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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 B.1 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 Expected frequencies of altruists for each life-cycle

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

$$\mathbb{E}[\bar{X}] \approx v + \omega \frac{v(1-v)}{\mu} [b(\beta_D - \beta_I) - c(\gamma_D - \gamma_I)]. \quad (2) \quad \{\text{eq:EXapprox}\}$$

192 (Calculations leading to eq. (5) are presented in Appendix A.)

193 The mutation bias  $v$  corresponds to the expected proportion of altruists in the  
 194 population in the absence of selection (*i.e.*, when  $\omega = 0$ );  $\omega$  is the parameter  
 195 that scales the effects of interactions between individuals, which is assumed to  
 196 be small. The subscript  $D$  refers to “direct” effects, and the subscript  $I$  to “in-  
 197 direct” effects. “Direct” effects involve effects on primary beneficiaries of the  
 198 benefits ( $b$ ) and costs ( $c$ ) of social interactions (West & Gardner, 2010), *i.e.*, so-

199 cial interactants (for the benefits  $b$ ) and the focal individuals themselves (for the  
 200 costs  $c$ ). “Indirect” effects corresponds to effects on secondary interactants, *i.e.*,  
 201 to (kin) competition. By providing a benefit to a deme-mate and thereby in-  
 202 creasing its fecundity, a focal altruist indirectly harms others by reducing their  
 203 relative fecundity ( $\beta_I$  term in eq. (5)); by having a reduced fecundity due to the  
 204 cost of altruism, a focal altruist indirectly favors others by increasing their rela-  
 205 tive fecundity ( $\gamma_I$  term).

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

### 208 3.1.1 Direct effects

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

{eq:directeffects}

$$\beta_D^{BD} = \beta_D^{DB} = (1 - \mu) Q_{in}^M, \quad (3a) \quad \text{{eq:bBDD}}$$

$$\beta_D^{WF} = (1 - \mu) Q_{in}^{WF}; \quad (3b) \quad \text{{eq:bWFD}}$$

$$\gamma_D^{BD} = \gamma_D^{DB} = \gamma_D^{WF} = 1 - \mu. \quad (3c) \quad \text{{eq:cBDD}}$$

212 For both benefits and costs, direct effects only count when there is no mutation  
 213 (hence the  $(1 - \mu)$  factors). Direct effects of benefits  $b$  (eq. (6a) and eq. (6b)) only  
 214 count if the interaction takes place with an individual who is identical by de-  
 215 scent. With the population structure that we consider, social interactions only  
 216 occur within demes, so only  $Q_{in}$  is present in eq. (6a) and eq. (6b). On the other  
 217 hand, the direct effect of the fecundity cost  $c$  (eq. (6c)) does not depend on the  
 218 type of interactant, since the same cost  $c$  is paid by altruists irrespective of the  
 219 interactant’s identity.

220 As seen in the previous section,  $Q_{in}^M$  and  $Q_{in}^{WF}$  decrease with the emigration  
 221 probability  $m$  (actually only until  $m = \frac{d-1}{d}$  for the latter). Consequently, the mag-

nititude of the direct (beneficial) effects of benefits  $b$  provided by altruists ( $\beta_D$ ) decreases when the emigration probability  $m$  increases, while the direct (detrimental) effects ( $\gamma_D$ ) due to the direct cost of altruism  $c$  are constant. As a result, if we only considered direct effects, we would conclude that more emigration  $m$  is detrimental to the evolution of altruistic behaviour. However, there are also indirect effects at play.

### 3.1.2 Indirect effects

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

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

$$\begin{aligned}\beta_I^{\text{BD}} &= (1 - m) \left( \frac{n-1}{n} Q_{\text{in}}^{\text{M}} + \frac{1}{n} \right) + m Q_{\text{out}}^{\text{M}} - \mu \frac{1 + (n-1)Q_{\text{in}}^{\text{M}} + n(d-1)Q_{\text{out}}^{\text{M}}}{nd} \\ &= \gamma_I^{\text{BD}}.\end{aligned}\tag{4a} \quad \{\text{eq: bBDI}\}$$

(Calculation details are presented in Appendix A.)

The formulas are the same for the indirect effects associated to  $b$  and to  $c$ ; in other words, the balance between the two indirect effects remains the same when the emigration probability changes. The term  $\left( \frac{n-1}{n} Q_{\text{in}}^{\text{M}} + \frac{1}{n} \right)$ , which will appear again later, corresponds to the probability that two individuals sampled with replacement from the same deme are identical by descent. Indirect effects are

indeed also felt by the focal individual itself (*e.g.*, increasing the fecundity of another individual implies decreasing one's own relative fecundity).

Replacing  $Q_{\text{in}}$  and  $Q_{\text{out}}$  by their formula for the Moran life-cycle (eq. (B.32)), we conclude that  $\beta_I^{\text{BD}} = \gamma_I^{\text{BD}}$  are decreasing functions of the emigration probability  $m$  (calculations in the supplementary Mathematica file).

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

$$\begin{aligned}\beta_I^{\text{DB}} &= (1 - \mu) \left[ \left( \frac{1}{n} + \frac{(n-1)Q_{\text{in}}^{\text{M}}}{n} \right) \left( (1-m)^2 + \frac{m^2}{(d-1)} \right) \right. \\ &\quad \left. + Q_{\text{out}}^{\text{M}} \left( 2m(1-m) + (d-2) \frac{m^2}{(d-1)} \right) \right] \\ &= \gamma_I^{\text{DB}}\end{aligned}\tag{4b} \quad \{\text{eq: bDBI}\}$$

The brackets in eq. (7b) contain a sum of two terms. The first term corresponds to two individuals from the same deme (with replacement) whose offspring either do not emigrate, or emigrate together to the same deme. The second term corresponds to individuals initially from different demes who end up in the same deme (either one of their home demes, or a third deme).

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

Replacing  $Q_{\text{in}}$  and  $Q_{\text{out}}$  by their formulas given in eq. (B.32), we can conclude that  $\beta_I^{\text{DB}} = \gamma_I^{\text{DB}}$  first decreases with the emigration probability  $m$ , and increases again after a threshold value  $m'_c$ , which is smaller than  $m_c^{\text{WF}} = (d-1)/d$  (calculation details are presented in the supplementary Mathematica file).

266 **Wright-Fisher** With this life-cycle, generations are synchronous and all indi-  
 267 viduals again all have the same survival probability (now equal to 0 at all sites).  
 268 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  
 269 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. (B.36)).  
 270 Once this is done, we see that  $\beta_I^{\text{WF}} = \gamma_I^{\text{WF}}$  first decreases with the emigration  
 271 probability  $m$ , and increases again after the threshold value  $m_c^{\text{WF}} = (d-1)/d$ .  
 272 This emigration threshold was identified above as the emigration probability  
 273 such that offspring have an equal chance of landing in their natal deme or in  
 274 any other deme, *i.e.*,  $d_{\text{in}} = d_{\text{out}}$  (calculation details are presented in the supple-  
 275 mentary Mathematica file.)

## 276 3.2 Identifying threshold values of the mutation probability $\mu$

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

### 283 3.2.1 Moran Birth-Death

284 For this life-cycle, we find that the expected frequency of altruists  $\mathbb{E}[\bar{X}]$  is a mono-  
 285 tonic function of the emigration probability  $m$ ; the direction of the change de-  
 286 pends on the value of the mutation probability  $\mu$  compared to a threshold value  
 287  $\mu_c^{\text{BD}}$ . 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  
 288 with  $m$ . The critical value  $\mu_c^{\text{BD}}$  is given by

$$\mu_c^{\text{BD}} = 1 - \frac{b - c + \sqrt{(b - c)(4b(nd)^2 + b - c)}}{2bnd} \quad (5) \quad \{\text{eq:mucBD}\}$$

289 This result is illustrated in figure 1(b); with the parameters of the figure,  $\mu_c^{\text{BD}} \approx$   
 290 0.026.

### 291 3.2.2 Moran Death-Birth

292 The relationship between  $\mathbb{E}[\bar{X}]$  and  $m$  is a bit more complicated for this life-  
 293 cycle. For simplicity, we concentrate on what happens starting from low emi-  
 294 gration probabilities (*i.e.*, the sign of the slope of  $\mathbb{E}[\bar{X}]$  as a function of  $m$  when  
 295  $m \rightarrow 0$ ). If the benefits  $b$  provided by altruists are relatively low ( $b < c(n+1)$ ),  
 296  $\mathbb{E}[\bar{X}]$  initially increases with  $m$  provided the mutation probability  $\mu$  is greater  
 297 than a threshold value  $\mu_c^{\text{DB}}$  given in eq. (9) below; otherwise, when the benefits  
 298 are high enough,  $\mathbb{E}[\bar{X}]$  initially increases with  $m$  for any value of  $\mu$ . Combining  
 299 these results, we write

$$\mu_c^{\text{DB}} = \begin{cases} \frac{(n+1)c - b}{(2n-1)b - (n-1)c} & \text{if } b < c(n+1), \\ 0 & \text{otherwise.} \end{cases} \quad (6) \quad \{\text{eq:mucDB}\}$$

300 In figure 1(a), the parameters are such that  $\mu_c^{\text{DB}} = 0$ .

301 The expected frequency of altruists  $\mathbb{E}[\bar{X}]$  then reaches a maximum at an em-  
 302 igration probability  $m_c^{\text{DB}}$  (whose complicated equation is given in the supple-  
 303 mentary Mathematica file), as can be seen in figure 1(a). When the mutation  
 304 probability gets close to 0 ( $\mu \rightarrow 0$ ),  $m_c^{\text{DB}}$  also gets close to 0,

### 305 3.2.3 Wright-Fisher

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

$$\mu_c^{\text{WF}} = 1 - \sqrt{1 - \frac{c}{b}}, \quad (7)$$

309 and it is a minimum otherwise. With the parameters of figure 1(c),  $\mu_c^{\text{WF}} = 0.034$ .

### 310 3.3 Relaxing key assumptions

311 To derive our analytical results, we had to make a number of simplifying assumptions, such as the fact that selection is weak ( $\omega \ll 1$ ), and the fact that the structure of the population is regular (all demes have the same size  $n$ ). We explored  
312  
313 with numerical simulations the effect of relaxing these key assumptions. When  
314 selection is strong, the patterns that we identified not only still hold but are even  
315 more marked, as shown on figure S1.  
316

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

322 For the Moran model, it may seem odd that an offspring can replace its own  
323 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  $i$ ,  
324  $d_{ii} = d_{\text{self}} = 0$ ;  $d_{\text{in}} = (1 - m)/(n - 1)$  for two different sites in the same deme,  $d_{\text{out}}$   
325 remaining unchanged), confirms that this does affect our conclusions.  
326

## 327 4 Discussion

### 328 The expected frequency of altruists in a subdivided population can increase with the probability of emigration 329

330 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  
331 frequency of altruists maintained in a population could increase with the probability  
332 of emigration out of the parental deme, a parameter tuning population  
333

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 1(b)–(c)) or favorable (Taylor et al., 2007a, and dashed lines in figure 1(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 of population viscosity. Often however, evolutionary success is measured qualitatively, by comparing a quantity (an expected frequency, or, in models with no mutation, a probability of fixation) to the value it would have in the absence of selection. In our model, this amounts to saying that altruism is favored whenever  $\mathbb{E}[\bar{X}] > v$  ( $v$  is plotted as a horizontal dashed line in figure 1). Some of our conclusions change if we switch to this qualitative measure of evolutionary success: Under the Moran Birth-Death and Wright-Fisher life-cycles, population viscosity does not promote the evolution of altruism – actually, these two life-cycles cannot ever promote altruistic behavior for any regular population structure (Taylor et al., 2011), whichever the probability of mutation (Débarre, 2017). However, under a Moran Death-Birth life-cycle, altruism can be favored only at intermediate emigration probabilities (figure 1(a)): increased emigration can still favor the evolution of altruism under this qualitative criterion.

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

To explain how the frequency of altruists can increase with the emigration probability  $m$ , let us go back to the decomposition of the expected frequency of al-



truists in the population  $\mathbb{E}[\bar{X}]$  into different terms (eq. (5)). For all the life-cycles that we consider, the direct effect of helping others ( $\beta_D$ ) decreases with emigration  $m$ , while the direct effect of the cost of helping ( $\gamma_D$ ) does not change with  $m$ . If we (erroneously) considered only direct effects, we would conclude that the expected proportion of altruists decreases with the emigration probability  $m$ , because an increase in  $m$  reduces the probability that two interactants (two deme-mates in this model) are identical by descent. But this explanation ignores indirect, competitive, effects. In the three life-cycles that we considered,  $\beta_I = \gamma_I$ , so the overall indirect effects are given by  $-(b - c)\beta_I$ . Hence, any increase of  $\mathbb{E}[\bar{X}]$  with  $m$  is driven by  $\beta_I$ . Indirect effects correspond to competition: helping another individual indirectly harms others – even the individual who is providing help is indirectly harmed. This competition can be diluted by increasing the emigration probability  $m$ . The overall effect of  $m$  on the expected frequency of altruists depends on the balance between direct and indirect effects. This balance depends on the fidelity of parent-offspring transmission ( $\mu$ ), 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

387 considered any fidelity of transmission (any  $\mu$  between 0 and 1) and population  
388 size. However, most models considering subdivided populations assume nearly  
389 perfect strategy transmission ( $\mu \rightarrow 0$ ) and infinite population sizes (number of  
390 demes  $N_D \rightarrow \infty$ ). The order in which these limits are taken matters, *i.e.*, one  
391 needs to specify how small  $\mu$ , but also  $\omega$ , are compared to the inverse size of  
392 the population. This remark complements findings by Sample & Allen (2017),  
393 who highlighted the quantitative differences between different orders of weak  
394 selection and large population limits.

### 395 **Imperfect transmission and Rebellious Children**

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

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

### 409 **Interactions and dispersal graphs**

410 Compared to graphs classically used in evolutionary graph theory (*e.g.*, regular  
411 random graphs, grids), the island model is particular because the interaction  
412 graph and the dispersal graph are different: interactions take place only within

413 demes ( $e_{\text{out}} = 0$ ), while offspring can disperse out of their natal deme ( $d_{\text{out}} > 0$ ).  
414 One may wonder whether our result depends on this difference between the two  
415 graphs. Figure S4 shows that the result still holds when the dispersal and inter-  
416 action graphs are the same. In this figure indeed, we let a proportion  $m$  (equal  
417 to the dispersal probability) of interactions occur outside of the deme where the  
418 individuals live, and set  $d_{\text{self}}$ , the probability of self replacement, equal to 0, so  
419 that the dispersal and interactions graphs are the same.

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

421 This work also raises the question of what would happen if dispersal (*e.g.*, the  
422 emigration probability  $m$ ) could evolve as well. Recent work on the topic has  
423 shown that under some conditions disruptive selection could take place, lead-  
424 ing to a polymorphism between sessile altruists and mobile defectors (Parvinen,  
425 2013; Mullan et al., 2017). The assumptions of these studies however differ from  
426 ours in important ways, in that they consider continuous traits and use an adap-  
427 tive dynamics framework, where, notably, mutations are assumed to be very  
428 rare. It remains to be investigated how non-rare and potentially large mutations  
429 would affect their result.

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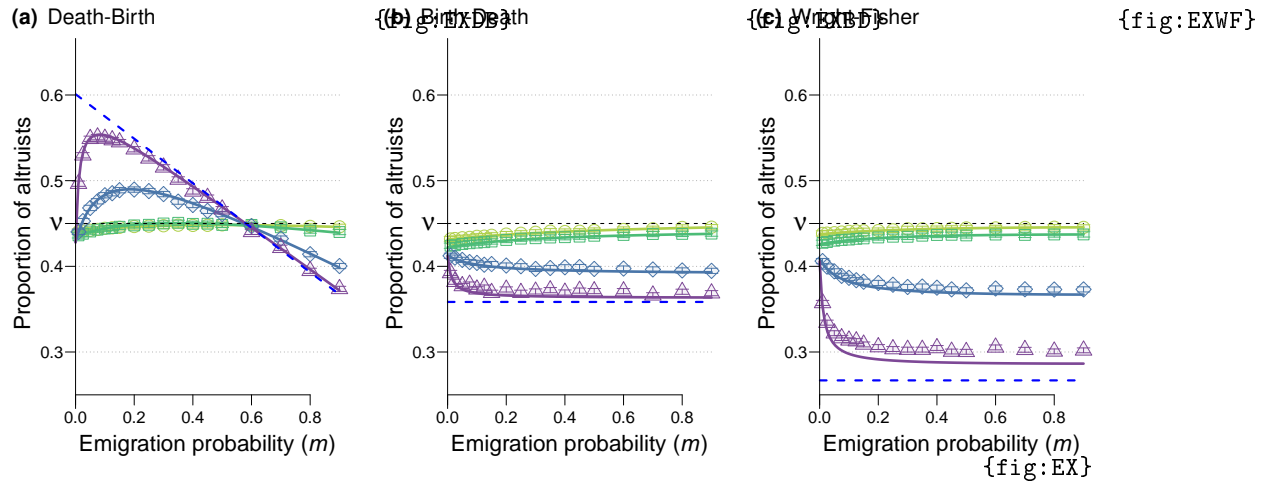
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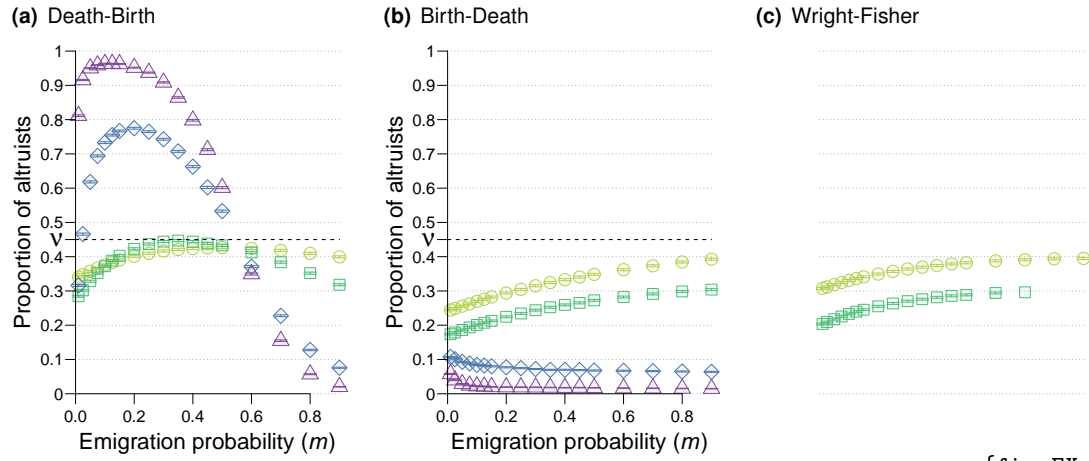
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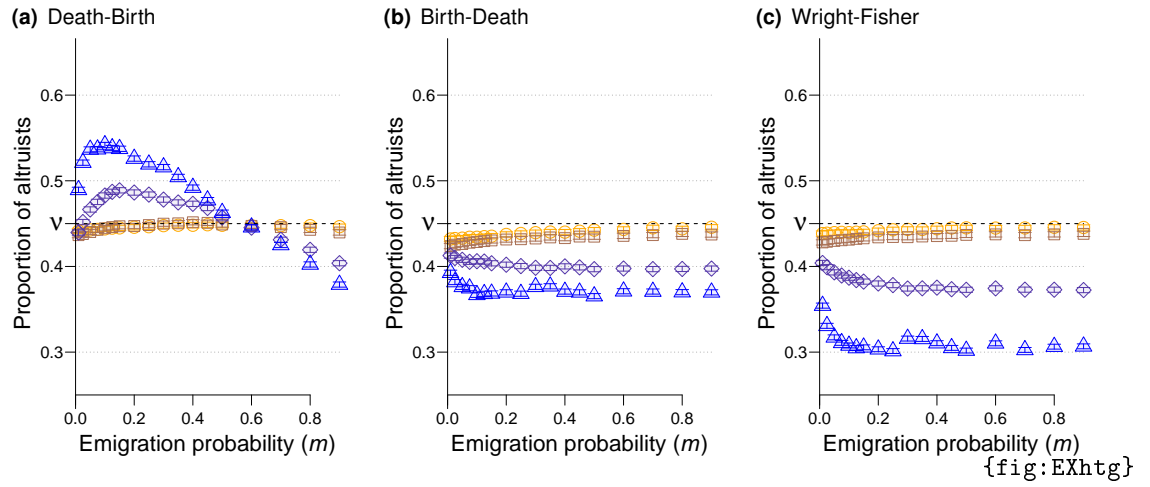
**Figure 1:** Expected proportion of altruists under weak selection, as a function of the emigration probability  $m$ , for different mutation values ( $\mu = 0.001$  (blue, dots),  $0.01$  (purple, squares),  $0.1$  (brown, diamonds),  $0.25$  (orange, triangles); the dashed blue lines correspond to  $\mu = 0$ ) 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.



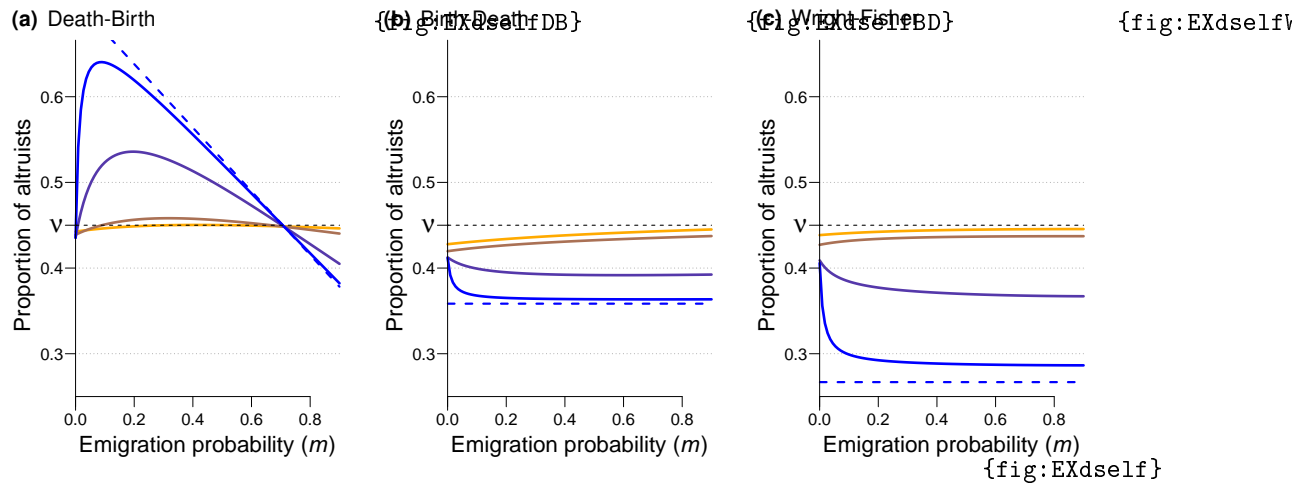
{fig:EXstrongsel}

**Figure S1:** Equivalent of figure 1 (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 1 (increasing mutation probabilities from blue dots to orange triangles).

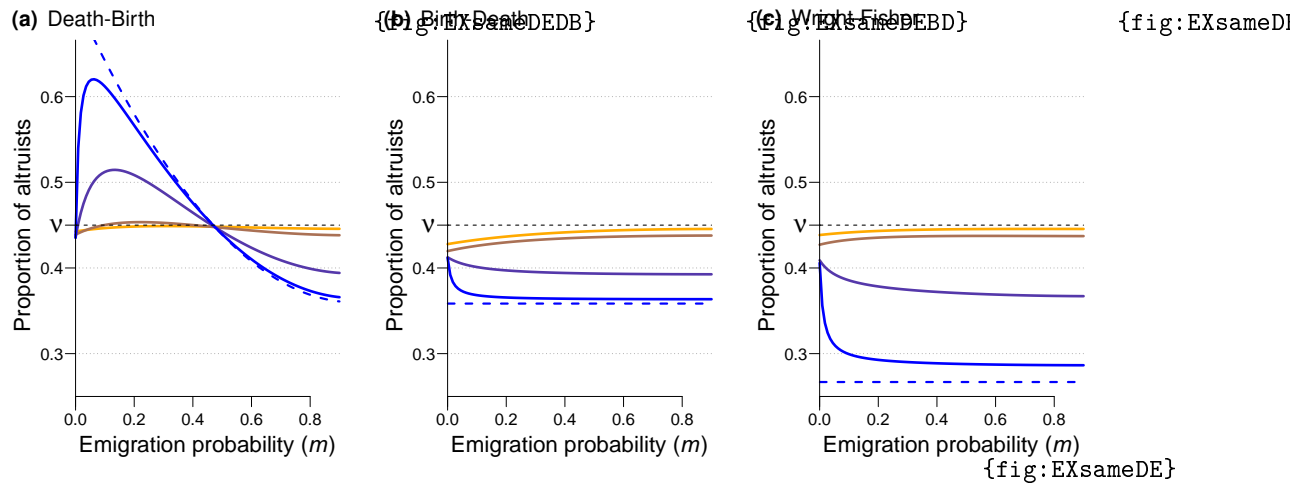




**Figure S2:** Equivalent of figure 1 (simulations only) but with a heterogeneous population structure: deme sizes range from 1 to 5 individuals per deme, the average deme size is 4 as in figure 1; all other parameters and legend are identical to those of figure 1.



**Figure S3:** Equivalent of figure 1 (analysis only), with no self-replacement ( $d_{ii} = d_{\text{self}} = 0$  for all sites).



**Figure S4:** Equivalent of figure 1 (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*.

524

## 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

544 the same probability of dying and the same probability of having successful off-  
 545 spring (*i.e.*, of having offspring that become adults at the next time step), so that  
 546

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

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

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

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

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

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

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

565 Now, we use the assumption of weak selection ( $\delta \ll 1$ ) and consider the first-  
 566 order expansion of eq. (A.3) for  $\delta$  close to 0. First, we note that in the absence  
 567 of selection ( $\delta = 0$ ), the population is at a mutation-drift balance; the expected  
 568 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  
 569 mutation bias parameter). Secondly, we note that for all the life-cycles that we  
 570 consider, the total number of deaths in the population during one time step does  
 571 not depend on population composition (it is exactly 1 death for the Moran life-  
 572 cycles, and exactly  $N$  for the Wright-Fisher life-cycle), so that  $\sum_{i,j=1}^N B_{ij}$  does not  
 573 depend on  $\delta$ . Consequently, the last term of eq. (A.3) vanishes when we take its  
 574 derivative with respect to  $\delta$ , for the life-cycles that we consider.

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

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

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

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

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

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

581 Now, we use a first time the law of total probabilities, taking individual pheno-  
582 types  $\phi_k$  are intermediate variables:

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

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

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

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

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

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

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

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

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

594 We can also replace the  $P$  terms by

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

595 In Appendix B.1, we will see that recursions on  $P_{ij}$  reveal that  $Q_{ij}$  can be inter-  
596 preted as a probability of identity by descent, *i.e.*, the probability that the individ-  
597 uals at sites  $i$  and  $j$  have a common ancestor and that no mutation has occurred  
598 on either lineage since the ancestor. Eq. (A.10) becomes

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

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

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

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

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

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

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

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

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

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

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

607 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  
608  $D_i$  terms by their formulas for each life-cycle (given in table S2).

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

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

{eq:dWBD}

### Moran Birth-Death

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

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

{eq:dWDB}

### Moran Death-Birth

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

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

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

{eq:dWWF}

### Wright-Fisher

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

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

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



## B Probabilities of identity by descent

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

{sec:app:IBD}

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 ( $\omega = 0$ ).

#### 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  $i$  it was the case at time  $t$  and neither site was replaced by a non-altruist (first term in eq. (B.20)), or  $ij$  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)):

$$\begin{aligned} \mathbb{E}[X_i X_j(t+1) | X(t) = \mathbf{X}] = & X_i X_j \left( 1 - \sum_{k=1}^N \frac{1}{N} (d_{ki} + d_{kj}) ((1 - X_k)(1 - \mu) + \mu(1 - \nu)) \right) \\ & + X_i(1 - X_j) \sum_{k=1}^N \frac{1}{N} d_{kj} (X_k(1 - \mu) + \mu\nu) \\ & + X_j(1 - X_i) \sum_{k=1}^N \frac{1}{N} d_{ki} (X_k(1 - \mu) + \mu\nu). \end{aligned} \quad (\text{B.20}) \quad \{\text{eq:app:PijM1}\}$$

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

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

while  $P_{ii} = \nu$ .

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

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

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

### 637 B.1.2 Wright-Fisher model

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

$$\begin{aligned} \mathbb{E}[X_i X_j(t+1) | X(t) = \mathbf{X}] = & \sum_{k, \ell=1}^N d_{ki} d_{\ell j} \left( X_k X_\ell (1 - \mu + \mu v)^2 \right. \\ & + (X_k(1 - X_\ell) + (1 - X_k)X_\ell) (1 - \mu + \mu v)(\mu v) \\ & \left. + (1 - X_k)(1 - X_\ell)(\mu v)^2 \right) \end{aligned} \quad (\text{B.23}) \quad \{\text{eq:app:PijWF1}\}$$

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

644 Taking the expectation and simplifying, we obtain

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

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

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

646 Again,  $Q_{ij}$  corresponds to a probability of identity by descent: the individuals at  
647 sites  $i$  and  $j$  are identical by descent if their parents were and if neither mutated  
648  $((1 - \mu)^2)$ .

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

{sec:app:Qsubdiv}

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

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

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

Here, we will 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  $\tilde{d}_{i_1 i_2}$  and  $\tilde{Q}_{i_1 i_2}$ , that correspond to the dispersal probability and probability of identity by descent to a site at distances  $i_1$  and  $i_2$  in the among-demes and within-deme dimensions (e.g.,  $\tilde{d}_{i_1 i_2} = d_{j_1 j_2'}$  where  $j_1 = i_1$  and  $j_2' = i_2$ ).

Also, in this section, we distinguish between  $\tilde{d}_{\text{self}} = d_{ii}$  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

$$\tilde{Q}_{r_1 r_2} = \frac{1}{N} \sum_{q_1=0}^{N_1-1} \sum_{q_2=0}^{N_2-1} \frac{\mu \lambda'_M}{1 - (1 - \mu) \tilde{D}_{q_1 q_2}} \exp\left(i \frac{2\pi q_1 r_1}{N_1}\right) \exp\left(i \frac{2\pi q_2 r_2}{N_2}\right) \quad (\text{B.27a}) \quad \{\text{eq:app:Q2DM}\}$$

with

$$\tilde{D}_{q_1 q_2} = \sum_{\ell_1=0}^{N_1-1} \sum_{\ell_2=0}^{N_2-1} \tilde{d}_{\ell_1 \ell_2} \exp\left(-i \frac{2\pi q_1 \ell_1}{N_1}\right) \exp\left(-i \frac{2\pi q_2 \ell_2}{N_2}\right), \quad (\text{B.27b}) \quad \{\text{eq:app:D2D}\}$$

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

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

672 ( $\delta_q$  is equal to 1 when  $q$  is equal to 0 modulo the relevant dimension, and to 0  
 673 otherwise). So for the three types of distances that we need to consider (distance  
 674 0, distance to another deme-mate, distance to individual in another deme), and  
 675 with  $N_1 = N_D$  and  $N_2 = n$ , we obtain

{eq:app:Dsystem}

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

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

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

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

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

{eq:app:Q2DMsol}

677 In particular,

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

{eq:app:Q2D1}

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

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

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

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

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

{eq:QM}

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

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

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

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

### 691 B.3 Wright-Fisher

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

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

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

$$\begin{aligned}
 \tilde{Q}_{r_1 r_2} &= \frac{1}{N} \left[ \frac{\mu \lambda'_{WF}}{1 - (1 - \mu)^2 (\tilde{\mathcal{D}}_0)^2} + \sum_{q_2=1}^{N_2-1} \frac{\mu \lambda'_{WF}}{1 - (1 - \mu)^2 (\tilde{\mathcal{D}}_{q_2})^2} \exp\left(-i \frac{2\pi q_2 r_2}{N_2}\right) \right. \\
 &\quad + \sum_{q_1=1}^{N_1-1} \frac{\mu \lambda'_{WF}}{1 - (1 - \mu)^2 (\tilde{\mathcal{D}}_{q_1})^2} \exp\left(-i \frac{2\pi q_1 r_1}{N_1}\right) \\
 &\quad \left. + \sum_{q_1=1}^{N_1-1} \sum_{q_2=1}^{N_2-1} \frac{\mu \lambda'_{WF}}{1 - (1 - \mu)^2 (\tilde{\mathcal{D}}_{q_1})^2} \exp\left(-i \frac{2\pi q_1 r_1}{N_1}\right) \exp\left(-i \frac{2\pi q_2 r_2}{N_2}\right) \right] \\
 &= \frac{\mu \lambda'_{WF}}{N} \left[ \frac{1}{1 - (1 - \mu)^2} + \frac{1}{1 - (1 - \mu)^2 (d_{\text{self}} - d_{\text{in}})^2} (\delta_{q_2} N_2 - 1) \right. \\
 &\quad + \frac{1}{1 - (1 - \mu)^2 (1 - m - \frac{m}{d-1})^2} (\delta_{q_1} N_1 - 1) \\
 &\quad \left. + \frac{1}{1 - (1 - \mu)^2 (d_{\text{self}} - d_{\text{in}})^2} (\delta_{q_1} N_1 - 1) (\delta_{q_2} N_2 - 1) \right] \\
 &= \frac{\mu \lambda'_{WF}}{N} \left[ \frac{1}{1 - (1 - \mu)^2} + \frac{1}{1 - (1 - \mu)^2 (d_{\text{self}} - d_{\text{in}})^2} (\delta_{q_2} N_2 - 1) \delta_{q_1} N_1 \right. \\
 &\quad \left. + \frac{1}{1 - (1 - \mu)^2 (1 - m - \frac{m}{d-1})^2} (\delta_{q_1} N_1 - 1) \right]. \tag{B.34} \quad \{\text{eq:app:Q2DWFsol}\}
 \end{aligned}$$

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

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

Then from eq. (B.34) we deduce

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

and

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

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

{eq:QWF}

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

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

with

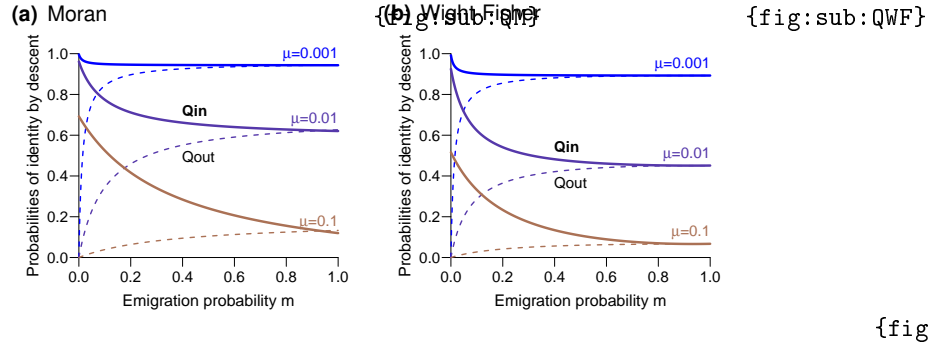
$$M_1 = \frac{N_D - 1}{1 - \frac{(1 - \mu)^2 (N_D (1 - m) - 1)^2}{(N_D - 1)^2}} \text{ and } M_2 = \frac{1}{1 - (1 - \mu)^2}.$$

(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.