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**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)

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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.

## 1 Introduction

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

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

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 muta-  
tion 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 in-  
teractions 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 individ-  
ual'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 prob-  
ability of moving from site  $i$  to site  $j$ , we have

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

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 also define

$$W_i := (1 - \mu) B_i + 1 - D_i, \quad (2) \quad \{\text{eq: def W}\}$$

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

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

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

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

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

## 161 2.2 Methods

### 162 2.2.1 Analytical part

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

170 The formula involves quantities that can be identified as neutral probabili-  
171 ties of identity by descent  $Q_{ij}$ , *i.e.*, the probability that individuals living at site  $i$   
172 and  $j$  share a common ancestor and that no mutation occurred on either lineage



173 since that ancestor, in a model with no selection ( $\omega = 0$ ; this is the “mutation def-  
174 inition” of identity by descent (Rousset & Billiard, 2000).)

175 These neutral probabilities of identity by descent depend on the chosen life-  
176 cycle, and are also computed by taking the long-term expectation of conditional  
177 expectations after one time step (see Appendix B.1 and B.2).

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

### 181 2.2.2 Stochastic simulations

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

188 All scripts are available at

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

## 190 3 Results

### 191 3.1 Expected frequencies of altruists for each life-cycle

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

$$\mathbb{E}[\bar{X}] \approx v + \frac{\delta}{\mu B^*} v(1-v)(1-Q_{\text{out}}) \times \left[ \underbrace{\frac{\partial W}{\partial f_{\bullet}}(-c) + \frac{\partial W}{\partial f_{\text{in}}}b}_{-C} + \underbrace{\left( \frac{\partial W}{\partial f_{\bullet}}b + (n-1)\frac{\partial W}{\partial f_{\text{in}}}(-c) + (n-2)\frac{\partial W}{\partial f_{\text{in}}}b \right)}_B \underbrace{\frac{Q_{\text{in}} - Q_{\text{out}}}{1 - Q_{\text{out}}}}_R \right], \quad (3) \quad \{\text{eq:EXapprox}\}$$

194 with  $W$  as defined in eq. (2). (Calculations leading to eq. (3) are presented in Ap-  
195 pendix A.)

196 The mutation bias  $v$  corresponds to the expected proportion of altruists in the  
197 population in the absence of selection (*i.e.*, when  $\delta = 0$ );  $\delta$  is the parameter that  
198 scales the effects of interactions between individuals, which is assumed to be  
199 small. The  $-\mathcal{C}$  term groups the effects corresponding to the effects of a change  
200 of a focal individual's phenotype on its own fitness (with the fitness definition  
201 given in eq. (2).) The  $\mathcal{B}$  term corresponds to effects on an individual's fitness of  
202 the change of a deme-mate's phenotype. It is multiplied by  $R$ , which is related-  
203 ness. Also note the overall  $(1 - Q_{\text{out}})$  factor. All of these terms depend on the  
204 chosen life-cycle, and on parameters such as the mutation probability  $\mu$  and the  
205 emigration probability  $m$ .

206 We now present the values of these different terms for the three life-cycles  
207 under study. The equations are obtained by replacing the derivatives of  $W$  by  
208 their specific formulas for each life-cycle, which are presented in Appendix A.2.  
209 The formulas of probabilities of identity by descent are more complicated, so  
210 not substituted, but they can be found in eq. (B.32) and eq. (B.36). The addi-  
211 tional superscripts correspond to the life-cycles (WF: Wright-Fisher, M: Moran  
212 (either), DB: Moran Death-Birth, BD: Moran Birth-Death.) Finally, for each life-  
213 cycle, we further decompose the  $-\mathcal{C}$  and  $\mathcal{B}$  terms into primary (subscript P) and  
214 secondary (subscript S) effects . Primary effects correspond to unmediated, di-  
215 rect consequences of interactions (they are included in  $\frac{\partial W}{\partial f_i}$ ), while secondary ef-  
216 fects correspond to consequences of interactions mediated by other individuals,  
217 competition. Primary and secondary effects correspond to what was called “di-  
218 rect” and “indirect” effects, respectively, in Débarre et al. (2014); Débarre (2017),  
219 but the terminology was updated for more consistency with other authors. All

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220 equations are of the form

$$\mathbb{E}[\bar{X}] \approx v + \frac{\delta}{\mu} v(1-v)(1-Q_{\text{out}}) \left[ \underbrace{\begin{pmatrix} -C_P \\ -C_S \end{pmatrix}}_{-C} + \underbrace{\begin{pmatrix} B_P \\ +B_S \end{pmatrix}}_B \underbrace{\frac{Q_{\text{in}} - Q_{\text{out}}}{1 - Q_{\text{out}}}}_R \right]. \quad (4) \quad \{\text{eq:EXgeneric}\}$$

221 **Moran Birth-Death** With the Birth-Death life-cycle, eq. (3) becomes

$$\mathbb{E}[\bar{X}] \approx v + \frac{\delta}{\mu} v(1-v)(1-Q_{\text{out}}^M) \times \left[ \underbrace{\begin{pmatrix} (1-\mu)(-c) \\ +(b-c)\left(\frac{\mu}{N} - \frac{1-m}{n}\right) \end{pmatrix}}_{-C^{\text{BD}}} + \underbrace{\begin{pmatrix} (1-\mu)b \\ +(b-c)(n-1)\left(\frac{\mu}{N} - \frac{1-m}{n}\right) \end{pmatrix}}_{B^{\text{BD}}} \underbrace{\frac{Q_{\text{in}}^M - Q_{\text{out}}^M}{1 - Q_{\text{out}}^M}}_{R^M} \right], \quad (5) \quad \{\text{eq:EXBD}\}$$

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

227 **Moran Death-Birth** With the Death-Birth life-cycle, eq. (3) becomes

$$\mathbb{E}[\bar{X}] \approx v + \frac{\delta}{\mu} v(1-v)(1-Q_{\text{out}}^M) \times \left[ \underbrace{\begin{pmatrix} (1-\mu)(-c) \\ -(b-c)(1-\mu)\left(\frac{(1-m)^2}{n} + \frac{m^2}{N-n}\right) \end{pmatrix}}_{-C^{\text{DB}}} + \underbrace{\begin{pmatrix} (1-\mu)b \\ -(b-c)(n-1)(1-\mu)\left(\frac{(1-m)^2}{n} + \frac{m^2}{N-n}\right) \end{pmatrix}}_{B^{\text{DB}}} \underbrace{\frac{Q_{\text{in}}^M - Q_{\text{out}}^M}{1 - Q_{\text{out}}^M}}_{R^M} \right], \quad (6) \quad \{\text{eq:EXDB}\}$$

228 With this life-cycle, Death occurs first, and the probability of dying is indepen-  
 229 dent from the state of the population (since we assume that social interactions  
 230 affect fecundity ). We can therefore factor a  $1 - \mu$  term in all terms. The primary  
 231 effects (first lines in the parentheses) remain the same as with the Birth-Death

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life-cycle. However, the Death-Birth life-cycle leads to different secondary ef-  
fects compared to the Birth-Death life-cycle: competition occurs at a different  
scale (Grafen & Archetti, 2008). Finally, with this life-cycle as we defined it, the  
probabilities of identity by descent are the same as with the Birth-Death model.

### Wright-Fisher

$$\mathbb{E}[\bar{X}] \approx v + \frac{\delta}{\mu} v(1-v)(1-Q_{\text{out}}^{\text{WF}}) \times$$

$$\left[ \underbrace{\left( \frac{(1-\mu)(-c)}{-(b-c)(1-\mu)\left(\frac{(1-m)^2}{n} + \frac{m^2}{N-n}\right)} \right)}_{-C^{\text{WF}}} + \underbrace{\left( \frac{(1-\mu)b}{-(b-c)(n-1)(1-\mu)\left(\frac{(1-m)^2}{n} + \frac{m^2}{N-n}\right)} \right)}_{B^{\text{WF}}} \right] \underbrace{\frac{Q_{\text{in}}^{\text{WF}} - Q_{\text{out}}^{\text{WF}}}{1 - Q_{\text{out}}^{\text{WF}}}}_{R^{\text{WF}}},$$

(7) {eq:EXWF}

The only – but important – different between eq. (7) and eq. (6) is the value of the  
probabilities of identity by descent, because the number of individuals that are  
updated at each time step differs.

### 3.2 Primary effects

Let us first focus on primary effects, shown on the first lines in the parentheses  
in eq. (5)–eq. (7). They are the same for the three life-cycles that we consider,  
and they do not depend on the emigration probability  $m$ . At the same time, as  
shown on figure 1, the relatedness terms  $R^{\text{M}}$  and  $R^{\text{WF}}$  decrease with  $m$  (keep-  
ing  $m < \frac{N_D-1}{N_D}$ .) Consequently, ignoring secondary effects, we would conclude  
that even with imperfect strategy transmission ( $\mu > 0$ ), increasing the emigra-  
tion probability  $m$  decreases the expected frequency of altruists in the popula-  
tion (as our intuition may suggest already.) However, secondary effects play a  
role as well.

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ure R

### 249 3.3 Changes with the emigration probability $m$

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

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

#### 259 3.3.1 Moran Birth-Death

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

$$\mu_c^{\text{BD}} = 1 - \frac{b - c + \sqrt{(b - c)(4bN^2 + b - c)}}{2bN} \quad (8) \quad \{\text{eq:mucBD}\}$$

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

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

### 271 3.3.2 Moran Death-Birth

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

$$\mu_c^{\text{DB}} = \begin{cases} \frac{(n+1)c - b}{(2n-1)b - (n-1)c} & \text{if } b < c(n+1), \\ 0 & \text{otherwise.} \end{cases} \quad (9) \quad \{\text{eq:mucDB}\}$$

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

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

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

### 290 3.3.3 Wright-Fisher

291 The expected frequency of altruists in the population reaches an extremum at  
 292 the highest admissible emigration value  $m = \frac{N_D-1}{N_D}$ . This extremum is a maxi-  
 293 mum when the mutation probability is higher than a threshold value  $\mu_c^{\text{WF}}$  given

294 by

$$\mu_c^{\text{WF}} = 1 - \sqrt{1 - \frac{c}{b}}, \quad (10)$$

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

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

### 298 3.4 Interpreting the effect of $m$ on $\mathbb{E}[\bar{X}]$

299 The result, that higher emigration probabilities can actually favor altruistic be-  
300 havior, may seem surprising, even though it is confirmed by simulations. The  
301 result may appear counterintuitive is because explanations for the effect of pop-  
302 ulation viscosity on the evolution of altruism often focus on primary effects. The  
303 role played by secondary effects is harder to grasp. To better understand the role  
304 played by the mutation probability  $\mu$ , we now focus on a qualitative condition  
305 for the evolution of altruism and on the Death-Birth life-cycle (having made sure  
306 that  $\mathcal{B}^{\text{DB}} > 0$ ):

$$\mathbb{E}[\bar{X}] > v \Leftrightarrow R^{\text{M}} > \frac{\mathcal{C}^{\text{DB}}}{\mathcal{B}^{\text{DB}}}. \quad (11)$$

307 With this life-cycle, the  $\mathcal{C}^{\text{DB}}/\mathcal{B}^{\text{DB}}$  ratio does not change with the mutation  
308 probability  $\mu$ , but it decreases with the emigration probability  $m$  ( $0 < m < 1 -$   
309  $1/N_D$ ). This decrease of the  $\mathcal{C}^{\text{DB}}/\mathcal{B}^{\text{DB}}$  ratio is due to secondary effects (com-  
310 petition) diminishing as emigration increases. Relatedness, on the other hand,  
311 decreases with both  $\mu$  and  $m$  (see figure 3(a)).

312 When the emigration probability  $m$  is vanishingly small,  $\lim_{m \rightarrow 0} R^{\text{M}} \leq \lim_{m \rightarrow 0} \frac{\mathcal{C}^{\text{DB}}}{\mathcal{B}^{\text{DB}}}$ ,  
313 the two only being equal when  $\mu = 0$ . Hence, it is only when strategy transmis-  
314 sion is perfect that condition eq. (11) is satisfied for vanishingly low  $m$ . Then,  
315 as  $m$  increases, the  $\frac{\mathcal{C}^{\text{DB}}}{\mathcal{B}^{\text{DB}}}$  ratio and relatedness  $R$  do not decrease with the same  
316 slope. Provided the mutation probability  $\mu$  is not too high, *i.e.*, that  $R$  initially is  
317 not too low already, there can be a range of emigration values  $m$  such that condi-

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tion (11) is satisfied (*i.e.*, the  $R$  curve is higher than the  $\mathcal{C}/\mathcal{B}$  curve in figure 3(a)).

### 3.5 Relaxing key assumptions

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

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

For the Moran model, it may seem odd that an offspring can replace its own parent (which can occur since  $d_{ii} \neq 0$ ). Figure S3, plotted with dispersal probabilities preventing immediate replacement of one's own parent (for all sites  $i$ ,  $d_{ii} = d_{\text{self}} = 0$ ;  $d_{\text{in}} = (1 - m)/(n - 1)$  for two different sites in the same deme,  $d_{\text{out}}$  remaining unchanged), confirms that this does affect our conclusions.

Finally, 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  $N_D \rightarrow \infty$ ).



## 340 4 Discussion

341 remove direct/indirect effects

342 discuss effects of  $n$  and  $N_D$

### 343 The expected frequency of altruists in a subdivided population can in- 344 crease with the probability of emigration

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

### 356 Quantitative vs. qualitative measures

357 Often, evolutionary success is measured qualitatively, by comparing a quantity  
358 (an expected frequency, or, in models with no mutation, a probability of fixation)  
359 to the value it would have in the absence of selection. In our model, this amounts  
360 to saying that altruism is favored whenever  $\mathbb{E}[\bar{X}] > v$  ( $v$  is plotted as a horizon-  
361 tal dashed line in figure 2). Some of our conclusions change if we switch to this  
362 qualitative measure of evolutionary success: Under the Moran Birth-Death and  
363 Wright-Fisher life-cycles, population viscosity does not promote the evolution of  
364 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 (figure 2(a)), altruism can be favored only at intermediate emigration probabilities: increased emigration can still favor the evolution of altruism under this qualitative criterion (see figure 3(b).)

### The result is due to secondary effects

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

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

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

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

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

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

#### 413 **Imperfect transmission and Rebellious Children**

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

418 Our model is mechanistic; relatedness  $r$  necessarily depends on the mutation  
419 probability  $\mu$ , because probabilities of identity by descent do.

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

## 427 Interactions and dispersal graphs

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

## 439 Coevolution of dispersal and social behavior

440 This work also raises the question of what would happen if dispersal (*e.g.*, the  
441 emigration probability  $m$ ) could evolve as well. Recent work on the topic has  
442 shown that under some conditions disruptive selection could take place, lead-  
443 ing to a polymorphism between sessile altruists and mobile defectors (Parvinen,

444 2013; Mullan et al., 2017). The assumptions of these studies however differ from  
445 ours in important ways, in that they consider continuous traits and use an adap-  
446 tive dynamics framework, where, notably, mutations are assumed to be very  
447 rare. It remains to be investigated how non-rare and potentially large mutations  
448 would affect their result.

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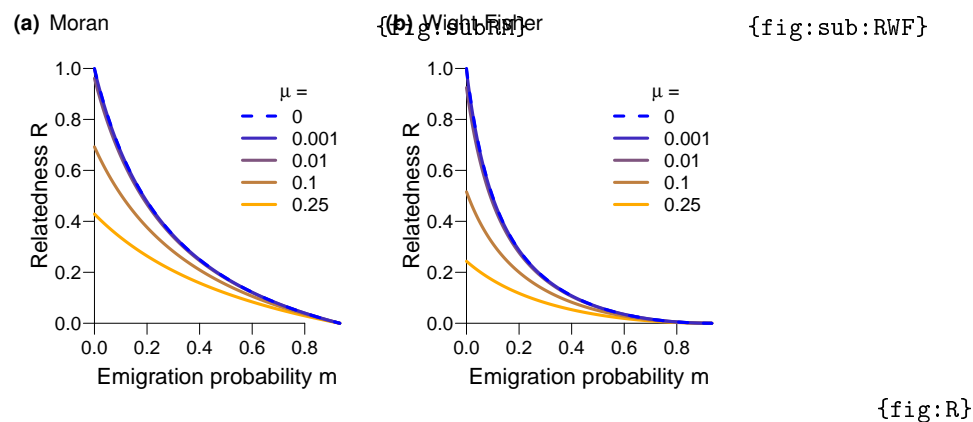
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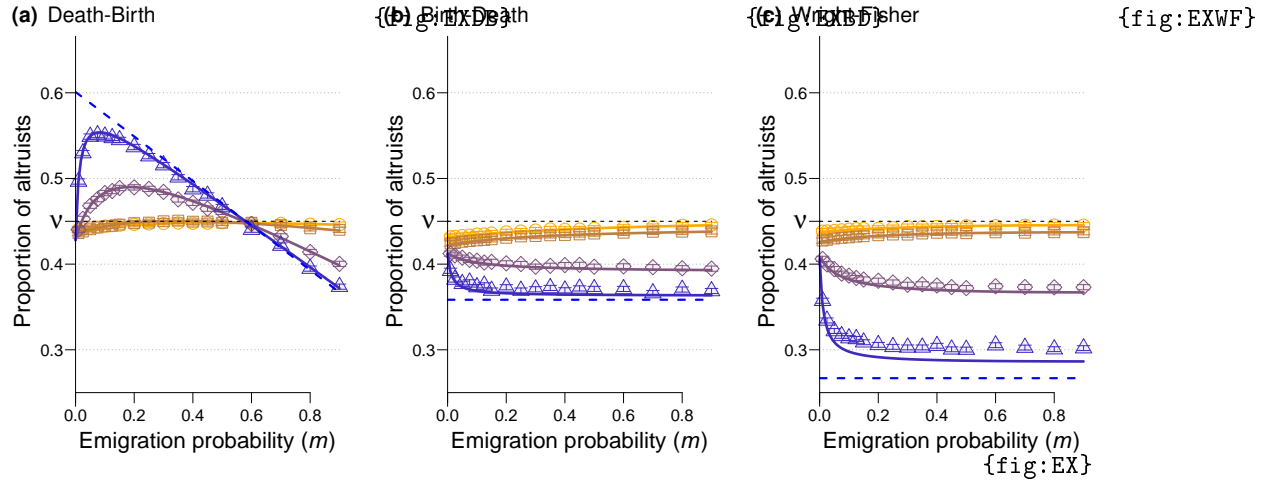
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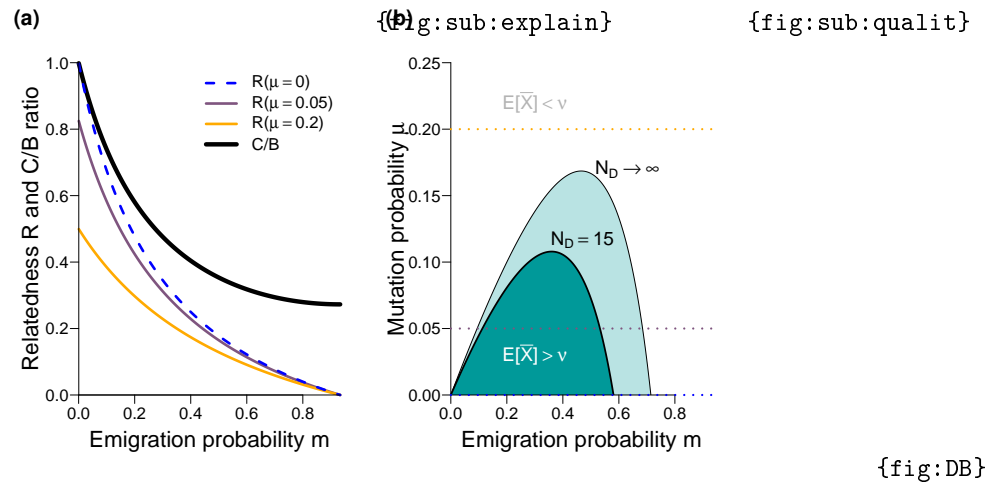




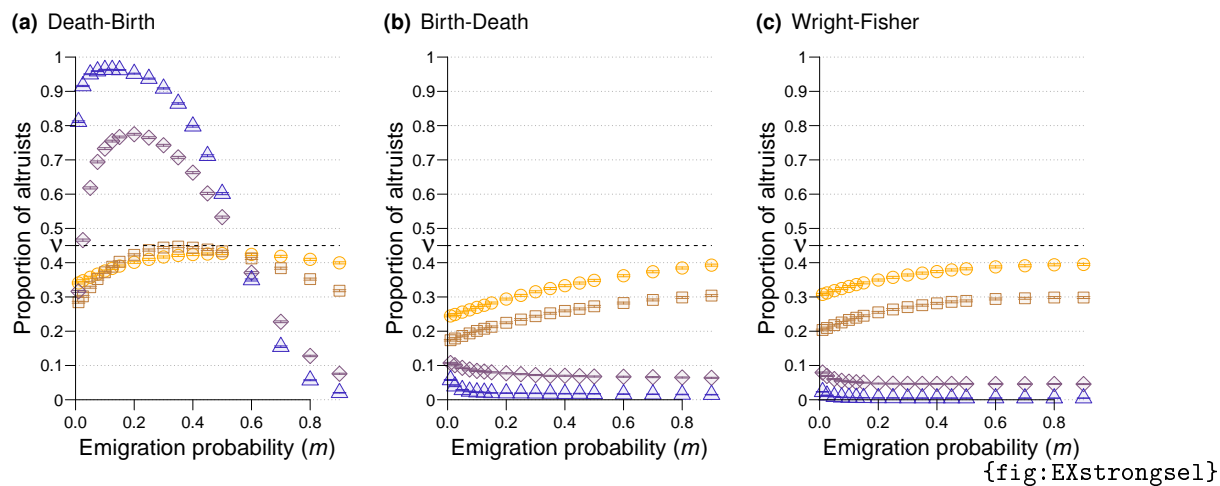
**Figure 1:** Within-deme relatedness of pairs of individuals, as a function of the emigration probability  $m$ , for different values of the mutation probability  $\mu$  (0, 0.001, 0.01, 0.1, 0.25), and for the two types of life-cycles ((a): Moran, (b): Wright-Fisher). Other parameters:  $n = 4$  individuals per deme,  $N_D = 15$  demes.



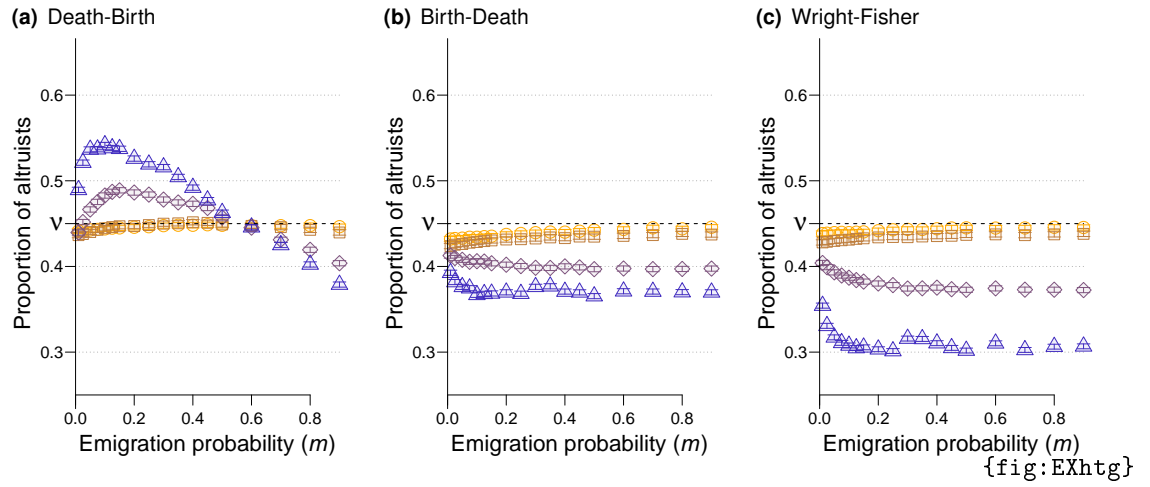
**Figure 2:** Expected proportion of altruists under weak selection, as a function of the emigration probability  $m$ , for different mutation values ( $\mu = 0.001$  (blue, dots),  $0.01$  (purple, squares),  $0.1$  (brown, diamonds),  $0.25$  (orange, triangles); the dashed blue lines correspond to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



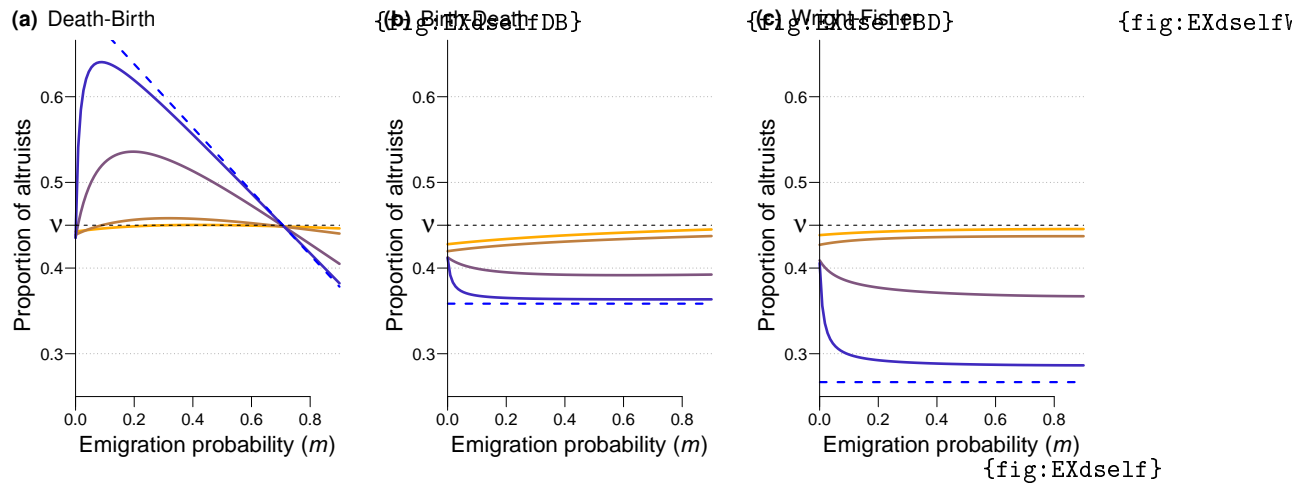
**Figure 3:** Understanding the effect of emigration  $m$  on whether altruism is favored in the Death-Birth life-cycle. (a) Comparison of relatedness  $R$  (thick red curve) and  $C/B$  ratio (thin curves) for different values of the mutation probability  $\mu$  (same color code as previously). (b)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



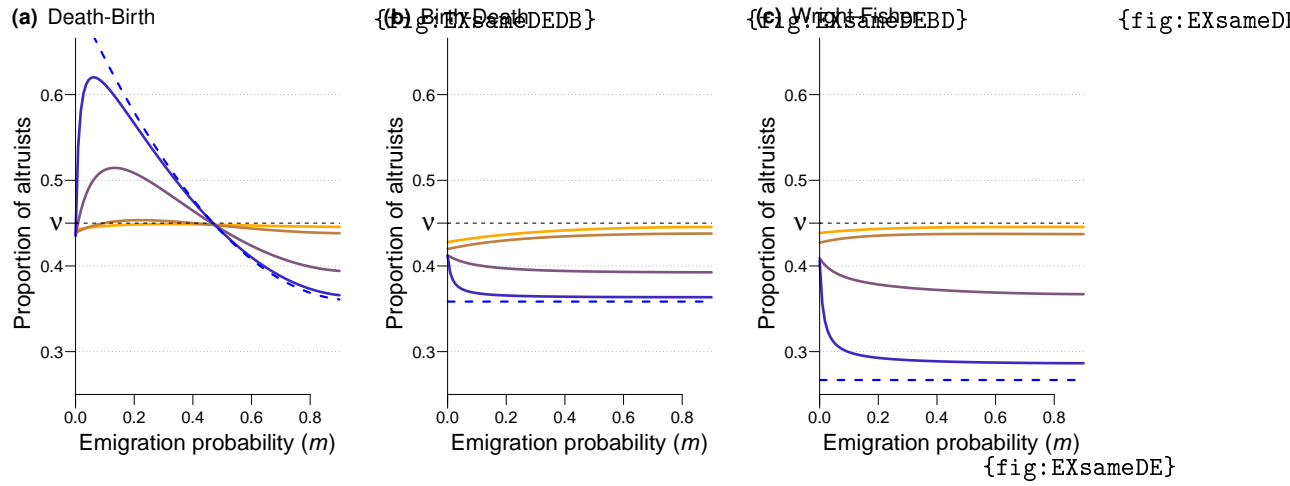
**Figure S1:** Equivalent of figure 2 (simulations only) but with strong selection ( $\omega = 0.1$ ); please note the change of scale on the vertical axis. All other parameters and legends are identical to those of figure 2 (increasing mutation probabilities from blue dots to orange triangles).



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



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



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

$b$	Fecundity benefit given by altruists to social interactants
$c$	Fecundity cost paid by altruists
$d_{ij}$	Dispersal probability from site $i$ to site $j$
$e_{ij}$	Interaction probability from site $i$ to site $j$
$n$	Deme size
$N_D$	Number of demes
$N$	Total population size ( $N = N_D n$ )
$m$	Emigration probability
$Q_{ij}$	(Long-term) Probability of identity by descent of individuals at sites $i$ and $j$
$X_i$	Indicator variable, equal to 1 if site $i$ is occupied by an altruist, to 0 otherwise (r.v.)
$\bar{X}$	Frequency of altruists in the population (r.v.)
$\beta$	Term associated to the benefits $b$
$\gamma$	Term associated to the costs $c$
$\mu$	Mutation probability
$\nu$	Mutation bias: probability that mutant is altruist
$\omega$	Parameter scaling the relative effect of social interactions on fecundity
D	Subscript corresponding to direct/primary effects
I	Subscript corresponding to indirect/secondary effects
in	Subscript used when $i \neq j$ and the two sites are in the same deme
out	Subscript used when the two sites $i$ and $j$ are in different demes
self	Subscript used when $i = j$
BD	Superscript corresponding to the Moran Birth-Death model
DB	Superscript corresponding to the Moran Death-Birth model
M	Superscript corresponding to a Moran model
WF	Superscript corresponding to the Wright-Fisher model

{tab:symbols}

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

548

## Appendix

### A Expected frequency of altruists

{sec:app:EX}

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

{sec:app:generic}

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

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

{tab:BD}

**Table S2:** Formulas of  $B_{ji}$  and  $D_i$  for each of the life-cycles that we consider;  $f_i$  (shorthand notation for  $f_i(X, \delta)$ ) is the fecundity of the individual living at site  $i$ , and  $d_{ji}$  is a dispersal probability, given in eq. (1).

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

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

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



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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

618 We can also replace the  $P$  terms by

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

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

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

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

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

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

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

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

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

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

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

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

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

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

632 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

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

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

{sec:app:dW}

635 Using the formulas presented in table S2, and the definition of  $W = W_i$  given in  
636 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

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

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

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

{eq:dWWF}

### Wright-Fisher

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

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

638 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 ( $1 - \mu$ ).

### 662 B.1.2 Wright-Fisher model

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

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

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

669 Taking the expectation and simplifying, we obtain

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

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

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

671 Again,  $Q_{ij}$  corresponds to a probability of identity by descent: the individuals at  
672 sites  $i$  and  $j$  are identical by descent if their parents were and if neither mutated  
673  $((1 - \mu)^2)$ .

## 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  $N_2 = n$ :

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

697 ( $\delta_q$  is equal to 1 when  $q$  is equal to 0 modulo the relevant dimension, and to 0  
 698 otherwise). So for the three types of distances that we need to consider (distance  
 699 0, distance to another deme-mate, distance to individual in another deme), and  
 700 with  $N_1 = N_D$  and  $N_2 = n$ , we obtain

{eq:app:Dsystem}

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

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

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

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

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

{eq:app:Q2DMsol}

702 In particular,

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

{eq:app:Q2D1}

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

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



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

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

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

{eq:QM}

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

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

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

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

### 716 B.2.2 Wright-Fisher

717 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

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

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:

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

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

with

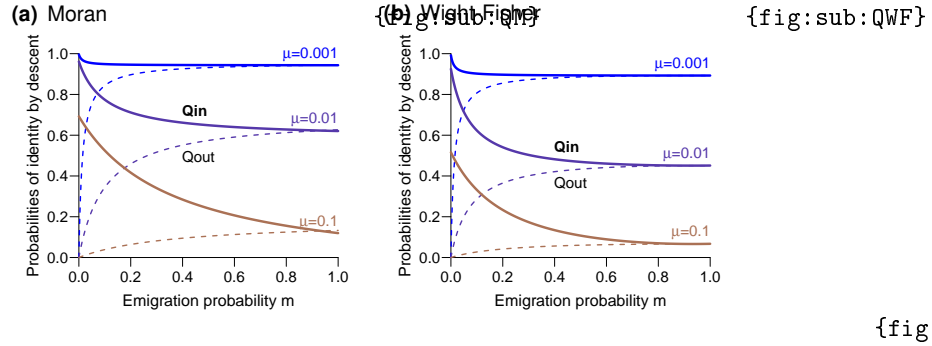
$$M_1 = \frac{N_D - 1}{1 - \frac{(1 - \mu)^2 (N_D (1 - m) - 1)^2}{(N_D - 1)^2}} \text{ and } M_2 = \frac{1}{1 - (1 - \mu)^2}.$$

(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.