

**Article Type:** Letter

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

**Author:** Florence Débarre – Centre Interdisciplinaire de Recherche en Biologie (CIRB), Collège de France, CNRS UMR 7241 - Inserm U1050, 11 place Marcelin Berthelot, 75231 Paris Cedex 05, France. [florence.debarre@normalesup.org](mailto:florence.debarre@normalesup.org)

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

**Keywords:** Altruism, Subdivided population, Mutation, Migration, Cooperation, Island model, Wright-Fisher, Moran.

<b>Word Count:</b>	Abstract	148
	Impact summary	285 words
	Total	4213 words

## 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. Predictions were first obtained analytically assuming weak se-  
13 lection and equal deme sizes, then confirmed with stochastic simulations relax-  
14 ing these assumptions. This result challenges the notion that the evolution of  
15 altruism requires limited dispersal.

## 16 **Impact Summary**

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

## 42 1 Introduction

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

51 Yet, living next to your kin also implies competing against them (West et al.,  
52 2002), which is detrimental to the evolution of altruism. The evolution of so-  
53 cial traits hence depends on the balance between the positive effects of inter-  
54 actions with related individuals and the detrimental consequences of kin com-  
55 petition. Under specific conditions, the two effects can even compensate each  
56 other, thereby annihilating the impact of population viscosity on the evolution  
57 of altruism. First identified with computer simulations (Wilson et al., 1992), this  
58 cancellation result was analyzed by Taylor (1992a) in a model with synchronous  
59 generations (*i.e.*, Wright-Fisher model) and a subdivided population of constant,  
60 infinite size. The cancellation result was later extended to heterogeneous pop-  
61 ulations (Rodrigues & Gardner, 2012, with synchronous generations and infinite  
62 population size), and other life-cycles, with generic regular population struc-  
63 tures (Taylor et al., 2011, with synchronous generations but also with continuous  
64 generations and Birth-Death updating). However, small changes in the model's  
65 assumptions, such as overlapping generations (Taylor & Irwin, 2000) or the pres-  
66 ence of empty sites (Alizon & Taylor, 2008) can tip the balance back in the favor  
67 of altruism. This high dependence on life-cycle specificities highlights the dif-  
68 ficulty of making general statements about the role of spatial structure on the

69 evolution of altruism. In this study, we will consider three different life-cycles:  
70 Wright-Fisher, where the whole population is renewed at each time step, and  
71 two Moran life-cycles (Birth-Death and Death-Birth), where a single individual  
72 dies and is replaced at each time step. These life-cycles are classically used in  
73 studies on altruism in structured populations, and are already known to have  
74 different outcomes in models with perfect parent-offspring transmission (*e.g.*,  
75 Taylor, 1992a; Rousset, 2004; Ohtsuki et al., 2006; Lehmann et al., 2007; Taylor,  
76 2010).

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

97 When strategy transmission is purely genetic, it makes sense to assume that  
 98 mutation is relatively weak. A social strategy can however also be culturally  
 99 transmitted from parent to offspring, in which case “rebellion” (as in Frank’s Re-  
 100 bellious Child Model (Frank, 1997)) does not have to be rare. Imperfect strategy  
 101 transmission can alter evolutionary dynamics, in particular in spatially struc-  
 102 tured populations (see *e.g.*, Allen et al., 2012; Débarre, 2017, for graph-structured  
 103 populations). Here, we want to explore the consequences of imperfect strategy  
 104 transmission from parents to their offspring on the evolution of altruistic behav-  
 105 ior in subdivided populations<sup>1</sup>. The question was tackled by Frank (1997), but  
 106 with a non fully dynamic model. His method, done “in the spirit of comparative  
 107 statics” (p.1721), precluded the exploration of the effects of population viscosity  
 108 on the evolution altruism.

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

## 114 2 Model and methods

### 115 2.1 Assumptions

116 We consider a population of size  $N$ , subdivided into  $N_D$  demes connected by  
 117 dispersal, each deme hosting exactly  $n$  individuals (*i.e.*, each deme contains  $n$   
 118 sites, each of which is occupied by exactly one individual; we have  $nN_D = N$ ).  
 119 Each site has a unique label  $i$ ,  $1 \leq i \leq N$ . There are two types of individuals in  
 120 the population, altruists and defectors. The type of the individual living at site  $i$   
 121 ( $1 \leq i \leq N$ ) is given by an indicator variable  $X_i$ , equal to 1 if the individual is an

---

<sup>1</sup>Note 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.

122 altruist, and to 0 if it is a defector. The state of the entire population is given by  
 123 a  $N$ -long vector  $\mathbf{X}$ . For a given population state  $\mathbf{X}$ , the proportion of altruists is  
 124  $\bar{X} = \sum_{i=1}^N X_i$ . All symbols are summarized in table S1.

125 Reproduction is asexual. Parents transmit their strategy to their offspring  
 126 with probability  $1 - \mu$ ; this transmission can be genetic or cultural (vertical cul-  
 127 tural transmission), but for simplicity, we refer to the parameter  $\mu$  as a mutation  
 128 probability. With probability  $\mu$ , offspring do not inherit their strategy from their  
 129 parent but instead get one randomly: with probability  $\nu$ , they become altruists,  
 130 with probability  $1 - \nu$  they become defectors. We call the parameter  $\nu$  the muta-  
 131 tion bias.

132 An individual of type  $X_k$  expresses a social phenotype  $\phi_k = \delta X_k$ , where  $\delta$  is  
 133 assumed to be small ( $\delta \ll 1$ ). Social interactions take place within each deme,  
 134 benefits are shared with the  $n - 1$  other deme-mates. We assume that social in-  
 135 teractions affect individual fecundity;  $f_k$  denotes the fecundity of the individual  
 136 at site  $k$ . We denote by  $b$  the sum of the marginal effects of deme-mates' phe-  
 137 notypes on the fecundity of a focal individual, and by  $-c$  the marginal effect of  
 138 a focal individual's phenotype on its own fecundity ( $c \leq b$ ; see system (A.14) for  
 139 formal definitions).

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

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

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

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

$$W_i := (1 - \mu)B_i + 1 - D_i, \quad (2)$$

153 which is a definition of fitness were only unmutated offspring are counted.

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

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

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

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

## 167 2.2 Methods

### 168 2.2.1 Analytical part

169 The calculation steps to obtain the expected (*i.e.*, long-term) proportion of al-  
 170 truists are given in Appendix A. They go as follows: first, we write an equation for  
 171 the expected frequency of altruists in the population at time  $t + 1$ , conditional

172 on the composition of the population at time  $t$ ; we then take the expectation of  
 173 this quantity and consider large times  $t$ . After this, we write a first order expan-  
 174 sion for phenotypic differences  $\delta$  close to 0 (this corresponds to weak selection  
 175 approximation).

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

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

182 These neutral probabilities of identity by descent depend on the chosen life-  
 183 cycle, and are also computed by taking the long-term expectation of conditional  
 184 expectations after one time step (see Appendix B.1 and B.2 and supplementary  
 185 Mathematica file (Wolfram Research, Inc., 2017).)

### 186 2.2.2 Stochastic simulations

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



### 194 3 Results

#### 195 3.1 Expected frequencies of altruists for each life-cycle

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

$$\mathbb{E}[\bar{X}] \approx v + \frac{\delta}{\mu B^*} v(1-v)(1-Q_{\text{out}}) \times \left[ \underbrace{\frac{\partial W}{\partial f_o}(-c) + \frac{\partial W}{\partial f_{\text{in}}}b}_{-\mathcal{C}} + \underbrace{\left( \frac{\partial W}{\partial f_o}b + (n-1)\frac{\partial W}{\partial f_{\text{in}}}(-c) + (n-2)\frac{\partial W}{\partial f_{\text{in}}}b \right)}_{\mathcal{B}} \underbrace{\frac{Q_{\text{in}} - Q_{\text{out}}}{1 - Q_{\text{out}}}}_R \right], \quad (4)$$

198 with  $W$  as defined in eq. (2). (Calculations leading to eq. (4) are presented in Ap-  
 199 pendix A; notations are recapitulated in table S1)

200 The mutation bias  $v$  corresponds to the expected proportion of altruists in the  
 201 population in the absence of selection (*i.e.*, when  $\delta = 0$ );  $\delta$  is the parameter that  
 202 scales the strength of selection ( $\delta \ll 1$ ). The  $-\mathcal{C}$  term groups the effects corre-  
 203 sponding to the effects of a change of a focal individual's phenotype on its own  
 204 fitness (with the fitness definition given in eq. (2).) The  $\mathcal{B}$  term corresponds to  
 205 the sum of the effects on an individual's fitness of the change of deme-mates'  
 206 phenotypes. It is multiplied by  $R$ , which is relatedness. Also note the overall  
 207  $(1 - Q_{\text{out}})$  factor. All of these terms depend on the chosen life-cycle, and on pa-  
 208 rameters such as the mutation probability  $\mu$  and the emigration probability  $m$ .

209 We now present the values of these different terms for the three life-cycles  
 210 under study. The equations are obtained by replacing the derivatives of  $W$  by  
 211 their specific formulas for each life-cycle, which are presented in Appendix A.2.  
 212 The formulas of probabilities of identity by descent are more complicated, so not  
 213 substituted, but they can be found in eq. (B.32) and eq. (B.36). The additional su-  
 214 perscripts correspond to the life-cycles (WF: Wright-Fisher, M: Moran (either),  
 215 DB: Moran Death-Birth, BD: Moran Birth-Death.) Finally, for each life-cycle,  
 216 we further decompose the  $-\mathcal{C}$  and  $\mathcal{B}$  terms into primary (subscript P) and sec-

217 onday (subscript S) effects (West & Gardner, 2010). Primary effects correspond  
 218 to unmediated consequences of interactions (they are included in  $\frac{\partial W}{\partial f_o}$ ), while  
 219 secondary effects correspond to consequences of interactions mediated by other  
 220 individuals, including competition. Primary and secondary effects correspond  
 221 to what was called “direct” and “indirect” effects, respectively, in Débarre et al.  
 222 (2014); Débarre (2017), but the terminology was updated for more consistency  
 223 with other authors. All equations are of the form

$$\mathbb{E}[\bar{X}] \approx v + \frac{\delta}{\mu} v(1-v)(1-Q_{\text{out}}) \left[ \underbrace{\begin{pmatrix} -\mathcal{C}_P \\ -\mathcal{C}_S \end{pmatrix}}_{-\mathcal{C}} + \underbrace{\begin{pmatrix} \mathcal{B}_P \\ +\mathcal{B}_S \end{pmatrix}}_{\mathcal{B}} \underbrace{\frac{Q_{\text{in}} - Q_{\text{out}}}{1 - Q_{\text{out}}}}_R \right]. \quad (5)$$

224 **Moran Birth-Death** With the Birth-Death life-cycle, eq. (4) becomes

$$\mathbb{E}[\bar{X}] \approx v + \frac{\delta}{\mu} v(1-v)(1-Q_{\text{out}}^M) \times \left[ \underbrace{\begin{pmatrix} (1-\mu)(-c) \\ +(b-c)\left(\frac{\mu}{N} - \frac{1-m}{n}\right) \end{pmatrix}}_{-\mathcal{C}^{\text{BD}}} + \underbrace{\begin{pmatrix} (1-\mu)b \\ +(b-c)(n-1)\left(\frac{\mu}{N} - \frac{1-m}{n}\right) \end{pmatrix}}_{\mathcal{B}^{\text{BD}}} \underbrace{\frac{Q_{\text{in}}^M - Q_{\text{out}}^M}{1 - Q_{\text{out}}^M}}_{R^M} \right], \quad (6)$$

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

230 **Moran Death-Birth** With the Death-Birth life-cycle, eq. (4) becomes

$$\mathbb{E}[\bar{X}] \approx \nu + \frac{\delta}{\mu} \nu (1 - \nu) (1 - Q_{\text{out}}^{\text{M}}) \times \left[ \underbrace{\left( \frac{(1 - \mu)(-c)}{-(b - c)(1 - \mu) \left( \frac{(1 - m)^2}{n} + \frac{m^2}{N - n} \right)} \right)}_{-\mathcal{C}^{\text{DB}}} + \underbrace{\left( \frac{(1 - \mu)b}{-(b - c)(n - 1)(1 - \mu) \left( \frac{(1 - m)^2}{n} + \frac{m^2}{N - n} \right)} \right)}_{\mathcal{B}^{\text{DB}}} \underbrace{\left( \frac{Q_{\text{in}}^{\text{M}} - Q_{\text{out}}^{\text{M}}}{1 - Q_{\text{out}}^{\text{M}}} \right)}_{R^{\text{M}}} \right], \quad (7)$$

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

### Wright-Fisher

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

239 The only – but important – different between eq. (8) and eq. (7) is the value of the  
 240 probabilities of identity by descent, because the number of individuals that are  
 241 updated at each time step differs.

## 242 3.2 Primary effects

243 Let us first focus on primary effects, shown on the first lines in the parentheses  
244 in eq. (6)–eq. (8). They are the same for the three life-cycles that we consider,  
245 and they do not depend on the emigration probability  $m$ . At the same time, as  
246 shown on figure 1, the relatedness terms  $R^M$  and  $R^{WF}$  decrease with  $m$  (keeping  
247  $m < 1 - \frac{1}{N_D}$ ; see figure 1) Consequently, if we ignored secondary effects, we would  
248 conclude that even with imperfect strategy transmission ( $\mu > 0$ ), increasing the  
249 emigration probability  $m$  decreases the expected frequency of altruists in the  
250 population (as our intuition may suggest already.) However, secondary effects  
251 play a role as well.

## 252 3.3 Changes with the emigration probability $m$

253 For the three life-cycles, the secondary effects are negative (with  $0 < m < 1 - \frac{1}{N_D}$ )  
254 and they increase with the emigration probability  $m$ . In other words, these detri-  
255 mental secondary effects weaken when the emigration probability increases. This  
256 effect goes against the reduction of relatedness  $R$  as  $m$  increases. Hence, we  
257 need to consider the entire equations to know the overall effect of the emigra-  
258 tion probability  $m$  on the expected frequency of altruists  $\mathbb{E}[\bar{X}]$  and on how it is  
259 affected by the (in)fidelity of parent-offspring transmission  $\mu$  (see Figure 2).

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

### 262 3.3.1 Moran Birth-Death

263 For the Moran Birth-Death life-cycle, we find that the expected frequency of al-  
264 truists  $\mathbb{E}[\bar{X}]$  is a monotonic function of the emigration probability  $m$ ; the direc-  
265 tion of the change depends on the value of the mutation probability  $\mu$  compared  
266 to a threshold value  $\mu_c^{BD}$ . When  $\mu < \mu_c^{BD}$ ,  $\mathbb{E}[\bar{X}]$  decreases with  $m$ , while when

267  $\mu > \mu_c^{\text{BD}}$ ,  $\mathbb{E}[\bar{X}]$  increases with  $m$ . The critical value  $\mu_c^{\text{BD}}$  is given by

$$\mu_c^{\text{BD}} = 1 - \frac{b - c + \sqrt{(b - c)(4bN^2 + b - c)}}{2bN} \quad (9)$$

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

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

### 274 3.3.2 Moran Death-Birth

275 The relationship between  $\mathbb{E}[\bar{X}]$  and  $m$  is a bit more complicated for the Moran  
 276 Death-Birth life-cycle. For simplicity, we concentrate on what happens starting  
 277 from low emigration probabilities (*i.e.*, on the sign of the slope of  $\mathbb{E}[\bar{X}]$  as a func-  
 278 tion of  $m$  when  $m \rightarrow 0$ ). If the benefits  $b$  provided by altruists are relatively low  
 279 ( $b < c(n + 1)$ ),  $\mathbb{E}[\bar{X}]$  initially increases with  $m$  provided the mutation probability  
 280  $\mu$  is greater than a threshold value  $\mu_c^{\text{DB}}$  given in eq. (10) below; otherwise, when  
 281 the benefits are high enough,  $\mathbb{E}[\bar{X}]$  initially increases with  $m$  for any value of  $\mu$ .  
 282 Combining these results, we write

$$\mu_c^{\text{DB}} = \begin{cases} \frac{(n + 1)c - b}{(2n - 1)b - (n - 1)c} & \text{if } b < c(n + 1), \\ 0 & \text{otherwise.} \end{cases} \quad (10)$$

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

286 When  $\mu > \mu_c^{\text{DB}}$ , the expected frequency of altruists  $\mathbb{E}[\bar{X}]$  reaches a maximum  
 287 at an emigration probability  $m_c^{\text{DB}}$  (whose complicated equation is given in the

supplementary Mathematica file), as can be seen in figure 2(a). When the mutation probability gets close to 0 ( $\mu \rightarrow 0$ ),  $m_c^{\text{DB}}$  also gets close to 0.

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

### 3.3.3 Wright-Fisher

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

$$\mu_c^{\text{WF}} = 1 - \sqrt{1 - \frac{c}{b}}, \quad (11)$$

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

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

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

The result, that higher emigration probabilities can actually favor altruistic behavior, may seem surprising, even though it is confirmed by simulations. The result may appear counterintuitive because explanations for the effect of population viscosity on the evolution of altruism often focus on primary effects. The role played by secondary effects is harder to grasp. To better understand the role played by the mutation probability  $\mu$ , we now focus on a qualitative condition for the evolution of altruism and on the Death-Birth life-cycle:

$$\mathbb{E}[\bar{X}] > v \Leftrightarrow R^{\text{M}} > \frac{\mathcal{C}^{\text{DB}}}{\mathcal{B}^{\text{DB}}}. \quad (12)$$

309 (having made sure that  $\mathcal{B}^{\text{DB}} > 0$ , as shown in the supplementary Mathematical  
 310 file). With this life-cycle, the  $\mathcal{C}^{\text{DB}}/\mathcal{B}^{\text{DB}}$  ratio does not change with the muta-  
 311 tion probability  $\mu$ , but it decreases with the emigration probability  $m$  ( $0 < m <$   
 312  $1 - 1/N_D$ ). This decrease of the  $\mathcal{C}^{\text{DB}}/\mathcal{B}^{\text{DB}}$  ratio is due to secondary effects (com-  
 313 petition) diminishing as emigration increases. Relatedness, on the other hand,  
 314 decreases with both  $\mu$  and  $m$  (see figure 3(a)).

315 When the emigration probability  $m$  is vanishingly small,  $\lim_{m \rightarrow 0} R^{\text{M}} \leq \lim_{m \rightarrow 0} \frac{\mathcal{C}^{\text{DB}}}{\mathcal{B}^{\text{DB}}}$ ,  
 316 the two only being equal when  $\mu = 0$ . Hence, it is only when strategy transmis-  
 317 sion is perfect that condition (12) is satisfied for vanishingly low  $m$ . Then, as  $m$   
 318 increases, the  $\frac{\mathcal{C}^{\text{DB}}}{\mathcal{B}^{\text{DB}}}$  ratio and relatedness  $R$  do not decrease with the same slope.  
 319 Provided the mutation probability  $\mu$  is not too high, *i.e.*, that  $R$  initially is not too  
 320 low already, there can be a range of emigration values  $m$  such that condition (12)  
 321 is satisfied (*i.e.*, the  $R$  curve is higher than the  $\mathcal{C}/\mathcal{B}$  curve in figure 3(a)).

### 322 3.5 Relaxing key assumptions

323 To derive our analytical results, we had to make a number of simplifying assump-  
 324 tions, such as the fact that selection is weak ( $\delta \ll 1$ ), and the fact that the struc-  
 325 ture of the population is regular (all demes have the same size  $n$ ). We explored  
 326 with numerical simulations the effect of relaxing these key assumptions.

327 When selection is strong, the patterns that we identified not only still hold  
 328 but are even more marked, as shown on figure S1.

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

334 For the Moran model, it may seem odd that an offspring can replace its own  
 335 parent (which can occur since  $d_{ii} \neq 0$ ). Figure S3, plotted with dispersal prob-

abilities 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.

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

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



## 354 4 Discussion

### 355 The expected frequency of altruists in a subdivided population can in- 356 crease with the probability of emigration

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

### 368 Quantitative vs. qualitative measures

369 Often, evolutionary success is measured qualitatively, by comparing a quantity  
370 (an expected frequency, or, in models with no mutation, a probability of fixation)  
371 to the value it would have in the absence of selection. In our model, this amounts  
372 to saying that altruism is favored whenever  $\mathbb{E}[\bar{X}] > v$  ( $v$  is plotted as a horizon-  
373 tal dashed line in figure 2). Some of our conclusions change if we switch to this  
374 qualitative measure of evolutionary success: Under the Moran Birth-Death and  
375 Wright-Fisher life-cycles, population viscosity does not promote the evolution of  
376 altruism – actually, these two life-cycles cannot ever promote altruistic behavior  
377 for any regular population structure (Taylor et al., 2011), whichever the probab-  
378 ility of mutation (Débarre, 2017). However, under a Moran Death-Birth life-cycle  
379 (figure 2(a)), altruism can be favored only at intermediate emigration probab-

ities. 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.  $R > \mathcal{C}/\mathcal{B}$ ; 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  $\mathcal{C}/\mathcal{B}$  ratio tend to 1. An increase in the mutation probability  $\mu$  reduces  $R$  while leaving  $\mathcal{C}/\mathcal{B}$  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  $\mathcal{C}/\mathcal{B}$  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 values of  $m$ : competition is already small enough that reducing it further does not outweigh the reduction in relatedness  $R$ .

Secondary effects are less straightforward to understand than primary effects, and yet they play a crucial role for social evolution in spatially structured populations. Competition among relatives is for instance the reason for 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 ( $\delta \ll 1$ ). 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 ( $\mu \rightarrow 1$ ) and infinite population sizes (number of demes  $N_D \rightarrow \infty$ ). The point is technical, but it is important to know that the order in which these limits are taken matters, *i.e.*, one needs to specify how small  $\mu$  and  $\delta$  are compared to the inverse size of the population. This remark complements findings by Sample & Allen (2017), who highlighted the quantitative differences between different orders of weak selection and large population limits.

### Imperfect transmission and Rebellious Children

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

433 probability  $\mu$ , because probabilities of identity by descent do.

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

#### 441 **Cultural transmission**

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

445 The model could nevertheless be interpreted as a representation of horizon-  
446 tal transmission, if we described reproduction as an instance of an individual  
447 convincing another one to update its strategy. The Moran Death-Birth model  
448 can be interpreted as a modified imitation scheme (Boyd & Richerson, 2002; Oht-  
449 suki et al., 2006) – with a specific function specifying who is imitated –, with mu-  
450 tation (Kandori et al., 1993). First, we choose uniformly at random an individual  
451 who may change its strategy; with probability  $\mu$  the individual chooses a random  
452 strategy (altruistic with probability  $\nu$ ), and with probability  $1 - \mu$  it imitates an-  
453 other individual. Who is imitated depends on the distance to the focal individual  
454 (with probability  $m$  it is a random individual in another deme) and on the “fe-  
455 cundities” of those individuals (as shown in table S2). With this interpretation of  
456 the updating rule however, there is not reproduction nor death anymore.

457 It remains to be investigated how imperfect strategy transmission would af-  
458 fect the effect of population viscosity on the evolution of altruism in a model im-  
459 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, leading to a polymorphism between sessile altruists and mobile defectors (Parvinen, 2013; Mullan et al., 2017). The assumptions of these studies however differ from ours in important ways, in that they consider continuous traits and use an adaptive dynamics framework, where, notably, mutations are assumed to be very rare. It remains to be investigated how non-rare and potentially large mutations would affect their result.

## Acknowledgements

Thanks to Charles Mullan for detailed comments on a previous version of the manuscript, and for suggesting the  $\mathcal{BR}-\mathcal{C}$  decomposition. At ESEB 2017, Sébastien Lion suggested using the  $R$  vs.  $\mathcal{C}/\mathcal{B}$  comparison to interpret the result. This work was funded by a ANR-14-ACHN-0003-01 grant.

## 477 References

- 478 Alizon, S. & Taylor, P. 2008: Empty sites can promote altruistic behavior. *Evolu-*  
479 *tion* 62(6):1335–1344.
- 480 Allen, B.; Lippner, G.; Chen, Y.-T.; Fotouhi, B.; Momeni, N.; Yau, S.-T. & Nowak,  
481 M. A. 2017: Evolutionary dynamics on any population structure. *Nature*  
482 544(7649):227–230.
- 483 Allen, B.; Traulsen, A.; Tarnita, C. E. & Nowak, M. A. 2012: How mutation affects  
484 evolutionary games on graphs. *Journal of Theoretical Biology* 299:97 – 105.  
485 *Evolution of Cooperation.*
- 486 Boyd, R. & Richerson, P. J. 2002: Group beneficial norms can spread rapidly in a  
487 structured population. *Journal of theoretical biology* 215(3):287–296.
- 488 Brockhurst, M. A.; Buckling, A. & Gardner, A. 2007: Cooperation peaks at inter-  
489 mediate disturbance. *Current Biology* 17(9):761–765.
- 490 Cockerham, C. C. & Weir, B. 1987: Correlations, descent measures: drift with  
491 migration and mutation. *Proceedings of the National Academy of Sciences*  
492 84(23):8512–8514.
- 493 Débarre, F. 2017: Fidelity of parent-offspring transmission and the evolution  
494 of social behavior in structured populations. *Journal of Theoretical Biology*  
495 420:26 – 35.
- 496 Débarre, F.; Hauert, C. & Doebeli, M. 2014: Social evolution in structured popu-  
497 lations. *Nature Communications* 5.
- 498 Fletcher, J. A. & Doebeli, M. 2009: A simple and general explanation for the evo-  
499 lution of altruism. *Proceedings of the Royal Society B: Biological Sciences*  
500 276(1654):13–19.
- 501 Frank, S. A. 1997: The Price equation, Fisher’s fundamental theorem, kin selec-  
502 tion, and causal analysis. *Evolution* 51(6):1712–1729.
- 503 Frank, S. A. 2010: Microbial secretor–cheater dynamics. *Philosophical Transac-*  
504 *tions of the Royal Society of London B: Biological Sciences* 365(1552):2515–  
505 2522.
- 506 Grafen, A. & Archetti, M. 2008: Natural selection of altruism in inelastic viscous  
507 homogeneous populations. *Journal of Theoretical Biology* 252(4):694 – 710.
- 508 Hamilton, W. 1964: The genetical evolution of social behaviour. i. *Journal of*  
509 *Theoretical Biology* 7(1):1 – 16.
- 510 Hamilton, W. D. 1975: Innate social aptitudes of man: an approach from evolu-  
511 tionary genetics. *Biosocial anthropology* 53:133–55.

512 Kandori, M.; Mailath, G. J. & Rob, R. 1993: Learning, mutation, and long run  
513 equilibria in games. *Econometrica* 61(1):29–56.

514 Lehmann, L.; Feldman, M. & Foster, K. 2008: Cultural transmission can inhibit  
515 the evolution of altruistic helping. *The American Naturalist* 172(1):12–24.  
516 PMID: 18500938.

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

520 Lehmann, L. & Rousset, F. 2014: The genetical theory of social behaviour. *Philo-*  
521 *sophical Transactions of the Royal Society of London B: Biological Sciences*  
522 369(1642).

523 Leturque, H. & Rousset, F. 2002: Dispersal, kin competition, and the ideal free  
524 distribution in a spatially heterogeneous population. *Theoretical Population*  
525 *Biology* 62(2):169 – 180.

526 Lion, S. 2016: Moment equations in spatial evolutionary ecology. *Journal of the-*  
527 *oretical biology* 405:46–57.

528 Mullon, C.; Keller, L. & Lehmann, L. 2017: Co-evolution of dispersal with be-  
529 haviour favours social polymorphism. *bioRxiv* .

530 Mullon, C. & Lehmann, L. 2014: The robustness of the weak selection approxi-  
531 mation for the evolution of altruism against strong selection. *Journal of evo-*  
532 *lutionary biology* 27(10):2272–2282.

533 Ohtsuki, H.; Hauert, C.; Lieberman, E. & Nowak, M. A. 2006: A simple rule  
534 for the evolution of cooperation on graphs and social networks. *Nature*  
535 441(7092):502–505.

536 Parvinen, K. 2013: Joint evolution of altruistic cooperation and dispersal in a  
537 metapopulation of small local populations. *Theoretical population biology*  
538 85:12–19.

539 R Core Team. 2015: R: A Language and Environment for Statistical Computing.  
540 R Foundation for Statistical Computing, Vienna, Austria.

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

543 Rousset, F. 2004: Genetic Structure and Selection in Subdivided Populations.  
544 Princeton University Press, Princeton, NJ.

545 Rousset, F. & Billiard, S. 2000: A theoretical basis for measures of kin selection in  
546 subdivided populations: finite populations and localized dispersal. *Journal of*  
547 *Evolutionary Biology* 13(5):814–825.

548 Sample, C. & Allen, B. 2017: The limits of weak selection and large population  
549 size in evolutionary game theory. *Journal of mathematical biology* pages 1–  
550 33.

551 Tarnita, C. E. & Taylor, P. D. 2014: Measures of relative fitness of social behaviors  
552 in finite structured population models. *The American Naturalist* 184(4):477–  
553 488.

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

556 Taylor, P. 2010: Birth–death symmetry in the evolution of a social trait. *Journal of*  
557 *Evolutionary Biology* 23(12):2569–2578.

558 Taylor, P.; Lillicrap, T. & Cownden, D. 2011: Inclusive fitness analysis on mathe-  
559 matical groups. *Evolution* 65(3):849–859.

560 Taylor, P. D. 1992b: Inclusive fitness in a homogeneous environment. *Pro-*  
561 *ceedings of the Royal Society of London. Series B: Biological Sciences*  
562 249(1326):299–302.

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

565 Taylor, P. D.; Day, T. & Wild, G. 2007b: From inclusive fitness to fixation proba-  
566 bility in homogeneous structured populations. *Journal of Theoretical Biology*  
567 249(1):101 – 110.

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

570 Van Cleve, J. 2015: Social evolution and genetic interactions in the short and long  
571 term. *Theoretical Population Biology* 103:2 – 26.

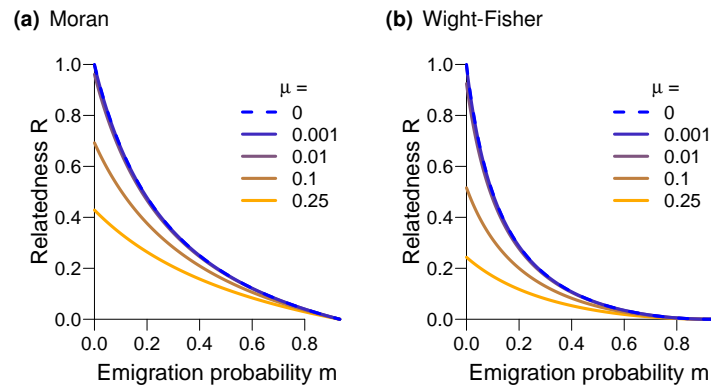
572 West, S. A. & Gardner, A. 2010: Altruism, spite, and greenbeards. *Science*  
573 327(5971):1341–1344.

574 West, S. A.; Pen, I. & Griffin, A. S. 2002: Cooperation and competition between  
575 relatives. *Science* 296(5565):72–75.

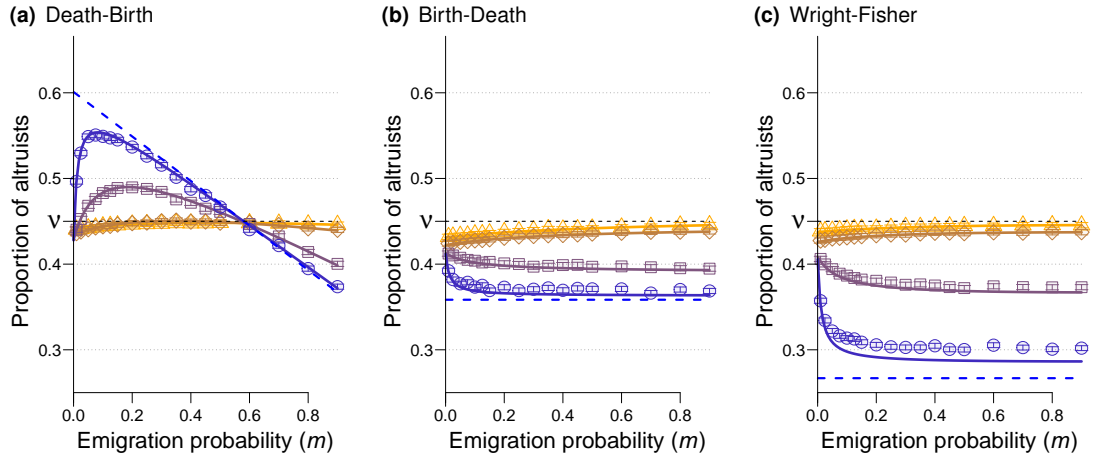
576 Wilson, D. S.; Pollock, G. B. & Dugatkin, L. A. 1992: Can altruism evolve in purely  
577 viscous populations? *Evolutionary Ecology* 6(4):331–341.

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

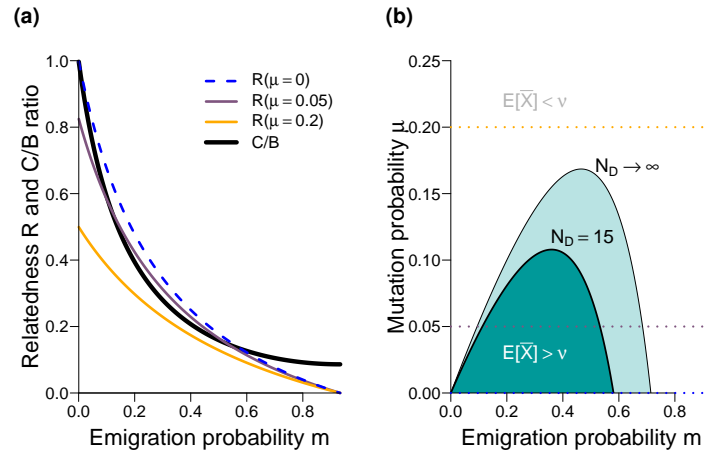




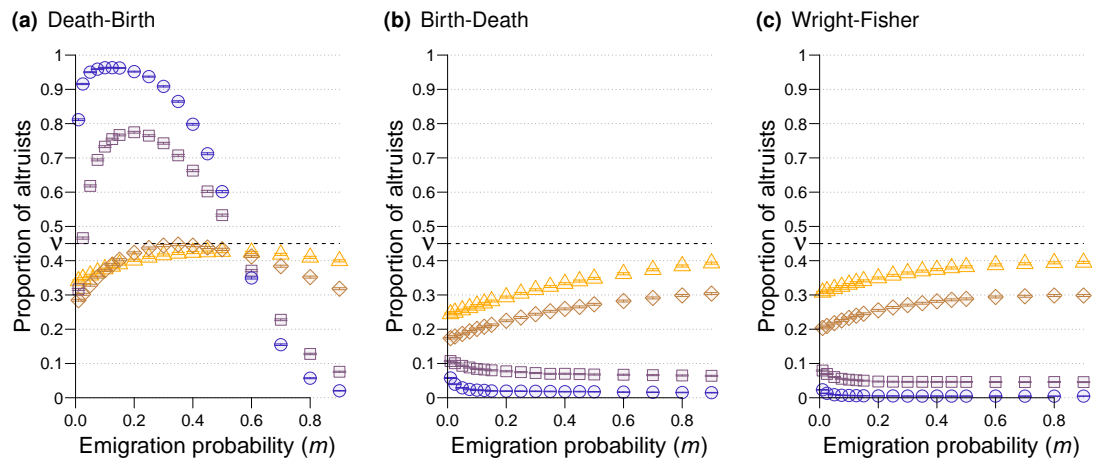
**Figure 1:** Within-deme relatedness of pairs of individuals, as a function of the emigration probability  $m$ , for different values of the mutation probability  $\mu$  (from 0 [blue] to 0.25 [orange]), and for the two types of life-cycles ((a): Moran, (b): Wright-Fisher). Other parameters:  $n = 4$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



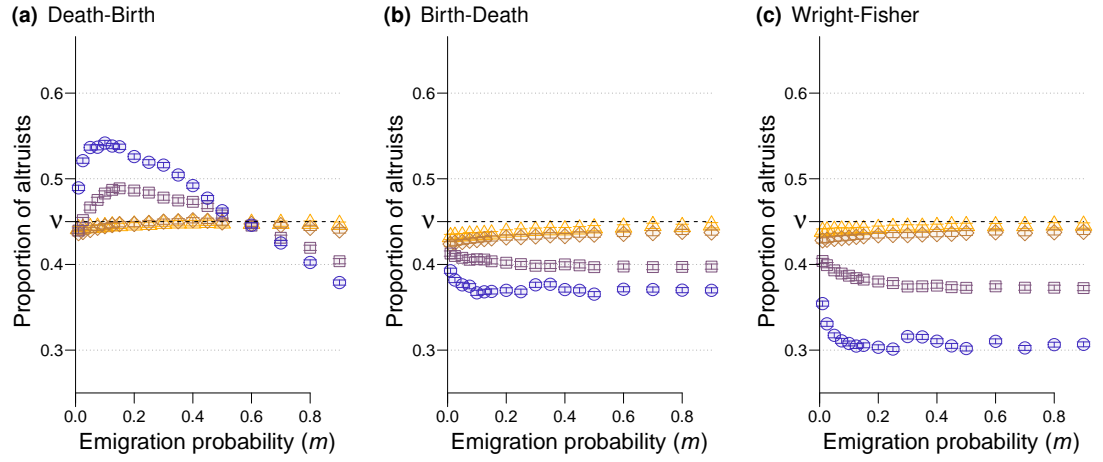
**Figure 2:** Expected proportion of altruists under weak selection, as a function of the emigration probability  $m$ , for different mutation values ( $\mu = 0.001$  (blue, dots),  $0.01$  (purple, squares),  $0.1$  (brown, diamonds),  $0.25$  (orange, triangles)); the dashed blue lines correspond to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



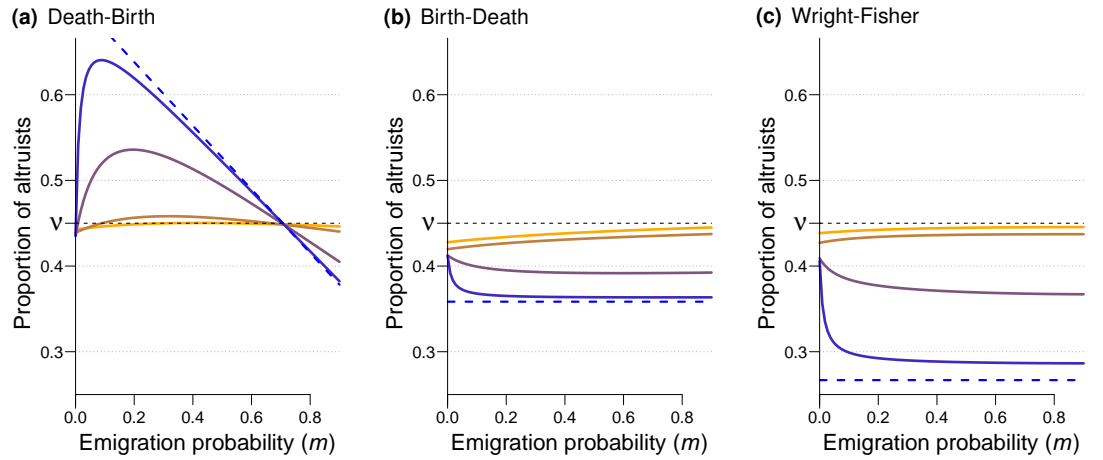
**Figure 3:** Understanding the effect of emigration  $m$  on whether altruism is favored in the Death-Birth life-cycle. (a) Comparison of the  $C/B$  ratio (thick black curve) and relatedness  $R$  (thin curves) for different values of the mutation probability  $\mu$  (same color code as previously). (b)  $(m, \mu)$  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.



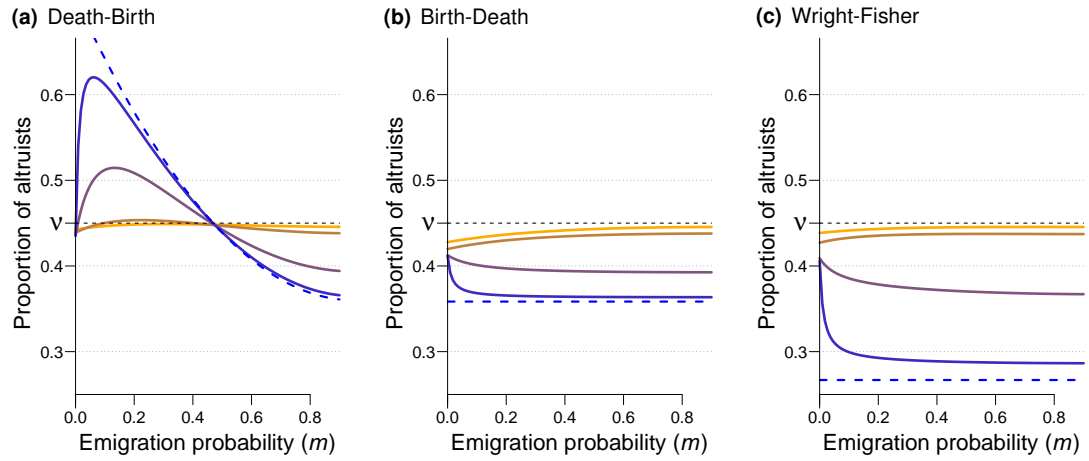
**Figure S1:** Equivalent of figure 2 (simulations only) but with strong selection ( $\delta = 0.1$ ); please note the change of scale on the vertical axis. All other parameters and legends are identical to those of figure 2 (increasing mutation probabilities from blue dots to orange triangles).



**Figure 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).

$b$	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. (4))
$W_i$	Measure of fitness, counting offspring only when unmutated (see eq. (2))
$X_i$	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.)
$\delta$	Phenotypic distance between altruists and defectors; strength of selection
$\phi_i$	Phenotype of the individual living at site $i$ ; $\phi_i = \delta X_i$ (r.v.)
$\mu$	Mutation probability
$\nu$	Mutation bias: probability that mutant is altruist
P	Subscript corresponding to primary effects
S	Subscript corresponding to secondary effects
$o$	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

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

## Appendix

582

### A Expected frequency of altruists

#### A.1 For a generic life-cycle

585 We want to compute the expected proportion of altruists in the population. We  
 586 represent the state of the population at a given time  $t$  using indicator variables  
 587  $X_i(t)$ ,  $1 \leq i \leq N$ , equal to 1 if the individual living at site  $i$  at time  $t$  is an altru-  
 588 ist, and equal to 0 if it is a defector; these indicator variables are gathered in a  
 589  $N$ -long vector  $\mathbf{X}(t)$ . The set of all possible population states is  $\Omega = \{0, 1\}^N$ . The  
 590 proportion of altruists in the population is written  $\bar{X}(t) = \sum_{i=1}^N X_i(t)$ . We denote  
 591 by  $B_{ji}(X(t), \delta)$ , written  $B_{ji}$  for simplicity, the probability that the individual at  
 592 site  $j$  at time  $t+1$  is the newly established offspring of the individual living at site  
 593  $i$  at time  $t$ . The expected number of successful offspring produced by the indi-  
 594 vidual living at site  $i$  at time  $t$  is given by  $B_i = \sum_{j=1}^N B_{ji}$ . We denote by  $D_i(X(t), \delta)$   
 595 ( $D_i$  for simplicity) the probability that the individual living at site  $i$  at time  $t$  has  
 596 been replaced (*i.e.*, died) at time  $t+1$ . These quantities depend on the chosen  
 597 life-cycle and on the state of the population; they are given in table S2 for each  
 598 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

**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).

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

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

600 holds for all sites  $i$ . The structure of the population is also such that in the ab-  
 601 sence 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

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

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

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

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  $\nu$ ), 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  $\delta$  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:

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

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

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

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

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

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

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

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

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

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

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

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 given that the size of the population is fixed ( $\sum_{i=1}^N (B_i - D_i) = 0$ ), and given that 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)

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

With this, eq. (A.8) becomes

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

We can also replace the  $P$  terms by

$$\begin{aligned} P_{ij} &= Q_{ij}\nu + (1 - Q_{ij})\nu^2 \\ &= \nu^2 + \nu(1 - \nu)Q_{ij}. \end{aligned} \quad (\text{A.11})$$

In Appendix B.1, we will see using recursions on  $P_{ij}$  that  $Q_{ij}$  can be interpreted as a probability of identity by descent, *i.e.*, the probability that the individuals at sites  $i$  and  $j$  have a common ancestor and that no mutation has occurred on either lineage since the ancestor. Eq. (A.10) becomes

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

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

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

With our notation, and given that social interactions take place within demes and affect fecundity, we have

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

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

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

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

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

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

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

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

666 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  
 667  $D_i$  terms by their formulas for each life-cycle (given in table S2).

## 668 A.2 Derivatives for the specific life-cycles

669 Using the formulas presented in table S2, and the definition of  $W = W_i$  given in  
 670 eq. (A.5), we obtain the following equations:

### Moran Birth-Death

$$\left. \frac{\partial W^{\text{BD}}}{\partial f_o} \right|_{\delta=0} = (1-\mu) \left( \frac{1}{N} - \frac{1}{N^2} \right) - \left( \frac{1-m}{nN} - \frac{1}{N^2} \right) = \frac{1-\mu}{N} + \frac{\mu}{N^2} - \frac{1-m}{nN}, \quad (\text{A.17a})$$

$$\left. \frac{\partial W^{\text{BD}}}{\partial f_{\text{in}}} \right|_{\delta=0} = (1-\mu) \left( -\frac{1}{N^2} \right) - \left( \frac{1-m}{nN} - \frac{1}{N^2} \right) = \frac{\mu}{N^2} - \frac{1-m}{nN}. \quad (\text{A.17b})$$

### Moran Death-Birth

$$\left. \frac{\partial W^{\text{DB}}}{\partial f_o} \right|_{\delta=0} = \frac{1-\mu}{N} \left[ 1 - \left( \frac{(1-m)^2}{n} + \frac{m^2}{N-n} \right) \right], \quad (\text{A.18a})$$

$$\left. \frac{\partial W^{\text{DB}}}{\partial f_{\text{in}}} \right|_{\delta=0} = -\frac{1-\mu}{N} \left( \frac{(1-m)^2}{n} + \frac{m^2}{N-n} \right). \quad (\text{A.18b})$$

671 In addition, for both Moran life-cycles, we have  $B_M^* = 1/N$ .

### Wright-Fisher

$$\left. \frac{\partial W^{\text{WF}}}{\partial f_o} \right|_{\delta=0} = (1-\mu) \left[ 1 - \left( \frac{(1-m)^2}{n} + \frac{m^2}{N-n} \right) \right], \quad (\text{A.19a})$$

$$\left. \frac{\partial W^{\text{WF}}}{\partial f_{\text{in}}} \right|_{\delta=0} = -(1-\mu) \left( \frac{(1-m)^2}{n} + \frac{m^2}{N-n} \right). \quad (\text{A.19b})$$

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

673 Combining these equations with eq. (A.16) and eq. (A.15) given eqs. (6)–(8)  
 674 in the main text.

## B Probabilities of identity by descent

### B.1 Expected state of pairs of sites and probabilities of identity by descent

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

#### B.1.1 Moran model

In a Moran model, exactly one individual dies and one individual reproduces during one time step. Given a state  $\mathbf{X}$  at time  $t$ , at time  $t + 1$  both sites  $i$  and  $j \neq i$  are occupied by altruists, if  $i\bar{i}$  it was the case at time  $t$  and neither site was replaced by a non-altruist (first term in eq. (B.20)), or  $i\bar{i}$  if exactly one of the two sites was occupied by a non-altruist at time  $t$ , but the site was replaced by an altruist (second and third terms of eq. (B.20)):

$$\begin{aligned} \mathbb{E}[X_i X_j(t+1) | X(t) = \mathbf{X}] = & X_i X_j \left( 1 - \sum_{k=1}^N \frac{1}{N} (d_{ki} + d_{kj}) ((1 - X_k)(1 - \mu) + \mu(1 - \nu)) \right) \\ & + X_i(1 - X_j) \sum_{k=1}^N \frac{1}{N} d_{kj} (X_k(1 - \mu) + \mu\nu) \\ & + X_j(1 - X_i) \sum_{k=1}^N \frac{1}{N} d_{ki} (X_k(1 - \mu) + \mu\nu). \end{aligned} \quad (\text{B.20})$$

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

$$P_{ij} = \frac{1}{2} \left( \sum_{k=1}^N (1 - \mu) (d_{kj} P_{ki} + d_{ki} P_{kj}) \right) + \mu\nu^2 \quad (i \neq j), \quad (\text{B.21})$$

while  $P_{ii} = \nu$ .

Now we substitute  $P_{ij} = \nu^2 + \nu(1 - \nu)Q_{ij}$  in eq. (B.21), we obtain

$$Q_{ij} = \frac{1}{2} \sum_{k=1}^N (1 - \mu) (d_{ki} Q_{kj} + d_{kj} Q_{ki}), \quad (\text{B.22})$$

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

698 **B.1.2 Wright-Fisher model**

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

$$\begin{aligned} \mathbb{E}[X_i X_j(t+1) | X(t) = \mathbf{X}] = \sum_{k, \ell=1}^N d_{ki} d_{\ell j} & \left( X_k X_\ell (1 - \mu + \mu v)^2 \right. \\ & + (X_k(1 - X_\ell) + (1 - X_k)X_\ell) (1 - \mu + \mu v)(\mu v) \\ & \left. + (1 - X_k)(1 - X_\ell)(\mu v)^2 \right) \end{aligned} \quad (\text{B.23})$$

701 The first term of eq. (B.23) corresponds to both parents being altruists, and hav-  
702 ing altruist offspring; the second line corresponds to exactly one parent being  
703 altruist, and the third line to both parents being non-altruists (in this latter case,  
704 the two offspring have to be both mutants to be altruists).

705 Taking the expectation and simplifying, we obtain

$$P_{ij} = \sum_{k, \ell=1}^N (P_{kl}(1 - \mu)^2) + (2 - \mu)\mu v^2. \quad (\text{B.24})$$

706 Replacing  $P_{ij}$  by  $v^2 + v(1 - v)Q_{ij}$ , eq. (B.24) becomes

$$Q_{ij} = \sum_{k, \ell=1}^N d_{ki} d_{\ell j} Q_{k\ell} (1 - \mu)^2. \quad (\text{B.25})$$

707 Again,  $Q_{ij}$  corresponds to a probability of identity by descent: the individuals at  
708 sites  $i$  and  $j$  are identical by descent if their parents were and if neither mutated  
709  $((1 - \mu)^2)$ .

## 710 B.2 Probabilities of identity by descent in a subdivided population

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

$$Q_{ij} = \begin{cases} 1 & \text{when } i = j; \\ Q_{\text{in}} & \text{when } i \neq j \text{ and both sites are in the same deme;} \\ Q_{\text{out}} & \text{when sites } i \text{ and } j \text{ are in different demes.} \end{cases} \quad (\text{B.26})$$

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

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

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

### 728 B.2.1 Moran model

729 In Débarre (2017), it was shown that

$$\tilde{\mathcal{Q}}_{r_1 r_2} = \frac{1}{N} \sum_{q_1=0}^{N_1-1} \sum_{q_2=0}^{N_2-1} \frac{\mu \lambda'_M}{1 - (1-\mu)\tilde{\mathcal{Q}}_{q_1 q_2}} \exp\left(i \frac{2\pi q_1 r_1}{N_1}\right) \exp\left(i \frac{2\pi q_2 r_2}{N_2}\right) \quad (\text{B.27a})$$

730 with

$$\tilde{\mathcal{Q}}_{q_1 q_2} = \sum_{\ell_1=0}^{N_1-1} \sum_{\ell_2=0}^{N_2-1} \tilde{d}_{\ell_1 \ell_2} \exp\left(-i \frac{2\pi q_1 \ell_1}{N_1}\right) \exp\left(-i \frac{2\pi q_2 \ell_2}{N_2}\right), \quad (\text{B.27b})$$

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

$$\begin{aligned} \tilde{\mathcal{Q}}_{q_1 q_2} &= d_{\text{self}} + \sum_{\ell_2=1}^{N_2-1} d_{\text{in}} \exp\left(-i \frac{2\pi q_2 \ell_2}{N_2}\right) + \sum_{\ell_1=1}^{N_1-1} \sum_{\ell_2=0}^{N_2-1} d_{\text{out}} \exp\left(-i \frac{2\pi q_1 \ell_1}{N_1}\right) \exp\left(-i \frac{2\pi q_2 \ell_2}{N_2}\right) \\ &= d_{\text{self}} + (\delta_{q_2}(N_2-1) + (1-\delta_{q_2})(-1)) d_{\text{in}} + (\delta_{q_1}(N_1-1) + (1-\delta_{q_1})(-1)) (\delta_{q_2} N_2) d_{\text{out}} \\ &= d_{\text{self}} + (\delta_{q_2} N_2 - 1) d_{\text{in}} + (\delta_{q_1} N_1 - 1) \delta_{q_2} N_2 d_{\text{out}}. \end{aligned} \quad (\text{B.28a})$$

733 ( $\delta_q$  is equal to 1 when  $q$  is equal to 0 modulo the relevant dimension, and to 0  
 734 otherwise). So for the three types of distances that we need to consider (distance  
 735 0, distance to another deme-mate, distance to individual in another deme), and  
 736 with  $N_1 = N_D$  and  $N_2 = n$ , we obtain

$$\tilde{\mathcal{D}}_0 = 1, \quad (\text{B.29a})$$

$$\tilde{\mathcal{D}}_{q_1} = 1 - m - \frac{m}{N_D - 1} \quad (q_1 \not\equiv 0 \pmod{N_1}), \quad (\text{B.29b})$$

$$\tilde{\mathcal{D}}_{q_1} = d_{\text{self}} - d_{\text{in}} \quad (q_2 \not\equiv 0 \pmod{N_2}). \quad (\text{B.29c})$$

737 So for  $\tilde{\mathcal{Q}}$ , using system (B.29) in eq. (B.27a),

$$\begin{aligned} \tilde{\mathcal{Q}}_{r_1} &= \frac{\mu \lambda'_M}{N} \left[ \frac{1}{1 - (1 - \mu) \tilde{\mathcal{D}}_0} + \sum_{q_2=1}^{N_2-1} \frac{1}{1 - (1 - \mu) \tilde{\mathcal{D}}_{q_2}} \exp\left(-i \frac{2\pi q_2 r_2}{N_2}\right) \right. \\ &\quad + \sum_{q_1=1}^{N_1-1} \frac{1}{1 - (1 - \mu) \tilde{\mathcal{D}}_{q_1}} \exp\left(-i \frac{2\pi q_1 r_1}{N_1}\right) \\ &\quad \left. + \sum_{q_1=1}^{N_1-1} \sum_{q_2=1}^{N_2-1} \frac{1}{1 - (1 - \mu) \tilde{\mathcal{D}}_{q_1}} \exp\left(-i \frac{2\pi q_1 r_1}{N_1}\right) \exp\left(-i \frac{2\pi q_2 r_2}{N_2}\right) \right] \\ &= \frac{\mu \lambda'_M}{N} \left[ \frac{1}{1 - (1 - \mu)} + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})} (\delta_{r_2} N_2 - 1) \right. \\ &\quad + \frac{1}{1 - (1 - \mu)(1 - m - \frac{m}{N_D - 1})} (\delta_{r_1} N_1 - 1) \\ &\quad \left. + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})} (\delta_{r_1} N_1 - 1)(\delta_{r_2} N_2 - 1) \right]. \quad (\text{B.30}) \end{aligned}$$

738 In particular,

$$\begin{aligned} \tilde{\mathcal{Q}}_0 &= \frac{\mu \lambda'_M}{N} \left[ \frac{1}{\mu} + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})} (n - 1) + \frac{1}{1 - (1 - \mu)(1 - m - \frac{m}{N_D - 1})} (N_D - 1) \right. \\ &\quad \left. + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})} (N_D - 1)(n - 1) \right] \\ &= 1. \quad (\text{B.31a}) \end{aligned}$$

739 We find  $\lambda'_M$  using eq. (B.31a). Let's now go back to eq. (B.30): when  $r_1 = 0$ , the  
 740 two individuals are in the same deme. They are different when  $r_2 \neq 0$ , and so:

$$\begin{aligned} Q_{\text{in}} &= \frac{\mu \lambda'_M}{N} \left[ \frac{1}{\mu} + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})} (-1) + \frac{1}{1 - (1 - \mu)(1 - m - \frac{m}{N_D - 1})} (D - 1) \right. \\ &\quad \left. + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})} (D - 1)(-1) \right]. \quad (\text{B.31b}) \end{aligned}$$



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

$$Q_{\text{out}} = \frac{\mu \lambda'_M}{N} \left[ \frac{1}{\mu} + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})} (-1) + \frac{1}{1 - (1 - \mu)(1 - m - \frac{m}{N_D - 1})} (-1) + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})} \right]. \quad (\text{B.31c})$$

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

$$Q_{\text{in}}^M = \frac{(1 - \mu)(m + \mu(N_D(1 - m) - 1))}{(1 - \mu)m(N_D\mu(n - 1) + 1) + (N_D - 1)\mu(\mu(n - 1) + 1)}, \quad (\text{B.32a})$$

$$Q_{\text{out}}^M = \frac{(1 - \mu)m}{(1 - \mu)m(N_D\mu(n - 1) + 1) + (N_D - 1)\mu(\mu(n - 1) + 1)}. \quad (\text{B.32b})$$

743 The probability that two different deme-mates are identical by descent,  $Q_{\text{in}}^M$ , de-  
 744 creases monotonically with the emigration probability  $m$ , while  $Q_{\text{out}}^M$  monoton-  
 745 ically increases with  $m$  (see figure S5(a)).

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

### 752 B.2.2 Wright-Fisher

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

$$\tilde{\mathcal{Q}}_{r_1}^{r_2} = \frac{1}{N} \sum_{q_1=0}^{N_1-1} \sum_{q_2=0}^{N_2-1} \frac{\mu \lambda'_{WF}}{1 - (1 - \mu)^2 (\tilde{\mathcal{Q}}_{q_1}^{q_2})^2} \exp\left(-i \frac{2\pi q_1 r_1}{N_1}\right) \exp\left(-i \frac{2\pi q_2 r_2}{N_2}\right), \quad (\text{B.33})$$

754 with  $\tilde{\mathcal{Q}}$  given in eq. (B.27b). In a subdivided population, with  $N_1 = N_D$  and  $N_2 =$   
 755  $n$ , this becomes

$$\begin{aligned}
 \tilde{\mathcal{Q}}_{r_1, r_2} &= \frac{1}{N} \left[ \frac{\mu \lambda'_{WF}}{1 - (1 - \mu)^2 (\tilde{\mathcal{Q}}_0)^2} + \sum_{q_2=1}^{N_2-1} \frac{\mu \lambda'_{WF}}{1 - (1 - \mu)^2 (\tilde{\mathcal{Q}}_{q_2})^2} \exp \left( -\iota \frac{2\pi q_2 r_2}{N_2} \right) \right. \\
 &\quad + \sum_{q_1=1}^{N_1-1} \frac{\mu \lambda'_{WF}}{1 - (1 - \mu)^2 (\tilde{\mathcal{Q}}_{q_1})^2} \exp \left( -\iota \frac{2\pi q_1 r_1}{N_1} \right) \\
 &\quad \left. + \sum_{q_1=1}^{N_1-1} \sum_{q_2=1}^{N_2-1} \frac{\mu \lambda'_{WF}}{1 - (1 - \mu)^2 (\tilde{\mathcal{Q}}_{q_1})^2} \exp \left( -\iota \frac{2\pi q_1 r_1}{N_1} \right) \exp \left( -\iota \frac{2\pi q_2 r_2}{N_2} \right) \right] \\
 &= \frac{\mu \lambda'_{WF}}{N} \left[ \frac{1}{1 - (1 - \mu)^2} + \frac{1}{1 - (1 - \mu)^2 (d_{\text{self}} - d_{\text{in}})^2} (\delta_{q_2} N_2 - 1) \right. \\
 &\quad + \frac{1}{1 - (1 - \mu)^2 (1 - m - \frac{m}{N_D - 1})^2} (\delta_{q_1} N_1 - 1) \\
 &\quad \left. + \frac{1}{1 - (1 - \mu)^2 (d_{\text{self}} - d_{\text{in}})^2} (\delta_{q_1} N_1 - 1) (\delta_{q_2} N_2 - 1) \right] \\
 &= \frac{\mu \lambda'_{WF}}{N} \left[ \frac{1}{1 - (1 - \mu)^2} + \frac{1}{1 - (1 - \mu)^2 (d_{\text{self}} - d_{\text{in}})^2} (\delta_{q_2} N_2 - 1) \delta_{q_1} N_1 \right. \\
 &\quad \left. + \frac{1}{1 - (1 - \mu)^2 (1 - m - \frac{m}{N_D - 1})^2} (\delta_{q_1} N_1 - 1) \right]. \tag{B.34}
 \end{aligned}$$

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

$$1 = \frac{\mu \lambda'_{WF}}{N} \left[ \frac{1}{1 - (1 - \mu)^2} + \frac{1}{1 - (1 - \mu)^2 (d_{\text{self}} - d_{\text{in}})^2} (N_2 - 1) N_1 + \frac{1}{1 - (1 - \mu)^2 (1 - m - \frac{m}{N_D - 1})^2} (N_1 - 1) \right]. \tag{B.35a}$$

757 Then from eq. (B.34) we deduce

$$Q_{\text{in}} = \frac{\mu \lambda'_{WF}}{N} \left[ \frac{1}{1 - (1 - \mu)^2} - \frac{1}{1 - (1 - \mu)^2 (d_{\text{self}} - d_{\text{in}})^2} N_1 + \frac{1}{1 - (1 - \mu)^2 (1 - m - \frac{m}{N_D - 1})^2} (N_1 - 1) \right]. \tag{B.35b}$$

758 and

$$Q_{\text{out}} = \frac{\mu \lambda'_{WF}}{N} \left[ \frac{1}{1 - (1 - \mu)^2} - \frac{1}{1 - (1 - \mu)^2 (1 - m - \frac{m}{d - 1})^2} \right]. \tag{B.35c}$$

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

$$Q_{\text{in}}^{\text{WF}} = \frac{-N_D + M_1 + M_2}{(n - 1)N_D + M_1 + M_2}, \tag{B.36a}$$

$$Q_{\text{out}}^{\text{WF}} = \frac{-\frac{1}{N_D - 1} M_1 + M_2}{(n - 1)N_D + M_1 + M_2}, \tag{B.36b}$$

760 with

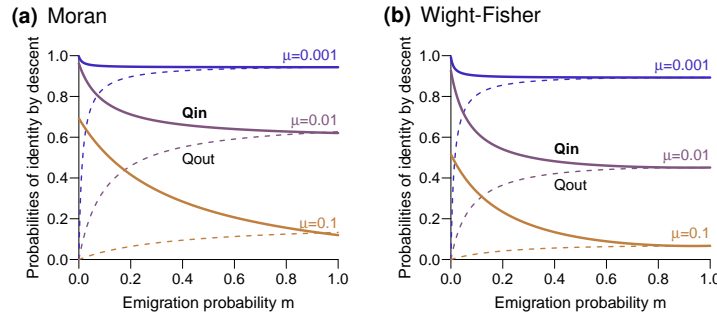
$$M_1 = \frac{N_D - 1}{1 - \frac{(1 - \mu)^2 (N_D (1 - m) - 1)^2}{(N_D - 1)^2}} \text{ and } M_2 = \frac{1}{1 - (1 - \mu)^2}.$$

(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  $m_c^{\text{WF}}$  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  $\mu$  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,  $Q_{\text{in}}$  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 S5(a) and S5(b)).



**Figure S5:** Probabilities of identity by descent, for two different individuals within the same deme ( $Q_{\text{in}}$ , full curves) and two individuals in different demes ( $Q_{\text{out}}$ , 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.