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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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Check  $\omega$  removes entirely + explain delta in table

## 1 Abstract

2 Population viscosity, *i.e.*, low emigration out of the natal deme, leads to high  
3 within-deme relatedness, which is beneficial to the evolution of altruistic behav-  
4 ior when social interactions take place among deme-mates. At the same time  
5 however, it increases competition among related individuals. The evolution of  
6 altruism depends on the balance between these opposite effects. This balance  
7 is already known to be affected by details of the life-cycle; we show here that  
8 it further depends on the fidelity of strategy transmission from parents to their  
9 offspring. We consider different life-cycles (Wright-Fisher, with synchronous  
10 non-overlapping generations, Moran Death-Birth and Moran Birth-Death, both  
11 with exactly one individual dying and reproducing at each time step) and we  
12 identify thresholds of parent-offspring strategy transmission inaccuracy, above  
13 which the effect of population viscosity on the frequency of altruists maintained  
14 in the population qualitatively changes. Analytical predictions are first obtained  
15 analytically under weak selection and equal deme sizes, then confirmed with

16 stochastic simulations relaxing these assumptions. This result challenges the  
17 notion that the evolution of altruism requires limited dispersal.

## 18 **Impact Summary**

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

## 44 1 Introduction

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

53 Yet, living next to your kin also implies competing against them (West et al.,  
54 2002). The evolution of social traits hence depends on the balance between the  
55 positive effects of interactions with related individuals and the detrimental con-  
56 sequences of kin competition. Under specific conditions, the two effects can  
57 even compensate each other, thereby annihilating the impact of population vis-  
58 cosity on the evolution of altruism. First identified with computer simulations  
59 (Wilson et al., 1992), this cancellation result was analyzed by Taylor (1992a) in  
60 a model with synchronous generations (*i.e.*, Wright-Fisher model) and a sub-  
61 divided population of constant, infinite size. The cancellation result was later  
62 extended to heterogeneous populations (Rodrigues & Gardner, 2012, with syn-  
63 chronous generations and infinite population size), and other life-cycles, with  
64 generic regular population structures (Taylor et al., 2011, with synchronous gen-  
65 erations but also with continuous generations and Birth-Death updating). How-  
66 ever, small changes in the model's assumptions, such as overlapping generations  
67 (Taylor & Irwin, 2000) or the presence of empty sites (Alizon & Taylor, 2008) can  
68 tip the balance back in the favor of altruism. This high dependence on life-  
69 cycle specificities highlights the difficulty of making general statements about  
70 the role of spatial structure on the evolution of altruism. In this study, we will

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

74 A large number of studies on the evolution of social behavior consider simple  
75 population structures (typically, homogeneous populations *sensu* Taylor et al.  
76 (2007a)) and often also infinite population sizes (but see Allen et al., 2017, for  
77 results on any structure). These studies also make use of weak selection ap-  
78 proximations, and commonly assume rare (*e.g.*, Leturque & Rousset, 2002; Tay-  
79 lor et al., 2007b; Tarnita & Taylor, 2014) or absent mutation (for models assum-  
80 ing infinite population sizes, or models concentrating on fixation probabilities  
81 Lehmann & Rousset, 2014; Van Cleve, 2015, for recent reviews). Often, these sim-  
82 plifying assumptions are a necessary step towards obtaining explicit analytical  
83 results. Although artificial, simple population structures (*e.g.*, regular graphs, or  
84 subdivided populations with demes of equal sizes) help reduce the dimension-  
85 ality of the system under study, in particular when the structure of the popula-  
86 tion displays symmetries such that all sites behave the same way in expectation.  
87 Weak selection approximations are crucial for disentangling spatial moments  
88 (Lion, 2016), that is, changes in global *vs.* local frequencies (though they can in  
89 some cases be relaxed, as in Mullon & Lehmann, 2014). Mutation, however, is  
90 usually ignored by classical models of inclusive fitness because these models as-  
91 sume infinite population sizes, so that there is no need to add mechanisms that  
92 restore genetic diversity (Tarnita & Taylor, 2014). In populations of finite size,  
93 this diversifying effect can be obtained thanks to mutation.

94 When strategy transmission is purely genetic, it makes sense to assume that  
95 mutation is relatively weak. A social strategy can however also be culturally  
96 transmitted from parent to offspring, in which case “rebellion” (as in Frank’s Re-  
97 bellious Child Model (Frank, 1997)) does not have to be rare. Imperfect strategy  
98 transmission can alter evolutionary dynamics, in particular in spatially struc-

99 tured populations (see *e.g.*, Allen et al., 2012; Débarre, 2017, for graph-structured  
100 populations). Here, we want to explore the consequences of imperfect strategy  
101 transmission from parents to their offspring on the evolution of altruistic behav-  
102 ior in subdivided populations. For the sake of concision, we use the word “mu-  
103 tation” throughout the paper, keeping in mind that strategy transmission does  
104 not have to be genetic.

105 For each of the three life-cycles that we consider, we compute the expected  
106 (*i.e.*, long-term) frequency of altruists maintained in a subdivided population,  
107 and investigate how it is affected by mutation and emigration. We find that, con-  
108 trary to what happens with perfect strategy transmission, higher emigration can  
109 increase the expected frequency of altruists in the population.

## 110 2 Model and methods

### 111 2.1 Assumptions

112 We consider a population of size  $N$ , subdivided into  $N_D$  demes, each hosting  
113 exactly  $n$  individuals (*i.e.*, each deme contains  $n$  sites, each of which is occupied  
114 by exactly one individual; we have  $nN_D = N$ ). Each site has a unique label  $i$ ,  
115  $1 \leq i \leq N$ . There are two types of individuals in the population, altruists and  
116 defectors. The type of the individual living at site  $i$  ( $1 \leq i \leq N$ ) is given by an  
117 indicator variable  $X_i$ , equal to 1 if the individual is an altruist, and to 0 if it is a  
118 defector. The state of the entire population is given by a  $N$ -long vector  $\mathbf{X}$ . For a  
119 given population state  $\mathbf{X}$ , the proportion of altruists is  $\bar{X} = \sum_{i=1}^N X_i$ . All symbols  
120 are summarized in table S1.

121 Reproduction is asexual. Parents transmit their strategy to their offspring  
122 with probability  $1 - \mu$ ; this transmission can be genetic or cultural (vertical cul-  
123 tural transmission), but for simplicity, we refer to the parameter  $\mu$  as a mutation  
124 probability. With probability  $\mu$ , offspring do not inherit their strategy from their

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

An individual of type  $X_k$  expresses a social phenotype  $\phi_k = \delta X_k$ , where  $\delta$  is assumed to be small ( $\delta \ll 1$ ). Social interactions take place within each deme; each individual interacts with the  $n - 1$  other deme members. Denoting by  $e_{ij}$  the interaction probability between individuals living at sites  $i$  and  $j$ , we have  $e_{ij} = 1/(n - 1)$  if  $i$  and  $j$  are two different sites in the same deme, and  $e_{ij} = 0$  otherwise. We assume that social interactions affect individual fecundity;  $f_k$  denotes the fecundity of the individual at site  $k$ . The baseline fecundity, *i.e.* individual fecundity when no altruists are present in the population, is set equal to 1. 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 ( $c \leq b$ ). With these assumptions and notation, at the first order in  $\delta$ , the fecundity of the individual living at site  $k$  is given by

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

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

$$d_{ij} = \begin{cases} d_{\text{in}} = \frac{1-m}{n} & \text{if both sites are in the same deme;} \\ d_{\text{out}} = \frac{m}{(N_D-1)n} & \text{if the two sites are in different demes,} \end{cases} \quad (2)$$

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

remove?

individual living at site  $i$  (successful means alive at the next time step), and by  $D_i = D_i(\mathbf{X}, \delta)$  the probability that the individual living at site  $i$  dies. Both depend on the state of the population  $\mathbf{X}$ , but also on the way the population is updated from one time step to the next, *i.e.*, on the chosen life-cycle (also called updating rule). We will specifically explore three different life-cycles. At the beginning of each step of each life-cycle, all individuals produce offspring, that can be mutated; then these juveniles move, within the parental deme or outside of it, and land on a site. The next events occurring during the time step depend on the life-cycle:

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

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

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

## 2.2 Methods

### 2.2.1 Analytical part

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



172 The formula involves quantities that can be identified as neutral probabili-  
173 ties of identity by descent  $Q_{ij}$ , *i.e.*, the probability that individuals living at site  $i$   
174 and  $j$  share a common ancestor and that no mutation occurred on either lineage  
175 since that ancestor, in a model with no selection ( $\omega = 0$ ) – this is the “mutation  
176 definition” of identity by descent (Rousset & Billiard, 2000).

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

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

### 183 2.2.2 Stochastic simulations

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

190 All scripts are available at

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

## 192 3 Results

### 193 3.1 Probabilities of identity by descent

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

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

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

#### 201 3.1.1 Moran updating

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

$$Q_{ij}^{\text{M}} = \frac{1-\mu}{2} \sum_{k=1}^N (d_{kj} Q_{ki}^{\text{M}} + d_{ki} Q_{kj}^{\text{M}}). \quad (4)$$

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

210 steps):

$$Q_{\text{in}}^M = \frac{(1-\mu)(m + \mu(N_D(1-m) - 1))}{(1-\mu)m(N_D\mu(n-1) + 1) + (N_D - 1)\mu(\mu(n-1) + 1)}, \quad (5a)$$

$$Q_{\text{out}}^M = \frac{(1-\mu)m}{(1-\mu)m(N_D\mu(n-1) + 1) + (N_D - 1)\mu(\mu(n-1) + 1)}. \quad (5b)$$

211 The probability that two different deme-mates are identical by descent,  $Q_{\text{in}}^M$ , de-  
 212 creases monotonically with the emigration probability  $m$ , while  $Q_{\text{out}}^M$  monoton-  
 213 ically increases with  $m$  (see figure 1(a)).

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

### 220 3.1.2 Wright-Fisher updating

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

$$Q_{ij}^{\text{WF}} = (1-\mu)^2 \sum_{k, \ell=1}^N d_{ki} d_{\ell j} Q_{kl}^{\text{WF}}. \quad (6)$$

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

227 Replacing the dispersal probabilities  $d_{ij}$  by their values (given in eq. (2)) and

228 skipping calculation steps (but see Appendix A.2 for details), we obtain:

$$Q_{\text{in}}^{\text{WF}} = \frac{-N_D + M_1 + M_2}{(n-1)N_D + M_1 + M_2}, \quad (7a)$$

$$Q_{\text{out}}^{\text{WF}} = \frac{-\frac{1}{N_D-1}M_1 + M_2}{(n-1)N_D + M_1 + M_2}, \quad (7b)$$

229 with

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

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

232 In the Wright-Fisher life-cycle,  $Q_{\text{in}}^{\text{WF}}$  decreases until  $m = m_c^{\text{WF}} = \frac{d-1}{d}$ , then in-  
233 creases again, while  $Q_{\text{out}}^{\text{WF}}$  follows the opposite pattern. The threshold value  $m_c^{\text{WF}}$   
234 corresponds to an emigration probability so high that an individual's offspring is  
235 as likely to land in its parent's deme as in any other deme (*i.e.*,  $d_{\text{in}} = d_{\text{out}}$ ).

236 The two probabilities of identity by descent go to 1 when the mutation prob-  
237 ability  $\mu$  is very small ( $\mu \rightarrow 0$ ), except if we first assume that the number of demes  
238 is very large ( $N_D \rightarrow \infty$ ); for instance, with this life-cycle as well,  $\lim_{N_D \rightarrow \infty} Q_{\text{out}}^{\text{WF}} =$   
239 0.

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

## 243 3.2 Expected frequencies of altruists for each life-cycle

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

$$\mathbb{E}[\bar{X}] \approx v + \omega \frac{v(1-v)}{\mu} [b(\beta_D - \beta_I) - c(\gamma_D - \gamma_I)]. \quad (8)$$

246 (Calculations leading to eq. (10) are presented in Appendix A.)

247 The mutation bias  $v$  corresponds to the expected proportion of altruists in the  
248 population in the absence of selection (*i.e.*, when  $\omega = 0$ );  $\omega$  is the parameter  
249 that scales the effects of interactions between individuals, which is assumed to  
250 be small. The subscript <sub>D</sub> refers to “direct” effects, and the subscript <sub>I</sub> to “in-  
251 direct” effects. “Direct” effects involve effects on primary beneficiaries of the  
252 benefits ( $b$ ) and costs ( $c$ ) of social interactions (West & Gardner, 2010), *i.e.*, so-  
253 cial interactants (for the benefits  $b$ ) and the focal individuals themselves (for the  
254 costs  $c$ ). “Indirect” effects corresponds to effects on secondary interactants, *i.e.*,  
255 to (kin) competition. By providing a benefit to a deme-mate and thereby increas-  
256 ing its fecundity, a focal altruist indirectly harms others by reducing their relative  
257 fecundity ( $\beta_I$  term in eq. (10)); by having a reduced fecundity due to the cost of  
258 altruism, a focal altruist indirectly favors others by increasing their relative fe-  
259 cundity ( $\gamma_I$  term).

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

### 262 3.2.1 Direct effects

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

tion, they differ between Moran and Wright-Fisher life-cycles):

$$\beta_D^{BD} = \beta_D^{DB} = (1 - \mu) Q_{in}^M, \quad (9a)$$

$$\beta_D^{WF} = (1 - \mu) Q_{in}^{WF}; \quad (9b)$$

$$\gamma_D^{BD} = \gamma_D^{DB} = \gamma_D^{WF} = 1 - \mu. \quad (9c)$$

For both benefits and costs, direct effects only count when there is no mutation (hence the  $(1 - \mu)$  factors). Direct effects of benefits  $b$  (eq. (11a) and eq. (11b)) only count if the interaction takes place with an individual who is identical by descent. With the population structure that we consider, social interactions only occur within demes, so only  $Q_{in}$  is present in eq. (11a) and eq. (11b). On the other hand, the direct effect of the fecundity cost  $c$  (eq. (11c)) does not depend on the type of interactant, since the same cost  $c$  is paid by altruists irrespective of the interactant's identity.

As seen in the previous section,  $Q_{in}^M$  and  $Q_{in}^{WF}$  decrease with the emigration probability  $m$  (actually only until  $m = \frac{d-1}{d}$  for the latter). Consequently, the 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 considered direct effects, we would conclude that more emigration  $m$  is detrimental to the evolution of altruistic behaviour. However, there are also indirect effects at play.

### 3.2.2 Indirect effects

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

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

$$\begin{aligned}\beta_1^{\text{BD}} &= (1 - m) \left( \frac{n-1}{n} Q_{\text{in}}^{\text{M}} + \frac{1}{n} \right) + m Q_{\text{out}}^{\text{M}} - \mu \frac{1 + (n-1)Q_{\text{in}}^{\text{M}} + n(d-1)Q_{\text{out}}^{\text{M}}}{nd} \\ &= \gamma_1^{\text{BD}}.\end{aligned}\quad (10a)$$

293 (Calculation details are presented in Appendix A.)

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

301 Replacing  $Q_{\text{in}}$  and  $Q_{\text{out}}$  by their formula for the Moran life-cycle (eq. (7)), we  
 302 conclude that  $\beta_1^{\text{BD}} = \gamma_1^{\text{BD}}$  are decreasing functions of the emigration probabil-  
 303 ity  $m$  (calculations in the supplementary Mathematica file).

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

308 descent to it. We obtain

$$\begin{aligned}
 \beta_I^{\text{DB}} &= (1 - \mu) \left[ \left( \frac{1}{n} + \frac{(n-1)Q_{\text{in}}^{\text{M}}}{n} \right) \left( (1-m)^2 + \frac{m^2}{(d-1)} \right) \right. \\
 &\quad \left. + Q_{\text{out}}^{\text{M}} \left( 2m(1-m) + (d-2) \frac{m^2}{(d-1)} \right) \right] \\
 &= \gamma_I^{\text{DB}}
 \end{aligned} \tag{10b}$$

309 The brackets in eq. (12b) contain a sum of two terms. The first term corresponds  
 310 two individuals from the same deme (with replacement) whose offspring either  
 311 do not emigrate, or emigrate together to the same deme. The second term cor-  
 312 responds to individuals initially from different demes who end up in the same  
 313 deme (either one of their home demes, or a third deme).

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

316 Replacing  $Q_{\text{in}}$  and  $Q_{\text{out}}$  by their formulas given in eq. (7), we can conclude  
 317 that  $\beta_I^{\text{DB}} = \gamma_I^{\text{DB}}$  first decreases with the emigration probability  $m$ , and increases  
 318 again after a threshold value  $m'_c$ , which is smaller than  $m_c^{\text{WF}} = (d-1)/d$  (calcu-  
 319 lation details are presented in the supplementary Mathematica file).

320 **Wright-Fisher** With this life-cycle, generations are synchronous and all indi-  
 321 viduals again all have the same survival probability (now equal to 0 at all sites).  
 322 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  
 323 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. (9)). Once  
 324 this is done, we see that  $\beta_I^{\text{WF}} = \gamma_I^{\text{WF}}$  first decreases with the emigration probab-  
 325 ility  $m$ , and increases again after the threshold value  $m_c^{\text{WF}} = (d-1)/d$ . This em-  
 326 igration threshold was identified above as the emigration probability such that  
 327 offspring have an equal chance of landing in their natal deme or in any other  
 328 deme, *i.e.*,  $d_{\text{in}} = d_{\text{out}}$  (calculation details are presented in the supplementary  
 329 Mathematica file.)



### 330 3.3 Identifying threshold values of the mutation probability $\mu$

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

#### 337 3.3.1 Moran Birth-Death

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

$$\mu_c^{\text{BD}} = 1 - \frac{b - c + \sqrt{(b - c)(4b(nd)^2 + b - c)}}{2bnd} \quad (11)$$

343 This result is illustrated in figure 2(b); with the parameters of the figure,  $\mu_c^{\text{BD}} \approx$   
 344 0.026.

#### 345 3.3.2 Moran Death-Birth

346 The relationship between  $\mathbb{E}[\bar{X}]$  and  $m$  is a bit more complicated for this life-  
 347 cycle. For simplicity, we concentrate on what happens starting from low emi-  
 348 gration probabilities (*i.e.*, the sign of the slope of  $\mathbb{E}[\bar{X}]$  as a function of  $m$  when  
 349  $m \rightarrow 0$ ). If the benefits  $b$  provided by altruists are relatively low ( $b < c(n + 1)$ ),  
 350  $\mathbb{E}[\bar{X}]$  initially increases with  $m$  provided the mutation probability  $\mu$  is greater  
 351 than a threshold value  $\mu_c^{\text{DB}}$  given in eq. (14) below; otherwise, when the benefits  
 352 are high enough,  $\mathbb{E}[\bar{X}]$  initially increases with  $m$  for any value of  $\mu$ . Combining

353 these results, we write

$$\mu_c^{\text{DB}} = \begin{cases} \frac{(n+1)c - b}{(2n-1)b - (n-1)c} & \text{if } b < c(n+1), \\ 0 & \text{otherwise.} \end{cases} \quad (12)$$

354 In figure 2(a), the parameters are such that  $\mu_c^{\text{DB}} = 0$ .

355 The expected frequency of altruists  $\mathbb{E}[\bar{X}]$  then reaches a maximum at an em-  
 356 igration probability  $m_c^{\text{DB}}$  (whose complicated equation is given in the supple-  
 357 imentary Mathematica file), as can be seen in figure 2(a). When the mutation  
 358 probability gets close to 0 ( $\mu \rightarrow 0$ ),  $m_c^{\text{DB}}$  also gets close to 0,

### 359 3.3.3 Wright-Fisher

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

$$\mu_c^{\text{WF}} = 1 - \sqrt{1 - \frac{c}{b}}, \quad (13)$$

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

## 364 3.4 Relaxing key assumptions

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

371 To relax the assumption of equal deme sizes, we randomly drew deme sizes  
 372 at the beginning of simulations, with sizes ranging from 2 to 6 individuals and

on average  $\bar{n} = 4$  individuals per deme as previously. As shown in figure S2, the patterns initially obtained with a homogeneous population structure are robust when the structure is heterogeneous.

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

## 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 2(b)–(c)) or favorable (Taylor et al., 2007a, and dashed lines in figure 2(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

398 of population viscosity. Often however, evolutionary success is measured quali-  
 399 tatively, by comparing a quantity (an expected frequency, or, in models with no  
 400 mutation, a probability of fixation) to the value it would have in the absence of  
 401 selection. In our model, this amounts to saying that altruism is favored whenever  
 402  $\mathbb{E}[\bar{X}] > \nu$  ( $\nu$  is plotted as a horizontal dashed line in figure 2). Some of our con-  
 403 clusions change if we switch to this qualitative measure of evolutionary success:  
 404 Under the Moran Birth-Death and Wright-Fisher life-cycles, population viscosity  
 405 does not promote the evolution of altruism – actually, these two life-cycles can-  
 406 not ever promote altruistic behavior for any regular population structure (Taylor  
 407 et al., 2011), whichever the probability of mutation (Débarre, 2017). However,  
 408 under a Moran Death-Birth life-cycle, altruism can be favored only at interme-  
 409 diate emigration probabilities (figure 2(a)): increased emigration can still favor  
 410 the evolution of altruism under this qualitative criterion.

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

412 To explain how the frequency of altruists can increase with the emigration prob-  
 413 ability  $m$ , let us go back to the decomposition of the expected frequency of altru-  
 414 ists in the population  $\mathbb{E}[\bar{X}]$  into different terms (eq. (10)). For all the life-cycles  
 415 that we consider, the direct effect of helping others ( $\beta_D$ ) decreases with emigra-  
 416 tion  $m$ , while the direct effect of the cost of helping ( $\gamma_D$ ) does not change with  
 417  $m$ . If we (erroneously) considered only direct effects, we would conclude that  
 418 the expected proportion of altruists decreases with the emigration probability  
 419  $m$ , because an increase in  $m$  reduces the probability that two interactants (two  
 420 deme-mates in this model) are identical by descent. But this explanation ignores  
 421 indirect, competitive, effects. In the three life-cycles that we considered,  $\beta_I = \gamma_I$ ,  
 422 so the overall indirect effects are given by  $-(b - c)\beta_I$ . Hence, any increase of  
 423  $\mathbb{E}[\bar{X}]$  with  $m$  is driven by  $\beta_I$ . Indirect effects correspond to competition: helping  
 424 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 ( $\mu$ ), in particular because probabilities of identity by descent depend on  $\mu$ .

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

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

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

## 449 **Imperfect transmission and Rebellious Children**

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

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

## 463 **Interactions and dispersal graphs**

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

## 474 Coevolution of dispersal and social behavior

475 This work also raises the question of what would happen if dispersal (*e.g.*, the  
476 emigration probability  $m$ ) could evolve as well. Recent work on the topic has  
477 shown that under some conditions disruptive selection could take place, lead-  
478 ing to a polymorphism between sessile altruists and mobile defectors (Parvinen,  
479 2013; Mullon et al., 2017). The assumptions of these studies however differ from  
480 ours in important ways, in that they consider continuous traits and use an adap-  
481 tive dynamics framework, where, notably, mutations are assumed to be very  
482 rare. It remains to be investigated how non-rare and potentially large mutations  
483 would affect their result.

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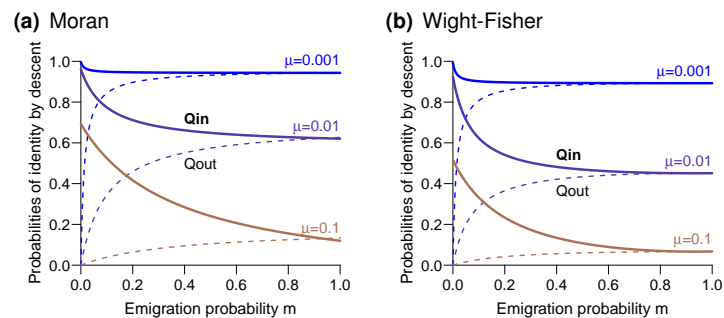
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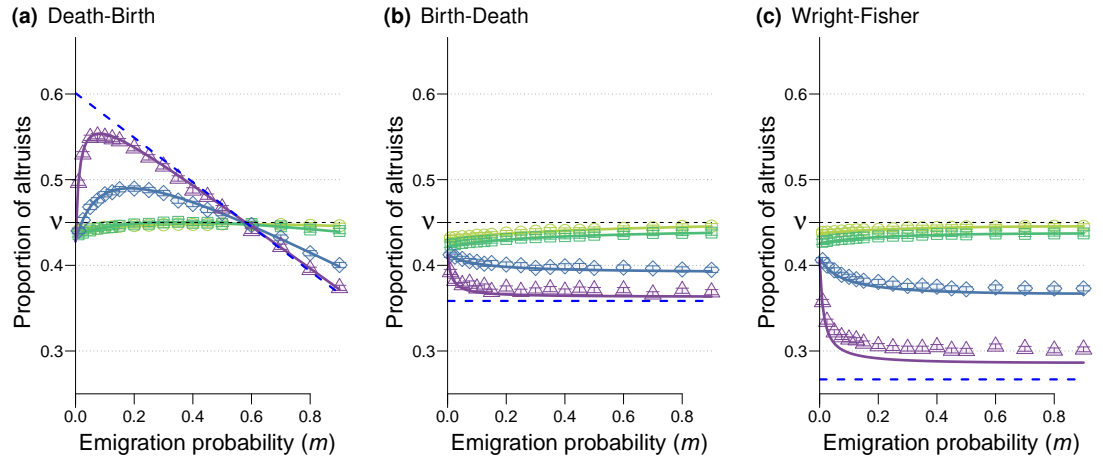
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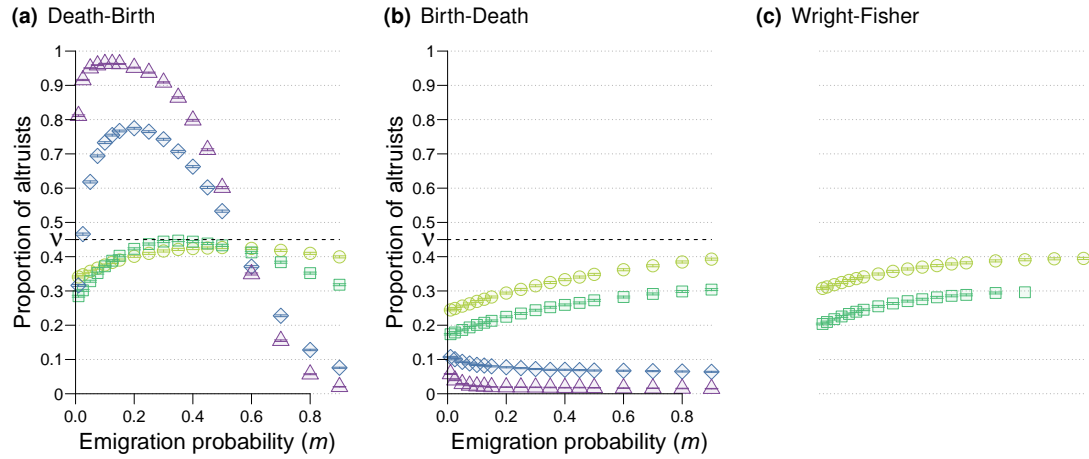
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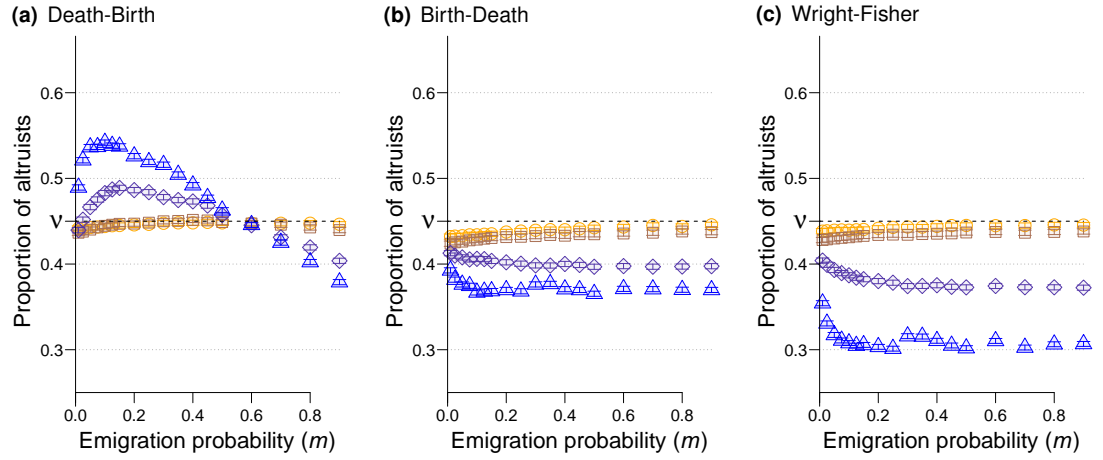
**Figure 1:** Probabilities of identity by descent, for two different individuals within the same deme ( $Q_{in}$ , full curves) and two individuals in different demes ( $Q_{out}$ , dashed curves), as a function of the emigration probability  $m$ , for different values of the mutation probability  $\mu$  (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.



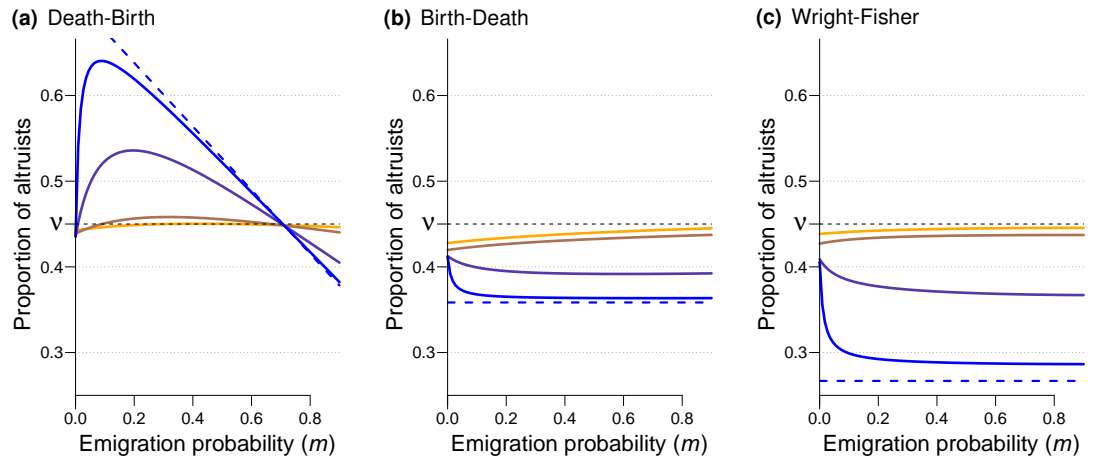
**Figure 2:** Expected proportion of altruists under weak selection, as a function of the emigration probability  $m$ , for different mutation values ( $\mu = 0.001$  (blue, dots),  $0.01$  (purple, squares),  $0.1$  (brown, diamonds),  $0.25$  (orange, triangles); the dashed blue lines correspond to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



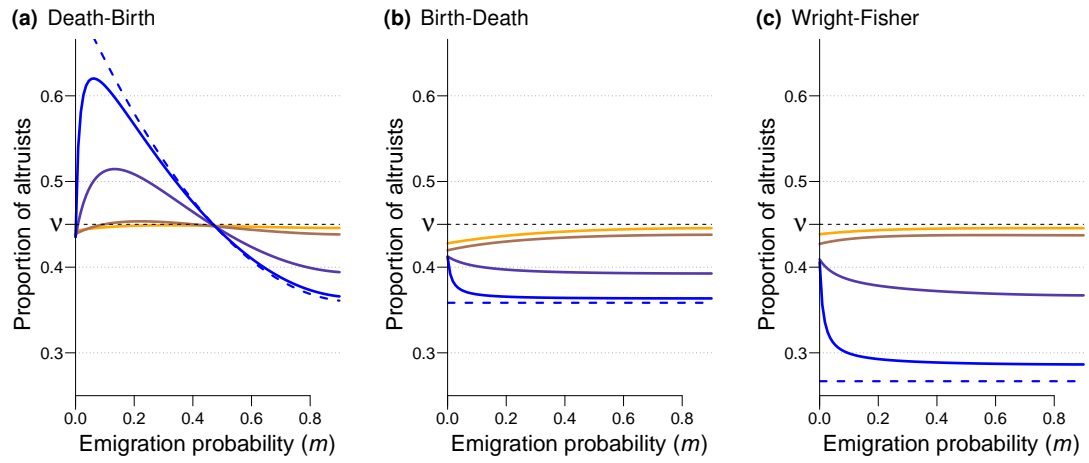
**Figure S1:** Equivalent of figure 2 (simulations only) but with strong selection ( $\omega = 0.1$ ); please note the change of scale on the vertical axis. All other parameters and legends are identical to those of figure 2 (increasing mutation probabilities from blue dots to orange triangles).



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



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



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

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

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



## Appendix

### A Expected frequency of altruists

*Note: The calculation steps are the same as the ones presented in Débarre (2017); they are presented here so that the article is self-contained, but there are no new results in Appendix A.*

In this section, we work with a generic regular population structure (with symmetries such that all individuals behave the same way in expectation), of which the island model is a particular case.

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

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  $B_{ji}(X(t), \omega)$ , 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  $t$ . We denote by  $D_i(X(t), \omega)$  ( $D_i$  for simplicity) the probability that the individual living at site  $i$  at time  $t$  has been replaced (*i.e.*, died) at time  $t+1$ . Both 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	$B_{ij}$	$D_i$
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

**Table S2:** Formulas of  $B_{ij}$  and  $D_i$  for each of the life-cycles 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. (1).

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

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

600 holds for all sites  $i$ . The structure of the population is also such that in the ab-  
 601 sence of selection ( $\omega = 0$ , so that  $f_i = 1$  for all sites  $1 \leq i \leq N$ ), all individuals have  
 602 the same probability of dying and the same probability of having successful off-  
 603 spring (*i.e.*, of having offspring that become adults at the next time step), so that  
 604

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

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

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

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

612 The first term within the brackets corresponds to births: the type of the individ-  
 613 ual living at  $i$  at time  $t + 1$  depends on the type of its parent (living at site  $j$ ), and  
 614 on whether mutation occurred. The second term in the brackets of eq. (A.2a)  
 615 corresponds to the survival of the individual living at site  $i$ .

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

$$0 = \frac{1}{N} \sum_{\mathbf{X} \in \Omega} \sum_{i=1}^N \left[ \sum_{j=1}^N B_{ij} (X_j(1-\mu) + \mu\nu) - D_i X_i \right] \xi(\mathbf{X}, \omega, \mu). \quad (\text{A.3})$$

623 Now, we use the assumption of weak selection ( $\omega \ll 1$ ) and consider the first-  
 624 order expansion of eq. (A.3) for  $\omega$  close to 0. First, we note that in the absence  
 625 of selection ( $\omega = 0$ ), the population is at a mutation-drift balance; the expected  
 626 state of every site  $i$  is then  $\mathbb{E}_0[X_i] = \sum_{\mathbf{X} \in \Omega} X_i \xi(\mathbf{X}, 0, \mu) = \nu$  (recall that  $\nu$  is the mu-  
 627 tation bias parameter). Secondly, we further expand derivatives of  $B_{ji}$  and  $D_i$   
 628 thanks to the chain rule, using the variables  $f_k$  ( $1 \leq k \leq N$ ), corresponding to in-  
 629 dividual fecundities (also, recall that  $f_k = 1$  when  $\omega = 0$ ). Thirdly, we note that for

all the life-cycles that we consider, the total number of deaths in the population during one time step does not depend on population composition (it is exactly 1 death for the Moran life-cycles, and exactly  $N$  for the Wright-Fisher life-cycle), so that  $\sum_{i,j=1}^N B_{ij}$  does not depend on  $\omega$ . After simplification and reorganization, the first order expansion of eq. (A.3) yields

$$0 = \frac{1}{N} \sum_{i,k=1}^N \left[ \frac{\partial \left( \sum_{j=1}^N (1-\mu) B_{ji} - D_i \right)}{\partial f_k} \right]_{f_k=1} \times \left( \sum_{\ell=1}^N e_{\ell k} b \sum_{X \in \Omega} X_{\ell} X_i \xi(\mathbf{X}, 0, \mu) - c \sum_{X \in \Omega} X_k X_i \xi(\mathbf{X}, 0, \mu) \right) - B^* \mu \frac{\partial \mathbb{E}[\bar{X}]}{\partial \omega} \Big|_{\omega=0} + O(\omega^2). \quad (\text{A.4})$$

The terms  $\sum_{X \in \Omega} X_i X_j \xi(\mathbf{X}, 0, \mu)$ , that we will 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

$$P_{ij} = v^2 + v(1-v)Q_{ij}. \quad (\text{A.5})$$

In Appendix A.2, we will see that recursions on  $P_{ij}$  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

$$\mathbb{E}[\bar{X}] = v + \omega \frac{\partial \mathbb{E}[\bar{X}]}{\partial \omega} \Big|_{\omega=0} + O(\omega^2), \quad (\text{A.6})$$

where  $\frac{\partial \mathbb{E}[\bar{X}]}{\partial \omega} \Big|_{\omega=0}$  is obtained from eq. (A.4). We then need to replace the  $B_{ij}$  and  $D_j$  terms by their formulas for each life-cycle (given in table S2), and the  $d_{ij}$  and  $e_{ij}$  terms by their formulas (given in eq. (2)) and eq. (??), respectively). For each life-cycle we can group terms as

$$\frac{\partial \mathbb{E}[\bar{X}]}{\partial \omega} \Big|_{\omega=0} \approx \frac{v(1-v)}{\mu} [b(\beta_D - \beta_I) - c(\gamma_D - \gamma_I)], \quad (\text{A.7})$$

where D terms come from the numerators of  $B_{ij}$  and  $D_i$ , and I terms come from the denominator of  $B_{ij}$  and  $D_i$ ; replacing  $B_{ij}$  and  $D_i$  by their formulas given in table S2, we obtain the following sets of equations for each life-cycle:

### Moran Birth-Death

$$\beta_D^{BD} = \sum_{k,\ell=1}^N \frac{1-\mu}{N} e_{k\ell} Q_{\ell k}^M, \quad (\text{A.8a})$$

$$\beta_I^{BD} = \sum_{j,k,\ell=1}^N \left( \frac{d_{\ell j}}{N} - \frac{\mu}{N^2} \right) e_{k\ell} Q_{jk}^M, \quad (\text{A.8b})$$

$$\gamma_D^{BD} = 1 - \mu, \quad (\text{A.8c})$$

$$\gamma_I^{BD} = \sum_{j,k=1}^N \left( \frac{d_{kj}}{N} - \frac{\mu}{N^2} \right) Q_{jk}^M. \quad (\text{A.8d})$$

### Moran Death-Birth

$$\beta_D^{DB} = \sum_{k,\ell=1}^N \frac{1-\mu}{N} e_{k\ell} Q_{\ell k}^M, \quad (\text{A.9a})$$

$$\beta_I^{DB} = (1 - \mu) \sum_{i,j,k,\ell=1}^N \frac{d_{ji} d_{\ell i}}{N} e_{k\ell} Q_{jk}^M, \quad (\text{A.9b})$$

$$\gamma_D^{DB} = 1 - \mu, \quad (\text{A.9c})$$

$$\gamma_I^{DB} = (1 - \mu) \sum_{i,j,k=1}^N \frac{d_{ji} d_{ki}}{N} Q_{jk}^M. \quad (\text{A.9d})$$

### Wright-Fisher

$$\beta_D^{WF} = \sum_{k,\ell=1}^N \frac{1-\mu}{N} e_{k\ell} Q_{\ell k}^{WF}, \quad (\text{A.10a})$$

$$\beta_I^{WF} = (1 - \mu) \sum_{i,j,k,\ell=1}^N \frac{d_{ji} d_{\ell i}}{N} e_{k\ell} Q_{jk}^{WF}, \quad (\text{A.10b})$$

$$\gamma_D^{WF} = 1 - \mu, \quad (\text{A.10c})$$

$$\gamma_I^{WF} = (1 - \mu) \sum_{i,j,k=1}^N \frac{d_{ji} d_{ki}}{N} Q_{jk}^{WF}. \quad (\text{A.10d})$$

System (A.10) is the same set of equations as for the Moran Death-Birth model (system (A.1)), except for the values of probabilities of identity by descent... that we now need to compute.

## A.2 Probabilities of identity by descent

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

### 659 A.2.1 Moran model

660 In a Moran model, exactly one individual dies and one individual reproduces  
 661 during one time step. Given a state  $\mathbf{X}$  at time  $t$ , at time  $t + 1$  both sites  $i$  and  
 662  $j \neq i$  are occupied by altruists, if  $i$  it was the case at time  $t$  and neither site was  
 663 replaced by a non-altruist (first term in eq. (A.11)), or  $ij$  if exactly one of the two  
 664 sites was occupied by a non-altruist at time  $t$ , but the site was replaced by an  
 665 altruist (second and third terms of eq. (A.11)):

$$\begin{aligned} \mathbb{E}[X_i X_j(t+1) | X(t) = \mathbf{X}] = & X_i X_j \left( 1 - \sum_{k=1}^N \frac{1}{N} (d_{ki} + d_{kj}) ((1 - X_k)(1 - \mu) + \mu(1 - \nu)) \right) \\ & + X_i(1 - X_j) \sum_{k=1}^N \frac{1}{N} d_{kj} (X_k(1 - \mu) + \mu\nu) \\ & + X_j(1 - X_i) \sum_{k=1}^N \frac{1}{N} d_{ki} (X_k(1 - \mu) + \mu\nu). \end{aligned} \quad (\text{A.11})$$

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

$$P_{ij} = \frac{1}{2} \left( \sum_{k=1}^N (1 - \mu) (d_{kj} P_{ki} + d_{ki} P_{kj}) \right) + \mu\nu^2 \quad (i \neq j), \quad (\text{A.12})$$

668 while  $P_{ii} = \nu$ .

669 Now we substitute  $P_{ij} = \nu^2 + \nu(1 - \nu)Q_{ij}$  in eq. (A.12), we obtain

$$Q_{ij} = \frac{1}{2} \sum_{k=1}^N (1 - \mu) (d_{ki} Q_{kj} + d_{kj} Q_{ki}), \quad (\text{A.13})$$

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

### 675 A.2.2 Wright-Fisher model

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

$$\begin{aligned} \mathbb{E}[X_i X_j(t+1) | X(t) = \mathbf{X}] = & \sum_{k, \ell=1}^N d_{ki} d_{\ell j} \left( X_k X_\ell (1 - \mu + \mu\nu)^2 \right. \\ & + (X_k(1 - X_\ell) + (1 - X_k)X_\ell) (1 - \mu + \mu\nu)(\mu\nu) \\ & \left. + (1 - X_k)(1 - X_\ell)(\mu\nu)^2 \right) \end{aligned} \quad (\text{A.14})$$

678 The first term of eq. (A.14) corresponds to both parents being altruists, and hav-  
 679 ing altruist offspring; the second line corresponds to exactly one parent being  
 680 altruist, and the third line to both parents being non-altruists (in this latter case,  
 681 the two offspring have to be both mutants to be altruists).  
 682 Taking the expectation and simplifying, we obtain

$$P_{ij} = \sum_{k,\ell=1}^N (P_{kl}(1-\mu)^2) + (2-\mu)\mu v^2. \quad (\text{A.15})$$

683 Replacing  $P_{ij}$  by  $v^2 + v(1-v)Q_{ij}$ , eq. (A.15) becomes

$$Q_{ij} = \sum_{k,\ell=1}^N d_{ki}d_{\ell j}Q_{k\ell}(1-\mu)^2. \quad (\text{A.16})$$

684 Again,  $Q_{ij}$  corresponds to a probability of identity by descent: the individuals at  
 685 sites  $i$  and  $j$  are identical by descent if their parents were and if neither mutated  
 686  $((1-\mu)^2)$ .

## 687 B In a subdivided population

### 688 B.1 $\beta$ and $\gamma$

689 Now, we need to adapt the results presented in Appendix A to our structure of  
 690 interest, a subdivided population, with dispersal and interaction probabilities  
 691 given by eq. (2) and eq. (??). For the  $\beta$  and  $\gamma$  terms, we use a brute-force ap-  
 692 proach, replacing  $d_{ij}$  and  $e_{ij}$  by their values in a subdivided population, and  
 693 simplifying the equations (for instance, there are 60 different cases to consider  
 694 for the four sums that appear in  $\beta_1^{\text{DB}}$ , shown in the table in section B.4 below).  
 695 The calculations and subsequent simplifications are detailed in the supplemen-  
 696 tary Mathematica file, and the results are presented in the main text (system (11),  
 697 eq. (12a), and eq. (12b)).

### 698 B.2 Probabilities of identity by descent

699 For the probabilities of identity by descent, we could also use a brute-force ap-  
 700 proach, but calculations are faster if we use formulas derived in Débarre (2017)  
 701 for “two-dimensional population structures”. The name comes from the fact that  
 702 we only need two types of transformations to go from any site to any other site  
 703 in the population: permutations on the deme index, and permutations on the  
 704 within-deme index.

705 We rewrite site labels ( $1 \leq i \leq N$ ) as  $(\ell_1, \ell_2)$ , where  $\ell_1$  is the index of the deme  
 706 ( $1 \leq \ell_1 \leq N_D$ ) and  $\ell_2$  the position of the site within the deme ( $1 \leq \ell_2 \leq n$ ). Then,  
 707 we introduce notations  $\tilde{d}_{i_1}^{i_2}$  and  $\tilde{Q}_{i_1}^{i_2}$ , that correspond to the dispersal probab-  
 708 ity and probability of identity by descent to a site at distances  $i_1$  and  $i_2$  in the  
 709 among-demes and within-deme dimensions (e.g.,  $\tilde{d}_{i_1}^{i_2} = d_{j_1 j_1 + i_1}^{j_2' j_2 + i_2}$ ).

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

#### 712 B.2.1 Moran model

713 In Débarre (2017), it was shown that

$$\tilde{Q}_{r_1}^{r_2} = \frac{1}{N} \sum_{q_1=0}^{N_1-1} \sum_{q_2=0}^{N_2-1} \frac{\mu \lambda'_M}{1 - (1 - \mu) \tilde{D}_{q_1}^{q_2}} \exp\left(i \frac{2\pi q_1 r_1}{N_1}\right) \exp\left(i \frac{2\pi q_2 r_2}{N_2}\right) \quad (\text{B.17a})$$

714 with

$$\tilde{D}_{q_1}^{q_2} = \sum_{\ell_1=0}^{N_1-1} \sum_{\ell_2=0}^{N_2-1} \tilde{d}_{\ell_1}^{\ell_2} \exp\left(-i \frac{2\pi q_1 \ell_1}{N_1}\right) \exp\left(-i \frac{2\pi q_2 \ell_2}{N_2}\right), \quad (\text{B.17b})$$

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

$$\begin{aligned}\tilde{D}_{q_1} &= d_{\text{self}} + \sum_{\ell_2=1}^{N_2-1} d_{\text{in}} \exp\left(-\iota \frac{2\pi q_2 \ell_2}{N_2}\right) + \sum_{\ell_1=1}^{N_1-1} \sum_{\ell_2=0}^{N_2-1} d_{\text{out}} \exp\left(-\iota \frac{2\pi q_1 \ell_1}{N_1}\right) \exp\left(-\iota \frac{2\pi q_2 \ell_2}{N_2}\right) \\ &= d_{\text{self}} + (\delta_{q_2}(N_2 - 1) + (1 - \delta_{q_2})(-1)) d_{\text{in}} + (\delta_{q_1}(N_1 - 1) + (1 - \delta_{q_1})(-1)) (\delta_{q_2} N_2) d_{\text{out}} \\ &= d_{\text{self}} + (\delta_{q_2} N_2 - 1) d_{\text{in}} + (\delta_{q_1} N_1 - 1) \delta_{q_2} N_2 d_{\text{out}}.\end{aligned}\quad (\text{B.18a})$$

717 ( $\delta_q$  is equal to 1 when  $q$  is equal to 0 modulo the relevant dimension, and to 0  
718 otherwise). So for the three types of distances that we need to consider (distance  
719 0, distance to another deme-mate, distance to individual in another deme), and  
720 with  $N_1 = N_D$  and  $N_2 = n$ , we obtain

$$\tilde{D}_0 = 1, \quad (\text{B.19a})$$

$$\tilde{D}_0^{q_1} = 1 - m - \frac{m}{d-1} \quad (q_1 \not\equiv 0 \pmod{N_1}), \quad (\text{B.19b})$$

$$\tilde{D}_{q_1}^{q_2} = d_{\text{self}} - d_{\text{in}} \quad (q_2 \not\equiv 0 \pmod{N_2}). \quad (\text{B.19c})$$

721 So for  $\tilde{Q}$ , using system (B.19) in eq. (B.17a),

$$\begin{aligned}\tilde{Q}_{r_1} &= \frac{\mu \lambda'_M}{N} \left[ \frac{1}{1 - (1 - \mu) \tilde{D}_0} + \sum_{q_2=1}^{N_2-1} \frac{1}{1 - (1 - \mu) \tilde{D}_0^{q_2}} \exp\left(-\iota \frac{2\pi q_2 r_2}{N_2}\right) \right. \\ &\quad + \sum_{q_1=1}^{N_1-1} \frac{1}{1 - (1 - \mu) \tilde{D}_0^{q_1}} \exp\left(-\iota \frac{2\pi q_1 r_1}{N_1}\right) \\ &\quad \left. + \sum_{q_1=1}^{N_1-1} \sum_{q_2=1}^{N_2-1} \frac{1}{1 - (1 - \mu) \tilde{D}_{q_1}^{q_2}} \exp\left(-\iota \frac{2\pi q_1 r_1}{N_1}\right) \exp\left(-\iota \frac{2\pi q_2 r_2}{N_2}\right) \right] \\ &= \frac{\mu \lambda'_M}{N} \left[ \frac{1}{1 - (1 - \mu)} + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})} (\delta_{r_2} N_2 - 1) \right. \\ &\quad + \frac{1}{1 - (1 - \mu)(1 - m - \frac{m}{d-1})} (\delta_{r_1} N_1 - 1) \\ &\quad \left. + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})} (\delta_{r_1} N_1 - 1)(\delta_{r_2} N_2 - 1) \right].\end{aligned}\quad (\text{B.20})$$

722 In particular,

$$\begin{aligned}\tilde{Q}_0 &= \frac{\mu \lambda'_M}{N} \left[ \frac{1}{\mu} + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})} (n - 1) + \frac{1}{1 - (1 - \mu)(1 - m - \frac{m}{d-1})} (D - 1) \right. \\ &\quad \left. + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})} (D - 1)(n - 1) \right] \\ &= 1.\end{aligned}\quad (\text{B.21a})$$



723 We find  $\lambda'_M$  using the eq. (B.21a). Going back to eq. (B.20), when  $r_1 = 0$ , the two  
724 individuals are in the same deme. They are different when  $r_2 \neq 0$ , and so:

$$Q_{\text{in}} = \frac{\mu\lambda'_M}{N} \left[ \frac{1}{\mu} + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})}(-1) + \frac{1}{1 - (1 - \mu)(1 - m - \frac{m}{d-1})}(D-1) \right. \\ \left. + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})}(D-1)(-1) \right]. \quad (\text{B.21b})$$

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

$$Q_{\text{out}} = \frac{\mu\lambda'_M}{N} \left[ \frac{1}{\mu} + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})}(-1) + \frac{1}{1 - (1 - \mu)(1 - m - \frac{m}{d-1})}(-1) \right. \\ \left. + \frac{1}{1 - (1 - \mu)(d_{\text{self}} - d_{\text{in}})} \right]. \quad (\text{B.21c})$$

726 With  $d_{\text{self}} = d_{\text{in}} = (1 - m)/n$ , we recover the equations given in the main text (sys-  
727 tem (7)).

### 728 B.3 Wright-Fisher

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

$$\tilde{Q}_{r_1, r_2} = \frac{1}{N} \sum_{q_1=0}^{N_1-1} \sum_{q_2=0}^{N_2-1} \frac{\mu\lambda'_{WF}}{1 - (1 - \mu)^2 (\tilde{D}_{q_1})^2} \exp\left(-i \frac{2\pi q_1 r_1}{N_1}\right) \exp\left(-i \frac{2\pi q_2 r_2}{N_2}\right), \quad (\text{B.22})$$

730 with  $\tilde{\mathcal{D}}$  given in eq. (B.17b). In a subdivided population, with  $N_1 = N_D$  and  $N_2 =$   
 731  $n$ , this becomes

$$\begin{aligned}
 \tilde{Q}_{r_1} &= \frac{1}{N} \left[ \frac{\mu \lambda'_{WF}}{1 - (1 - \mu)^2 (\tilde{\mathcal{D}}_0)^2} + \sum_{q_2=1}^{N_2-1} \frac{\mu \lambda'_{WF}}{1 - (1 - \mu)^2 (\tilde{\mathcal{D}}_{q_2})^2} \exp\left(-i \frac{2\pi q_2 r_2}{N_2}\right) \right. \\
 &\quad + \sum_{q_1=1}^{N_1-1} \frac{\mu \lambda'_{WF}}{1 - (1 - \mu)^2 (\tilde{\mathcal{D}}_{q_1})^2} \exp\left(-i \frac{2\pi q_1 r_1}{N_1}\right) \\
 &\quad \left. + \sum_{q_1=1}^{N_1-1} \sum_{q_2=1}^{N_2-1} \frac{\mu \lambda'_{WF}}{1 - (1 - \mu)^2 (\tilde{\mathcal{D}}_{q_1})^2} \exp\left(-i \frac{2\pi q_1 r_1}{N_1}\right) \exp\left(-i \frac{2\pi q_2 r_2}{N_2}\right) \right] \\
 &= \frac{\mu \lambda'_{WF}}{N} \left[ \frac{1}{1 - (1 - \mu)^2} + \frac{1}{1 - (1 - \mu)^2 (d_{\text{self}} - d_{\text{in}})^2} (\delta_{q_2} N_2 - 1) \right. \\
 &\quad + \frac{1}{1 - (1 - \mu)^2 (1 - m - \frac{m}{d-1})^2} (\delta_{q_1} N_1 - 1) \\
 &\quad \left. + \frac{1}{1 - (1 - \mu)^2 (d_{\text{self}} - d_{\text{in}})^2} (\delta_{q_1} N_1 - 1) (\delta_{q_2} N_2 - 1) \right] \\
 &= \frac{\mu \lambda'_{WF}}{N} \left[ \frac{1}{1 - (1 - \mu)^2} + \frac{1}{1 - (1 - \mu)^2 (d_{\text{self}} - d_{\text{in}})^2} (\delta_{q_2} N_2 - 1) \delta_{q_1} N_1 \right. \\
 &\quad \left. + \frac{1}{1 - (1 - \mu)^2 (1 - m - \frac{m}{d-1})^2} (\delta_{q_1} N_1 - 1) \right]. \tag{B.23}
 \end{aligned}$$

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

$$1 = \frac{\mu \lambda'_{WF}}{N} \left[ \frac{1}{1 - (1 - \mu)^2} + \frac{1}{1 - (1 - \mu)^2 (d_{\text{self}} - d_{\text{in}})^2} (N_2 - 1) N_1 + \frac{1}{1 - (1 - \mu)^2 (1 - m - \frac{m}{d-1})^2} (N_1 - 1) \right]. \tag{B.24a}$$

733 Then from eq. (B.23) we deduce

$$Q_{\text{in}} = \frac{\mu \lambda'_{WF}}{N} \left[ \frac{1}{1 - (1 - \mu)^2} - \frac{1}{1 - (1 - \mu)^2 (d_{\text{self}} - d_{\text{in}})^2} N_1 + \frac{1}{1 - (1 - \mu)^2 (1 - m - \frac{m}{d-1})^2} (N_1 - 1) \right]. \tag{B.24b}$$

734 and

$$Q_{\text{out}} = \frac{\mu \lambda'_{WF}}{N} \left[ \frac{1}{1 - (1 - \mu)^2} - \frac{1}{1 - (1 - \mu)^2 (1 - m - \frac{m}{d-1})^2} \right]. \tag{B.24c}$$

735 With  $d_{\text{self}} = d_{\text{in}} = (1 - m)/n$ , we recover the equations given in the main text (sys-  
 736 tem (9)).

737 **B.4 Unpacking  $\beta_i^{\text{DB}}$** 

738 The table below contains all combinations for  $i, j, k, l$  involved in the four sums.  $(i, j)$ : means  
 739 that  $i$  and  $j$  are different sites in the same deme;  $G_i$ : deme containing site  $i$ .

	$j$	$k$	$l$	Notation	Count	$d_{ji}$	$d_{li}$	$e_{kl}$	$Q_{jk}$
1	$j = i$	$k = i$	$l = i$	$(i = j = k = l)$	1	$d_{\text{self}}$	$d_{\text{self}}$	$e_{\text{self}}$	1
2	$j = i$	$k = i$	$l \neq i; l \in G_i$	$(i = j = k, l)$	$n - 1$	$d_{\text{self}}$	$d_{\text{in}}$	$e_{\text{in}}$	1
3	$j = i$	$k = i$	$l \notin G_i$	$(i = j = k), (l)$	$N - n$	$d_{\text{self}}$	$d_{\text{out}}$	$e_{\text{out}}$	1
4	$j = i$	$k \neq i; k \in G_i$	$l = i$	$(i = j = l, k)$	$n - 1$	$d_{\text{self}}$	$d_{\text{self}}$	$e_{\text{in}}$	$Q_{\text{in}}$
5	$j = i$	$k \neq i; k \in G_i$	$l = k$	$(i = j, k = l)$	$n - 1$	$d_{\text{self}}$	$d_{\text{in}}$	$e_{\text{self}}$	$Q_{\text{in}}$
6	$j = i$	$k \neq i; k \in G_i$	$l \neq i, k; l \in G_i$	$(i = j, k, l)$	$(n - 1)(n - 2)$	$d_{\text{self}}$	$d_{\text{in}}$	$e_{\text{in}}$	$Q_{\text{in}}$
7	$j = i$	$k \neq i; k \in G_i$	$l \notin G_i$	$(i = j, k), (l)$	$(n - 1)(N - n)$	$d_{\text{self}}$	$d_{\text{out}}$	$e_{\text{out}}$	$Q_{\text{in}}$
8	$j = i$	$k \notin G_i$	$l = i = j$	$(i = j = l), (k)$	$(N - n)$	$d_{\text{self}}$	$d_{\text{self}}$	$e_{\text{out}}$	$Q_{\text{out}}$
9	$j = i$	$k \notin G_i$	$l \neq i, l \in G_i$	$(i = j, l), (k)$	$(N - n)(n - 1)$	$d_{\text{self}}$	$d_{\text{in}}$	$e_{\text{out}}$	$Q_{\text{out}}$
10	$j = i$	$k \notin G_i$	$l = k$	$(i = j), (k = l)$	$(N - n)$	$d_{\text{self}}$	$d_{\text{out}}$	$e_{\text{self}}$	$Q_{\text{out}}$
11	$j = i$	$k \notin G_i$	$l \neq k; l \in G_k$	$(i = j), (k, l)$	$(N - n)(n - 1)$	$d_{\text{self}}$	$d_{\text{out}}$	$e_{\text{in}}$	$Q_{\text{out}}$
12	$j = i$	$k \notin G_i$	$l \notin G_i, G_k$	$(i = j), (k), (l)$	$(N - n)(N - 2n)$	$d_{\text{self}}$	$d_{\text{out}}$	$e_{\text{out}}$	$Q_{\text{out}}$
13	$j \neq i, j \in G_i$	$k = i$	$l = i$	$(i = k = l, j)$	$(n - 1)$	$d_{\text{in}}$	$d_{\text{self}}$	$e_{\text{self}}$	$Q_{\text{in}}$
14	$j \neq i, j \in G_i$	$k = i$	$l = j$	$(i = k, j = l)$	$(n - 1)$	$d_{\text{in}}$	$d_{\text{in}}$	$e_{\text{in}}$	$Q_{\text{in}}$
15	$j \neq i, j \in G_i$	$k = i$	$l \neq i, j; l \in G_i$	$(i = k, j, l)$	$(n - 1)(n - 2)$	$d_{\text{in}}$	$d_{\text{in}}$	$e_{\text{in}}$	$Q_{\text{in}}$
16	$j \neq i, j \in G_i$	$k = i$	$l \notin G_i$	$(i = k, j), (l)$	$(n - 1)(N - n)$	$d_{\text{in}}$	$d_{\text{out}}$	$e_{\text{out}}$	$Q_{\text{in}}$
17	$j \neq i, j \in G_i$	$k = j$	$l = i$	$(i = l, j = k)$	$(n - 1)$	$d_{\text{in}}$	$d_{\text{self}}$	$e_{\text{in}}$	1
18	$j \neq i, j \in G_i$	$k = j$	$l = j$	$(i, j = k = l)$	$(n - 1)$	$d_{\text{in}}$	$d_{\text{in}}$	$e_{\text{self}}$	1
19	$j \neq i, j \in G_i$	$k = j$	$l \neq i, j; l \in G_i$	$(i, j = k, l)$	$(n - 1)(n - 2)$	$d_{\text{in}}$	$d_{\text{in}}$	$e_{\text{in}}$	1
20	$j \neq i, j \in G_i$	$k = j$	$l \notin G_i$	$(i, j = k), (l)$	$(n - 1)(N - n)$	$d_{\text{in}}$	$d_{\text{out}}$	$e_{\text{out}}$	1
21	$j \neq i, j \in G_i$	$k \neq i, j; k \in G_i$	$l = i$	$(i = l, j, k)$	$(n - 1)(n - 2)$	$d_{\text{in}}$	$d_{\text{self}}$	$e_{\text{in}}$	$Q_{\text{in}}$
22	$j \neq i, j \in G_i$	$k \neq i, j; k \in G_i$	$l = j$	$(i, j = l, k)$	$(n - 1)(n - 2)$	$d_{\text{in}}$	$d_{\text{in}}$	$e_{\text{in}}$	$Q_{\text{in}}$
23	$j \neq i, j \in G_i$	$k \neq i, j; k \in G_i$	$l = k$	$(i, j, k = l)$	$(n - 1)(n - 2)$	$d_{\text{in}}$	$d_{\text{in}}$	$e_{\text{self}}$	$Q_{\text{in}}$
24	$j \neq i, j \in G_i$	$k \neq i, j; k \in G_i$	$l \neq i, j, k; l \in G_i$	$(i, j, k, l)$	$(n - 1)(n - 2)(n - 3)$	$d_{\text{in}}$	$d_{\text{in}}$	$e_{\text{in}}$	$Q_{\text{in}}$
25	$j \neq i, j \in G_i$	$k \neq i, j; k \in G_i$	$l \notin G_i$	$(i, j, k), (l)$	$(n - 1)(n - 2)(N - n)$	$d_{\text{in}}$	$d_{\text{out}}$	$e_{\text{out}}$	$Q_{\text{in}}$
26	$j \neq i, j \in G_i$	$k \notin G_i$	$l = i$	$(i = l, j), (k)$	$(n - 1)(N - n)$	$d_{\text{in}}$	$d_{\text{self}}$	$e_{\text{out}}$	$Q_{\text{out}}$
27	$j \neq i, j \in G_i$	$k \notin G_i$	$l = j$	$(i, j = l), (k)$	$(n - 1)(N - n)$	$d_{\text{in}}$	$d_{\text{in}}$	$e_{\text{out}}$	$Q_{\text{out}}$
28	$j \neq i, j \in G_i$	$k \notin G_i$	$l \neq i, j; l \in G_i$	$(i, j, l), (k)$	$(n - 1)(N - n)(n - 2)$	$d_{\text{in}}$	$d_{\text{in}}$	$e_{\text{out}}$	$Q_{\text{out}}$
29	$j \neq i, j \in G_i$	$k \notin G_i$	$l = k$	$(i, j), (k = l)$	$(n - 1)(N - n)$	$d_{\text{in}}$	$d_{\text{out}}$	$e_{\text{self}}$	$Q_{\text{out}}$
30	$j \neq i, j \in G_i$	$k \notin G_i$	$l \neq k; l \in G_k$	$(i, j), (k, l)$	$(n - 1)(N - n)(n - 1)$	$d_{\text{in}}$	$d_{\text{out}}$	$e_{\text{in}}$	$Q_{\text{out}}$
31	$j \neq i, j \in G_i$	$k \notin G_i$	$l \notin G_i, G_k$	$(i, j), (k), (l)$	$(n - 1)(N - n)(N - 2n)$	$d_{\text{in}}$	$d_{\text{out}}$	$e_{\text{out}}$	$Q_{\text{out}}$
32	$j \notin G_i$	$k = i$	$l = i$	$(i = k = l), (j)$	$(N - n)$	$d_{\text{out}}$	$d_{\text{self}}$	$e_{\text{self}}$	$Q_{\text{out}}$
33	$j \notin G_i$	$k = i$	$l \neq i; l \in G_i$	$(i = k, l), (j)$	$(N - n)(n - 1)$	$d_{\text{out}}$	$d_{\text{in}}$	$e_{\text{in}}$	$Q_{\text{out}}$
34	$j \notin G_i$	$k = i$	$l = j$	$(i = k), (j = l)$	$(N - n)$	$d_{\text{out}}$	$d_{\text{out}}$	$e_{\text{out}}$	$Q_{\text{out}}$
35	$j \notin G_i$	$k = i$	$l \neq j; l \in G_j$	$(i = k), (j, l)$	$(N - n)(n - 1)$	$d_{\text{out}}$	$d_{\text{out}}$	$e_{\text{out}}$	$Q_{\text{out}}$
36	$j \notin G_i$	$k = i$	$l \notin G_i, G_j$	$(i = k), (j), (l)$	$(N - n)(N - 2n)$	$d_{\text{out}}$	$d_{\text{out}}$	$e_{\text{out}}$	$Q_{\text{out}}$
37	$j \notin G_i$	$k \neq i; k \in G_i$	$l = i$	$(i = l, k), (j)$	$(N - n)(n - 1)$	$d_{\text{out}}$	$d_{\text{self}}$	$e_{\text{in}}$	$Q_{\text{out}}$
38	$j \notin G_i$	$k \neq i; k \in G_i$	$l = k$	$(i, k = l), (j)$	$(N - n)(n - 1)$	$d_{\text{out}}$	$d_{\text{in}}$	$e_{\text{self}}$	$Q_{\text{out}}$
39	$j \notin G_i$	$k \neq i; k \in G_i$	$l \neq i, k; l \in G_i$	$(i, k, l), (j)$	$(N - n)(n - 1)(n - 2)$	$d_{\text{out}}$	$d_{\text{in}}$	$e_{\text{in}}$	$Q_{\text{out}}$
40	$j \notin G_i$	$k \neq i; k \in G_i$	$l = j$	$(i, k), (j = l)$	$(N - n)(n - 1)$	$d_{\text{out}}$	$d_{\text{out}}$	$e_{\text{out}}$	$Q_{\text{out}}$
41	$j \notin G_i$	$k \neq i; k \in G_i$	$l \neq j; l \in G_j$	$(i, k), (j, l)$	$(N - n)(n - 1)(n - 1)$	$d_{\text{out}}$	$d_{\text{out}}$	$e_{\text{out}}$	$Q_{\text{out}}$
42	$j \notin G_i$	$k \neq i; k \in G_i$	$l \notin G_i, G_j$	$(i, k), (j), (l)$	$(N - n)(n - 1)(N - 2n)$	$d_{\text{out}}$	$d_{\text{out}}$	$e_{\text{out}}$	$Q_{\text{out}}$
43	$j \notin G_i$	$k = j$	$l = i$	$(i = l), (j = k)$	$(N - n)$	$d_{\text{out}}$	$d_{\text{self}}$	$e_{\text{out}}$	1
44	$j \notin G_i$	$k = j$	$l \neq i; l \in G_i$	$(i, l), (j = k)$	$(N - n)(n - 1)$	$d_{\text{out}}$	$d_{\text{in}}$	$e_{\text{out}}$	1
45	$j \notin G_i$	$k = j$	$l = j$	$(i), (j = k = l)$	$(N - n)$	$d_{\text{out}}$	$d_{\text{out}}$	$e_{\text{self}}$	1
46	$j \notin G_i$	$k = j$	$l \neq j; l \in G_j$	$(i), (j = k, l)$	$(N - n)(n - 1)$	$d_{\text{out}}$	$d_{\text{out}}$	$e_{\text{in}}$	1
47	$j \notin G_i$	$k = j$	$l \notin G_i, G_j$	$(i), (j = k), (l)$	$(N - n)(N - 2n)$	$d_{\text{out}}$	$d_{\text{out}}$	$e_{\text{out}}$	1
48	$j \notin G_i$	$k \neq j; k \in G_j$	$l = i$	$(i = l), (j, k)$	$(N - n)(n - 1)$	$d_{\text{out}}$	$d_{\text{self}}$	$e_{\text{out}}$	$Q_{\text{in}}$
49	$j \notin G_i$	$k \neq j; k \in G_j$	$l \neq i; l \in G_i$	$(i, l), (j, k)$	$(N - n)(n - 1)(n - 1)$	$d_{\text{out}}$	$d_{\text{in}}$	$e_{\text{out}}$	$Q_{\text{in}}$
50	$j \notin G_i$	$k \neq j; k \in G_j$	$l = j$	$(i), (j = l, k)$	$(N - n)(n - 1)$	$d_{\text{out}}$	$d_{\text{out}}$	$e_{\text{in}}$	$Q_{\text{in}}$
51	$j \notin G_i$	$k \neq j; k \in G_j$	$l = k$	$(i), (j, k = l)$	$(N - n)(n - 1)$	$d_{\text{out}}$	$d_{\text{out}}$	$e_{\text{self}}$	$Q_{\text{in}}$
52	$j \notin G_i$	$k \neq j; k \in G_j$	$l \neq j, k; l \in G_j$	$(i), (j, k, l)$	$(N - n)(n - 1)(n - 2)$	$d_{\text{out}}$	$d_{\text{out}}$	$e_{\text{in}}$	$Q_{\text{in}}$
53	$j \notin G_i$	$k \neq j; k \in G_j$	$l \notin G_i, G_j$	$(i), (j, k), (l)$	$(N - n)(n - 1)(N - 2n)$	$d_{\text{out}}$	$d_{\text{out}}$	$e_{\text{out}}$	$Q_{\text{in}}$
54	$j \notin G_i$	$k \notin G_i, G_j$	$l = i$	$(i = l), (j), (k)$	$(N - n)(N - 2n)$	$d_{\text{out}}$	$d_{\text{self}}$	$e_{\text{out}}$	$Q_{\text{out}}$
55	$j \notin G_i$	$k \notin G_i, G_j$	$l \neq i; l \in G_i$	$(i, l), (j), (k)$	$(N - n)(N - 2n)(n - 1)$	$d_{\text{out}}$	$d_{\text{in}}$	$e_{\text{out}}$	$Q_{\text{out}}$
56	$j \notin G_i$	$k \notin G_i, G_j$	$l = j$	$(i), (j = l), (k)$	$(N - n)(N - 2n)$	$d_{\text{out}}$	$d_{\text{out}}$	$e_{\text{out}}$	$Q_{\text{out}}$
57	$j \notin G_i$	$k \notin G_i, G_j$	$l \neq j; l \in G_j$	$(i), (j, l), (k)$	$(N - n)(N - 2n)(n - 1)$	$d_{\text{out}}$	$d_{\text{out}}$	$e_{\text{out}}$	$Q_{\text{out}}$
58	$j \notin G_i$	$k \notin G_i, G_j$	$l = k$	$(i), (j), (k = l)$	$(N - n)(N - 2n)$	$d_{\text{out}}$	$d_{\text{out}}$	$e_{\text{self}}$	$Q_{\text{out}}$
59	$j \notin G_i$	$k \notin G_i, G_j$	$l \neq k; l \in G_k$	$(i), (j), (k, l)$	$(N - n)(N - 2n)(n - 1)$	$d_{\text{out}}$	$d_{\text{out}}$	$e_{\text{in}}$	$Q_{\text{out}}$
60	$j \notin G_i$	$k \notin G_i, G_j$	$l \notin G_i, G_j, G_k$	$(i), (j), (k), (l)$	$(N - n)(N - 2n)(N - 3n)$	$d_{\text{out}}$	$d_{\text{out}}$	$e_{\text{out}}$	$Q_{\text{out}}$