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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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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 Mullan & 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 μ as a mutation
124 probability. With probability μ , offspring do not inherit their strategy from their

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

An individual of type X_k expresses a social phenotype $\phi_k = \delta X_k$, where δ 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 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 δ 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

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

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 $\delta = 0$); δ is the parameter that
 198 scales the effects of interactions between individuals, which is assumed to be
 199 small. The $-C$ 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 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 μ and the
 205 emigration probability m .

206 For each life-cycle, we will further decompose the $-C$ and B terms into pri-
 207 mary and secondary effects TODO CITE Gardner . Primary effects correspond
 208 to unmediated, direct consequences of interactions (they are included in $\frac{\partial W}{\partial f_{\bullet}}$),
 209 while secondary effects correspond to consequences of interactions mediated
 210 by other individuals, competition.

211 We now present the values of these different terms for the three life-cycles

212 under study.

Moran Birth-Death

$$\mathbb{E}[\bar{X}] \approx \nu + \frac{\delta}{\mu} \nu (1 - \nu) (1 - Q_{\text{out}}^M) \times \left[\underbrace{\left(\frac{(1 - \mu)(-c)}{+(b - c) \left(\frac{\mu}{N} - \frac{1 - m}{n} \right)} \right)}_{-C^{\text{BD}}} + \underbrace{\left(\frac{(1 - \mu)b}{+(b - c)(n - 1) \left(\frac{\mu}{N} - \frac{1 - m}{n} \right)} \right)}_{B^{\text{BD}}} \underbrace{\left(\frac{Q_{\text{in}}^M - Q_{\text{out}}^M}{1 - Q_{\text{out}}^M} \right)}_{R^M} \right], \quad (4) \quad \{\text{eq: EXBD}\}$$

Moran Death-Birth

$$\mathbb{E}[\bar{X}] \approx \nu + \frac{\delta}{\mu} \nu (1 - \nu) (1 - Q_{\text{out}}^M) \times \left[\underbrace{\left(\frac{(1 - \mu)(-c)}{-(b - c)(1 - \mu) \left(\frac{(1 - m)^2}{n} + \frac{m^2}{N - n} \right)} \right)}_{-C^{\text{DB}}} + \underbrace{\left(\frac{(1 - \mu)b}{-(b - c)(n - 1) \left(\frac{(1 - m)^2}{n} + \frac{m^2}{N - n} \right)} \right)}_{B^{\text{DB}}} \underbrace{\left(\frac{Q_{\text{in}}^M - Q_{\text{out}}^M}{1 - Q_{\text{out}}^M} \right)}_{R^M} \right], \quad (5) \quad \{\text{eq: EXDB}\}$$

Wright-Fisher

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

213 3.1.1 Direct effects

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

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

$$\beta_D^{BD} = \beta_D^{DB} = (1 - \mu) Q_{in}^M, \quad (7a) \quad \{eq:bBDD\}$$

$$\beta_D^{WF} = (1 - \mu) Q_{in}^{WF}; \quad (7b) \quad \{eq:bWFD\}$$

$$\gamma_D^{BD} = \gamma_D^{DB} = \gamma_D^{WF} = 1 - \mu. \quad (7c) \quad \{eq:cBDD\}$$

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

225 As seen in the previous section, Q_{in}^M and Q_{in}^{WF} decrease with the emigration
 226 probability m (actually only until $m = \frac{d-1}{d}$ for the latter). Consequently, the mag-
 227 nitude of the direct (beneficial) effects of benefits b provided by altruists (β_D)
 228 decreases when the emigration probability m increases, while the direct (detrimental)
 229 effects (γ_D) due to the direct cost of altruism c are constant. As a result,
 230 if we only considered direct effects, we would conclude that more emigration m
 231 is detrimental to the evolution of altruistic behaviour. However, there are also
 232 indirect effects at play.

233 3.1.2 Indirect effects

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

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

$$\begin{aligned}\beta_I^{\text{BD}} &= (1 - m) \left(\frac{n-1}{n} Q_{\text{in}}^{\text{M}} + \frac{1}{n} \right) + m Q_{\text{out}}^{\text{M}} - \mu \frac{1 + (n-1)Q_{\text{in}}^{\text{M}} + n(d-1)Q_{\text{out}}^{\text{M}}}{nd} \\ &= \gamma_I^{\text{BD}}.\end{aligned}\tag{8a} \quad \{\text{eq:bBDI}\}$$

244 (Calculation details are presented in Appendix A.)

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

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

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

259 descent to it. We obtain

$$\begin{aligned}
 \beta_I^{\text{DB}} &= (1 - \mu) \left[\left(\frac{1}{n} + \frac{(n-1)Q_{\text{in}}^{\text{M}}}{n} \right) \left((1-m)^2 + \frac{m^2}{(d-1)} \right) \right. \\
 &\quad \left. + Q_{\text{out}}^{\text{M}} \left(2m(1-m) + (d-2) \frac{m^2}{(d-1)} \right) \right] \quad (8b) \quad \{\text{eq: bDBI}\} \\
 &= \gamma_I^{\text{DB}}
 \end{aligned}$$

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

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

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

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

281 3.2 Identifying threshold values of the mutation probability μ

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

288 3.2.1 Moran Birth-Death

289 For this life-cycle, we find that the expected frequency of altruists $\mathbb{E}[\bar{X}]$ is a mono-
 290 tonic function of the emigration probability m ; the direction of the change de-
 291 pends on the value of the mutation probability μ compared to a threshold value
 292 μ_c^{BD} . When $\mu < \mu_c^{\text{BD}}$, $\mathbb{E}[\bar{X}]$ decreases with m , while when $\mu > \mu_c^{\text{BD}}$, $\mathbb{E}[\bar{X}]$ increases
 293 with m . The critical value μ_c^{BD} is given by

$$\mu_c^{\text{BD}} = 1 - \frac{b - c + \sqrt{(b - c)(4b(nd)^2 + b - c)}}{2bnd} \quad (9) \quad \{\text{eq:mucBD}\}$$

294 This result is illustrated in figure 1(b); with the parameters of the figure, $\mu_c^{\text{BD}} \approx$
 295 0.026.

296 3.2.2 Moran Death-Birth

297 The relationship between $\mathbb{E}[\bar{X}]$ and m is a bit more complicated for this life-
 298 cycle. For simplicity, we concentrate on what happens starting from low emi-
 299 gration probabilities (*i.e.*, the sign of the slope of $\mathbb{E}[\bar{X}]$ as a function of m when
 300 $m \rightarrow 0$). If the benefits b provided by altruists are relatively low ($b < c(n + 1)$),
 301 $\mathbb{E}[\bar{X}]$ initially increases with m provided the mutation probability μ is greater
 302 than a threshold value μ_c^{DB} given in eq. (9) below; otherwise, when the benefits
 303 are high enough, $\mathbb{E}[\bar{X}]$ initially increases with m for any value of μ . Combining

304 these results, we write

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

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

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

310 3.2.3 Wright-Fisher

311 The expected frequency of altruists in the population reaches an extremum when
 312 $m = m_c^{\text{WF}} = \frac{d-1}{d}$. This extremum is a maximum when the mutation probability
 313 is higher than a threshold value μ_c^{WF} given by

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

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

315 3.3 Relaxing key assumptions

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

322 To relax the assumption of equal deme sizes, we randomly drew deme sizes
 323 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_{out} remaining unchanged), confirms that this does affect our conclusions.

4 Discussion

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

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

349 of population viscosity. Often however, evolutionary success is measured quali-
 350 tatively, by comparing a quantity (an expected frequency, or, in models with no
 351 mutation, a probability of fixation) to the value it would have in the absence of
 352 selection. In our model, this amounts to saying that altruism is favored whenever
 353 $\mathbb{E}[\bar{X}] > \nu$ (ν is plotted as a horizontal dashed line in figure 1). Some of our con-
 354 clusions change if we switch to this qualitative measure of evolutionary success:
 355 Under the Moran Birth-Death and Wright-Fisher life-cycles, population viscosity
 356 does not promote the evolution of altruism – actually, these two life-cycles can-
 357 not ever promote altruistic behavior for any regular population structure (Taylor
 358 et al., 2011), whichever the probability of mutation (Débarre, 2017). However,
 359 under a Moran Death-Birth life-cycle, altruism can be favored only at interme-
 360 diate emigration probabilities (figure 1(a)): increased emigration can still favor
 361 the evolution of altruism under this qualitative criterion.

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

363 To explain how the frequency of altruists can increase with the emigration prob-
 364 ability m , let us go back to the decomposition of the expected frequency of al-
 365 truists in the population $\mathbb{E}[\bar{X}]$ into different terms (eq. (3)). For all the life-cycles
 366 that we consider, the direct effect of helping others (β_D) decreases with emigra-
 367 tion m , while the direct effect of the cost of helping (γ_D) does not change with
 368 m . If we (erroneously) considered only direct effects, we would conclude that
 369 the expected proportion of altruists decreases with the emigration probability
 370 m , because an increase in m reduces the probability that two interactants (two
 371 deme-mates in this model) are identical by descent. But this explanation ignores
 372 indirect, competitive, effects. In the three life-cycles that we considered, $\beta_I = \gamma_I$,
 373 so the overall indirect effects are given by $-(b - c)\beta_I$. Hence, any increase of
 374 $\mathbb{E}[\bar{X}]$ with m is driven by β_I . Indirect effects correspond to competition: helping
 375 another individual indirectly harms others – even the individual who is provid-

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

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

How small is small and how large is large?

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

400 **Imperfect transmission and Rebellious Children**

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

407 Mutation was also previously included in models investigating the mainte-
408 nance of cooperative microorganisms in the presence of cheaters (Brockhurst
409 et al., 2007; Frank, 2010). In both of these models however, only loss-of-function
410 mutation was considered, which corresponds to setting the mutation bias at
411 $\nu = 0$ in our model. This means that the all-cheaters state is absorbing; no matter
412 how favored cooperators may otherwise be, in the long run, a finite population
413 will only consist of cheaters.

414 **Interactions and dispersal graphs**

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

425 **Coevolution of dispersal and social behavior**

426 This work also raises the question of what would happen if dispersal (*e.g.*, the
427 emigration probability m) could evolve as well. Recent work on the topic has
428 shown that under some conditions disruptive selection could take place, lead-
429 ing to a polymorphism between sessile altruists and mobile defectors (Parvinen,
430 2013; Mullon et al., 2017). The assumptions of these studies however differ from
431 ours in important ways, in that they consider continuous traits and use an adap-
432 tive dynamics framework, where, notably, mutations are assumed to be very
433 rare. It remains to be investigated how non-rare and potentially large mutations
434 would affect their result.

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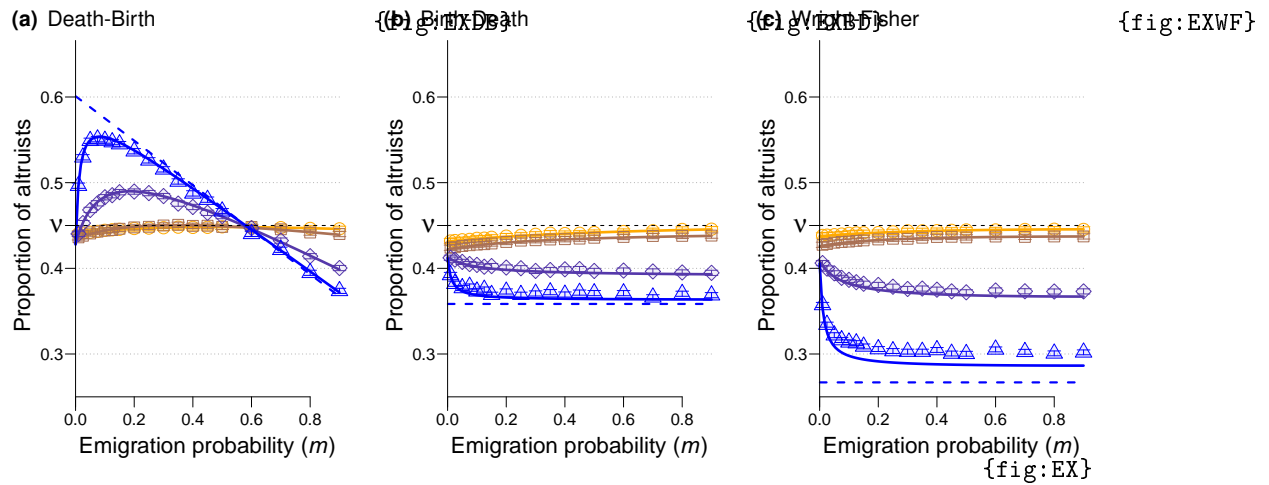


Figure 1: Expected proportion of altruists under weak selection, as a function of the emigration probability m , for different mutation values ($\mu = 0.001$ (blue, dots), 0.01 (purple, squares), 0.1 (brown, diamonds), 0.25 (orange, triangles); the dashed blue lines correspond to $\mu = 0$) and different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

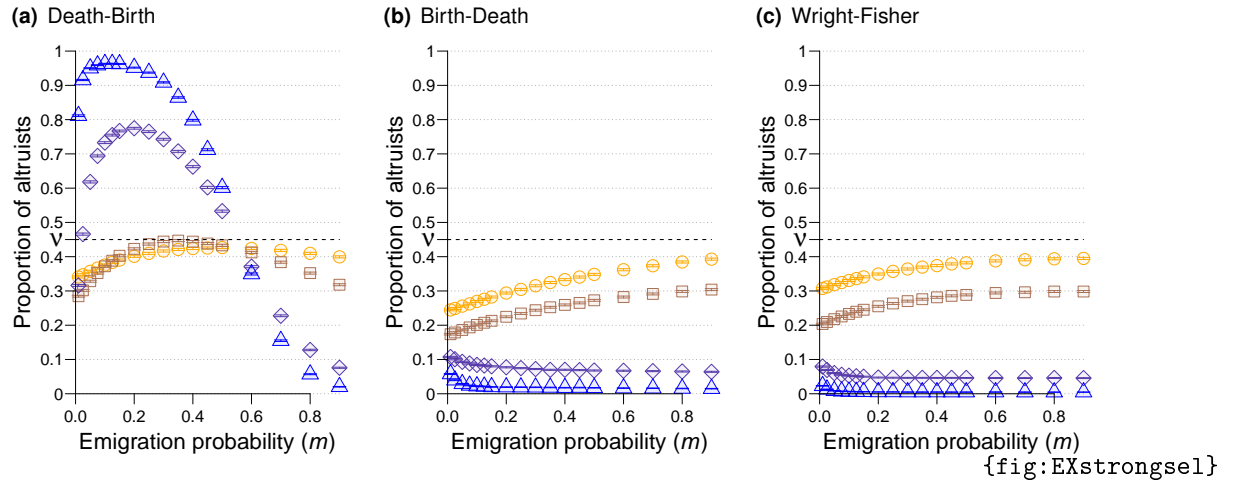


Figure S1: Equivalent of figure 1 (simulations only) but with strong selection ($\omega = 0.1$); please note the change of scale on the vertical axis. All other parameters and legends are identical to those of figure 1 (increasing mutation probabilities from blue dots to orange triangles).

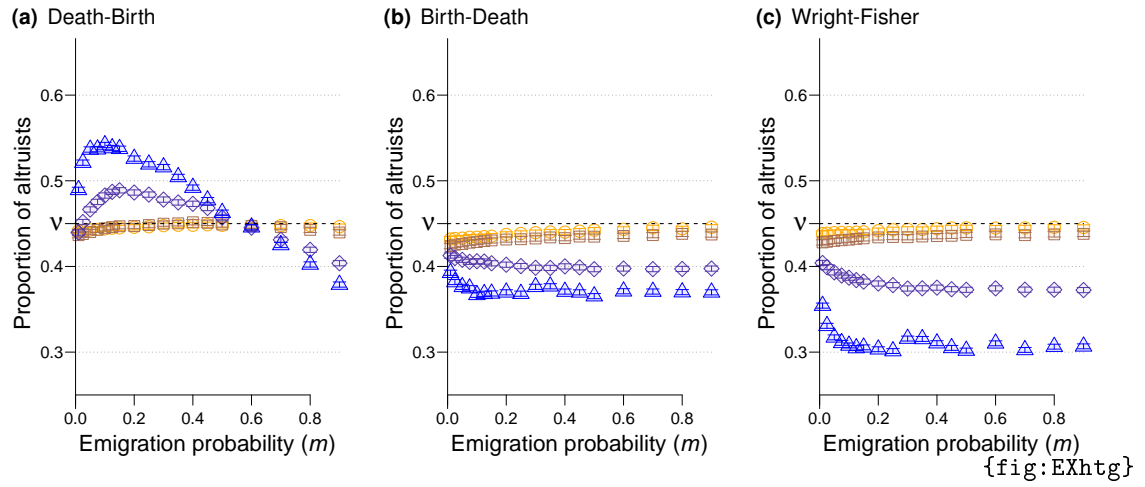


Figure S2: Equivalent of figure 1 (simulations only) but with a heterogeneous population structure: deme sizes range from 1 to 5 individuals per deme, the average deme size is 4 as in figure 1; all other parameters and legend are identical to those of figure 1.

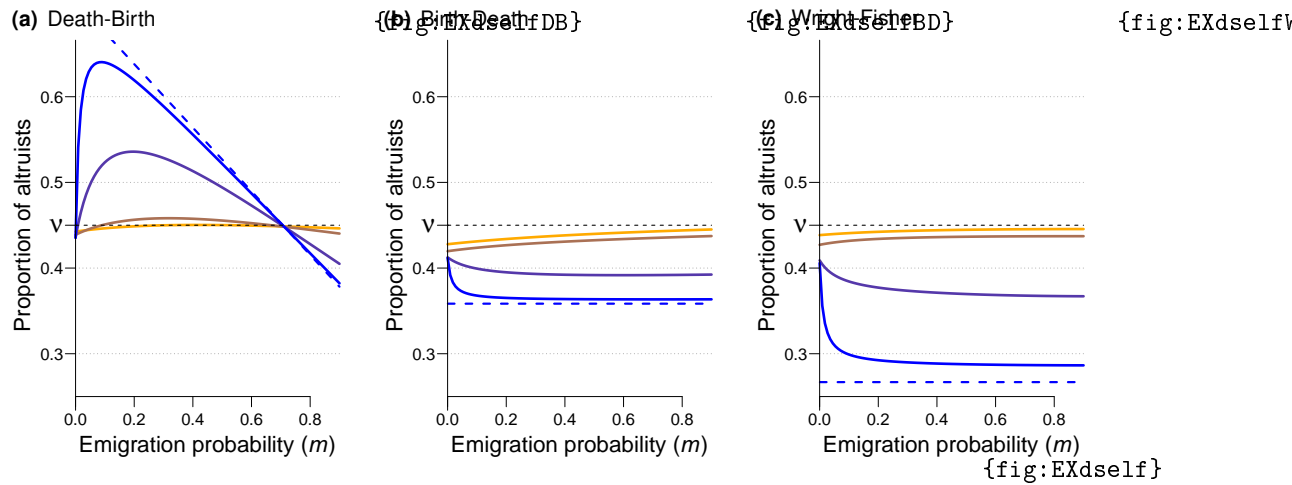


Figure S3: Equivalent of figure 1 (analysis only), with no self-replacement ($d_{ii} = d_{\text{self}} = 0$ for all sites).

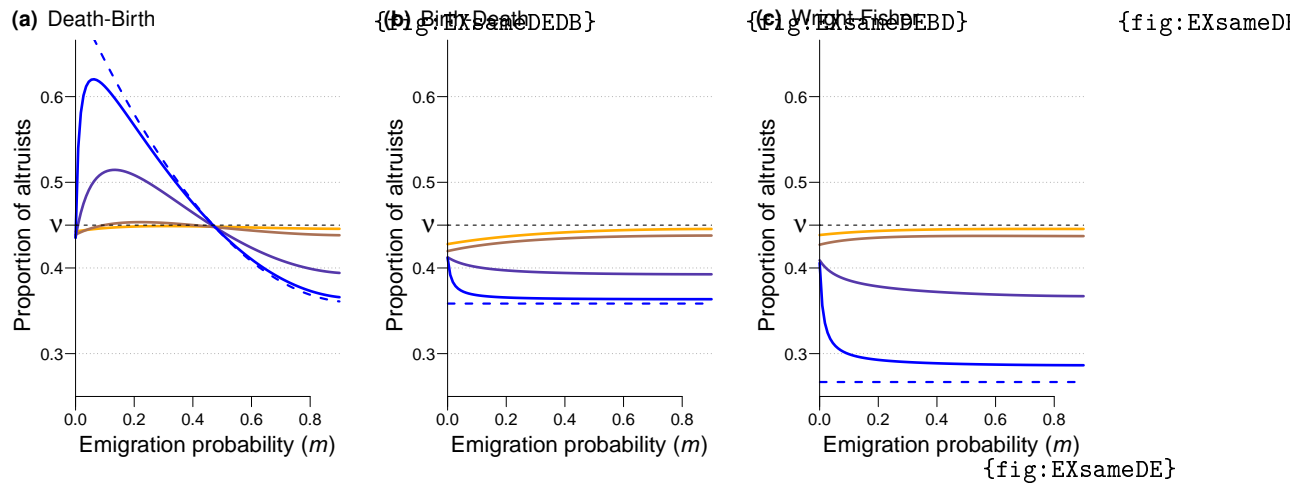


Figure S4: Equivalent of figure 1 (analysis only), with equal dispersal and interaction graphs (*i.e.*, no self-replacement [$d_{ii} = d_{\text{self}} = 0$ for all sites], and a proportion m of the interactions occurring outside of the home deme).

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.)
β	Term associated to the benefits b
γ	Term associated to the costs c
μ	Mutation probability
ν	Mutation bias: probability that mutant is altruist
ω	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*.

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

549 the same probability of dying and the same probability of having successful off-
 550 spring (*i.e.*, of having offspring that become adults at the next time step), so that
 551

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

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

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

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

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

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

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

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

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

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

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

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

583 a measure of fitness counting offspring only when they are unmutated. With
 584 this, using the expectation notation, and denoting by $\mathbb{E}_0[\cdot]$ expectations under
 585 $\delta = 0$, we can rewrite and reorganize eq. (A.4) as

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

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

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

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

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

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

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

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

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

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

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

599 We can also replace the P terms by

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

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

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

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

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

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

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

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

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

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

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

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

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

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

613 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

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

615 A.2 Derivatives for the specific life-cycles

616 Using the formulas presented in table S2, and the definition of $W = W_i$ given in
617 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

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

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

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

{eq:dWWF}

Wright-Fisher

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

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

619 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 ($1 - \mu$).

643 B.1.2 Wright-Fisher model

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

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

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

650 Taking the expectation and simplifying, we obtain

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

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

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

652 Again, Q_{ij} corresponds to a probability of identity by descent: the individuals at
653 sites i and j are identical by descent if their parents were and if neither mutated
654 $((1 - \mu)^2)$.

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_{in} and Q_{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 (ℓ_1, ℓ_2) , where ℓ_1 is the index of the deme ($1 \leq \ell_1 \leq N_D$) and ℓ_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_{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 λ'_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 $N_2 = n$:

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

678 (δ_q is equal to 1 when q is equal to 0 modulo the relevant dimension, and to 0
 679 otherwise). So for the three types of distances that we need to consider (distance
 680 0, distance to another deme-mate, distance to individual in another deme), and
 681 with $N_1 = N_D$ and $N_2 = n$, we obtain

{eq:app:Dsystem}

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

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

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

682 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}

683 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}

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

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

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

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

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

{eq:QM}

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

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

The probability that two different deme-mates are identical by descent, Q_{in}^M , decreases monotonically with the emigration probability m , while Q_{out}^M monotonically increases with m (see figure S5(a)).

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

B.3 Wright-Fisher

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

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

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

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

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

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

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

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

703 and

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

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

{eq:QWF}

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

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

705 with

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

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

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

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

Also, because more sites (all of them, actually) are updated at each time step, Q_{in} is lower for the Wright-Fisher updating than for a Moran updating, under which only one site is updated at each time step (compare figure S5(a) and S5(b)).

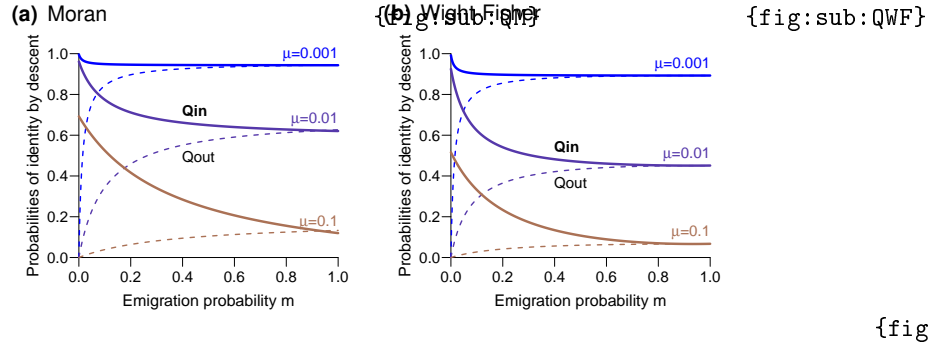


Figure S5: Probabilities of identity by descent, for two different individuals within the same deme (Q_{in} , full curves) and two individuals in different demes (Q_{out} , dashed curves), as a function of the emigration probability m , for different values of the mutation probability μ (0.001, 0.01, 0.1), and for the two types of life-cycles ((a): Moran, (b): Wright-Fisher). Other parameters: $n = 4$ individuals per deme, $N_D = 15$ demes.