

Mon titre

# 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 (1992) 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 consider three different life-cycles: Wright-Fisher, where the whole population is renewed at each time step, and two Moran life-cycles (Birth-Death and Death-Birth), where a single individual dies and is replaced at each time step.

A large number of studies on the evolution of social behavior consider simple population structures (typically, homogeneous populations *sensu* Taylor et al. (2007a)) and often also infinite population sizes (but see Allen et al., 2017, for results on any structure). These studies also make use of weak selection approximations, and commonly assume rare (*e.g.*, Leturque & Rousset, 2002; Taylor et al., 2007b; Tarnita & Taylor, 2014) or absent mutation (for models assuming infinite population sizes, or models concentrating on fixation probabilities). Often, these simplifying assumptions are a necessary step towards obtaining explicit analytical results. Although artificial, simple population structures (*e.g.*,

refs?

40 regular graphs, or subdivided populations with demes of equal sizes) help re-  
41 duce the dimensionality of the system under study, in particular when the struc-  
42 ture of the population displays symmetries such that all sites behave the same  
43 way in expectation. Weak selection approximations are crucial for disentangling  
44 spatial moments (Lion, 2016), that is, changes in global *vs.* local frequencies  
45 (though they can in some cases be relaxed, as in Mullon & Lehmann, 2014).  
46 Mutation, however, is usually ignored by classical models of inclusive fitness be-  
47 cause these models assume infinite population sizes, so that there is no need to  
48 add mechanisms that restore genetic diversity (Tarnita & Taylor, 2014). In popu-  
49 lations of finite size, this diversifying effect can be obtained thanks to mutation.

50 When strategy transmission is purely genetic, it makes sense to assume that  
51 mutation is relatively weak. A social strategy can however also be culturally  
52 transmitted from parent to offspring, in which case “rebellion” (as in Frank’s Re-  
53 bellious Child Model (Frank, 1997)) does not have to be rare. Imperfect strategy  
54 transmission can alter evolutionary dynamics, in particular in spatially struc-  
55 tured populations (see *e.g.*, Allen et al., 2012; Débarre, 2017, for graph-structured  
56 populations). Here, we want to explore the consequences of imperfect strategy  
57 transmission from parents to their offspring on the evolution of altruistic be-  
58 havior in subdivided populations. For the sake of concision, we use the word  
59 “mutation” throughout the paper, keeping in mind that strategy transmission  
60 does not have to be genetic.

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

## 2 Model and methods

### 2.1 Assumptions

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

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

Social interactions take place within each deme; each individual interacts with the  $n - 1$  other deme members. We assume that social interactions affect individual fecundity, whose baseline is set equal to 1. Each interaction with an altruist increases an individual's fecundity by  $\omega b$ ; altruists pay a fecundity cost  $\omega c$  ( $c \leq b$ ). The parameter  $\omega$  scales the relative effect of social interactions on fecundity, and is assumed to be small ( $\omega \ll 1$ ).

Denoting by  $e_{ij}$  the interaction probability between individuals living at sites  $i$  and  $j$ , we have

$$e_{ij} = \begin{cases} 0 & \text{if } i = j; \\ \frac{1}{n-1} & \text{if } i \neq j \text{ and both sites are in the same deme;} \\ 0 & \text{if the two sites are in different demes.} \end{cases} \quad (1) \quad \{\text{eq: defE}\}$$

Given our assumptions and with this notation, the fecundity of the individual living at site  $k$  is given by

$$f_k(\mathbf{X}, \omega) = 1 + \omega \left( \sum_{\ell=1}^N e_{\ell k} b X_\ell - c X_k \right). \quad (2) \quad \{\text{eq: defF}\}$$

Although our assumptions may seem restrictive: we assume that fecundity benefits are unconditional, *i.e.*, the same which ever the type of the recipient, and the fecundity effects are additive, *i.e.*, the effect of interacting with  $k$  altruists is

96  $k$  times the effect of interacting with one altruist. And yet, the same fecundities  
 97 are obtained with a generic fecundity function, after linearization, under the as-  
 98 sumption that altruists and defectors are phenotypically close (see Appendix A  
 99 for details).

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

$$d_{ij} = \begin{cases} d_{\text{in}} = \frac{1-m}{n} & \text{if both sites are in the same deme;} \\ d_{\text{out}} = \frac{m}{(N_D-1)n} & \text{if the two sites are in different demes.} \end{cases} \quad (3) \quad \{\text{eq: defD}\}$$

105 The way the population is updated from one time step to the next depends  
 106 on the chosen life-cycle (also called updating rule). We will specifically explore  
 107 three different life-cycles. At the beginning of each step of each life-cycle, all  
 108 individuals produce offspring, that can be mutated; then these juveniles move,  
 109 within the parental deme or outside of it, and land on a site. The next events  
 110 occurring during the time step depend on the life-cycle:

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

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

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

## 119 2.2 Methods

### 120 2.2.1 Analytical part

121 To derive the expected (*i.e.*, long-term) proportion of altruists in the population,  
 122 we use the toolbox presented in Débarre (2017), which is valid for any regular  
 123 population and any life-cycle. Calculation details are given in Appendix B; they  
 124 go as follows. First, we write an equation for the expected frequency of altruists  
 125 in the population at time  $t + 1$ , conditional on the composition of the population  
 126 at time  $t$ ; we then take the expectation of this quantity, for large times  $t$ . After  
 127 this, we use the assumption that selection is weak ( $\omega \ll 1$ ) and write a first order

128 expansion of the expression that we have obtained. By doing so, we let appear  
 129 quantities that can be identified as neutral probabilities of identity by descent  
 130  $Q_{ij}$ , *i.e.*, the probability that individuals living at site  $i$  and  $j$  share a common  
 131 ancestor and that no mutation occurred on either lineage since that ancestor, in  
 132 a model with no selection ( $\omega = 0$ ).

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

136 Check results with regular results

## 137 2.2.2 Stochastic simulations

138 We also ran stochastic simulations (coded in C). The simulations were run for  $10^8$   
 139 generations (one generation is one time step for the Wright-Fisher life-cycle, and  
 140  $N$  time steps for the Moran life-cycles). For each set of parameters and life-cycle,  
 141 we estimated the long-term frequency of altruists by sampling the population  
 142 every  $10^3$  generations and computing the average frequency of altruists.

143 add Code availability

# 144 3 Results

## 145 3.1 Probabilities of identity by descent

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

$$Q_{ij} = \begin{cases} 1 & \text{when } i = j; \\ Q_{\text{in}} & \text{when } i \neq j \text{ and both sites are in the same deme;} \\ Q_{\text{out}} & \text{when sites } i \text{ and } j \text{ are in different demes.} \end{cases} \quad (4)$$

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

### 153 3.1.1 Moran updating

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

$$Q_{ij}^M = \frac{1-\mu}{2} \sum_{k=1}^N (d_{kj} Q_{ki}^M + d_{ki} Q_{kj}^M). \quad (5)$$

156 Given the law of total probabilities, we first consider the site that was last up-  
157 dated (1/2 chance that it was  $j$  rather than  $i$ ); then we consider each potential  
158 parent  $k$ , weighted by the dispersal probabilities  $d_{kj}$ . Then the individuals at  
159 sites  $i$  and  $j$  are identical by descent (IBD) if  $i$  and  $j$ 's parent were IBD ( $Q_{ki}^M$ ) and  
160 if no mutation occurred ( $1-\mu$ ). Replacing the dispersal probabilities  $d_{ij}$  by their  
161 values (given in eq. (3)), we eventually obtain (see Appendix B.2 for calculation  
162 steps):

{eq:QM}

$$Q_{\text{in}}^M = \frac{(1-\mu)(m + \mu(N_D(1-m) - 1))}{(1-\mu)m(N_D\mu(n-1) + 1) + (N_D - 1)\mu(\mu(n-1) + 1)}, \quad (6a)$$

$$Q_{\text{out}}^M = \frac{(1-\mu)m}{(1-\mu)m(N_D\mu(n-1) + 1) + (N_D - 1)\mu(\mu(n-1) + 1)}. \quad (6b)$$

163 The probability that two different deme-mates are identical by descent,  $Q_{\text{in}}^M$ ,  
164 monotonically decreases with the emigration probability  $m$ , while  $Q_{\text{out}}^M$  mono-  
165 tonically increases with  $m$  (see figure 1(a)).

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

### 172 3.1.2 Wright-Fisher updating

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

$$Q_{ij}^{\text{WF}} = (1-\mu)^2 \sum_{k,\ell=1}^N d_{ki} d_{\ell j} Q_{kl}^{\text{WF}}. \quad (7)$$

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

179 Replacing the dispersal probabilities  $d_{ij}$  by their values (given in eq. (3)) and  
 180 skipping calculation steps (but see Appendix B.2 for details), we obtain: {eq: QWF}

$$Q_{\text{in}}^{\text{WF}} = \frac{-N_D + M_1 + M_2}{(n-1)N_D + M_1 + M_2}, \quad (8a)$$

$$Q_{\text{out}}^{\text{WF}} = \frac{-\frac{1}{N_D-1}M_1 + M_2}{(n-1)N_D + M_1 + M_2}, \quad (8b)$$

181 with

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

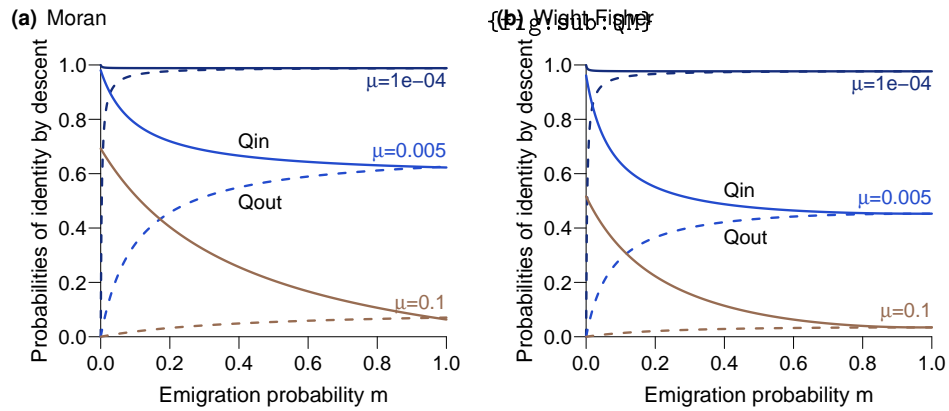
182 Here,  $Q_{\text{in}}^{\text{WF}}$  decreases until  $m = m_c^{\text{WF}} = \frac{d-1}{d}$ , then increases again, while  $Q_{\text{out}}^{\text{WF}}$   
 183 follows the opposite pattern. The threshold value  $m_c^{\text{WF}}$  corresponds to an emi-  
 184 gration probability so high that an individual's offspring is as likely to land in its  
 185 parent's deme as in any other deme (*i.e.*,  $d_{\text{in}} = d_{\text{out}}$ ).

186 The two probabilities of identity by descent go to 1 when the mutation prob-  
 187 ability  $\mu$  is very small ( $\mu \rightarrow 0$ ), except if we first assume that the number of demes  
 188 is very large ( $N_D \rightarrow \infty$ ); for instance, with this life-cycle as well,  $\lim_{N_D \rightarrow \infty} Q_{\text{out}}^{\text{WF}} =$   
 189 0.

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

Change d  
= 30





**Figure 1:** Probabilities of identity by descent, for two different individuals within the same deme ( $Q_{in}$ , full curves) and two individuals in different demes ( $Q_{out}$ , dashed curves), as a function of the emigration probability  $m$ , for different values of the mutation probability  $\mu$  ( $10^{-4}$ , 0.005, 0.1), and for the two types of life-cycles: Moran (a) and Wright-Fisher (b). Other parameters:  $n = 4$  individuals per deme,  $N_D = 30$  demes.

## 193 3.2 Expected frequencies of altruists for each life-cycle

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

$$\mathbb{E}[\bar{X}] \approx v + \omega \frac{v(1-v)}{\mu} [b(\beta_D - \beta_I) - c(\gamma_D - \gamma_I)]. \quad (9) \quad \{\text{eq:EXapprox}\}$$

196 (Calculations leading to eq. (9) are presented in the Appendix B). The muta-  
197 tion bias  $v$  corresponds to the expected proportion of altruists in the popula-  
198 tion in the absence of selection (*i.e.*, when  $\omega = 0$ );  $\omega$  is the parameter that scales  
199 the effects of interactions between individuals and is assumed to be small; the  
200 subscript  $_D$  refers to “direct” effects, and the subscript  $_I$  to “indirect” effects.  
201 These indirect effects correspond to (kin) competition: by providing a benefit  
202 to a deme-mate and thereby increasing its fecundity, a focal altruist indirectly  
203 harms others by reducing their relative fecundity ( $\beta_I$  term in eq. (9)); by having  
204 a reduced fecundity due to the cost of altruism, a focal altruist indirectly favors  
205 others by increasing their relative fecundity ( $\gamma_I$  term).

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

### 208 3.2.1 Direct effects

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

$\{\text{eq:directeffects}\}$

$$\beta_D^{BD} = \beta_D^{DB} = (1 - \mu) Q_{in}^M, \quad (10a) \quad \{\text{eq:bBDD}\}$$

$$\beta_D^{WF} = (1 - \mu) Q_{in}^{WF}; \quad (10b) \quad \{\text{eq:bWFD}\}$$

$$\gamma_D^{BD} = \gamma_D^{DB} = \gamma_D^{WF} = 1 - \mu. \quad (10c) \quad \{\text{eq:cBDD}\}$$

212 For both benefits and costs, direct effects only count when there is no muta-  
213 tion ( $1 - \mu$ ). Direct effects of benefits  $b$  (eq. (10a) and eq. (10b)) only count if  
214 the interaction takes place with an individual who is identical by descent. With  
215 the population structure that we consider, social interactions only occur within  
216 demes, so only  $Q_{in}$  is present in eq. (10a) and eq. (10b). On the other hand, the  
217 direct effect of the fecundity cost  $c$  (eq. (10c)) does not depend on the type of  
218 interactant.

219 As seen in the previous section,  $Q_{in}^M$  and  $Q_{in}^{WF}$  decrease with the emigration  
220 probability  $m$  (actually only until  $m = \frac{d-1}{d}$  for the latter). Consequently, the  
221 magnitude of the direct (beneficial) effects of benefits  $b$  provided by altruists

( $\beta_D$ ) decreases when the emigration probability  $m$  increases, while the direct (detrimental) effects ( $\gamma_D$ ) due to the direct cost of altruism  $c$  are constant. As a result, if we only consider direct effects, more emigration  $m$  is detrimental to the evolution of altruistic behaviour. But there are also indirect effects at play.

### 3.2.2 Indirect effects

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

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

$$\begin{aligned}\beta_I^{\text{BD}} &= (1 - m) \left( \frac{n-1}{n} Q_{\text{in}}^{\text{M}} + \frac{1}{n} \right) + m Q_{\text{out}}^{\text{M}} - \mu \frac{1 + (n-1) Q_{\text{in}}^{\text{M}} + n(d-1) Q_{\text{out}}^{\text{M}}}{nd} \\ &= \gamma_I^{\text{BD}}.\end{aligned}\quad (11a) \quad \{\text{eq:bBDI}\}$$

(Calculation details are presented in Appendix B.)

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

Replacing  $Q_{\text{in}}$  and  $Q_{\text{out}}$  by their formula for the Moran life-cycle (eq. (6)), we conclude that  $\beta_I^{\text{BD}} = \gamma_I^{\text{BD}}$  are decreasing functions of the emigration probability  $m$ .

Add Mathematica

### 3.2.3 Moran Death-Birth

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

$$\begin{aligned}
\beta_I^{\text{DB}} &= (1 - \mu) \left[ \left( \frac{1}{n} + \frac{(n-1)Q_{\text{in}}^{\text{M}}}{n} \right) \left( (1-m)^2 + \frac{m^2}{(d-1)} \right) \right. \\
&\quad \left. + Q_{\text{out}}^{\text{M}} \left( 2m(1-m) + (d-2) \frac{m^2}{(d-1)} \right) \right] \\
&= \gamma_I^{\text{DB}}
\end{aligned} \tag{11b} \quad \{\text{eq:bDBI}\}$$

The brackets in eq. (11b) contain a sum of two terms. The first term corresponds to two individuals from the same deme (with replacement) whose offspring either do not emigrate, or emigrate together to the same deme. The second term corresponds to individuals initially from different demes who end up in the same deme (either one of their home demes, or a third deme).

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

Replacing  $Q_{\text{in}}$  and  $Q_{\text{out}}$  by their formulas given in eq. (6), we can conclude that  $\beta_I^{\text{DB}} = \gamma_I^{\text{DB}}$  first decreases with the emigration probability  $m$ , and increases again after a threshold value  $m'_c$  (given in the appendix;  $m'_c < (d-1)/d$ ).

Mathematica

name

#### 3.2.4 Wright-Fisher

With this life-cycle, generations are synchronous and all individuals again all have the same survival probability (now equal to 0 at all sites). As a result, the formulas for  $\beta_I^{\text{WF}}$  and  $\gamma_I^{\text{WF}}$  are the same as  $\beta_I^{\text{DB}}$  and  $\gamma_I^{\text{DB}}$ , except that instead of  $Q_{\text{in}}^{\text{M}}$  and  $Q_{\text{out}}^{\text{M}}$ , we need to use  $Q_{\text{in}}^{\text{WF}}$  and  $Q_{\text{out}}^{\text{WF}}$  (given in eq. (8)). Once this is done, we see that  $\beta_I^{\text{WF}} = \gamma_I^{\text{WF}}$  first decreases with the emigration probability  $m$ , and increases again after the threshold value  $m_c^{\text{WF}} = (d-1)/d$  (which was identified previously as the emigration probability such that offspring have an equal chance of landing in their natal deme or in any other deme, *i.e.*,  $d_{\text{in}} = d_{\text{out}}$ ).

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

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

### 278 3.3.1 Moran Birth-Death

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

$$\mu_c^{\text{BD}} = 1 - \frac{b - c + \sqrt{(b - c)(4b(nd)^2 + b - c)}}{2bnd} \quad (12) \quad \{\text{eq:mucBD}\}$$

284 This result is illustrated in figure 2(b).

donner la  
valeur

### 285 3.3.2 Moran Death-Birth

286 The relationship between  $\mathbb{E}[\bar{X}]$  and  $m$  is a bit more complicated for this life-  
 287 cycle. For simplicity, we concentrate on what happens starting from low emi-  
 288 gration probabilities (*i.e.*, the sign of the slope of  $\mathbb{E}[\bar{X}]$  as a function of  $m$  when  
 289  $m \rightarrow 0$ ). If the benefits  $b$  provided by altruists are relatively low ( $b < c(n + 1)$ ),  
 290  $\mathbb{E}[\bar{X}]$  initially increases with  $m$  provided the mutation probability  $\mu$  is greater  
 291 than a threshold value  $\mu_c^{\text{DB}}$  given in eq. (13) below; otherwise, when the benefits  
 292 are high enough,  $\mathbb{E}[\bar{X}]$  initially increases with  $m$  for any value of  $\mu$ . Combining  
 293 these results, we write

$$\mu_c^{\text{DB}} = \begin{cases} \frac{b - (n + 1)c}{(n - 1)c - (2n - 1)b} & \text{if } b < c(n + 1), \\ 0 & \text{otherwise.} \end{cases} \quad (13) \quad \{\text{eq:mucDB}\}$$

294 The expected frequency of altruists  $\mathbb{E}[\bar{X}]$  reaches a maximum for an emigration  
 295 probability  $m_c^{\text{DB}}$  (whose complicated equation is in the [appendix](#)), as can be seen  
 296 in figure 2(a). The limit of this critical emigration probability  $m_c^{\text{DB}}$  when  $\mu \rightarrow 0$  is  
 297 0: we recover the result that more emigration is detrimental to the evolution of  
 298 altruism when the mutation probability is either null or vanishingly small.

do

attention  
order of  
limits

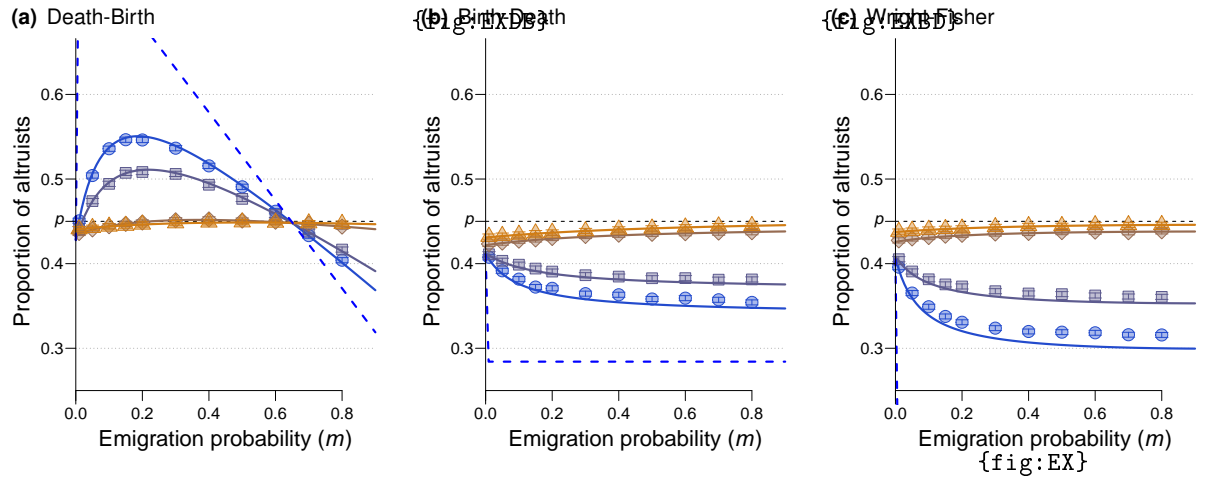
### 299 3.3.3 Wright-Fisher

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

$$\mu_c^{\text{WF}} = 1 - \sqrt{1 - \frac{c}{b}}, \quad (14)$$

303 and it is a minimum otherwise (see figure 2(c)).

appendix



**Figure 2:** Expected proportion of altruists under weak selection, as a function of the emigration probability  $m$ , for different mutation values  $\mu = 0.005$  (blue, dots),  $0.01$  (purple, squares),  $0.1$  (brown, diamonds), and  $0.25$  (orange, triangles) and 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:  $\omega = 0.005$ ,  $p = 0.45$ ,  $b = 15$ ,  $c = 1$ ,  $n = 4$  individuals per deme,  $N_D = 30$  demes.

### 3.4 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. The patterns that we identified hold when selection is strong (see figure S1, done with  $\omega = 0.1$ ), but also when the demes have different sizes. Deme sizes are drawn randomly at the beginning of a simulation; the range from 1 to 5 individuals per deme and the average size is 4 individuals as in the other figures. Here as well, the same patterns hold as those obtained with a homogeneous structure (figure S2).

For the Moran model, it may seem odd that an individual can replace its parent. We can do the same analysis assuming that for all sites  $i$ ,  $d_{ii} = d_{\text{self}} = 0$  (and so  $d_{\text{in}} = (1 - m)/(n - 1)$  for two different sites in the same deme,  $d_{\text{out}}$  remaining unchanged). Figure S3 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 (decreased emigration probability) is either neutral (Taylor, 1992) or favorable (Taylor et al., 2007a) to the evolution of altruistic behavior.

### Quantitative vs. qualitative measures

We used a quantitative measure, the expected frequency of altruists in the population ( $\mathbb{E}[\bar{X}]$ ), to explore how non-zero mutation probabilities altered the impact of population viscosity. Often however, evolutionary success is measured qualitatively, by comparing a quantity (an expected frequency, or, in models with no mutation, a probability of fixation) to the value it would have in the absence of

Cite (?)

add ref  
to fig and  
dashed  
line

338 selection. In our model, this amounts to saying that altruism is favored when-  
 339 ever  $\mathbb{E}[\bar{X}] > v$  ( $v$  is plotted as a horizontal dashed line in figure 2). Some of our  
 340 conclusions change if we switch to this qualitative measure of evolutionary suc-  
 341 cess: Under the Moran Birth-Death and Wright-Fisher life-cycles, population  
 342 viscosity does not promote the evolution of altruism – actually, these two life-  
 343 cycles cannot ever promote altruistic behavior for any regular population struc-  
 344 ture (Taylor et al., 2011), whichever the probability of mutation (Débarre, 2017).  
 345 However, under a Moran Death-Birth life-cycle, altruism can be favored only  
 346 at intermediate emigration probabilities (figure 2(a)): increased emigration can  
 347 still favor the evolution of altruism under this qualitative criterion.

a changer  
aussi en  
nu

### 348 **The result is due to indirect, competitive, effects**

349 To explain how the frequency of altruists can increase with the emigration prob-  
 350 ability  $m$ , let us go back to the decomposition of the expected frequency of al-  
 351 truists in the population  $\mathbb{E}[\bar{X}]$  into different terms (eq. (9)). For all the life-cycles  
 352 that we consider, the direct effect of helping others ( $\beta_D$ ) decreases with emigra-  
 353 tion  $m$ , while the direct effect of the cost of helping ( $\gamma_D$ ) does not change with  
 354  $m$ . If we (erroneously) considered only direct effects, we would conclude that  
 355 the expected proportion of altruists decreases with the emigration probability  
 356  $m$ , because an increase in  $m$  reduces the probability that two interactants (two  
 357 deme-mates in this model) are identical by descent. But this explanation ignores  
 358 indirect, competitive, effects. In the three life-cycles that we considered,  $\beta_I = \gamma_I$ ,  
 359 so the overall indirect effects are given by  $-(b - c)\beta_I$ . Hence, any increase of  
 360  $\mathbb{E}[\bar{X}]$  with  $m$  is driven by  $\beta_I$ . Indirect effects correspond to competition: helping  
 361 another individual indirectly harms others – even the individual who is provid-  
 362 ing help is indirectly harmed. This competition can be diluted by increasing the  
 363 emigration probability  $m$ . The overall effect of  $m$  on the expected frequency of  
 364 altruists depends on the balance between direct and indirect effects. This bal-  
 365 ance depends on the fidelity of parent-offspring transmission ( $\mu$ ), in particular  
 366 because probabilities of identity by descent depend on  $\mu$ .

367 Primary and secondary recipients West and Gardner 2010.

368 Competitive effects are less straightforward to explain than direct

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

370 Our results were derived under the assumption of weak selection, assuming that  
 371 the phenotypic difference between altruists and defectors is small ( $\delta \ll 0$ ). We  
 372 considered any fidelity of transmission (any  $\mu$  between 0 and 1) and population  
 373 size. However, most models considering subdivided populations assume nearly



374 perfect strategy transmission ( $\mu \rightarrow 0$ ) and infinite population sizes (number of  
375 demes  $N_D \rightarrow \infty$ ). The order in which these limits are taken matters, *i.e.*, one  
376 needs to specify how small  $\mu$ , but also  $\omega$ , are compared to the inverse size of the  
377 population. This remark complements findings by  $\text{?}$ , who highlighted the quan-  
378 titative differences between different orders of weak selection and large popula-  
379 tion limits.

## 380 Imperfect transmission and Rebellious Children

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

387 Mutation was also previously included in models investigating the mainte-  
388 nance of cooperative microorganisms in the presence of cheaters (Brockhurst  
389 et al., 2007; Frank, 2010). In both of these models however, only loss-of-function  
390 mutation was considered, which corresponds to setting the mutation bias at  
391  $p = 0$  in our model. This means that the all-cheaters state is absorbing; no mat-  
392 ter how favored cooperators may otherwise be, in the long run, a finite popula-  
393 tion will only consist of cheaters.

394

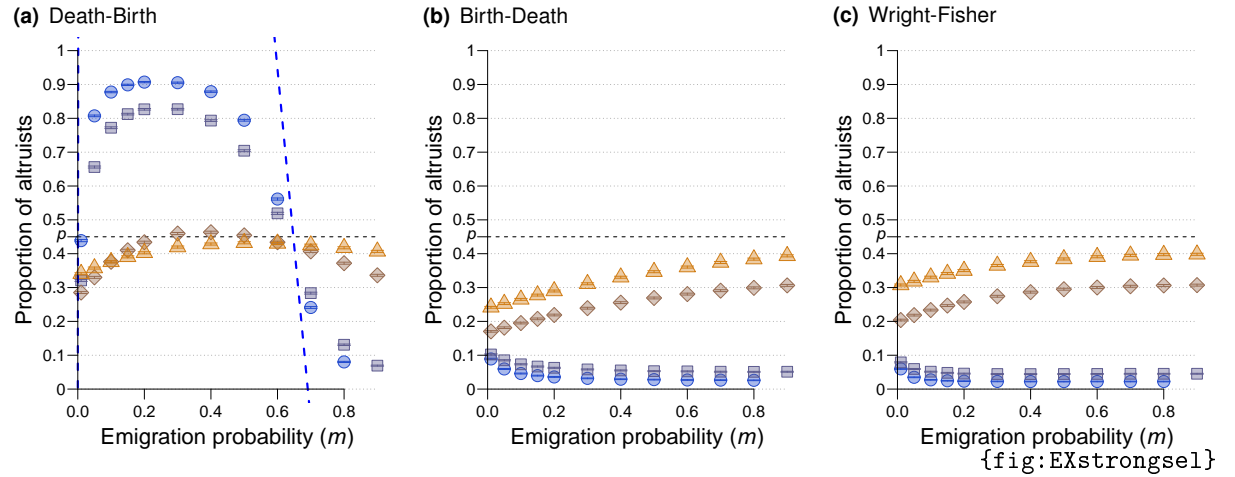
Voter  
model  
Ayana  
Graphs  
et dire  
que on  
peut avoir  
 $e = d$ .  
Faire fig-  
ure avant  
de com-  
mencer a  
discuter  
ca.

## References

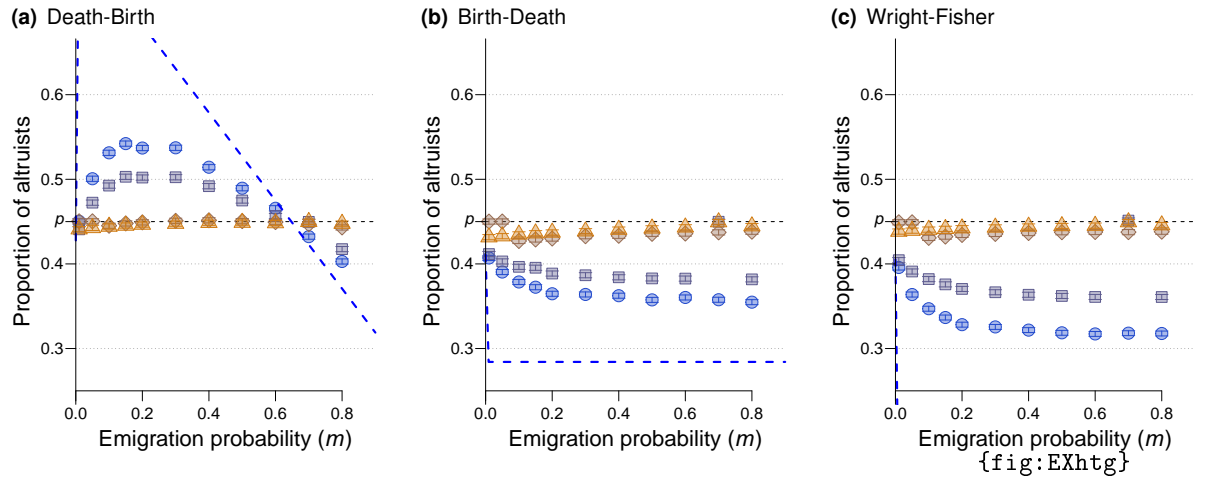
- Alizon, S. & Taylor, P. 2008: Empty sites can promote altruistic behavior. *Evolution* 62(6):1335–1344.
- Allen, B.; Lippner, G.; Chen, Y.-T.; Fotouhi, B.; Momeni, N.; Yau, S.-T. & Nowak, M. A. 2017: Evolutionary dynamics on any population structure. *Nature* 544(7649):227–230.
- Allen, B.; Traulsen, A.; Tarnita, C. E. & Nowak, M. A. 2012: How mutation affects evolutionary games on graphs. *Journal of Theoretical Biology* 299:97 – 105. *Evolution of Cooperation*.
- Brockhurst, M. A.; Buckling, A. & Gardner, A. 2007: Cooperation peaks at intermediate disturbance. *Current Biology* 17(9):761–765.
- Débarre, F. 2017: Fidelity of parent-offspring transmission and the evolution of social behavior in structured populations. *Journal of Theoretical Biology* 420:26 – 35.
- Fletcher, J. A. & Doebeli, M. 2009: A simple and general explanation for the evolution of altruism. *Proceedings of the Royal Society B: Biological Sciences* 276(1654):13–19.
- Frank, S. A. 1997: The price equation, fisher's fundamental theorem, kin selection, and causal analysis. *Evolution* 51(6):1712–1729.
- Frank, S. A. 2010: Microbial secretor–cheater dynamics. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 365(1552):2515–2522.
- Hamilton, W. 1964: The genetical evolution of social behaviour. i. *Journal of Theoretical Biology* 7(1):1 – 16.
- Hamilton, W. D. 1975: Innate social aptitudes of man: an approach from evolutionary genetics. *Biosocial anthropology* 53:133–55.
- Lehmann, L.; Keller, L. & Sumpter, D. J. T. 2007: The evolution of helping and harming on graphs: the return of the inclusive fitness effect. *Journal of Evolutionary Biology* 20(6):2284–2295.
- Leturque, H. & Rousset, F. 2002: Dispersal, kin competition, and the ideal free distribution in a spatially heterogeneous population. *Theoretical Population Biology* 62(2):169 – 180.

- 427 Lion, S. 2016: Moment equations in spatial evolutionary ecology. *Journal of the-*  
428 *oretical biology* 405:46–57.
- 429 Mullon, C. & Lehmann, L. 2014: The robustness of the weak selection approxi-  
430 *mation for the evolution of altruism against strong selection. Journal of evo-*  
431 *lutionary biology* 27(10):2272–2282.
- 432 Ohtsuki, H.; Hauert, C.; Lieberman, E. & Nowak, M. A. 2006: A simple rule  
433 *for the evolution of cooperation on graphs and social networks. Nature*  
434 *441(7092):502–505.*
- 435 Rodrigues, A. M. M. & Gardner, A. 2012: Evolution of helping and harming in  
436 *heterogeneous populations. Evolution* 66(7):2065–2079.
- 437 Sample, C. & Allen, B. 2016: The limits of weak selection and large population  
438 *size in evolutionary game theory. ArXiv .*
- 439 Tarnita, C. E. & Taylor, P. D. 2014: Measures of relative fitness of social behaviors  
440 *in finite structured population models. The American Naturalist* 184(4):477–  
441 *488.*
- 442 Taylor, P. 1992: Altruism in viscous populations—an inclusive fitness model.  
443 *Evolutionary ecology* 6(4):352–356.
- 444 Taylor, P.; Lillicrap, T. & Cownden, D. 2011: Inclusive fitness analysis on mathe-  
445 *matical groups. Evolution* 65(3):849–859.
- 446 Taylor, P. D.; Day, T. & Wild, G. 2007a: Evolution of cooperation in a finite homo-  
447 *geneous graph. Nature* 447(7143):469–472.
- 448 Taylor, P. D.; Day, T. & Wild, G. 2007b: From inclusive fitness to fixation proba-  
449 *bility in homogeneous structured populations. Journal of Theoretical Biology*  
450 *249(1):101 – 110.*
- 451 Taylor, P. D. & Irwin, A. J. 2000: Overlapping generations can promote altruistic  
452 *behavior. Evolution* 54(4):1135–1141.
- 453 West, S. A.; Pen, I. & Griffin, A. S. 2002: Cooperation and competition between  
454 *relatives. Science* 296(5565):72–75.
- 455 Wilson, D. S.; Pollock, G. B. & Dugatkin, L. A. 1992: Can altruism evolve in purely  
456 *viscous populations? Evolutionary Ecology* 6(4):331–341.

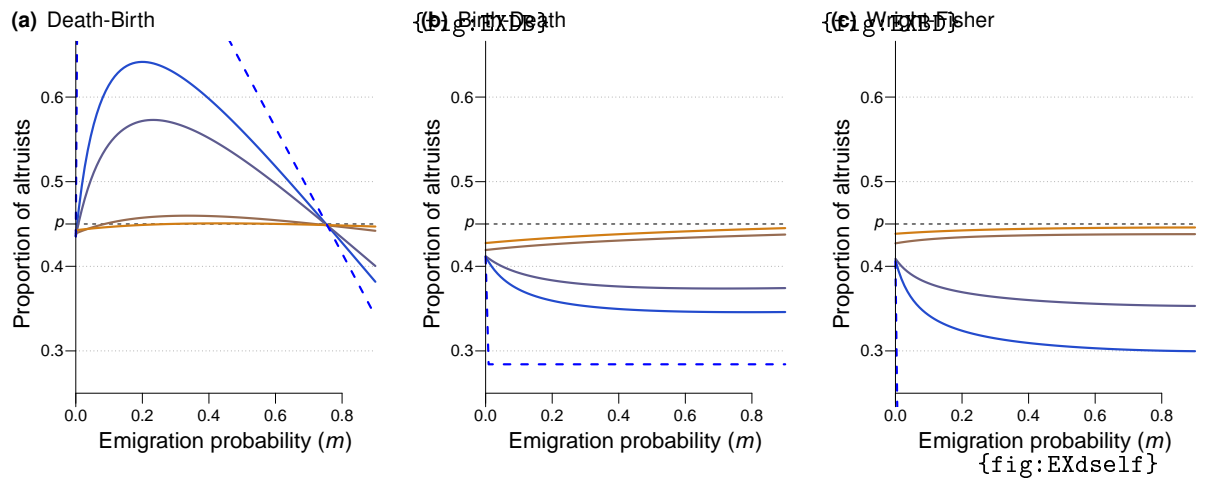
## Supplementary figures



**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).

# Appendix

## A Fecundity and weak selection approximation

{sec:app:F}

Here we show that the fecundity function presented in eq. (2) can be obtained from a generic fecundity function, under the assumption of small phenotypic differences between altruists and defectors. Let us denote by  $\phi_i$  the phenotype of the individual living at site  $i$ , and assume that the phenotypic value of altruists and defectors differs by  $\omega \ll 1$ , so that

$$\phi_i = \phi^{(0)} + \omega X_i, \quad (\text{A.1}) \quad \{\text{eq:app:phidef}\}$$

where  $\phi^{(0)}$  is the phenotype of defectors (and  $\phi_0 + \omega$  the phenotype of altruists). Then we consider a generic fecundity function, that depends on the focal individual's phenotype, and on the phenotype of all the individuals that it interacts with, weighted by the probability of interaction ( $e_{ki}$  for an individual at site  $k$ ,  $1 \leq k \leq N$ ). For instance, the fecundity of an individual at site  $i$  is given by a function with  $N + 1$  arguments

$$F_i = \mathcal{F}(e_{1,i}\phi_1, \dots, e_{N,i}\phi_N; \phi_i),$$

which, using eq. (A.1), becomes

$$F_i = \mathcal{F}(e_{1,i}(\phi^{(0)} + \omega X_1), \dots, e_{N,i}(\phi^{(0)} + \omega X_N); \phi^{(0)} + \omega X_i). \quad (\text{A.2}) \quad \{\text{eq:app:Fi}\}$$

We then write a first-order expansion of eq. (A.2) for  $\omega \ll 1$ :

$$F_i = \mathcal{F}(e_{1,i}\phi^{(0)}, \dots, e_{N,i}\phi^{(0)}; \phi^{(0)}) + \omega \left[ \sum_{k=1}^N e_{ki} X_k \partial_{(k)} \mathcal{F}|_{\omega=0} + X_i \partial_{(N+1)} \mathcal{F}|_{\omega=0} \right] + O(\omega^2), \quad (\text{A.3}) \quad \{\text{eq:app:DLF}\}$$

where  $\partial_{(k)} \mathcal{F}|_{\omega=0}$  is the derivative of  $\mathcal{F}$  with respect to its  $k^{\text{th}}$  argument, evaluated at  $\omega = 0$ . The first term in eq. (A.3) is the fecundity of individual  $i$  when there is not a single altruist in the population. Given the chosen structure of the population, all individuals have the same number of social interactions, so they end up having the same fecundity when the population is fixed for the defector type. Without loss of generality, we set this baseline fecundity equal to 1. If we now consider that it does not matter where the benefits of social interactions come from, only that they are received by the focal individual, then  $\partial_{(k)} \mathcal{F}$  is the same for all  $k$ ,  $1 \leq k \leq N$ ; let us denote it by  $b$ . If we denote by  $-c$  the marginal effect

482 of the focal individual's phenotype on its own fecundity (*i.e.*,  $-c = \partial_{N+1} \mathcal{F}|_{\omega=0}$ ),  
 483 then we obtain

$$F_i = 1 + \omega \left( b \sum_{k=1}^N e_{ki} X_i - c X_i \right) + O(\omega^2), \quad (\text{A.4})$$

484 which is equal to  $f_i$  as defined in eq. (2), neglecting terms in  $\omega^2$  and higher.

## 485 **B Expected frequency of altruists**

{sec:app:EX}

486 Note: The calculation steps are the same as the ones presented in Débarre (2017);  
 487 they are presented here so that the article is self-contained, but there are no new  
 488 results in section B. In this section, we work with a generic regular population  
 489 structure (with symmetries such that all individuals behave the same way in ex-  
 490 pectation), of which the island model is a particular case.

### 491 **B.1 For a generic life-cycle**

{sec:app:generic}

492 We want to compute the expected proportion of altruists in the population. Some  
 493 steps can be done without specifying the life-cycle. We represent the state of the  
 494 population at a given time  $t$  using indicator variables  $X_i(t)$ ,  $1 \leq i \leq N$ , equal  
 495 to 1 if the individual living at site  $i$  at time  $t$  is an altruist, and equal to 0 if it is  
 496 a defector; these indicator variables are gathered in a  $N$ -long vector  $\mathbf{X}(t)$ . The  
 497 set of all possible population states is  $\Omega = \{0, 1\}^N$ . The proportion of altruists in  
 498 the population is written  $\bar{X}(t) = \sum_{i=1}^N X_i(t)$ . We denote by  $B_{ji}(X(t), \omega)$ , written  
 499  $B_{ji}$  for simplicity, the probability that the individual at site  $j$  at time  $t+1$  is the  
 500 newly established offspring of the individual living at site  $i$  at time  $t$ . We denote  
 501 by  $D_i(X(t), \omega)$  ( $D_i$  for simplicity) the probability that the individual living at site  
 502  $i$  at time  $t$  has been replaced (*i.e.*, died) at time  $t+1$ . Both quantities depend  
 503 on the chosen life-cycle and on the state of the population; they are given in  
 504 table S1 for each of the life-cycles that we consider.

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

$$D_i = \sum_{j=1}^N B_{ij} \quad (\text{B.5a}) \quad \{\text{eq:DBequiv}\}$$

506 holds for all sites  $i$ . The structure of the population is also such that in the ab-  
 507 sence of selection ( $\omega = 0$ , so that  $f_i = 1$  for all sites  $1 \leq i \leq N$ ), all individuals have  
 508 the same probability of dying and the same probability of having successful off-  
 509 spring (*i.e.*, offspring that become adults), so that

$$D_i^0 = \sum_{j=1}^N B_{ji}^0 = B^*, \quad (\text{B.5b}) \quad \{\text{eq:DBRV}\}$$

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

{tab:BD}

**Table S1:** Formulas of  $B_{ij}$  and  $D_i$  for each of the life-cycle that we consider;  $f_i$  (shorthand notation for  $f_i(X, \omega)$ ) is the fecundity of the individual living at site  $i$ , as defined in eq. (2).

where the <sup>0</sup> subscript means that the quantities are evaluated for  $\omega = 0$ ; 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 with eq. (B.5a) 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

$$\mathbb{E}[\bar{X}(t+1)|\mathbf{X}(t)] = \frac{1}{N} \sum_{i=1}^N \left[ \sum_{j=1}^N B_{ij} (X_j(1-\mu) + \mu p) + (1 - D_i) X_i \right]. \quad (\text{B.6a}) \quad \{\text{eq:conditionalchange}\}$$

The first term within the brackets corresponds to births: the type of the individual living at  $i$  at time  $t + 1$  depends on the type of its parent (living at site  $j$ ), and on whether mutation occurred. The second term in the brackets of eq. (B.6a) corresponds to the survival of the individual living at site  $i$ .

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, so that the expected frequency of altruists does not change anymore for large times  $t$  (realized frequencies of course keep changing). We denote by  $\xi(\mathbf{X}, \omega, \mu)$  the probability that the population is in state  $\mathbf{X}$ , given the strength of selection  $\omega$  and the mutation probability  $\mu$ . Taking the expectation of eq. (B.6a) ( $\mathbb{E}[\bar{X}] = \sum_{\mathbf{X} \in \Omega} \bar{X} \xi(\mathbf{X}, \omega, \mu)$ ), we obtain, after reorganizing:

$$0 = \frac{1}{N} \sum_{\mathbf{X} \in \Omega} \sum_{i=1}^N \left[ \sum_{j=1}^N B_{ij} (X_j(1-\mu) + \mu p) - D_i X_i \right] \xi(\mathbf{X}, \omega, \mu). \quad (\text{B.7}) \quad \{\text{eq:statdist}\}$$



Now, we use the assumption of weak selection ( $\omega \ll 1$ ) and consider the first-order expansion of eq. (B.7) for  $\omega$  close to 0. First, we note that in the absence of selection ( $\omega = 0$ ), the population is at a mutation-drift balance, and the expected state of every site  $i$  is then  $\mathbb{E}_0[X_i] = \sum_{X \in \Omega} X_i \xi(X, 0, \mu) = p$ , the mutation bias. Secondly, we further expand derivatives of  $B_{ji}$  and  $D_i$  thanks to the chain rule, using the variables  $f_k$  ( $1 \leq k \leq N$ ), corresponding to individual fecundities (also, recall that  $f_k = 1$  when  $\omega = 0$ ). Thirdly, we note that for all the life-cycles that we consider, the number of deaths in the population during one time step does not depend on population composition (exactly 1 death for the Moran life-cycles, and exactly  $N$  for the Wright-Fisher life-cycle), so that  $\partial \sum_{i,j=1}^N B_{ij} / \partial \omega$  does not depend on  $\omega$ . After simplification and reorganization, the first order expansion of eq. (B.7) yields

$$0 = \frac{1}{N} \sum_{i,k=1}^N \left[ \frac{\partial \left( \sum_{j=1}^N (1-\mu) B_{ji} - D_i \right)}{\partial f_k} \right]_{f_k=1} \times \left( \sum_{\ell=1}^N e_{\ell k} b \sum_{X \in \Omega} X_{\ell} X_i \xi(\mathbf{X}, 0, \mu) - c \sum_{X \in \Omega} X_k X_i \xi(\mathbf{X}, 0, \mu) \right) - B^* \mu \frac{\partial \mathbb{E}[\bar{X}]}{\partial \omega} \Big|_{\omega=0} + O(\omega^2). \quad (\text{B.8}) \quad \{\text{eq:weaksel1}\}$$

The terms  $\sum_{X \in \Omega} X_i X_j \xi(\mathbf{X}, 0, \mu)$ , that we will also denote by  $P_{ij}$ , correspond to the expected state of the pair of sites  $(i, j)$ , evaluated in the absence of selection ( $\omega = 0$ ). We can also replace these terms by

$$P_{ij} = p^2 + p(1-p)Q_{ij}. \quad (\text{B.9}) \quad \{\text{eq:QP}\}$$

In Appendix B.2, we will see that recursions on  $P_{ij}$  will reveal that  $Q_{ij}$  can be interpreted as a probability of identity by descent, *i.e.*, the probability that the individuals at sites  $i$  and  $j$  have a common ancestor and that no mutation has occurred on either lineage since the ancestor.

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

$$\mathbb{E}[\bar{X}] = p + \omega \frac{\partial \mathbb{E}[\bar{X}]}{\partial \omega} \Big|_{\omega=0} + O(\omega^2), \quad (\text{B.10}) \quad \{\text{eq:EXgeneric}\}$$

where  $\frac{\partial \mathbb{E}[\bar{X}]}{\partial \omega} \Big|_{\omega=0}$  is obtained from eq. (B.8). We then need to replace the  $B_{ij}$  and  $D_j$  terms by their formulas for each life-cycle (given in table S1), and the  $d_{ij}$  and

551  $e_{ij}$  terms by their formulas (given in eq. (3)) and eq. (1), respectively). For each  
 552 life-cycle we can group terms as

$$\left. \frac{\partial \mathbb{E}[\bar{X}]}{\partial \omega} \right|_{\omega=0} \approx \frac{p(1-p)}{\mu} [b(\beta_D - \beta_I) - c(\gamma_D - \gamma_I)], \quad (\text{B.11})$$

553 where D terms come from the numerators of  $B_{ij}$  and  $D_i$ , and I terms come from  
 554 the denominator of  $B_{ij}$  and  $D_i$ ; replacing  $B_{ij}$  and  $D_i$  by their formulas given in  
 555 table S1, we obtain

### Moran Birth-Death

$$\beta_D^{\text{BD}} = \sum_{k,\ell=1}^N \frac{1-\mu}{N} e_{k\ell} Q_{\ell k}^{\text{M}}, \quad (\text{B.12a}) \quad \{\text{eq:EXBDsums}\}$$

$$\beta_I^{\text{BD}} = \sum_{j,k,\ell=1}^N \left( \frac{d_{\ell j}}{N} - \frac{\mu}{N^2} \right) e_{k\ell} Q_{jk}^{\text{M}}, \quad (\text{B.12b})$$

$$\gamma_D^{\text{BD}} = 1 - \mu, \quad (\text{B.12c})$$

$$\gamma_I^{\text{BD}} = \sum_{j,k=1}^N \left( \frac{d_{kj}}{N} - \frac{\mu}{N^2} \right) Q_{jk}^{\text{M}}. \quad (\text{B.12d})$$

### Moran Death-Birth

$$\beta_D^{\text{DB}} = \sum_{k,\ell=1}^N \frac{1-\mu}{N} e_{k\ell} Q_{\ell k}^{\text{M}}, \quad (\text{B.13a})$$

$$\beta_I^{\text{DB}} = (1-\mu) \sum_{i,j,k,\ell=1}^N \frac{d_{ji} d_{\ell i}}{N} e_{k\ell} Q_{jk}^{\text{M}}, \quad (\text{B.13b})$$

$$\gamma_D^{\text{DB}} = 1 - \mu, \quad (\text{B.13c})$$

$$\gamma_I^{\text{DB}} = (1-\mu) \sum_{i,j,k=1}^N \frac{d_{ji} d_{ki}}{N} Q_{jk}^{\text{M}}. \quad (\text{B.13d})$$

## Wright-Fisher

$$\beta_D^{\text{WF}} = \sum_{k,\ell=1}^N \frac{1-\mu}{N} e_{k\ell} Q_{\ell k}^{\text{WF}}, \quad (\text{B.14a})$$

$$\beta_I^{\text{WF}} = (1-\mu) \sum_{i,j,k,\ell=1}^N \frac{d_{ji}d_{\ell i}}{N} e_{k\ell} Q_{jk}^{\text{WF}}, \quad (\text{B.14b})$$

$$\gamma_D^{\text{WF}} = 1 - \mu, \quad (\text{B.14c})$$

$$\gamma_I^{\text{WF}} = (1-\mu) \sum_{i,j,k=1}^N \frac{d_{ji}d_{ki}}{N} Q_{jk}^{\text{WF}}, \quad (\text{B.14d})$$

which is the same set of equations as for the Moran Death-Birth model, except for the values of probabilities of identity by descent... that we now need to compute.

## B.2 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  $Q_{ij}$ .

### B.2.1 Moran model

In a Moran model, exactly one individual died 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 (or say mutants, since there is no selection and hence no benefits or costs provided by altruists), if  $i$ ) it was the case at time  $t$  and neither site was replaced by a non-mutant (first term in eq. (B.15)), or  $ii$ ) if exactly one of the two sites was occupied by a non-mutant at time  $t$ , but the site was replaced by a mutant (second and third terms of eq. (B.15)):

$$\begin{aligned} \mathbb{E}[X_i X_j(t+1) | X(t) = \mathbf{X}] = & X_i X_j \left( 1 - \sum_{k=1}^N \frac{1}{N} (d_{ki} + d_{kj}) ((1 - X_k)(1 - \mu) + \mu(1 - p)) \right) \\ & + X_i(1 - X_j) \sum_{k=1}^N \frac{1}{N} d_{kj} (X_k(1 - \mu) + \mu p) \\ & + X_j(1 - X_i) \sum_{k=1}^N \frac{1}{N} d_{ki} (X_k(1 - \mu) + \mu p). \end{aligned} \quad (\text{B.15}) \quad \{\text{eq:app:PijM1}\}$$

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

573

$$P_{ij} = \frac{1}{2} \left( \sum_{k=1}^N (1-\mu) (d_{kj} P_{ki} + d_{ki} P_{kj}) \right) + \mu p^2 \quad (i \neq j), \quad (\text{B.16}) \quad \{\text{eq:app:PijM}\}$$

574 while  $P_{ii} = p$ .575 Now we substitute  $P_{ij} = p^2 + p(1-p)Q_{ij}$  in eq. (B.16), obtain

$$Q_{ij} = \frac{1}{2} \sum_{k=1}^N (1-\mu) (d_{ki} Q_{kj} + d_{kj} Q_{ki}), \quad (\text{B.17}) \quad \{\text{eq:app:QijM}\}$$

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

581 **B.2.2 Wright-Fisher model**

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

$$\begin{aligned} \mathbb{E}[X_i X_j(t+1) | X(t) = \mathbf{X}] &= \sum_{k,\ell=1}^N d_{ki} d_{\ell j} \left( X_k X_\ell (1-\mu + \mu p)^2 \right. \\ &\quad + (X_k(1-X_\ell) + (1-X_k)X_\ell) (1-\mu + \mu p)(\mu p) \\ &\quad \left. + (1-X_k)(1-X_\ell)(\mu p)^2 \right) \end{aligned} \quad (\text{B.18}) \quad \{\text{eq:app:PijWF1}\}$$

584 Taking the expectation and simplifying, we obtain

$$P_{ij} = \sum_{k,\ell=1}^N (P_{kl}(1-\mu)^2) + (2-\mu)\mu p^2. \quad (\text{B.19}) \quad \{\text{eq:app:PijWF}\}$$

585 Replacing  $P_{ij}$  by  $p^2 + p(1-p)Q_{ij}$ , eq. (B.19) becomes

$$Q_{ij} = \sum_{k,\ell=1}^N d_{ki} d_{\ell j} Q_{k\ell} (1-\mu)^2. \quad (\text{B.20}) \quad \{\text{eq:app:QijWF}\}$$

586 Again,  $Q_{ij}$  corresponds to a probability of identity by descent: the individuals at  
 587 sites  $i$  and  $j$  are identical by descent if their parents were and if neither mutated  
 588  $((1-\mu)^2)$ .

## 589 C In a subdivided population

### 590 C.1 $\beta$ and $\gamma$

591 Now, we need to adapt the results presented in Appendix B to our structure of  
 592 interest, a subdivided population, with dispersal and interaction probabilities  
 593 given by eq. (3) and eq. (1). For the  $\beta$  and  $\gamma$  terms, we use a brute-force approach,  
 594 replacing  $d_{ij}$  and  $e_{ij}$  by their values in a subdivided population, and simplifying  
 595 the equations (for instance, there are 60 different cases to consider for the four  
 596 sums that appear in  $\beta_1^{\text{DB}}$ ). The calculations are detailed in an accompanying  
 597 Mathematica file, [and the results are presented in the main text.](#)

todo

### 598 C.2 Probabilities of identity by descent

599 For the probabilities of identity by descent, we could also use a brute-force ap-  
 600 proach, but calculations are faster if we use formulas derived in Débarre (2017)  
 601 for “two-dimensional population structures”. The name comes from the fact  
 602 that we only need two types of transformations to go from any site to any other  
 603 site in the population: permutations on the deme index, and permutations on  
 604 the within-deme index. We introduce notations  $\tilde{d}_i$  and  $\tilde{Q}_i$ , that correspond to  
 605 the dispersal probability to a site at distance  $i$  (e.g., for all  $j, 1 \leq j \leq N$ ,  $\tilde{d}_1 =$   
 606  $d_{j,j+1}$ ) and the probability of identity by descent with a site at distance  $i$  (e.g.,  
 607 for all  $j, 1 \leq j \leq N$ ,  $\tilde{Q}_1 = Q_{j,j+1}$ ), respectively. Finally, we can rewrite site labels  
 608 ( $1 \leq i \leq N$ ) as  $(l_1, l_2)$ , where  $l_1$  is the number of the deme ( $1 \leq l_1 \leq N_D$ ) and  $l_2$  the  
 609 position of the site within the deme ( $1 \leq l_2 \leq n$ ).

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

#### 612 C.2.1 Moran model

613 In Débarre (2017), it was shown that

$$\tilde{Q}_{r_1} = \frac{1}{N} \sum_{q_1=0}^{N_1-1} \sum_{q_2=0}^{N_2-1} \frac{\mu \lambda'_M}{1 - (1 - \mu) \tilde{D}_{q_1}} \exp\left(i \frac{2\pi q_1 r_1}{N_1}\right) \exp\left(i \frac{2\pi q_2 r_2}{N_2}\right) \quad (\text{C.21a}) \quad \{\text{eq:app:Q2DM}\}$$

614 with

$$\tilde{D}_{q_1} = \sum_{l_1=0}^{N_1-1} \sum_{l_2=0}^{N_2-1} \tilde{d}_{l_1} \exp\left(-i \frac{2\pi q_1 l_1}{N_1}\right) \exp\left(-i \frac{2\pi q_2 l_2}{N_2}\right), \quad (\text{C.21b}) \quad \{\text{eq:app:D2D}\}$$

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

$$\begin{aligned}\tilde{D}_{q_1} &= d_{\text{self}} + \sum_{l_2=1}^{N_2-1} d_{\text{in}} \exp\left(-i \frac{2\pi q_2 l_2}{N_2}\right) + \sum_{l_1=1}^{N_1-1} \sum_{l_2=0}^{N_2-1} d_{\text{out}} \exp\left(-i \frac{2\pi q_1 l_1}{N_1}\right) \exp\left(-i \frac{2\pi q_2 l_2}{N_2}\right) \\ &= d_{\text{self}} + (\delta_{q_2}(N_2 - 1) + (1 - \delta_{q_2})(-1)) d_{\text{in}} + (\delta_{q_1}(N_1 - 1) + (1 - \delta_{q_1})(-1)) (\delta_{q_2} N_2) d_{\text{out}} \\ &= d_{\text{self}} + (\delta_{q_2} N_2 - 1) d_{\text{in}} + (\delta_{q_1} N_1 - 1) \delta_{q_2} N_2 d_{\text{out}}.\end{aligned}\quad (\text{C.22a})$$

617 ( $\delta_q$  is equal to 1 when  $q$  is equal to 0 modulo the relevant dimension, and to 0  
 618 otherwise). So for the three types of distances that we need to consider (distance  
 619 0, distance to another deme-mate, distance to individual in another deme), and  
 620 with  $N_1 = N_D$  and  $N_2 = n$ , we obtain {eq:app:Dsystem}

$$\tilde{D}_0 = 1, \quad (\text{C.23a})$$

$$\tilde{D}_{q_1} = 1 - m - \frac{m}{d-1} \quad (q_1 \not\equiv 0 \pmod{N_1}), \quad (\text{C.23b})$$

$$\tilde{D}_{q_1} = d_{\text{self}} - d_{\text{in}} \quad (q_2 \not\equiv 0 \pmod{N_2}). \quad (\text{C.23c})$$

621 So for  $\tilde{Q}$ , using system (C.23) in eq. (C.21a),

$$\begin{aligned}\tilde{Q}_{r_1} &= \frac{\mu \lambda'_M}{N} \left[ \frac{1}{1 - (1 - \mu) \tilde{D}_0} + \sum_{q_2=1}^{N_2-1} \frac{1}{1 - (1 - \mu) \tilde{D}_{q_2}} \exp\left(-i \frac{2\pi q_2 r_2}{N_2}\right) + \sum_{q_1=1}^{N_1-1} \frac{1}{1 - (1 - \mu) \tilde{D}_{q_1}} \exp\left(-i \frac{2\pi q_1 r_1}{N_1}\right) \right. \\ &\quad \left. + \sum_{q_1=1}^{N_1-1} \sum_{q_2=1}^{N_2-1} \frac{1}{1 - (1 - \mu) \tilde{D}_{q_1}} \exp\left(-i \frac{2\pi q_1 r_1}{N_1}\right) \exp\left(-i \frac{2\pi q_2 r_2}{N_2}\right) \right] \\ &= \frac{\mu \lambda'_M}{N} \left[ \frac{1}{1 - (1 - \mu)} + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})} (\delta_{r_2} N_2 - 1) + \frac{1}{1 - (1 - \mu)(1 - m - \frac{m}{d-1})} (\delta_{r_1} N_1 - 1) \right. \\ &\quad \left. + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})} (\delta_{r_1} N_1 - 1) (\delta_{r_2} N_2 - 1) \right].\end{aligned}\quad (\text{C.24}) \quad \{\text{eq:app:Q2DMsol}\}$$

622 In particular,

$$\begin{aligned}\tilde{Q}_0 &= \frac{\mu \lambda'_M}{N} \left[ \frac{1}{\mu} + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})} (n - 1) + \frac{1}{1 - (1 - \mu)(1 - m - \frac{m}{d-1})} (D - 1) \right. \\ &\quad \left. + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})} (D - 1)(n - 1) \right] \\ &= 1.\end{aligned}\quad (\text{C.25a}) \quad \{\text{eq:app:Q2D1}\}$$

623 We find  $\lambda'_M$  using the eq. (C.25a). Going back to eq. (C.24), when  $r_1 = 0$ , the two  
 624 individuals are in the same deme. They are different when  $r_2 \neq 0$ , and so:

$$Q_{\text{in}} = \frac{\mu\lambda'_M}{N} \left[ \frac{1}{\mu} + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})}(-1) + \frac{1}{1 - (1 - \mu)(1 - m - \frac{m}{d-1})}(D-1) \right. \\ \left. + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})}(D-1)(-1) \right]. \quad (\text{C.25b})$$

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

$$Q_{\text{out}} = \frac{\mu\lambda'_M}{N} \left[ \frac{1}{\mu} + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})}(-1) + \frac{1}{1 - (1 - \mu)(1 - m - \frac{m}{d-1})}(-1) \right. \\ \left. + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})} \right]. \quad (\text{C.25c})$$

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

### 628 **C.3 Wright-Fisher**

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

$$\tilde{Q}_{r_1} = \frac{1}{N} \sum_{q_1=0}^{N_1-1} \sum_{q_2=0}^{N_2-1} \frac{\mu\lambda'_{WF}}{1 - (1 - \mu)^2 (\tilde{\mathcal{D}}_{q_1})^2} \exp\left(-i \frac{2\pi q_1 r_1}{N_1}\right) \exp\left(-i \frac{2\pi q_2 r_2}{N_2}\right), \quad (\text{C.26})$$

630 with  $\tilde{D}$  given in eq. (C.21b). In a subdivided population, with  $N_1 = N_D$  and  $N_2 =$   
 631  $n$ , this becomes

$$\begin{aligned}
 \tilde{Q}_{r_1 r_2} &= \frac{1}{N} \left[ \frac{\mu \lambda'_{WF}}{1 - (1 - \mu)^2 (\tilde{D}_0)^2} + \sum_{q_2=1}^{N_2-1} \frac{\mu \lambda'_{WF}}{1 - (1 - \mu)^2 (\tilde{D}_{q_2})^2} \exp \left( -i \frac{2\pi q_2 r_2}{N_2} \right) \right. \\
 &\quad + \sum_{q_1=1}^{N_1-1} \frac{\mu \lambda'_{WF}}{1 - (1 - \mu)^2 (\tilde{D}_{q_1})^2} \exp \left( -i \frac{2\pi q_1 r_1}{N_1} \right) \\
 &\quad \left. + \sum_{q_1=1}^{N_1-1} \sum_{q_2=1}^{N_2-1} \frac{\mu \lambda'_{WF}}{1 - (1 - \mu)^2 (\tilde{D}_{q_1})^2} \exp \left( -i \frac{2\pi q_1 r_1}{N_1} \right) \exp \left( -i \frac{2\pi q_2 r_2}{N_2} \right) \right] \\
 &= \frac{\mu \lambda'_{WF}}{N} \left[ \frac{1}{1 - (1 - \mu)^2} + \frac{1}{1 - (1 - \mu)^2 (d_{\text{self}} - d_{\text{in}})^2} (\delta_{q_2} N_2 - 1) \right. \\
 &\quad + \frac{1}{1 - (1 - \mu)^2 (1 - m - \frac{m}{d-1})^2} (\delta_{q_1} N_1 - 1) \\
 &\quad \left. + \frac{1}{1 - (1 - \mu)^2 (d_{\text{self}} - d_{\text{in}})^2} (\delta_{q_1} N_1 - 1) (\delta_{q_2} N_2 - 1) \right] \\
 &= \frac{\mu \lambda'_{WF}}{N} \left[ \frac{1}{1 - (1 - \mu)^2} + \frac{1}{1 - (1 - \mu)^2 (d_{\text{self}} - d_{\text{in}})^2} (\delta_{q_2} N_2 - 1) \delta_{q_1} N_1 \right. \\
 &\quad \left. + \frac{1}{1 - (1 - \mu)^2 (1 - m - \frac{m}{d-1})^2} (\delta_{q_1} N_1 - 1) \right]. \tag{C.27} \quad \{\text{eq:app:Q2DWFsol}\}
 \end{aligned}$$

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

$$1 = \frac{\mu \lambda'_{WF}}{N} \left[ \frac{1}{1 - (1 - \mu)^2} + \frac{1}{1 - (1 - \mu)^2 (d_{\text{self}} - d_{\text{in}})^2} (N_2 - 1) N_1 + \frac{1}{1 - (1 - \mu)^2 (1 - m - \frac{m}{d-1})^2} (N_1 - 1) \right]. \tag{C.28a}$$

633 Then from eq. (C.27) we deduce

$$Q_{\text{in}} = \frac{\mu \lambda'_{WF}}{N} \left[ \frac{1}{1 - (1 - \mu)^2} - \frac{1}{1 - (1 - \mu)^2 (d_{\text{self}} - d_{\text{in}})^2} N_1 + \frac{1}{1 - (1 - \mu)^2 (1 - m - \frac{m}{d-1})^2} (N_1 - 1) \right]. \tag{C.28b}$$

634 and

$$Q_{\text{out}} = \frac{\mu \lambda'_{WF}}{N} \left[ \frac{1}{1 - (1 - \mu)^2} - \frac{1}{1 - (1 - \mu)^2 (1 - m - \frac{m}{d-1})^2} \right]. \tag{C.28c}$$

635 With  $d_{\text{self}} = d_{\text{in}} = (1 - m)/n$ , we recover the equations given in the main text  
 636 (system (8)).