{\text{self}} = d_{\text{in}}$ ).

#### B.2.1 Moran model

In Débarre (2017), it was shown that

$$\tilde{Q}_{r_1} = \frac{1}{N} \sum_{q_1=0}^{N_1-1} \sum_{q_2=0}^{N_2-1} \frac{\mu \lambda'_M}{1 - (1 - \mu) \tilde{D}_{q_1}} \exp\left(i \frac{2\pi q_1 r_1}{N_1}\right) \exp\left(i \frac{2\pi q_2 r_2}{N_2}\right) \quad (\text{B.23a}) \quad \{\text{eq:app:Q2DM}\}$$

with

$$\tilde{D}_{q_1} = \sum_{\ell_1=0}^{N_1-1} \sum_{\ell_2=0}^{N_2-1} \tilde{d}_{\ell_1} \exp\left(-i \frac{2\pi q_1 \ell_1}{N_1}\right) \exp\left(-i \frac{2\pi q_2 \ell_2}{N_2}\right), \quad (\text{B.23b}) \quad \{\text{eq:app:D2D}\}$$

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

$$\begin{aligned}\tilde{D}_{q_1} &= d_{\text{self}} + \sum_{\ell_2=1}^{N_2-1} d_{\text{in}} \exp\left(-\iota \frac{2\pi q_2 \ell_2}{N_2}\right) + \sum_{\ell_1=1}^{N_1-1} \sum_{\ell_2=0}^{N_2-1} d_{\text{out}} \exp\left(-\iota \frac{2\pi q_1 \ell_1}{N_1}\right) \exp\left(-\iota \frac{2\pi q_2 \ell_2}{N_2}\right) \\ &= d_{\text{self}} + (\delta_{q_2}(N_2 - 1) + (1 - \delta_{q_2})(-1)) d_{\text{in}} + (\delta_{q_1}(N_1 - 1) + (1 - \delta_{q_1})(-1)) (\delta_{q_2} N_2) d_{\text{out}} \\ &= d_{\text{self}} + (\delta_{q_2} N_2 - 1) d_{\text{in}} + (\delta_{q_1} N_1 - 1) \delta_{q_2} N_2 d_{\text{out}}.\end{aligned}\quad (\text{B.24a})$$

722 ( $\delta_q$  is equal to 1 when  $q$  is equal to 0 modulo the relevant dimension, and to 0  
723 otherwise). So for the three types of distances that we need to consider (distance  
724 0, distance to another deme-mate, distance to individual in another deme), and  
725 with  $N_1 = N_D$  and  $N_2 = n$ , we obtain {eq:app:Dsystem}

$$\tilde{D}_0 = 1, \quad (\text{B.25a})$$

$$\tilde{D}_0 = 1 - m - \frac{m}{d-1} \quad (q_1 \not\equiv 0 \pmod{N_1}), \quad (\text{B.25b})$$

$$\tilde{D}_{q_1} = d_{\text{self}} - d_{\text{in}} \quad (q_2 \not\equiv 0 \pmod{N_2}). \quad (\text{B.25c})$$

726 So for  $\tilde{Q}$ , using system (B.25) in eq. (B.23a),

$$\begin{aligned}\tilde{Q}_{r_1} &= \frac{\mu \lambda'_M}{N} \left[ \frac{1}{1 - (1 - \mu) \tilde{D}_0} + \sum_{q_2=1}^{N_2-1} \frac{1}{1 - (1 - \mu) \tilde{D}_0} \exp\left(-\iota \frac{2\pi q_2 r_2}{N_2}\right) \right. \\ &\quad + \sum_{q_1=1}^{N_1-1} \frac{1}{1 - (1 - \mu) \tilde{D}_0} \exp\left(-\iota \frac{2\pi q_1 r_1}{N_1}\right) \\ &\quad \left. + \sum_{q_1=1}^{N_1-1} \sum_{q_2=1}^{N_2-1} \frac{1}{1 - (1 - \mu) \tilde{D}_{q_1}} \exp\left(-\iota \frac{2\pi q_1 r_1}{N_1}\right) \exp\left(-\iota \frac{2\pi q_2 r_2}{N_2}\right) \right] \\ &= \frac{\mu \lambda'_M}{N} \left[ \frac{1}{1 - (1 - \mu)} + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})} (\delta_{r_2} N_2 - 1) \right. \\ &\quad + \frac{1}{1 - (1 - \mu)(1 - m - \frac{m}{d-1})} (\delta_{r_1} N_1 - 1) \\ &\quad \left. + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})} (\delta_{r_1} N_1 - 1)(\delta_{r_2} N_2 - 1) \right].\end{aligned}\quad (\text{B.26}) \quad \{\text{eq:app:Q2DMsol}\}$$

727 In particular,

$$\begin{aligned}\tilde{Q}_0 &= \frac{\mu \lambda'_M}{N} \left[ \frac{1}{\mu} + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})} (n - 1) + \frac{1}{1 - (1 - \mu)(1 - m - \frac{m}{d-1})} (D - 1) \right. \\ &\quad \left. + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})} (D - 1)(n - 1) \right] \\ &= 1.\end{aligned}\quad (\text{B.27a}) \quad \{\text{eq:app:Q2D1}\}$$



728 We find  $\lambda'_M$  using the eq. (B.27a). Going back to eq. (B.26), when  $r_1 = 0$ , the two  
 729 individuals are in the same deme. They are different when  $r_2 \neq 0$ , and so:

$$Q_{\text{in}} = \frac{\mu\lambda'_M}{N} \left[ \frac{1}{\mu} + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})}(-1) + \frac{1}{1 - (1 - \mu)(1 - m - \frac{m}{d-1})}(D-1) \right. \\ \left. + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})}(D-1)(-1) \right]. \quad (\text{B.27b})$$

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

$$Q_{\text{out}} = \frac{\mu\lambda'_M}{N} \left[ \frac{1}{\mu} + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})}(-1) + \frac{1}{1 - (1 - \mu)(1 - m - \frac{m}{d-1})}(-1) \right. \\ \left. + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})} \right]. \quad (\text{B.27c})$$

731 With  $d_{\text{self}} = d_{\text{in}} = (1 - m)/n$ , we recover the equations given in the main text (sys-  
 732 tem (4)).

### 733 B.3 Wright-Fisher

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

$$\tilde{Q}_{r_1, r_2} = \frac{1}{N} \sum_{q_1=0}^{N_1-1} \sum_{q_2=0}^{N_2-1} \frac{\mu\lambda'_{WF}}{1 - (1 - \mu)^2 (\tilde{D}_{q_1})^2} \exp\left(-i \frac{2\pi q_1 r_1}{N_1}\right) \exp\left(-i \frac{2\pi q_2 r_2}{N_2}\right), \quad (\text{B.28})$$

with  $\tilde{\mathcal{D}}$  given in eq. (B.23b). In a subdivided population, with  $N_1 = N_D$  and  $N_2 = n$ , this becomes

$$\begin{aligned}
 \tilde{Q}_{r_1} &= \frac{1}{N} \left[ \frac{\mu \lambda'_{WF}}{1 - (1 - \mu)^2 (\tilde{\mathcal{D}}_0)^2} + \sum_{q_2=1}^{N_2-1} \frac{\mu \lambda'_{WF}}{1 - (1 - \mu)^2 (\tilde{\mathcal{D}}_{q_2})^2} \exp\left(-i \frac{2\pi q_2 r_2}{N_2}\right) \right. \\
 &\quad + \sum_{q_1=1}^{N_1-1} \frac{\mu \lambda'_{WF}}{1 - (1 - \mu)^2 (\tilde{\mathcal{D}}_{q_1})^2} \exp\left(-i \frac{2\pi q_1 r_1}{N_1}\right) \\
 &\quad \left. + \sum_{q_1=1}^{N_1-1} \sum_{q_2=1}^{N_2-1} \frac{\mu \lambda'_{WF}}{1 - (1 - \mu)^2 (\tilde{\mathcal{D}}_{q_1})^2} \exp\left(-i \frac{2\pi q_1 r_1}{N_1}\right) \exp\left(-i \frac{2\pi q_2 r_2}{N_2}\right) \right] \\
 &= \frac{\mu \lambda'_{WF}}{N} \left[ \frac{1}{1 - (1 - \mu)^2} + \frac{1}{1 - (1 - \mu)^2 (d_{\text{self}} - d_{\text{in}})^2} (\delta_{q_2} N_2 - 1) \right. \\
 &\quad + \frac{1}{1 - (1 - \mu)^2 (1 - m - \frac{m}{d-1})^2} (\delta_{q_1} N_1 - 1) \\
 &\quad \left. + \frac{1}{1 - (1 - \mu)^2 (d_{\text{self}} - d_{\text{in}})^2} (\delta_{q_1} N_1 - 1) (\delta_{q_2} N_2 - 1) \right] \\
 &= \frac{\mu \lambda'_{WF}}{N} \left[ \frac{1}{1 - (1 - \mu)^2} + \frac{1}{1 - (1 - \mu)^2 (d_{\text{self}} - d_{\text{in}})^2} (\delta_{q_2} N_2 - 1) \delta_{q_1} N_1 \right. \\
 &\quad \left. + \frac{1}{1 - (1 - \mu)^2 (1 - m - \frac{m}{d-1})^2} (\delta_{q_1} N_1 - 1) \right]. \tag{B.29}
 \end{aligned}$$

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

$$1 = \frac{\mu \lambda'_{WF}}{N} \left[ \frac{1}{1 - (1 - \mu)^2} + \frac{1}{1 - (1 - \mu)^2 (d_{\text{self}} - d_{\text{in}})^2} (N_2 - 1) N_1 + \frac{1}{1 - (1 - \mu)^2 (1 - m - \frac{m}{d-1})^2} (N_1 - 1) \right]. \tag{B.30a}$$

Then from eq. (B.29) we deduce

$$Q_{\text{in}} = \frac{\mu \lambda'_{WF}}{N} \left[ \frac{1}{1 - (1 - \mu)^2} - \frac{1}{1 - (1 - \mu)^2 (d_{\text{self}} - d_{\text{in}})^2} N_1 + \frac{1}{1 - (1 - \mu)^2 (1 - m - \frac{m}{d-1})^2} (N_1 - 1) \right]. \tag{B.30b}$$

and

$$Q_{\text{out}} = \frac{\mu \lambda'_{WF}}{N} \left[ \frac{1}{1 - (1 - \mu)^2} - \frac{1}{1 - (1 - \mu)^2 (1 - m - \frac{m}{d-1})^2} \right]. \tag{B.30c}$$

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