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**Article Title:** Imperfect strategy transmission can reverse the role of population viscosity on the evolution of altruism .

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1 **Abstract**

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

## 18 **Impact Summary**

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

## 44 1 Introduction

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

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

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

74 A large number of studies on the evolution of social behavior consider simple  
75 population structures (typically, homogeneous populations *sensu* Taylor et al.  
76 (2007a)) and often also infinite population sizes (but see Allen et al., 2017, for  
77 results on any structure). These studies also make use of weak selection ap-  
78 proximations, and commonly assume rare (*e.g.*, Leturque & Rousset, 2002; Tay-  
79 lor et al., 2007b; Tarnita & Taylor, 2014) or absent mutation (for models assum-  
80 ing infinite population sizes, or models concentrating on fixation probabilities  
81 Lehmann & Rousset, 2014; Van Cleve, 2015, for recent reviews). Often, these sim-  
82 plifying assumptions are a necessary step towards obtaining explicit analytical  
83 results. Although artificial, simple population structures (*e.g.*, regular graphs, or  
84 subdivided populations with demes of equal sizes) help reduce the dimension-  
85 ality of the system under study, in particular when the structure of the popula-  
86 tion displays symmetries such that all sites behave the same way in expectation.  
87 Weak selection approximations are crucial for disentangling spatial moments  
88 (Lion, 2016), that is, changes in global *vs.* local frequencies (though they can in  
89 some cases be relaxed, as in 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.*, containing  $n$  sites, each of which is occupied by exactly  
114 one individual; we have  $nN_D = N$ ). Each site has a unique label  $i$ ,  $1 \leq i \leq N$ .  
115 There are two types of individuals in the population, altruists and defectors. The  
116 type of the individual living at site  $i$  ( $1 \leq i \leq N$ ) is given by an indicator variable  
117  $X_i$ , equal to 1 if the individual is an altruist, and to 0 if it is a defector. The state  
118 of the entire population is given by a  $N$ -long vector  $\mathbf{X}$ . For a given population  
119 state  $\mathbf{X}$ , the proportion of altruists is  $\bar{X} = \sum_{i=1}^N X_i$ . All symbols are summarized in  
120 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.

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

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

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

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

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

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

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

The way the population is updated from one time step to the next depends 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

To derive the expected (*i.e.*, long-term) proportion of altruists in the population, we use the toolbox presented in Débarre (2017), which is valid for any regular

168 population and any life-cycle. Calculation details are given in Appendix B; they  
169 go as follows. First, we write an equation for the expected frequency of altruists  
170 in the population at time  $t + 1$ , conditional on the composition of the population  
171 at time  $t$ ; we then take the expectation of this quantity, for large times  $t$ . After  
172 this, we use the assumption that selection is weak ( $\omega \ll 1$ ) and write a first order  
173 expansion of the expression that we have obtained. By doing so, we let appear  
174 quantities that can be identified as neutral probabilities of identity by descent  
175  $Q_{ij}$ , *i.e.*, the probability that individuals living at site  $i$  and  $j$  share a common  
176 ancestor and that no mutation occurred on either lineage since that ancestor, in  
177 a model with no selection ( $\omega = 0$ ) – this is the “mutation definition of identity by  
178 descent (Rousset & Billiard, 2000).

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

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

### 185 2.2.2 Stochastic simulations

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

192 All scripts are available at

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



## 194 3 Results

### 195 3.1 Probabilities of identity by descent

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

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

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

#### 203 3.1.1 Moran updating

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

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

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

212 steps):

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

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

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

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

### 222 3.1.2 Wright-Fisher updating

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

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

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

229 Replacing the dispersal probabilities  $d_{ij}$  by their values (given in eq. (3)) and

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

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

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

231 with

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

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

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

238 The two probabilities of identity by descent go to 1 when the mutation prob-  
239 ability  $\mu$  is very small ( $\mu \rightarrow 0$ ), except if we first assume that the number of demes  
240 is very large ( $N_D \rightarrow \infty$ ); for instance, with this life-cycle as well,  $\lim_{N_D \rightarrow \infty} Q_{\text{out}}^{\text{WF}} =$   
241 0.

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

## 245 3.2 Expected frequencies of altruists for each life-cycle

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

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

248 (Calculations leading to eq. (9) are presented in Appendix B.)

249 The mutation bias  $v$  corresponds to the expected proportion of altruists in the  
250 population in the absence of selection (*i.e.*, when  $\omega = 0$ );  $\omega$  is the parameter  
251 that scales the effects of interactions between individuals, which is assumed to  
252 be small. The subscript <sub>D</sub> refers to “direct” effects, and the subscript <sub>I</sub> to “in-  
253 direct” effects. “Direct” effects involve effects on primary beneficiaries of the  
254 benefits ( $b$ ) and costs ( $c$ ) of social interactions (West & Gardner, 2010), *i.e.*, so-  
255 cial interactants (for the benefits  $b$ ) and the focal individuals themselves (for the  
256 costs  $c$ ). “Indirect” effects corresponds to effects on secondary interactants, *i.e.*,  
257 to (kin) competition. By providing a benefit to a deme-mate and thereby in-  
258 creasing its fecundity, a focal altruist indirectly harms others by reducing their  
259 relative fecundity ( $\beta_I$  term in eq. (9)); by having a reduced fecundity due to the  
260 cost of altruism, a focal altruist indirectly favors others by increasing their rela-  
261 tive fecundity ( $\gamma_I$  term).

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

### 264 3.2.1 Direct effects

265 Direct (/primary) effects are similar for the three life-cycles; the only difference  
266 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):

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

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

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

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. (10a) and eq. (10b)) 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. (10a) and eq. (10b). On the other hand, the direct effect of the fecundity cost  $c$  (eq. (10c)) 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.

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

$$\begin{aligned}\beta_1^{\text{BD}} &= (1 - m) \left( \frac{n-1}{n} Q_{\text{in}}^{\text{M}} + \frac{1}{n} \right) + m Q_{\text{out}}^{\text{M}} - \mu \frac{1 + (n-1)Q_{\text{in}}^{\text{M}} + n(d-1)Q_{\text{out}}^{\text{M}}}{nd} \\ &= \gamma_1^{\text{BD}}.\end{aligned}\quad (11a)$$

295 (Calculation details are presented in Appendix B.)

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

303 Replacing  $Q_{\text{in}}$  and  $Q_{\text{out}}$  by their formula for the Moran life-cycle (eq. (6)), we  
 304 conclude that  $\beta_1^{\text{BD}} = \gamma_1^{\text{BD}}$  are decreasing functions of the emigration probabil-  
 305 ity  $m$  (calculations in the supplementary Mathematica file).

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

310 descent to it. We obtain

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

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

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

318 Replacing  $Q_{\text{in}}$  and  $Q_{\text{out}}$  by their formulas given in eq. (6), we can conclude  
319 that  $\beta_I^{\text{DB}} = \gamma_I^{\text{DB}}$  first decreases with the emigration probability  $m$ , and increases  
320 again after a threshold value  $m'_c$ , which is smaller than  $m_c^{\text{WF}} = (d-1)/d$  (calcu-  
321 lation details are presented in the supplementary Mathematica file).

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

### 332 3.3 Identifying threshold values of the mutation probability $\mu$

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

#### 339 3.3.1 Moran Birth-Death

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

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

345 This result is illustrated in figure 2(b); with the parameters of the figure,  $\mu_c^{\text{BD}} \approx$   
 346 0.026.

#### 347 3.3.2 Moran Death-Birth

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



355 these results, we write

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

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

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

### 361 3.3.3 Wright-Fisher

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

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

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

## 366 3.4 Relaxing key assumptions

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

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

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

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

## 383 4 Discussion

### 384 The expected frequency of altruists in a subdivided population can in- 385 crease with the probability of emigration

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

### 397 Quantitative vs. qualitative measures

398 We used a quantitative measure, the expected frequency of altruists in the popu-  
399 lation ( $\mathbb{E}[\bar{X}]$ ), to explore how non-zero mutation probabilities altered the impact

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

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

414 To explain how the frequency of altruists can increase with the emigration prob-  
 415 ability  $m$ , let us go back to the decomposition of the expected frequency of al-  
 416 truists in the population  $\mathbb{E}[\bar{X}]$  into different terms (eq. (9)). For all the life-cycles  
 417 that we consider, the direct effect of helping others ( $\beta_D$ ) decreases with emigra-  
 418 tion  $m$ , while the direct effect of the cost of helping ( $\gamma_D$ ) does not change with  
 419  $m$ . If we (erroneously) considered only direct effects, we would conclude that  
 420 the expected proportion of altruists decreases with the emigration probability  
 421  $m$ , because an increase in  $m$  reduces the probability that two interactants (two  
 422 deme-mates in this model) are identical by descent. But this explanation ignores  
 423 indirect, competitive, effects. In the three life-cycles that we considered,  $\beta_I = \gamma_I$ ,  
 424 so the overall indirect effects are given by  $-(b - c)\beta_I$ . Hence, any increase of  
 425  $\mathbb{E}[\bar{X}]$  with  $m$  is driven by  $\beta_I$ . Indirect effects correspond to competition: helping  
 426 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.

## 451 **Imperfect transmission and Rebellious Children**

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

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

## 465 **Interactions and dispersal graphs**

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

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

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

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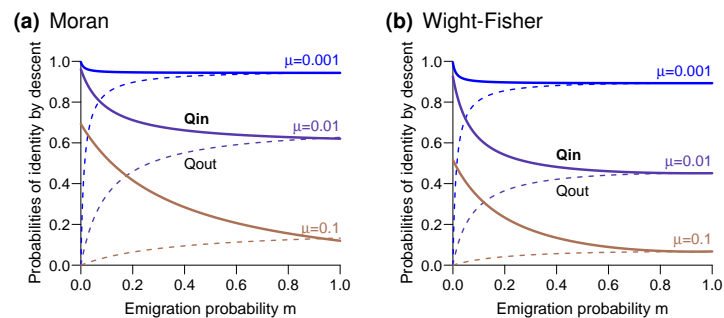
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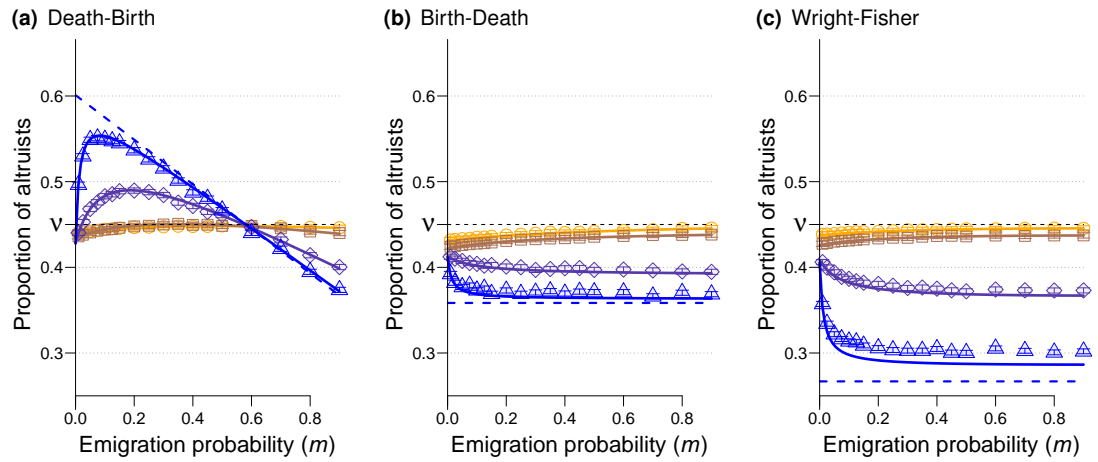
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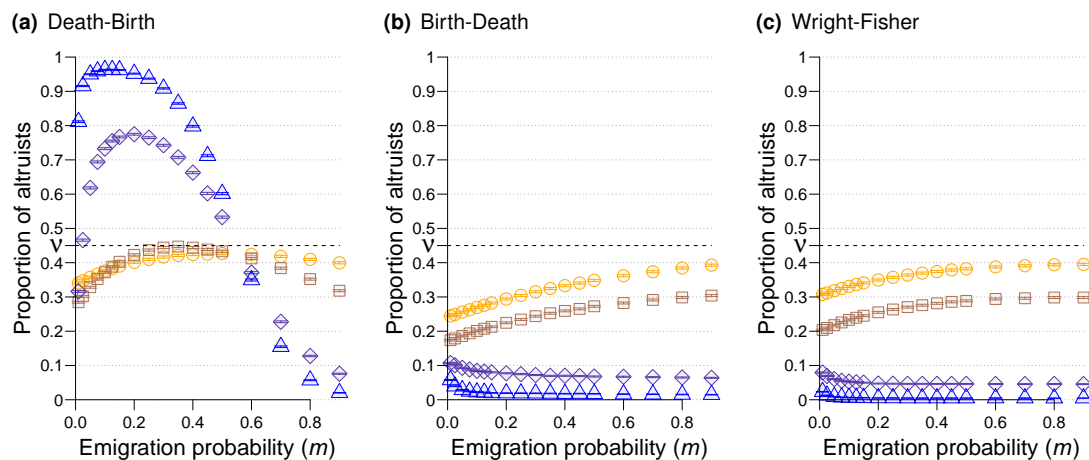
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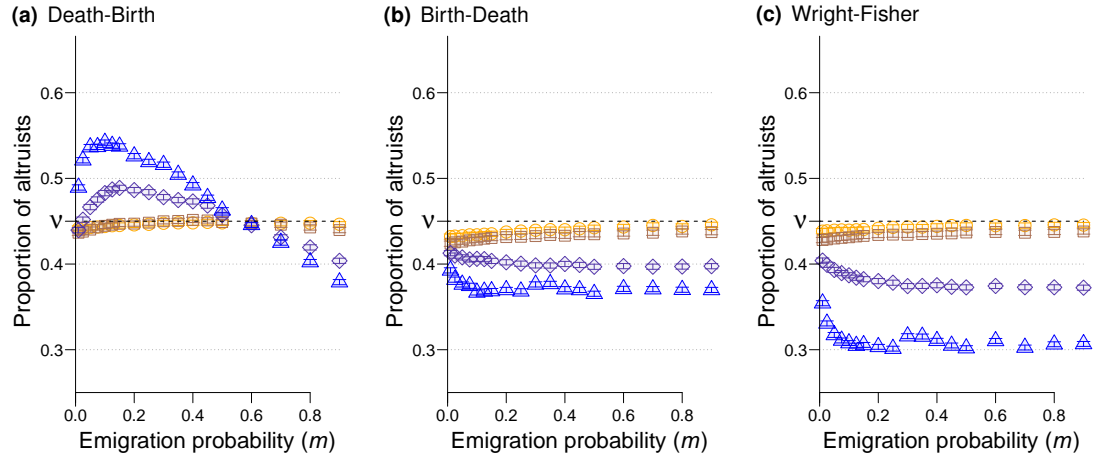
**Figure 1:** Probabilities of identity by descent, for two different individuals within the same deme ( $Q_{in}$ , full curves) and two individuals in different demes ( $Q_{out}$ , dashed curves), as a function of the emigration probability  $m$ , for different values of the mutation probability  $\mu$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



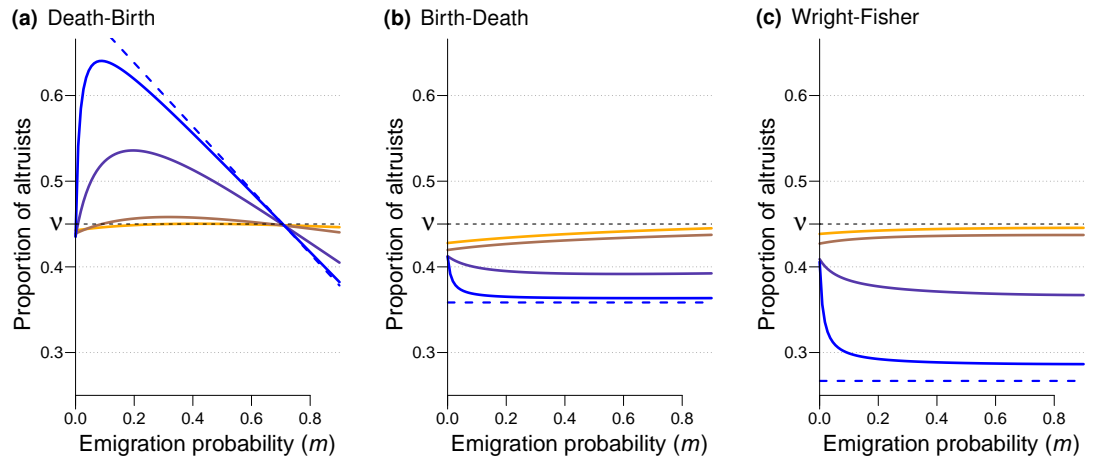
**Figure 2:** Expected proportion of altruists under weak selection, as a function of the emigration probability  $m$ , for different mutation values ( $\mu = 0.001$  (blue, dots), 0.01 (purple, squares), 0.1 (brown, diamonds), 0.25 (orange, triangles); the dashed blue lines correspond to  $\mu = 0$ ) 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:  $\omega = 0.005$ ,  $\nu = 0.45$ ,  $b = 15$ ,  $c = 1$ ,  $n = 4$  individuals per deme,  $N_D = 15$  demes.



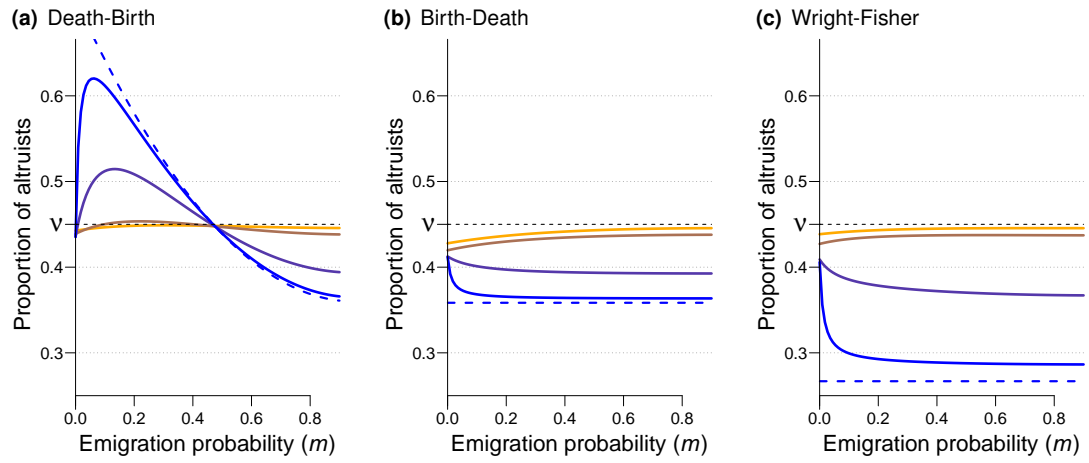
**Figure S1:** Equivalent of figure 2 (simulations only) but with strong selection ( $\omega = 0.1$ ); please note the change of scale on the vertical axis. All other parameters and legends are identical to those of figure 2 (increasing mutation probabilities from blue dots to orange triangles).



**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

580

### A Fecundity and weak selection approximation

582 Here we show that the fecundity function presented in eq. (2) can be obtained  
583 from a generic fecundity function, under the assumption of small phenotypic  
584 differences between altruists and defectors.

585 Let us denote by  $\phi_i$  the phenotype of the individual living at site  $i$ , and as-  
586 sume that the phenotypic value of altruists and defectors differs by  $\omega \ll 1$ , so  
587 that

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

588 where  $\phi^{(0)}$  is the phenotype of defectors (and  $\phi_0 + \omega$  the phenotype of altruists).

589 We consider a generic fecundity function, that depends on the focal indi-  
590 vidual's phenotype, and on the phenotype of all the individuals that it interacts  
591 with, weighted by the probability of interaction ( $e_{ki}$  for an individual at site  $k$ ,  
592  $1 \leq k \leq N$ ). For instance, the fecundity of an individual at site  $i$  is given by a  
593 function with  $N + 1$  arguments

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

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

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

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

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

596 where  $\partial_{(k)} \mathcal{F}|_{\omega=0}$  is the derivative of  $\mathcal{F}$  with respect to its  $k^{\text{th}}$  argument, evaluated  
597 at  $\omega = 0$ . The first term in eq. (A.3) is the fecundity of individual  $i$  when there is  
598 not a single altruist in the population.

599 Given the chosen structure of the population, all individuals have the same  
600 number of social interactions, so they end up having the same fecundity when  
601 the population is fixed for the defector type. Without loss of generality, we set  
602 this baseline fecundity equal to 1. If we now consider that it does not matter  
603 where the benefits of social interactions come from, only that they are received  
604 by the focal individual, then  $\partial_{(k)} \mathcal{F}$  is the same for all  $k$ ,  $1 \leq k \leq N$ ; let us denote  
605 it by  $b$ . If we denote by  $-c$  the marginal effect of the focal individual's phenotype



606 on its own fecundity (*i.e.*,  $-c = \partial_{N+1} \mathcal{F}|_{\omega=0}$ ), then we obtain

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

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

## 608 B Expected frequency of altruists

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

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

### 615 B.1 For a generic life-cycle

616 We want to compute the expected proportion of altruists in the population. We  
 617 represent the state of the population at a given time  $t$  using indicator variables  
 618  $X_i(t)$ ,  $1 \leq i \leq N$ , equal to 1 if the individual living at site  $i$  at time  $t$  is an altruist,  
 619 and equal to 0 if it is a defector; these indicator variables are gathered in a  $N$ -  
 620 long vector  $\mathbf{X}(t)$ . The set of all possible population states is  $\Omega = \{0, 1\}^N$ . The  
 621 proportion of altruists in the population is written  $\bar{X}(t) = \sum_{i=1}^N X_i(t)$ . We denote  
 622 by  $B_{ji}(X(t), \omega)$ , written  $B_{ji}$  for simplicity, the probability that the individual at  
 623 site  $j$  at time  $t+1$  is the newly established offspring of the individual living at site  
 624  $i$  at time  $t$ . We denote by  $D_i(X(t), \omega)$  ( $D_i$  for simplicity) the probability that the  
 625 individual living at site  $i$  at time  $t$  has been replaced (*i.e.*, died) at time  $t+1$ . Both  
 626 quantities depend on the chosen life-cycle and on the state of the population;  
 627 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. (2).

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

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

629 holds for all sites  $i$ . The structure of the population is also such that in the ab-

630 sence of selection ( $\omega = 0$ , so that  $f_i = 1$  for all sites  $1 \leq i \leq N$ ), all individuals have  
 631 the same probability of dying and the same probability of having successful off-  
 632 spring (*i.e.*, of having offspring that become adults at the next time step), so that  
 633

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

634 where the  $^0$  subscript means that the quantities are evaluated for  $\omega = 0$ . This  
 635 also implies that  $B_{ij}^0$  and  $D_i^0$  do not depend on the state  $\mathbf{X}$  of the population. For  
 636 the Moran life-cycles,  $B^* = 1/N$ , while for the Wright-Fisher life-cycle,  $B^* = 1$ .  
 637 (The difference between eq. (B.5b) and eq. (B.5a) is that we are now considering  
 638 offspring produced by  $i$  landing on  $j$ ).

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

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

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

645 Given that there is no absorbing population state (a lost strategy can always  
 646 be recreated by mutation), there is a stationary distribution of population states;  
 647 the expected frequency of altruists does not change anymore for large times  $t$   
 648 (realized frequencies of course keep changing). We denote by  $\xi(\mathbf{X}, \omega, \mu)$  the prob-  
 649 ability that the population is in state  $\mathbf{X}$ , given the strength of selection  $\omega$  and the  
 650 mutation probability  $\mu$ . Taking the expectation of eq. (B.6a) ( $\mathbb{E}[\bar{X}] = \sum_{\mathbf{X} \in \Omega} \bar{X} \xi(\mathbf{X}, \omega, \mu)$ ),  
 651 we obtain, after reorganizing:

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

652 Now, we use the assumption of weak selection ( $\omega \ll 1$ ) and consider the first-  
 653 order expansion of eq. (B.7) for  $\omega$  close to 0. First, we note that in the absence  
 654 of selection ( $\omega = 0$ ), the population is at a mutation-drift balance; the expected  
 655 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-  
 656 tation bias parameter). Secondly, we further expand derivatives of  $B_{ji}$  and  $D_i$   
 657 thanks to the chain rule, using the variables  $f_k$  ( $1 \leq k \leq N$ ), corresponding to in-  
 658 dividual fecundities (also, recall that  $f_k = 1$  when  $\omega = 0$ ). Thirdly, we note that for  
 659 all the life-cycles that we consider, the total number of deaths in the population  
 660 during one time step does not depend on population composition (it is exactly  
 661 1 death for the Moran life-cycles, and exactly  $N$  for the Wright-Fisher life-cycle),  
 662 so that  $\sum_{i,j=1}^N B_{ij}$  does not depend on  $\omega$ . After simplification and reorganization,

the first order expansion of eq. (B.7) yields

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

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

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

In Appendix B.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

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

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 S2), and the  $d_{ij}$  and  $e_{ij}$  terms by their formulas (given in eq. (3)) and eq. (1), respectively). For each life-cycle we can group terms as

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

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

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

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

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

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

### 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

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

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

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

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

System (B.14) has the same set of equations as for the Moran Death-Birth model (system (B.1)), except for the values of probabilities of identity by descent... that we now need to compute.

## B.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 ( $\omega = 0$ ).

### 688 B.2.1 Moran model

689 In a Moran model, exactly one individual dies and one individual reproduces  
 690 during one time step. Given a state  $\mathbf{X}$  at time  $t$ , at time  $t + 1$  both sites  $i$  and  
 691  $j \neq i$  are occupied by altruists, if  $i$  it was the case at time  $t$  and neither site was  
 692 replaced by a non-altruist (first term in eq. (B.15)), or  $ij$  if exactly one of the two  
 693 sites was occupied by a non-altruist at time  $t$ , but the site was replaced by an  
 694 altruist (second and third terms of eq. (B.15)):

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

695 We take the expectation of this quantity, and consider that the stationary dis-  
 696 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

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

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

698 Now we substitute  $P_{ij} = \nu^2 + \nu(1 - \nu)Q_{ij}$  in eq. (B.16), we obtain

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

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

### 704 B.2.2 Wright-Fisher model

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

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

707 The first term of eq. (B.18) corresponds to both parents being altruists, and hav-  
 708 ing altruist offspring; the second line corresponds to exactly one parent being  
 709 altruist, and the third line to both parents being non-altruists (in this latter case,  
 710 the two offspring have to be both mutants to be altruists).  
 711 Taking the expectation and simplifying, we obtain

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

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

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

713 Again,  $Q_{ij}$  corresponds to a probability of identity by descent: the individuals at  
 714 sites  $i$  and  $j$  are identical by descent if their parents were and if neither mutated  
 715  $((1-\mu)^2)$ .

## 716 C In a subdivided population

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

718 Now, we need to adapt the results presented in Appendix B to our structure of  
 719 interest, a subdivided population, with dispersal and interaction probabilities  
 720 given by eq. (3) and eq. (1). For the  $\beta$  and  $\gamma$  terms, we use a brute-force ap-  
 721 proach, replacing  $d_{ij}$  and  $e_{ij}$  by their values in a subdivided population, and  
 722 simplifying the equations (for instance, there are 60 different cases to consider  
 723 for the four sums that appear in  $\beta_1^{\text{DB}}$ , shown in the table in section C.4 below).  
 724 The calculations and subsequent simplifications are detailed in the supplemen-  
 725 tary Mathematica file, and the results are presented in the main text (system (10),  
 726 eq. (11a), and eq. (11b)).

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

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

734 We rewrite site labels ( $1 \leq i \leq N$ ) as  $(\ell_1, \ell_2)$ , where  $\ell_1$  is the index of the deme  
 735 ( $1 \leq \ell_1 \leq N_D$ ) and  $\ell_2$  the position of the site within the deme ( $1 \leq \ell_2 \leq n$ ). Then,  
 736 we introduce notations  $\tilde{d}_{i_1}^{i_2}$  and  $\tilde{Q}_{i_1}^{i_2}$ , that correspond to the dispersal probab-  
 737 ity and probability of identity by descent to a site at distances  $i_1$  and  $i_2$  in the  
 738 among-demes and within-deme dimensions (e.g.,  $\tilde{d}_{i_1}^{i_2} = d_{j_1 j_1 + i_1}^{j_2' j_2 + i_2}$ ).

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

#### 741 C.2.1 Moran model

742 In Débarre (2017), it was shown that

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

743 with

$$\tilde{D}_{q_1}^{q_2} = \sum_{\ell_1=0}^{N_1-1} \sum_{\ell_2=0}^{N_2-1} \tilde{d}_{\ell_1}^{\ell_2} \exp\left(-i \frac{2\pi q_1 \ell_1}{N_1}\right) \exp\left(-i \frac{2\pi q_2 \ell_2}{N_2}\right), \quad (\text{C.21b})$$



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

$$\begin{aligned}\tilde{D}_{q_1} &= d_{\text{self}} + \sum_{\ell_2=1}^{N_2-1} d_{\text{in}} \exp\left(-i \frac{2\pi q_2 \ell_2}{N_2}\right) + \sum_{\ell_1=1}^{N_1-1} \sum_{\ell_2=0}^{N_2-1} d_{\text{out}} \exp\left(-i \frac{2\pi q_1 \ell_1}{N_1}\right) \exp\left(-i \frac{2\pi q_2 \ell_2}{N_2}\right) \\ &= d_{\text{self}} + (\delta_{q_2}(N_2 - 1) + (1 - \delta_{q_2})(-1)) d_{\text{in}} + (\delta_{q_1}(N_1 - 1) + (1 - \delta_{q_1})(-1)) (\delta_{q_2} N_2) d_{\text{out}} \\ &= d_{\text{self}} + (\delta_{q_2} N_2 - 1) d_{\text{in}} + (\delta_{q_1} N_1 - 1) \delta_{q_2} N_2 d_{\text{out}}.\end{aligned}\quad (\text{C.22a})$$

746 ( $\delta_q$  is equal to 1 when  $q$  is equal to 0 modulo the relevant dimension, and to 0  
 747 otherwise). So for the three types of distances that we need to consider (distance  
 748 0, distance to another deme-mate, distance to individual in another deme), and  
 749 with  $N_1 = N_D$  and  $N_2 = n$ , we obtain

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

$$\tilde{D}_0^{q_1} = 1 - m - \frac{m}{d-1} \quad (q_1 \not\equiv 0 \pmod{N_1}), \quad (\text{C.23b})$$

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

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

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

751 In particular,

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

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

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

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

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

755 With  $d_{\text{self}} = d_{\text{in}} = (1 - m)/n$ , we recover the equations given in the main text (sys-  
 756 tem (6)).

### 757 C.3 Wright-Fisher

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

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

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

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

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

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

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

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

763 and

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

764 With  $d_{\text{self}} = d_{\text{in}} = (1 - m)/n$ , we recover the equations given in the main text (sys-  
 765 tem (8)).

766 **C.4 Unpacking  $\beta_i^{\text{DB}}$** 

767 The table below contains all combinations for  $i, j, k, l$  involved in the four sums.  $(i, j)$ : means  
 768 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	$j \notin G_i$	$k \notin G_i, G_j$	$l \notin G_i, G_j, G_k$	$(i), (j), (k), (l)$	$(N - n)(N - 2n)(N - 3n)$	$d_{\text{out}}$	$d_{\text{out}}$	$e_{\text{out}}$	$Q_{\text{out}}$