Title

Fidelity of parent-offspring transmission and the evolution of social behavior in structured populations

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Length

228	words in the abstract,
4998	words in the main text,
4	figures (color) [in the text + at the end],
1	supplementary material (Appendix),
1	zipped folder of scripts [uploaded on figshare, `https://figshare.com/articles/Mutation_and_social_evolution/3207748`]

Abstract

The theoretical investigation of how spatial structure affects the evolution of social behavior has mostly been done under the assumption that parent-offspring strategy transmission is perfect, *i.e.*, for genetically transmitted traits, that mutation is very weak or absent. Here, we investigate the evolution of social behavior in structured populations under arbitrary mutation probabilities. We consider populations of fixed size N, structured such that in the absence of selection, all individuals have the same probability of reproducing or dying (neutral reproductive values are the all same). Two types of individuals, A and B, corresponding to two types of social behavior, are competiting; the fidelity of strategy transmission from parent to offspring is tuned by a parameter μ. Social interactions have a direct effect on individual fecundities. Under the assumption of small phenotypic differences (weak selection), we provide a formula for the expected frequency of type A individuals in the population, and deduce conditions for the long-term success of one strategy against another. We then illustrate this result with three common life-cycles (Wright-Fisher, Moran Birth-Death and Moran Death-Birth), and specific population structures (graph-structured populations). Qualitatively, we find that some life-cycles (Moran Birth-Death, Wright-Fisher) prevent the evolution of altruistic behavior, confirming previous results obtained with perfect strategy transmission. We also show that computing the expected frequency of altruists on a regular graph may require knowing more than just the graph's size and degree.

Keywords

mutation, relatedness, altruism, evolutionary graph theory

1 Introduction

Most models on the evolution of social behavior in structured populations study the outcome of competition between individuals having different strategies and assume that strategy transmission from parents to their offspring is almost perfect (*i.e.*, when considering genetic transmission, that mutation is either vanishingly small or absent). This is for instance illustrated by the use of fixation probabilities to assess evolutionary success (*e.g.*, Nowak et al., 2004; Nowak, 2006; Ohtsuki et al., 2006). Yet, mutation has been shown to affect the evolutionary fate of social behavior (Frank, 1997; Tarnita et al., 2009) and is, more generally, a potentially important evolutionary force. Here, we explore the role of imperfect strategy transmission—genetic or cultural—from parents to offspring on the evolution of social behavior, when two types of individuals, with different social strategies, are competing. We are interested in evaluating the long-term success of one strategy over another.

A population in which mutation is not close (or equal) to zero will spend a non-negligible time in mixed states (*i.e.*, in states where both types of individuals are present), so instead of fixation probabilities, we need to consider long-term frequencies to assess evolutionary success (Tarnita et al., 2009; Wakano & Lehmann, 2014; Tarnita & Taylor, 2014). We will say that a strategy is favored by selection when its expected frequency is larger than what it would be in the absence of selection.

In this study, we consider populations such that, in the absence of selection (when social interactions have no effect on fitness), all individuals have equal chances of reproducing, and equal chances of dying. In other words, in such a population of size N, the neutral reproductive value of each site is $1/N$ (Taylor, 1990; Maciejewski, 2014; Tarnita & Taylor, 2014). We provide a formula that gives the long-term frequency of a social strategy in any such population, for arbitrary mutation rates, and for any life-cycle (provided population size remains equal to N). This formula is a function of the probabilities that pairs of individuals are identical by descent. These probabilities are obtained by solving a linear system of equations, and we present explicit solutions for population structures with a high level of symmetry (structures that we call "n-dimensional graphs"). We finally illustrate our results with widely used updating rules (Moran models, Wright-Fisher model) and specific population structures.

2 Models and Methods

Population structures

We consider a population of fixed size N, where each individual inhabits a site corresponding to the node of a graph $\mathcal{D}$; each site hosts exactly one individual. The edges of the graph, $\{d_{ij}\}_{1\leq i,j\leq N}$, define where individuals can send their offspring to; we consider graphs $\mathcal{D}$ that are connected, *i.e.*, such that following the edges of the graph, we can go from any node to any other node. Another graph, $\mathcal{E}$, with the same nodes as graph $\mathcal{D}$ but with edges $\{e_{ij}\}_{1\leq i,j\leq N}$, defines the social interactions between the individuals; $\mathcal{E}$ can be the same graph as $\mathcal{D}$, but does not have to be (Taylor et al., 2007a; Ohtsuki et al., 2007; Débarre et al., 2014). The edges of the two graphs can be weighted (*i.e.*, d_{ij} and e_{ij} can take any non-negative value) and directed (*i.e.*, we can have $d_{ij} \neq d_{ji}$ or $e_{ij} \neq e_{ji}$ for some sites i and j). Finally, we denote by $\mathbf{D}$ and $\mathbf{E}$ the adjacency matrices of the dispersal and interaction graphs, respectively.

Regular dispersal graphs In this study, we focus on dispersal graphs that are regular, *i.e.*, such that for all sites i, the sum of the edges to i and the sum of the edges from i are both equal to ν:

$$\sum_{j=1}^{N} d_{ij} = \sum_{j=1}^{N} d_{ji} = \nu, \tag{1}$$

where ν is called *degree* of the graph when the graph is unweighted. All the graphs depicted in the article satisfy eq. (1). Note that there is no specific constraint on the interaction graph $\mathcal{E}$.

More detailed results are then obtained for regular graphs that display some level of symmetry, that we now describe:

Transitive dispersal graphs A transitive graph is such that for any two nodes i and j of the graph, there is an isomorphism that maps i to j (Taylor et al., 2007a; **?**); in other words, the graph looks the same from every node. In figure 1, graphs (b)–(e) are transitive.

Transitive undirected dispersal graphs A graph is undirected if for any two nodes i and j, $d_{ij} = d_{ji}$. In figure 1, graphs (b), (c), (e) are both transitive and undirected.

“n-dimensional” dispersal graphs We call “n-dimensional graphs” transitive graphs whose nodes can be relabelled with n-long indices, such that the graph is unchanged by circular permutation of the indices in each dimension.

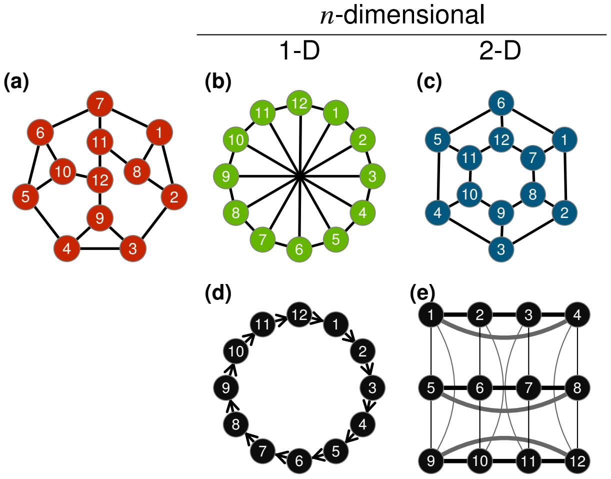

Figure 1: Examples of regular graphs of size 12. The graphs on the first line are unoriented and unweighted graphs of degree $v = 3$; Graph (d) is oriented, graph (e) is weighted. (a) is the Frucht graph, and has no symmetry. Graphs (b) and (d) are one-dimensional, graphs (c) and (e) are two-dimensional (see main text).

The graphs can be directed and weighted. We denote by $\mathcal{N}$ the ensemble of node indices: $\mathcal{N} = \{0, \dots, N_1 - 1\} \times \cdots \times \{0, \dots, N_n - 1\}$, with $\prod_{k=1}^{n} N_n = N$; numbering is done modulo N_k in dimension k. Then for all indices i, j and l of $\mathcal{N}$, node labelling is such that for all edges (modulo the size of each dimension),

$$d_{ij} = d_{i+k,j+k}. \tag{2}$$

In figure 1, graphs (b) and (d) are 1-dimensional: we can label their nodes such that the adjacency matrices are circulant. Graphs (c) and (e) are 2-dimensional: the adjacency matrices are block-circulant, with each block being circulant. In 1(c), one dimension corresponds to the angular position of a node ($N_1 = 6$ positions), and the other dimension to the radial position of a node ($N_2 = 2$ positions, inner or outer hexagon). In 2(e), one dimension corresponds to the horizontal position of a node ($N_1 = 4$ positions) and the other to the vertical position of a node ($N_2 = 3$ positions). Condition eq. (2) may sound strong, but is satisfied for the regular population structures classically studied, like stepping-stones (*e.g.*, cycle graphs, lattices), or island models (Taylor, 2010; Taylor et al., 2011).

Types of individuals and social interactions

There are two types (A and B) of individuals in the population, corresponding to two strategies of social behavior. There are no mixed strategies: an individual of type A plays strategy A, and individuals do not change strategies. The indicator variable X_i represents the type of the individual present at site i: X_i is equal to 1 if the individual at site i is of type A, and X_i is equal to 0 otherwise ($X_i = \mathbb{1}_A(i)$). A N-long vector X gathers the identities of all individuals in the population, and $\overline{X}$ is the population average of X ($\overline{X} = \sum_{i=1}^{N} X_i / N$).

Individuals in the population reproduce asexually. Fecundities are affected by social interactions, and are gathered in a N-long vector f. We assume that the genotype-phenotype map is such that the two types A and B are close in phenotype space: the individual living at site i expresses a phenotype δX_i, with $\delta \ll 1$ (a feature called "δ-weak selection" by Wild & Traulsen (2007)).

An individual's fecundity depends on its own phenotype and on its interaction neighborhood. Interaction neighborhoods are determined by the interaction graph $\mathcal{E}$, and the effect of social interactions on fecundity are given by a function ϕ. We assume that the baseline fecundity is $\phi(0,0) = 1$, so that

$$\begin{aligned} f_i(X,\delta) &= \phi\left(\delta X_i, \sum_l e_{li}\delta X_l\right) \\ &= 1 + \delta\left(X_i\,\partial_{(1)}\phi(0,0) + \sum_l e_{li}\,X_l\,\partial_{(2)}\phi(0,0)\right) + O(\delta^2), \end{aligned} \tag{3a}$$

where $\partial_{(n)}\phi(0,0)$ represents the partial derivative of ϕ with respect to its n^{th} element, evaluated at $(0,0)$, and $\sum_l$ refers to the sum $\sum_{l=1}^{N}$. If we write $\mathsf{b} = \partial_{(2)}\phi(0,0)$ and $-\mathsf{c} = \partial_{(1)}\phi(0,0)$, then eq. (3a) becomes

$$f_i(X,\delta) = 1 + \delta\left(-\mathsf{c}X_i + \mathsf{b}\sum_l e_{li}X_l\right) + O(\delta^2). \tag{3b}$$

Our results are valid for any b and c, but throughout the article, we will consider the case where $\mathsf{b} > 0$ and $\mathsf{c} > 0$, so that type-A individuals are "altruists", and we will seek to understand the impact of imperfect strategy transmission on the frequency of altruists. When $\delta = 0$, all individuals in the population, whichever their type, have the same fecundity: the trait is then neutral.

Reproduction and mutation

The expected number of successful offspring established at site j at the next time step, descending from the individual who is living at site i at the current time step, is denoted by $B_{ji}(f(X,\delta))$, written B_{ji} for simplicity. "Successful offspring" of a focal individual means individuals who descend from this focal individual and who are alive and established at the start of the next time step. Because there is exactly one individual per site, $0 \le B_{ji} \le 1$. Mutation among offspring occurs with probability μ, $0 < \mu \le 1$; when mutation occurs, the offspring are of type A with probability p and of type B otherwise $(0 < p < 1)$. For instance, under this mutation scheme, the offspring of an individual of type A is also of type A with probability $1-\mu+\mu p$ (Taylor et al., 2007b; Nowak et al., 2010; Tarnita & Taylor, 2014). The parameter p controls the asymmetry of mutation, and it is also the expected frequency of type-A individuals in the absence of selection (*i.e.*, when $\delta = 0$). Although we use the word "mutation", which hints at a genetic transmission of the trait, this framework can also describe vertical cultural transmission, so μ does not have to be small. The mutation probability, however, cannot be zero; if it were, the all-A and all-B states would be absorbing: we would end up either with only type-A or only type-B individuals in the population, and we would not be able to define a stationary distribution of population states—for similar reasons, p cannot be 0 nor 1.

We denote by $D_i(f(X,\delta))$ (or D_i for simplicity) the probability that the individual living at site i is dead at the beginning of the next time step, given that the population is currently in state X. This probability of death at site i can be expressed as a function of the probabilities of birth and establishment of offspring at site i, summing over the locations j of the potential parents:

$$D_i = \sum_{j=1}^{N} B_{ij}. \tag{4}$$

There is exactly one individual per site, so at a given site i, there can be at most one successfully established offspring at each time step, and $0 \le D_i \le 1$. On the other hand, the expected number of offspring of the parent currently living at site i is $0 \leq \sum_{j=1}^{N} B_{ji} \leq N$. We denote by

$$W_i = \sum_{j=1}^{N} B_{ji} + (1 - D_i) \tag{5}$$

the expected contribution to the next time step of the individual living in site j: this includes this individual's successful offspring, and the individual itself if it survived—a quantity that we can also refer to as "fitness".

Finally, we are considering population structures such that in the absence of selection ($\delta = 0$), all individuals have the same probability of reproducing, and all individuals have the same probability of dying—meaning that all sites in the population have the same reproductive value $1/N$ (Taylor, 1990; Caswell, 2001; Maciejewski, 2014); this implies that for all sites i

$$\sum_{j=1}^{N} B_{ji}(f(X,0)) = B^{*} = D_i(f(X,0)). \tag{6}$$

Life-cycles

Most of our results are derived without specifying a life-cycle (also called "updating rule"). In the *Illustrations* section, we will give specific examples using classical life-cycles: Moran models (Birth-Death and Death-Birth), with exactly one birth and one death during a time step, and the Wright-Fisher model, where all adults die and are replaced by new individuals at the end of a time step.

3 Results

Expected frequency of type-A individuals in the population

We describe here the key steps of the computation of the expected frequency of type-A individuals in the population and refer the reader to Appendix A for mathematical details.

The expected frequency of type-A individuals in the population, denoted by $\mathbb{E}[\overline{X}]$, can be computed from the stationary distribution of population states, considering what happens during one during step. We denote by Ω the set of all possible states of the population and by $\xi(X,\delta,\mu)$ the probability that the population is in state X, in a model with strength of selection (phenotype differences) δ and mutation probability μ (ξ is the stationary distribution of population states). Given state X of the population, at the end of the time step, the state of the individual living at site i depends on whether it has survived during the time step (first term within the brackets of eq. (7)), and, if it has been replaced, on the type of the newly established offspring (second term within the brackets); we then take the expectation over all population states, and obtain:

$$\mathbb{E}[\overline{X}] = \sum_{X\in\Omega} \frac{1}{N} \sum_{i=1}^{N} \left[(1-D_i)X_i + \sum_{j=1}^{N} B_{ij} \left(X_j (1-\mu) + \mu p \right) \right] \xi(X,\delta,\mu). \tag{7}$$

This is the expected frequency of type-A individuals in the population. For instance, if we run a simulation of the model for a very long time, the average over time of the frequency of type-A individuals will provide an estimation of $\mathbb{E}[\overline{X}]$; this quantity does not depend on the initial state of the population.

We then assume that selection is weak, *i.e.*, δ is small, and write a first-order expansion of eq. (7) that contains derivatives of ξ, D_i and B_{ij} with respect to δ. For the last two, we further use the chain rule with the variables f_k, which represent the fecundity of the individual living at site k. In doing so, we let appear quantities that are the expectations of the state of pairs of sites when no selection is acting (*i.e.*, when $\delta = 0$; we call these "neutral expectations" and $\xi(X, 0, \mu)$ is called neutral stationary distribution):

$$P_{jk} = \sum_{X \in \Omega} X_j X_k \xi(X, 0, \mu) = \mathbb{E}_0\left[X_j X_k\right]. \tag{8}$$

The fact that these neutral expectations appear in our equations does not mean that selection is initially not acting and then "turned on": selection is acting all the time, but it is weak because phenotypic differences are small ($\delta \ll 1$). At the first order in δ, we can ignore the effect of selection on the expected state of pairs of sites, and this is why we only need neutral expectations (eq. (8)).

Eventually, we deduce that the expected frequency of individuals of type A in the population can be written as

$$\mathbb{E}\left[\overline{X}\right] \approx p + \frac{\delta}{\mu B^*}\left(\frac{\beta \mathsf{b} - \gamma \mathsf{c}}{N}\right), \tag{9}$$

with

$$\beta = \sum_{j,k,l}\left(\sum_i (1-\mu)\,\partial_{f_k} B_{ij} - \partial_{f_k} D_j\right) e_{lk} P_{jl} + \mu \sum_{i,j,k,l} \partial_{f_k} B_{ij}\, e_{lk} p^2, \tag{10a}$$

$$\gamma = \sum_{j,k}\left(\sum_i (1-\mu)\,\partial_{f_k} B_{ij} - \partial_{f_k} D_j\right) P_{jk} + \mu \sum_{i,j,k} \partial_{f_k} B_{ij}\, p^2, \tag{10b}$$

with P as defined in eq. (8) and ∂_{f_k} being a shorthand notation for $\frac{\partial}{\partial f_k}\Big|_{\delta=0}$. Eq. (9)

is an approximation at the first order in δ (we neglect terms in δ^2 and higher). A weak mutation approximation of eq. (9) is presented in Appendix A.4.

The formulas for β and γ (eq. (10a)-eq. (10b)) are still implicit, because we need to evaluate the P_{ij} terms, which we now do.

Expected state of pairs of sites at neutrality

We recall that P_{ij}, defined in eq. (8), is also the probability that both sites i and j are occupied by individuals of type A, at neutrality (*i.e.*, when $\delta = 0$). Under vanishing mutation ($\mu \to 0$), convenient connections can be made between identity in state and identity-by-descent (Cockerham & Weir, 1993; Rousset et al., 2000), and then with coalescence times (Slatkin, 1991, 1993; Rousset, 2004; Allen et al., 2012). Here as well, we can characterize P_{ij} in terms of probabilities of identity-by-descent, Q_{ij}. Two individuals at sites i and j are said to be identical by descent (IBD) if they share a common ancestor and if no mutation occurred in their lineages since this common ancestor (Kimura & Crow, 1964, note though that the original definition is with an infinite allele model, where each mutation creates a new allele). If two individuals are IBD, then they are both of type A with probability p, the expected state of a single individual at neutrality. If two individuals are not IBD, then they are both of type A with probability p^2. Simplifying, we obtain

$$P_{ij} = p^2 + Q_{ij}\, p\,(1-p) \tag{11}$$

(Allen & Nowak, 2014) (see Appendix B.1 for more details). Eq. (11) also valid when $i = j$. So we can work with IBD relationships.

To find the probabilities of identity-by-descent, we first write the probability that two individuals at sites i and j are IBD given the state X of the population at the previous time step, and then take the expectation of this conditional probability. We can still do so without specifying the way the population is updated (using notation as in Allen et al. (2015)), and the resulting equation is presented in Appendix B.1, eq. (B.1). This equation can also be adapted to specific updating rules, as shown in the *Illustrations* section (details of the calculations are provided in Appendix B).

Keeping in mind that $Q_{ij} = Q_{ji}$ and that $Q_{ii} = 1$, we then have to solve a linear system of $N(N-1)/2$ equations to obtain explicit formulas for all the Q_{ij} terms, for any regular graph. More explicit formulas for Q_{ij} can be found for regular graphs, and in particular for n-dimensional graphs, as we will see in the *Illustrations* section. Finally, we can gather all probabilities of identity by descent in a matrix $\mathbf{Q}$.

Back to the expected frequency of type-A individuals

Using the relationship between the expected state of pairs of sites P_{ij} and probabilities of identity-by-descent Q_{ij} (eq. (11)), we can rewrite eq. (9) as follows:

$$\mathbb{E}[\overline{X}] \approx p + \delta \frac{p(1-p)}{\mu B^* N}\left[\mathsf{b}\left(\sum_{j,k,l} e_{kl}\,\partial_{f_l} W_j\; Q_{jk}\right) - \mathsf{c}\left(\sum_{j,k} \partial_{f_k} W_j\; Q_{jk}\right)\right], \tag{12}$$

where as before ∂_{f_k} is a shorthand notation for $\left.\frac{\partial}{\partial f_k}\right|_{\delta=0}$; W_j, the fitness of individual j, was defined in eq. (5).

Interpretation For each focal individual at site k, we consider the influence that this individual can have on an identical-by-descent individual at site j (Q_{jk}).

The focal k can directly provide a benefit to j ($\mathsf{b}\, e_{kj}$) and hence affect j's fitness ($\partial_{f_j} W_j$), but k can also provide a benefit to another individual l ($\mathsf{b}\, e_{kl}$), and the resulting change of l's fecundity affects j's fitness ($\partial_{f_l} W_j$). By paying the cost of being of type A (c), k affects its own fitness ($\partial_{f_k} W_k$) but also indirectly the fitness of j ($\partial_{f_k} W_j$).

Structure parameter We say that a strategy is favored if its frequency at the mutation-selection-drift equilibrium is higher than what it would be in the absence of selection. For type A, this translates into $\mathbb{E}[\overline{X}] > p$. With eq. (12), this condition becomes

$$\underbrace{\frac{\sum_{j,k,l} e_{kl}\, \partial_{f_l} W_j\, Q_{jk}}{\sum_{j,k} \partial_{f_k} W_j\, Q_{jk}}}_{\kappa} \mathsf{b} - \mathsf{c} > 0. \tag{13}$$

Hence, a single parameter, κ, summarizes, for a given life-cycle, the structure of the population and the effect of mutation (Tarnita et al., 2009; Taylor & Maciejewski, 2012); κ is interpreted as a scaled coefficient of relatedness, that includes the effect of competition (Lehmann & Rousset, 2010).

4 Illustrations

Updating rules

The results presented so far were valid for any updating rule, provided it is such that population size remains equal to N. We now express the expected frequency of type-A individuals for specific updating rules, commonly used in studies on the evolution of altruistic behavior in structured populations: the Moran model and the Wright-Fisher model. Under a Moran model (Moran, 1962), exactly one individual dies and one individual reproduces during one time step; hence, at neutrality, $B^* = 1/N$ (B^* was defined in eq. (6)). The order of the two events matters, so two updating rules are distinguished (Ohtsuki & Nowak, 2006; Ohtsuki et al., 2006): Birth-Death and Death-Birth. In both cases, payoffs are computed at the start of each time step, before anything happens.

Moran model, Birth-Death

Any regular graph Under a Birth-Death (BD) updating, an individual j is chosen to reproduce with a probability equal to its relative fecundity in the population ($f_j / \sum_l f_l$); then its offspring disperses at random along the $\mathcal{D}$ graph, and so displaces another individual i with a probability d_{ji}/ν, so that

$$B_{ij} = \frac{f_j}{\sum_l f_l} \frac{d_{ji}}{\nu}, \text{ and } D_j = \sum_{i=1}^{N} B_{ji} = \frac{\sum_i f_i \, d_{ij}}{\nu \sum_l f_l}. \tag{14}$$

Note that with this updating rule, the probability of dying D_j depends on the composition of the population. With these probabilities of reproducing and dying eq. (12) becomes, using the matrix notation,

$$\mathbb{E}\left[\overline{X}\right] \approx p + \delta \frac{p(1-p)}{\mu} \left[\mathsf{b}\left(\frac{1}{N} \mathrm{Tr}\left(\mathbf{E}\cdot\mathbf{Q}\right) - \frac{1}{N\nu} \mathrm{Tr}\left(\mathbf{E}\cdot\mathbf{D}\cdot\mathbf{Q}\right) \right) - \mathsf{c}\left(1 - \frac{1}{N\nu} \mathrm{Tr}\left(\mathbf{D}\cdot\mathbf{Q}\right) \right) \right], \tag{15}$$

where $\mathrm{Tr}(\mathbf{M})$ denotes the trace of a matrix $\mathbf{M}$, *i.e.*, the sum of its diagonal elements. The factors of the benefits b and costs c contain direct (first terms) and indirect (second terms) effects. The term $\mathrm{Tr}(\mathbf{E}\cdot\mathbf{Q})/N$, associated to direct effects of a benefit b, is the average probability of identity by descent with a social interactant. It is discounted by the indirect effects $\mathrm{Tr}(\mathbf{E}\cdot\mathbf{D}\cdot\mathbf{Q})/(N\nu)$, corresponding to the effects of a change in fecundity of competitors; with this updating rule, competitors are one dispersal step away. Under a Birth-Death updating rule indeed, the survival of an individual at site k is reduced if another individual j sends its offspring to site k, an event that occurs if the two are neighbors on the dispersal graph (d_{jk}). So the competition neighborhood is determined by $\mathbf{D}$ (Grafen & Archetti, 2008). Similarly, the direct cost of a social interaction is discounted by the effects on competitors ($\mathrm{Tr}(\mathbf{D}\cdot\mathbf{Q})/(N\nu)$). We can further note that for all dispersal graphs, $1-\frac{1}{N\nu}\mathrm{Tr}(\mathbf{D}\cdot\mathbf{Q})\geq 0$, *i.e.*, that costs are always costly. We will see below that benefits are not always beneficial (b's factor can be negative).

Probabilities of identity by descent With this updating rule, the probabilities of identity by descent satisfy, for any i and $j \neq i$,

$$Q_{ij} = \frac{1}{2\nu}\sum_k \left(d_{kj}Q_{ki} + d_{ki}Q_{kj}\right). \tag{16}$$

(see Appendix B.2 for details on the derivation). For generic regular graphs, we have to solve a system of $N(N-1)/2$ equations to find the probabilities of identity by descent.

Transitive undirected graphs When the graph is transitive and undirected, probabilities of identity by descent verify

$$\mathbf{Q} = \lambda_M\left(\mathbf{I}_N - \frac{1-\mu}{\nu}\mathbf{D}\right)^{-1}, \tag{17}$$

where $\mathbf{I}_N$ is the identity matrix, and λ_M is such that $Q_{i,i}=1$ for all i (the $_M$ index stands for "Moran"). In addition, we have $0\leq\lambda_M\leq 1$. With eq. (17), eq. (15)

simplifies into

$$\mathbb{E}\left[\overline{X}\right] \approx p + \delta \frac{p(1-p)}{\mu} \left[\mathsf{b} \left(\frac{-\mu}{1-\mu} \frac{\mathrm{Tr}\left(\mathbf{E} \cdot \mathbf{Q}\right)}{N} + \frac{\lambda_M}{1-\mu} \frac{\mathrm{Tr}\left(\mathbf{E}\right)}{N} \right) - \mathsf{c} \left(1 - \frac{1-\lambda_M}{1-\mu} \right) \right]. \quad (18)$$

The term $\mathrm{Tr}\left(\mathbf{E}\right)/N$ corresponds to social interactions with oneself; it is usually considered as null in the case of pairwise interactions, but is not for common good type of interactions (when benefits are pooled and then redistributed). So unless interactions with oneself are strong (large $\mathrm{Tr}\left(\mathbf{E}\right)/N$), the factor modulating the effect of benefits b is negative, and as a result the expected frequency of altruists cannot be greater than what it would be in the absence of selection (*i.e.*, $\mathbb{E}\left[\overline{X}\right] \leq p$.)

Evaluating probabilities of identity by descent in transitive regular graphs still requires the inversion of a N by N matrix (eq. (17)), which can limit applications. Results are simpler in graphs that match our definition of "n-dimensional graphs"; they depend on the dimensionality n of the graph and are presented in Appendix B.2.

Moral model, Death-Birth

Any regular graph Under a Death-Birth (DB) updating, the individual who is going to die is chosen first, uniformly at random (i is chosen with probability $1/N$). Then, all individuals produce offspring, and one of them (one offspring of parent j wins with probability $f_j d_{ji}/\sum_l f_l d_{li}$) displaces the individual chosen to die. When $d_{ii} \neq 0$, one needs to clarify whether the individual chosen to die reproduces before dying or not; here we assume that this is the case, but some alternative formulations do not. Under this updating rule, we have

$$D_j = \frac{1}{N}, \text{ and } B_{ij} = \frac{1}{N}\frac{f_j\, d_{ji}}{\sum_l f_l\, d_{li}}. \tag{19}$$

Using matrix notation, eq. (12) becomes

$$\mathbb{E}\left[\overline{X}\right] \approx p + \delta\frac{p(1-p)}{\mu}\left[\mathsf{b}\left(\frac{1}{N}\mathrm{Tr}\left(\mathbf{E}\cdot\mathbf{Q}\right) - \frac{1}{N v^2}\mathrm{Tr}\left(\mathbf{E}\cdot\mathbf{D}\cdot\mathbf{D}^T\cdot\mathbf{Q}\right)\right) - \mathsf{c}\left(1 - \frac{1}{N v^2}\mathrm{Tr}\left(\mathbf{D}\cdot\mathbf{D}^T\cdot\mathbf{Q}\right)\right)\right], \tag{20}$$

where ^{T} denotes transposition. We can again identify direct and indirect effects of benefits and costs; the direct effects are the same as for the Birth-Death updating rule, but the indirect effects differ, reflecting the fact that competitors are now two dispersal steps away (Grafen & Archetti, 2008; Débarre et al., 2014). Under a Death-Birth updating rule indeed, individuals j and k are competing for a site i whose occupant has just been chosen to die if both j and k can send their offspring to i; this depends on $d_{ji} d_{ki}$, leading to the $\mathbf{D}\cdot\mathbf{D}^T$ products in eq. (20). Again, we can also note that $1 - \frac{1}{Nv^2}\mathrm{Tr}\left(\mathbf{D}\cdot\mathbf{D}^T\cdot\mathbf{Q}\right) \geq 0$, *i.e.*, that the costs are indeed costly.

Probabilities of identity by descent With the Death-Birth model as defined above, the system of equations for the probabilities of identity by descent at neutrality is the same as in eq. (16).

Transitive undirected graphs When the graph is transitive and undirected, eq. (17) still holds and eq. (20) simplifies into

$$\mathbb{E}\left[\overline{X}\right] \approx p + \delta \frac{p(1-p)}{\mu}\left[\mathsf{b}\left(\left(\frac{-\mu\,(2-\mu)}{(1-\mu)^2}\right)\frac{\mathrm{Tr}\,(\mathbf{E}\cdot\mathbf{Q})}{N} + \frac{\lambda_M}{1-\mu}\frac{\mathrm{Tr}\,(\mathbf{E}\cdot\mathbf{D})}{N\nu} + \frac{\lambda_M}{(1-\mu)^2}\frac{\mathrm{Tr}\,(\mathbf{E})}{N}\right) - \mathsf{c}\left(\frac{-\mu\,(2-\mu)}{(1-\mu)^2} + \frac{\lambda_M}{1-\mu}\frac{\mathrm{Tr}\,(\mathbf{D})}{N\nu} + \frac{\lambda_M}{(1-\mu)^2}\right)\right]. \tag{21}$$

Wright-Fisher

Under a Wright-Fisher model, generations are non-overlapping: all adults produce offspring, then all adults die and the offspring disperse and compete for establishment, so that

$$D_j = 1, \text{ and } B_{ij} = \frac{f_j\, d_{ji}}{\sum_l f_l\, d_{li}}. \tag{22}$$

In a Wright-Fisher model, at neutrality, $B^* = 1$ (the entire population is renewed at each generation; in a Moran model we had $B^* = 1/N$); eq. (22) differing from its Moran Death-Birth equivalent (eq. (19)) by only a factor $1/N$, we end up with the same equation as eq. (20) for the expected frequency of type-A individuals in the population. The difference between the Moran Death-Birth and Wright-Fisher life-cycles however lies in the evaluation of probabilities of identity by descent.

Probabilities of identity by descent Under a Wright-Fisher model, the entire population is replaced, so the equation is different from the one obtained under a Moran model; probabilities of identity by descent of two different individuals satisfy ($i \neq j$)

$$Q_{ij} = (1-\mu)^2 \sum_{k,l} \frac{d_{ki}}{\nu} \frac{d_{lj}}{\nu} Q_{kl}. \tag{23}$$

(see Appendix B.3 for details of the derivation.)

Undirected transitive graphs When the dispersal graph is undirected ($\mathbf{D} = \mathbf{D}^T$) and transitive, the probabilities of identity by descent verify

$$\mathbf{Q} = \lambda_{WF} \left(\mathbf{I}_N - \frac{(1-\mu)^2}{\nu^2} \mathbf{DD} \right)^{-1}, \tag{24}$$

with λ_{WF} such that for all i, $Q_{ii} = 1$, and the $_{WF}$ index stands for "Wright-Fisher". With this, the expected frequency of type-A individuals becomes

$$\begin{aligned} \mathbb{E}\left[\overline{X}\right] \approx p + \delta \frac{p(1-p)}{\mu} \Bigg[\mathsf{b} \left(\frac{-\mu(2-\mu)}{(1-\mu)^2} \frac{\operatorname{Tr}(\mathbf{E}\cdot\mathbf{Q})}{N} + \frac{\lambda_{WF}}{(1-\mu)^2} \frac{\operatorname{Tr}(\mathbf{E})}{N} \right) \\ - \mathsf{c} \left(\frac{-\mu(2-\mu)}{(1-\mu)^2} + \frac{\lambda_{WF}}{(1-\mu)^2} \right) \Bigg]. \end{aligned} \tag{25}$$

We can immediately see the difference with the Moran Death-Birth case (eq. (21)), caused by a different equation for the probabilities of identity by descent $\mathbf{Q}$. Crucially missing in eq. (25) is the positive term $\frac{\lambda_M}{1-\mu} \frac{\operatorname{Tr}(\mathbf{E}\cdot\mathbf{D})}{N\nu}$: without it, the factor associated to the benefits b is negative unless interactions with oneself ($\operatorname{Tr}(\mathbf{E})$) are strong enough, as was the case with the Moran Birth-Death updating.

As for the Moran model, evaluating probabilities of identity by descent in undirected transitive graphs (eq. (24)) involves the computation of the inverse of a N by N matrix. More explicit results can be obtained for "n-dimensional graphs"; they are presented in Appendix B.3.

Specific population structures

All numerical examples given in this section are derived with $\mathsf{b} > 0$ and $\mathsf{c} > 0$, so type-A individuals can be called altruists.

As an illustration, we explore the impact of mutation on the expected proportion of type-A individuals in graph-structured populations, in which the same graph defines dispersal and interactions among individuals (Lieberman et al., 2005; Hindersin & Traulsen, 2015; McAvoy & Hauert, 2015), so that $\mathbf{E} = \mathbf{D}$.

Undirected transitive graphs When the graph undirected and transitive, the equations for the expected frequency of altruists (type-A individuals) can be further simplified as follows:

Moran, Birth-Death

$$\mathbb{E}\left[\overline{X}\right] \approx p + \delta \frac{p(1-p)}{\mu}\left[\mathsf{b}\left(\frac{-\mu\nu}{(1-\mu)^2}(1-\lambda_M) + \frac{\lambda_M}{1-\mu} d_{11}\right) - \mathsf{c}\left(\frac{\lambda_M - \mu}{1-\mu}\right)\right]. \tag{26}$$

Moran, Death-Birth

$$\mathbb{E}\left[\overline{X}\right] \approx p + \delta \frac{p(1-p)}{\mu}\left[\mathsf{b}\left(\frac{-\mu(2-\mu)\nu}{(1-\mu)^3}(1-\lambda_M) + \frac{\lambda_M}{1-\mu}\frac{\sum_k d_{1k}^2}{\nu} + \frac{\lambda_M}{(1-\mu)^2} d_{11}\right) - \mathsf{c}\left(\frac{-\mu(2-\mu)+\lambda_M}{(1-\mu)^2}\right) + \frac{\lambda_M}{(1-\mu)}\frac{d_{11}}{\nu}\right]. \tag{27}$$

In both cases, λ_M is obtained from eq. (17). Under a Wright-Fisher updating, eq. (25) cannot be much further simplified.

Small graphs

For regular graphs of small size, the probabilities of identity by descent can be calculated directly using eq. (16) (Moran model) or eq. (23) (Wright-Fisher). In figure 2, we show the value of $\mathbb{E}[\overline{X}]$ on three regular graphs that have the same size ($N = 12$) and the same degree ($\nu = 3$), and we consider three common life-cycles in populations of fixed size (Moran Death-Birth, Moran Birth-Death, Wright-Fisher). We compare the prediction based on eq. (9) (curves) to the outputs of stochastic simulations (points). For all life-cycles, increasing the mutation probability μ makes $\mathbb{E}[\overline{X}]$ closer to its value at the mutation-drift equilibrium (p). The curves corresponding to different structures are almost undistinguishable under a Moran model (figures 2(a) and (b))—the curve corresponding to the graph with no symmetry (red, squares) being a bit less similar though). In the Wright-Fisher model (figure 2(c)) however, the effects of the three structures are clearly different, even when μ becomes very small: knowing only the size (N) and degree (ν) of a regular graph is not enough in this case to precisely predict the expected frequency of altruists in the population.

Large graphs: variations on a circle

When the number of nodes gets larger, we have to concentrate on graphs with a high level of symmetry. Here we will consider 1-dimensional graphs (graphs whose nodes can be relabelled to satisfy eq. (2)) that are undirected, and hence that can be categorised as undirected transitive graphs. For simplicity, we can consider a circle graph, such that the nodes are arranged on a circle, and each node is connected to its two neighbors only. Here, we assume that the num-

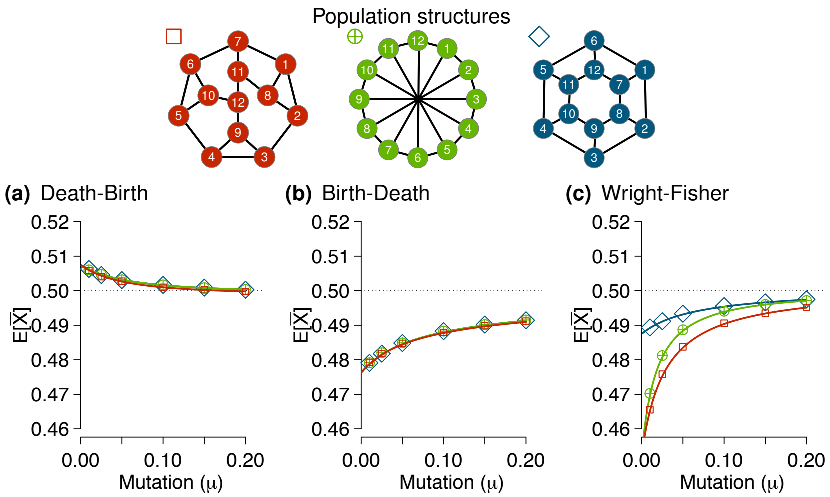

Figure 2: Expected frequency of type-A individuals $\mathbb{E}[\overline{X}]$, depending on population structure (legend on the first line), updating rule ((a): Moran Death-Birth, (b): Moran Birth-Death, (c): Wright-Fisher), and mutation probability μ (horizontal axis): Comparison between the theoretical prediction (curves) and the outcomes of numerical simulations (points). The horizontal dotted gray line corresponds to p, the expected frequency of type-A individuals when there is no selection (*i.e.*, when $\delta = 0$). Other parameters: δ=0.005, $p = 1/2$.

ber of nodes is infinite: $N \to \infty$. As previously, a given node hosts exactly one individual (see figure 3(a)).

Under a Moran model, using eq. (B.12b), we find for $\mu > 0$

$$\lambda_M = \sqrt{\mu(2-\mu)}, \tag{28a}$$

and, although the quantity is not needed to compute $\mathbb{E}[\overline{X}]$ under a Moran model, the probability of identity by descent between two neighbors on the circle is given by

$$Q_M = \frac{1-\sqrt{(2-\mu)\mu}}{1-\mu}, \tag{28b}$$

and we recover the formula presented in, *e.g.*, Allen et al. (2012) (see Appendix B.2.4 for details). This result is plotted in figure 3(c). We however need to note that the first-order approximation for $\mathbb{E}\left[\overline{X}\right]$ fails when both $\mu \to 0$ and $N \to \infty$: this is because the integral behind eq. (28a) does not converge when $\mu \to 0$. Similarly, for instance, the first order approximation for the probability that two neighbors are identical by descent $1-\mu(N-1)$, which was obtained by Taylor et al. (2007a), fails when N is too large compared to μ.

The circle graph is too particular a graph for a Wright-Fisher updating. Indeed, while we find the same equation for λ_{WF} as for λ_M in this case (eq. (28a)), the probability of identity by descent between neighbors is equal to 0. This is because all individuals reproduce at each time step, and their offspring can only establish on the node on the left or on the right of their parent, so that relatedness cannot build up. We can however modify the graph to allow for establishment in the parent's node: with probability $(1-m)$ the offspring remain where the parent was, otherwise they move to the right or the left-hand side node (with probability $m/2$ for each; see figure 32(b)). In this case, we find the following probability of identity by descent between neighbors:

$$Q_{WF} = \frac{\mu\,(2-\mu)+2\,(1-\mu)^2 m\,(1-m)-\sqrt{\mu\,(2-\mu)\,\big(\mu+2\,m\,(1-\mu)\big)\big(2-\mu-2\,m\,(1-\mu)\big)}}{2\,(1-\mu)^2 m\,(1-m)}. \tag{29}$$

(See Appendix B.3.4 for details.) The result is plotted in figure 3(d) for different values of the emigration probability m.

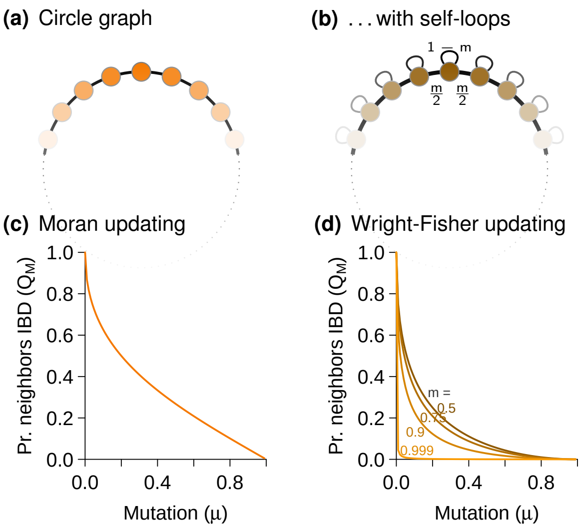

Figure 3: Circle graphs, without (a) or with self-loops ((b); the weight of the self-loop is $1-m$), and Probability that two neighbors on the graph are identical by descent, as function of the mutation probability μ, for the Moran updating on an infinite circle graph (c), and for the Wright-Fisher updating on an infinite circle graph with self loops (d). In (d), emigration probabilities m take values 0.5, 0.75, 0.9, 0.999 (increasingly lighted curves).

5 Discussion

While most studies on the evolution of cooperation assume an almost perfect fidelity of strategy transmission from parent to offspring, here, we explored the effect of arbitrary mutation on the evolution of social behavior in structured populations. We provide a formula (eq. (12)) that gives the expected frequency of a given strategy, for any life-cycle, any mutation probability, and that is valid in populations of fixed size that are such that the reproductive values of all sites are equal (*i.e.*, when all individuals have the same fecundity, they all have the same chance of actually reproducing). The formula depends on the probability of identity by descent of pairs of individuals, and we show how to compute those in general.

Identity by descent and expected state of pairs of sites

The effects of social interactions depend on the actual types of the individuals who interact. With imperfect strategy transmission from parents to their offspring ($\mu > 0$), common ancestry does not guarantee that two individuals are of the same type. The concept of identity by descent, as we use it in this article, adds to common ancestry the condition that no mutation has occured in the two individuals' lineages since the common ancestor (Kimura & Crow, 1964; Taylor et al., 2007b), and hence garanties that the two individuals are of the same type. Two individuals that are not IBD can be treated independently, and we can hence relate the probability that the individuals at two sites i and j to their expected state (eq. (11) and Allen & Nowak (2014)). Finally, equations with probabilities of identity by descent are much simpler than those for the expected state of pairs of sites.

A structure parameter κ

Tarnita et al. (2009) and Taylor & Maciejewski (2012) showed that, when social interactions affect fecundities, there exists a parameter independent of the terms of the interaction matrix that summarizes the effects of population structure (in terms of dispersal patterns and also of who interacts with whom) and depends on the rule chosen to update the population and on mutation; here we provide a generic formula for such a structure parameter. This parameter, κ, can be interpreted as a scaled relatedness (Queller, 1994; Lehmann & Rousset, 2010), which includes the effect of competition. Eq. (13) provides a generic formula for κ, for any life-cycle and population structure (provided condition eq. (1) is satisfied).

The actual value of the scaled relatedness κ depends on the life-cycle and on the mutation probability μ. First, κ includes competition (what we call "indirect effects"), and the scale of competition depends on the life-cycle (Grafen & Archetti, 2008; Débarre et al., 2014). Second, even direct effects—and so even what is referred to as relatedness—do depend on the life-cycle and μ.

Finally, there is a single structure parameter κ because social interactions only affect fecundity. Previous studies assuming vanishing or absent mutation have shown that the parameter will be different if social interactions instead influence survival (Nakamaru & Iwasa, 2006; Taylor, 2010) and that we need more than one parameter if social interactions affect both fecundity and survival (Débarre et al., 2014).

Updating rules and the evolution of altruism

We illustrate our results with specific updating rules, with either exactly new individual at each time step (Moran Birth-Death, Moran Death-Birth), or exactly N new individuals, *i.e.*, the entire population being renewed at each time step (Wright-Fisher). Previous studies done under the assumption of vanishing mutation rates (and with undirected transitive dispersal graphs) found that updating rules had a great impact on the evolution of altruism, and in particular, that selection did not favor altruism (benefits given to others exclusively) under a Wright-Fisher or Moran Birth-Death updating (the "cancellation result"; Taylor, 1992; Taylor et al., 2011; Ohtsuki et al., 2007; Lehmann et al., 2007); the result holds with imperfect strategy transmission as well. This is because the competition radius (individuals one dispersal step away [**D**] with a Moran Birth-Death updating, individuals two dispersal steps away [**D**.**D**] with a Wright-Fisher updating) matches the radius on which identities by descent are computed (see eq. (17) and eq. (24)). On the other hand, under a Death-Birth updating, competition is against individuals two dispersal steps away, but identity by descent is computed using individuals one dispersal step away: competition is "diluted", and altruism can be favored by selection. Again, note that the conclusions for the Moran model depend on which trait is affected by the social behavior: altruism is favored under a Birth-Death updating if survival, instead of fecundity, is affected by social behavior (Nakamaru & Iwasa, 2006; Taylor, 2010; Débarre et al., 2014).

Implications for adaptive dynamics

Our results are obtained by considering the changes that occur during one time step from a given population state, chosen from the stationary distribution of population states—hence the phrase "long-term", which differs from the use made by, for instance Van Cleve (2015), where it refers to a trait substitution sequence. Yet, our results can also be used in that context. The adaptive dynamics framework describes evolution as a series of trait substitutions (Geritz et al., 1997; Champagnat et al., 2006; Champagnat & Lambert, 2007; Lehmann, 2012; Lehmann & Rousset, 2014) and is based on the assumption that mutations are rare and incremental; in a finite population, trait evolution proceeds along a gradient of fixation probabilities. Computing those fixations probabilities can be challenging in spatially structured populations.

Yet, the existence of a single parameter (in this case, defined as $\sigma = (\kappa - 1)/(\kappa + 1)$, Tarnita et al., 2009) to characterize population structure and update rules led to the extension of the adaptive dynamics framework to populations with arbitrary structure (Allen et al., 2013), the structure parameter however remaining unspecified in general. Our formula for κ (eq. (13)) is valid for arbitrary mutation, so *a fortiori* for vanishing mutation probabilities, and can therefore be used to explicitly study adaptive dynamics in structured populations (provided the reproductive values of all sites are equal).

Data accessibility

All codes are provided as a zipped folder, and can be downloaded from `https://figshare.com/articles/Mutation_and_social_evolution/3207748`. They will be uploaded on Dryad when the manuscript is accepted.

Competing interests

I have no competing interests.

Acknowledgements

I thank Sally Otto and François Bienvenu for comments on the manuscript and Ben Allen for clarifications. The simulations were run on the Migale cluster (`http://migale.jouy.inra.fr/`).

Funding

We thank the Agence Nationale de la Recherche for funding (grant ANR-14-ACHN-0003-01).

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A Expected frequency of type-A individuals

Conditional expectations

We denote by $\mathbb{E}\left[X_i(t+1)|X(t)\right]$ the expected state of the individual at site i at time $t+1$, given that the population is in state X at time t. Because X_i is an indicator variable, $\mathbb{E}\left[X_i(t+1)|X(t)\right] = \mathbb{P}\left[X_i(t+1) = 1|X(t)\right]$. Site i is occupied by an individual of type A at time $t+1$ if: *i)* it was occupied by an individual of type A at time t and this individual has not been replaced (*i.e.*, has not died) between t and $t+1$ (first term in eq. (A.1)), or *ii)* the individual has been replaced by a new one, whose parent was in site j at t; in this case, either the parent was of type A and the offspring is not a mutant; or, whichever the type of the parent, the offspring is a mutant and mutated into type A (second term of eq. (A.1)):

$$\mathbb{E}\left[X_i(t+1)|X(t)\right] = (1-D_i)X_i + \sum_j B_{ij}\left(X_j(1-\mu) + \mu p\right). \tag{A.1}$$

Unconditional expectations

We now want to consider the long-term outcome of competition. We denote by $\xi(X,\delta,\mu)$ the probability that the population is in state X, given phenotype difference δ between the two types and a mutation rate μ, and by Ω the ensemble of all possible population states. By definition, the expectation of the state of the population is given by $\mathbb{E}\left[X\right] = \sum_{X\in\Omega} X\,\xi(X,\delta,\mu)$.

When the stationary distribution is reached (*i.e.*, for very large t), $\mathbb{E}\left[X(t+1)\right] = \mathbb{E}\left[X(t)\right] = \mathbb{E}\left[X\right]$; we consider the population average of X, $\overline{X} = \sum_i X_i/N$.

Appendix A

From eq. (A.1), we obtain

$$\mathbb{E}\left[\overline{X}\right] = \sum_{X\in\Omega}\sum_{i=1}^{N}\frac{1}{N}\left(\sum_{j=1}^{N}B_{ij}X_j - D_i X_i - \mu\sum_{j=1}^{N}B_{ij}(X_j-p) + X_i\right)\xi(X,\delta,\mu),$$

which, after simplifications , becomes

$$\sum_{X\in\Omega}\frac{1}{N}\left[\sum_{j=1}^{N}\left(\sum_{i}B_{ij}-D_j\right)X_j - \mu\sum_{i}\sum_{j}B_{ij}\,(X_j-p)\right]\xi(X,\delta,\mu) = 0. \qquad \text{(A.2)}$$

Weak selection approximation While eq. (A.2) is valid for any μ and δ, we now assume that δ, which scales the phenotype difference, is small, so that we can neglects terms of order δ^2 and higher. We note that in the absence of selection (*i.e.*, when the expressed phenotypes are identical, $\delta = 0$), the expected state of a site j when the stationary distribution is reached is equal to the probability that a mutated offspring is of type A (*i.e.*, $\sum_{X\in\Omega}X_j\xi(X,0,\mu) = p$; see section A.3 below for more details). Using eq. (6) and the compact notation ∂_δ to represent $\frac{\partial}{\partial\delta}\Big|_{\delta=0}$, a first-order expansion of eq. (A.2) yields, after simplifications:

$$\begin{aligned}0 = {} & \frac{\delta}{N}\sum_{X\in\Omega}\left[\sum_{j}\left(\sum_{i}\partial_\delta B_{ij} - \partial_\delta D_j\right)X_j - \mu\sum_{i}\sum_{j}\partial_\delta B_{ij}\,(X_j-p)\right]\xi(X,0,\mu)\\ & -\frac{\delta\mu}{N}\sum_{X\in\Omega}\left[\sum_{j}B^*\,(X_j-p)\right]\partial_\delta\xi(X,\delta,\mu) + O(\delta^2).\end{aligned} \qquad \text{(A.3a)}$$

Appendix A

Because ξ is a probability distribution, $\sum_{X\in\Omega}\partial_\delta\xi(X,\delta,\mu)=0$; reorganizing eq. (A.3a), we obtain

$$\partial_\delta\mathbb{E}\left[\overline{X}\right]=\frac{1}{\mu NB^*}\left(\sum_{X\in\Omega}\left[\sum_j\left(\sum_i\partial_\delta B_{ij}-\partial_\delta D_j\right)X_j\right]\xi(X,0,\mu)\right.$$
$$\left.-\sum_{X\in\Omega}\left[\mu\sum_{i,j}\partial_\delta B_{ij}\,(X_j-p)\right]\xi(X,0,\mu)\right)+O\left(\frac{\delta}{\mu B^*}\right).\qquad\text{(A.3b)}$$

We can now use the chain rule:

$$\partial_\delta B_{ij}=\sum_{k=0}^{N}\left.\frac{\partial B_{ij}}{\partial f_k}\right|_{\delta=0}\partial_\delta f_k,\qquad\text{(A.4a)}$$

$$\partial_\delta D_j=\sum_{k=0}^{N}\left.\frac{\partial D_j}{\partial f_k}\right|_{\delta=0}\partial_\delta f_k,\qquad\text{(A.4b)}$$

where the $\partial_\delta f_k$ terms are computed using the definition of f presented in eq. (3b). We also denote by P_{jk} the expected state of a pair of sites (j,k) evaluated when there are no social interactions ($\delta=0$):

$$P_{jk}=\sum_{X\in\Omega}X_jX_k\xi(X,0,\mu).\qquad\text{(A.5)}$$

Doing so, we realize that we can write eq. (A.3b) as

$$\partial_\delta\mathbb{E}\left[\overline{X}\right]=\frac{1}{\mu NB^*}\left(\beta\mathsf{b}-\gamma\mathsf{c}\right)+O\left(\frac{\delta}{\mu B^*}\right),\qquad\text{(A.6)}$$

with β and γ as defined in eq. (10).

Plugging eq. (A.6) in the following equation

$$\mathbb{E}\left[\overline{X}\right]=p+\delta\,\partial_\delta\mathbb{E}\left[\overline{X}\right]+O(\delta^2),\qquad\text{(A.7)}$$

we recover eq. (9).

In the absence of selection ($\delta = 0$)

In the absence of selection, neither D_i nor B_{ij} depend on the state of the population, because all individuals now have the same fecundity. Consequently, when $\delta = 0$, and given that neutral reproductive values are all equal (eq. (6) in the main text),eq. (A.1) becomes

$$\mathbb{E}\left[X_i(t+1)|X(t)\right] = (1-B^*)X_i + \sum_j B^0_{ij}\left(X_j(1-\mu)\right) + \mu p B^*. \tag{A.8}$$

We now take the expectation of eq. (A.8) over the neutral distribution of states ($\xi(X,0,\mu)$); since B^0_{ij} does not depend on X, we have

$$\mathbb{E}_0\left[X_i\right] = (1-B^*)\mathbb{E}_0\left[X_i\right] + \sum_j B^0_{ij}\left(\mathbb{E}_0\left[X_j\right](1-\mu)\right) + \mu p B^*, \tag{A.9a}$$

and we obtain after simplifying

$$\mathbb{E}_0\left[X_i\right] = p. \tag{A.9b}$$

Weak mutation

When $\mu = 0$, there is no stationary distribution of states, because the states $X = \mathbf{0}$ and $X = \mathbf{1}$ (loss of type-A and loss of type-B individuals, respectively) are absorbing. We can nevertheless extend ξ by continuity at $\mu = 0$, so that $\xi(X,\delta,0) = \lim_{\mu\to 0}\xi(X,\delta,\mu)$. Then, it does not matter whether we Taylor-expand ξ first in δ then in μ or first in μ and then in δ, and so we can consider $\mu \ll \delta$ and $\delta \ll \mu$

(Tarnita & Taylor, 2014).

Weak selection then weak mutation Starting from eq. (A.3a), a first order expansion near $\mu = 0$ yields

$$0 = \frac{1}{N}\sum_{X\in\Omega}\sum_{j}\left(\sum_{i}\partial_\delta B_{ij} - \partial_\delta D_j\right)X_j\partial_\mu\xi(X,0,\mu) - \frac{1}{N}\sum_{X\in\Omega}\sum_{i,j}\partial_\delta B_{ij}(X_j-p)\xi(X,0,0)$$
$$-\frac{1}{N}\sum_{X\in\Omega}\sum_{j}B^*(X_j-p)\partial_\delta\xi(X,\delta,0) + O\left(\frac{\delta}{\mu}\right) + O(\mu). \tag{A.10}$$

Here we have $\delta \ll \mu \ll 1$. Notation ∂_μ stands for $\left.\frac{\partial}{\partial\mu}\right|_{\mu=0}$.

Weak mutation then weak selection Starting from eq. (A.2), a first order expansion near $\mu = 0$ and then a first order expansion near $\delta = 0$ yields

$$0 = \frac{1}{N}\sum_{X\in\Omega}\sum_{j}\left(\sum_{i}\partial_\delta B_{ij} - \partial_\delta D_j\right)X_j\partial_\mu\xi(X,0,\mu) - \frac{1}{N}\sum_{X\in\Omega}\sum_{i,j}\partial_\delta B_{ij}(X_j-p)\xi(X,0,0)$$
$$-\frac{1}{N}\sum_{X\in\Omega}\sum_{j}B^*(X_j-p)\partial_\delta\xi(X,\delta,0) + O\left(\frac{\mu}{\delta}\right) + O(\delta). \tag{A.11}$$

Here we have $\mu \ll \delta \ll 1$.

At the first orders, eq. (A.10) and eq. (A.11) are the same.

When $\mu \to 0$, the population is either in state $X = \mathbf{0}$ or in state $X = \mathbf{1}$, so

$$\xi(\mathbf{1},\delta,0) = 1 - \xi(\mathbf{0},\delta,0) = \lim_{\mu\to 0}\mathbb{E}\left[\overline{X}\right], \tag{A.12a}$$

and as a result

$$\partial_\delta \xi(\mathbf{1},\delta,0) = -\partial_\delta \xi(\mathbf{0},\delta,0)\,. \tag{A.12b}$$

In addition, when $\delta = 0$,

$$\xi(\mathbf{1},0,\mu) = p. \tag{A.12c}$$

So at the first orders, reorganizing eq. (A.10) (or equivalently eq. (A.11)), we obtain the following equation for the derivative with respect to δ of the expected state of the population when $\mu \to 0$ (Tarnita & Taylor, 2014):

$$\begin{aligned}\partial_\delta \xi(\mathbf{1},\delta,0) \approx \frac{1}{B^*}\Bigg[&\frac{1}{N}\sum_{X\in\Omega}\sum_j\left(\sum_i \partial_\delta B_{ij} - \partial_\delta D_j\right) X_j \partial_\mu \xi(X,0,\mu)\\ &-\frac{1}{N}p(1-p)\sum_{i,j}\big(\partial_\delta B_{ij}(\mathbf{1}) - \partial_\delta B_{ij}(\mathbf{0})\big)\Bigg].\end{aligned} \tag{A.13}$$

B Probabilities of identity by descent

We first start by showing the link between the expected state of a pair of sites (P_{ij}) and probabilities of identity by descent (Q_{ij}), for any life-cycle.

Any life-cycle

Notation

To be able to consider any life-cycle, we use notation similar to what is used in Allen et al. (2015). At each time step, from 1 to N individuals are replaced, depending on the updating rule; R denotes the set of individuals that are replaced (*i.e.*, the sites where an individual is replaced by another one). For each site i where a replacement happened ($i \in R$), $\alpha(i)$ gives the index of the site where the parent of the new individual lived, while for individuals that were not replaced, $\forall i \in \{1,\dots,N\}\setminus R, \alpha(i) = i$[1]. Finally, $\rho(R,\alpha)$ denotes the probability of the replacement event (R,α). In the absence of selection, this probability does not depend on the current state of the population.

Expected state of a pair of sites

Considering two different sites i and j, depending on the updating rule, at each time step, *i)* either none of the individuals are replaced—then they are both of type A if they already were [first term in eq. (B.1)], *ii)* either one of the individuals (i or j) is replaced—then they are both of type A if the surviving individual is A and if either the parent of the other individual was of type A and no mu-

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[1] Here we extend the notation used in Allen et al. (2015), because in their study, $\alpha : R \to \{1,\dots,N\}$

tation occurred, or the offspring mutated into type A whichever the type of its parent [second and third terms in eq. (B.1)]), or finally *iii)* both individuals are replaced—then the probability that both offspring are of type A is $P_{\alpha(i)\alpha(j)}(1-\mu+\mu p)^2+2(p-P_{\alpha(i)\alpha(j)})(1-\mu+\mu p)(\mu p)+(1-2p+P_{\alpha(i)\alpha(j)})(\mu p)^2$, which simplifies into the fourth term in eq. (B.1)). We obtain the following equation:

$$\begin{aligned}
&\forall (i,j)\in\{1,\dots,N\}^2, i\neq j,\\
&\qquad P_{ij} = \sum_{\substack{R,\alpha\\ i\notin R, j\notin R}} q(R,\alpha)\, P_{\alpha(i)\alpha(j)}\\
&\qquad\quad + \sum_{\substack{R,\alpha\\ i\notin R, j\in R}} q(R,\alpha)\left[P_{\alpha(i)\alpha(j)}(1-\mu)+p\mu p\right]\\
&\qquad\quad + \sum_{\substack{R,\alpha\\ i\in R, j\notin R}} q(R,\alpha)\left[P_{\alpha(i)\alpha(j)}(1-\mu)+p\mu p\right]\\
&\qquad\quad + \sum_{\substack{R,\alpha\\ i\in R, j\in R}} q(R,\alpha)\left[P_{\alpha(i)\alpha(j)}(1-\mu)^2+(2-\mu)\mu p^2\right].
\end{aligned}\tag{B.1}$$

Identity by descent

Considering two different sites i and j, depending on the updating rule, at each time step, *i)* either none of the individuals are replaced—then they are identical by descent (IBD) if they already were [first term in eq. (B.1)], *ii)* either one of the individuals (i or j) is replaced—then they are both IBD if the surviving individual and the parent of the new individual were and no mutation occurred [second and third terms in eq. (B.1)]), or finally *iii)* both individuals are replaced—then then are IBD if their two parents were and no mutation occurred in either [fourth term in eq. (B.1)]. We obtain the following equation:

$$\begin{aligned}
&\forall (i,j) \in \{1,\dots,N\}^2, i \neq j,\\
&Q_{ij} = \sum_{\substack{R,\alpha\\ i\notin R, j\notin R}} \rho(R,\alpha)\, Q_{\alpha(i)\alpha(j)} + \sum_{\substack{R,\alpha\\ i\notin R, j\in R}} \rho(R,\alpha)\, Q_{\alpha(i)\alpha(j)}(1-\mu)\\
&\qquad + \sum_{\substack{R,\alpha\\ i\in R, j\notin R}} \rho(R,\alpha)\, Q_{\alpha(i)\alpha(j)}(1-\mu) + \sum_{\substack{R,\alpha\\ i\in R, j\in R}} \rho(R,\alpha)\, Q_{\alpha(i)\alpha(j)}(1-\mu)^2.
\end{aligned} \tag{B.2}$$

For all pairs $i \neq j$, eq. (B.1) and eq. (B.2) are equivalent when we set

$$Q_{ij} = \frac{P_{ij} - p^2}{p(1-p)}, \tag{B.3}$$

and eq. (B.3) is also valid when $i = j$ (in this case $Q_{ii} = 1$ and $P_{ii} = p$). So we can use the recursion on Q presented in eq. (B.2) together with eq. (B.3).

Finally, while Q_{ij} is an expectation over the stationary distribution of population states, we also introduce the indicator variable $q_{ij}(t)$, equal to 1 if, in a realization of the process, the individuals at sites i and j are IBD at time t. We also denote by $\mathbf{Q}$ the matrix gathering the Q_{ij} terms.

Moran model

In a Moran model, exactly one individual died and one individual reproduces during one time step. Given a state X at time t, for $i \neq j$, probabilities of identity by descent verify

$$\mathbb{E}\left[q_{ij}(t+1)|X(t)\right] = q_{ij}(t)\left(1 - \frac{2}{N}\right) + \frac{1-\mu}{N}\sum_k \frac{d_{kj}q_{ki}(t) + d_{ki}q_{kj}(t)}{\nu}. \tag{B.4}$$

Taking the expectation of this quantity over the stationary distribution of states, we obtain

$$Q_{ij} = \frac{1-\mu}{2\nu} \sum_k \left(d_{kj} Q_{ki} + d_{ki} Q_{kj}\right) \qquad (i \neq j), \tag{B.5}$$

and $Q_{ij} = 1$ when $i = j$. Eq. (B.5) is valid for any regular graph; all the Q_{ij} terms can be found by solving a system of $N(N-1)/2$ equations (since $Q_{ij} = Q_{ji}$). We can also write eq. (B.5) in matrix form:

$$\mathbf{Q} = \frac{1-\mu}{2\nu} (\mathbf{QD} + \mathbf{D}^T \mathbf{Q}) + \mathbf{L}, \tag{B.6}$$

where $\mathbf{D}$ is the adjacency matrix of the dispersal graph (with elements d_{ij}), ^{T} denotes transposition, and $\mathbf{L}$ is a diagonal matrix whose ith diagonal element is $1 - \sum_k d_{ki} Q_{ki}/\nu$ (*i.e.*, such that $Q_{ii} = 1$).

Transitive undirected graphs

When the dispersal graph is transitive, then all the elements on the diagonal of $\mathbf{L}$ are equal, so we can write $\mathbf{L} = \lambda_M \mathbf{I}_N$, where $\mathbf{I}_N$ is the N by N identity matrix. When the graph is also undirected, $\mathbf{D} = \mathbf{D}^T$, and we also show by induction that $\mathbf{DQ} = \mathbf{QD}$ (Grafen & Archetti, 2008).

Let us assume without loss of generality that initially $(t = 0)$ all individuals are IBD ($q_{ij}(0) = \mathbf{1}_{NN}$, where $\mathbf{1}_{NN}$ is the N-by-N matrix containing only ones) and of type B $(X(0) = \{0, \ldots, 0\})$. Also, let us denote by $\zeta_0(X, t)$ the probability that the population is in state X at time t given that it was in state $\{0, \ldots, 0\}$ at time 0, and by $\mathbb{E}_t[]$ expectations with respect to that distribution, at time t. Then from eq. (B.4), since $q_{ii} = 1$, and given that the graph is regular,

$$\mathbb{E}_1[\mathbf{q}] = \left(1 - \frac{2}{N}\right)\mathbf{1}_{NN} + 2\frac{1-\mu}{N}\mathbf{1}_{NN} + \lambda_1 \mathbf{I}_N, \tag{B.7}$$

so

$$\mathbf{D}\cdot\mathbb{E}_1[\mathbf{q}] = \left(1 - \frac{2}{N}\right)\nu\mathbf{1}_{NN} + 2\frac{1-\mu}{N}\nu\mathbf{1}_{NN} + \lambda_1 \mathbf{D} = \mathbb{E}_1[\mathbf{q}]\cdot\mathbf{D}. \tag{B.8}$$

Then, assuming that $\mathbf{D}$ and $\mathbb{E}_t[\mathbf{q}]$ commute, and given that we assume $\mathbf{D} = \mathbf{D}^T$,

$$\mathbb{E}_{t+1}[\mathbf{q}] = \left(1 - \frac{2}{N}\right)\mathbb{E}_t[\mathbf{q}] + \frac{2(1-\mu)}{N}\mathbf{D}\cdot\mathbb{E}_t[\mathbf{q}] + \lambda_t \mathbf{I}_N, \tag{B.9}$$

so

$$\mathbf{D}\cdot\mathbb{E}_{t+1}[\mathbf{q}] = \left(1 - \frac{2}{N}\right)\mathbf{D}\cdot\mathbb{E}_t[\mathbf{q}] + \frac{2(1-\mu)}{N}\mathbf{D}^2\cdot\mathbb{E}_t[\mathbf{q}] + \lambda_t\mathbf{D} = \mathbb{E}_{t+1}[\mathbf{q}]\cdot\mathbf{D} \tag{B.10}$$

And so, when $t \to \infty$, we have $\mathbf{D}\cdot\mathbf{Q} = \mathbf{Q}\cdot\mathbf{D}$. □

Then with a transitive undirected dispersal graph, eq. (B.6), simplifies into

$$\mathbf{Q} = \frac{1-\mu}{\nu}\mathbf{D}\cdot\mathbf{Q} + \lambda_M \mathbf{I}_N, \tag{B.11}$$

and so (for $\mu > 0$),

$$\mathbf{Q} = \lambda_M\left(\mathbf{I}_N - \frac{1-\mu}{\nu}\mathbf{D}\right)^{-1}, \tag{B.12a}$$

with

$$\lambda_M = \frac{1}{\left(\left(\mathbf{I}_N - \frac{1-\mu}{\nu}\mathbf{D}\right)^{-1}\right)_{1,1}}. \tag{B.12b}$$

Eq. (B.11) also implies

$$\mathbf{Q} = \frac{(1-\mu)^2}{\nu^2}\mathbf{D}\cdot\mathbf{D}\cdot\mathbf{Q} + \lambda_M \frac{1-\mu}{\nu}\mathbf{D} + \lambda_M \mathbf{I}_N. \tag{B.13}$$

It is possible to find more explicit formulae when the graphs are transitive and when they are n-dimensional, and we do so for 1-D and 2-D graphs.

One-dimensional graphs

On a 1-D graph, numbering the different nodes modulo N, for all i and j, by definition of a 1-D graph, $d_{ij} = d_{0,j-i} = \tilde{d}_{j-i}$, and as a result similar equalities hold for the expected states of pairs of sites: $Q_{ij} = Q_{0,j-i} = \tilde{Q}_{j-i}$. We can hence rewrite eq. (B.5) as follows, keeping in mind that $Q_{ij} = Q_{ji}$ and that node numbering is done modulo N:

$$\begin{aligned} Q_{ij} = \tilde{Q}_{j-i} &= \frac{1-\mu}{2\nu}\sum_k d_{0,j-k}Q_{0,k-i} + d_{0,i-k}Q_{0,j-k} \qquad (i \neq j) \\ &= \frac{1-\mu}{2\nu}\sum_k d_{0,k}P_{0,j-i-k} + d_{0,k}P_{0,j-i+k} \quad \text{[change of variables } k' = j-k\text{]} \\ &= \frac{1-\mu}{2\nu}\sum_k \tilde{d}_k\tilde{P}_{j-i-k} + \tilde{d}_k\tilde{P}_{j-i+k}, \end{aligned}$$

so that

$$\tilde{Q}_l = \frac{1-\mu}{2\nu}\left(\sum_k \tilde{d}_k\tilde{Q}_{l-k} + \tilde{d}_k\tilde{Q}_{l+k}\right) + \delta_l\lambda_M, \tag{B.14}$$

where $\delta_l = 1$ when $l \equiv 0$ and $\delta_l = 0$ otherwise, and λ is as defined in the previous section, *i.e.*, such that $\tilde{Q}_0 = 1$:

$$\lambda_M = 1 - \frac{1-\mu}{\nu} \sum_k \tilde{d}_k \tilde{Q}_k. \tag{B.15}$$

(Recall that $\tilde{Q}_l = \tilde{Q}_{-l}$).

To solve for $\tilde{Q}_l$, we can follow the same method as in Malécot (1975); Gandon & Rousset (1999) and use discrete Fourier transforms, defining the transforms of Q and of d as follows:

$$\mathscr{Q}_q = \sum_{l=0}^{N-1} \tilde{Q}_l \exp\left(-\imath \frac{2\pi q l}{N}\right), \tag{B.16a}$$

$$\mathscr{D}_q = \sum_{l=0}^{N-1} \tilde{d}_l \exp\left(-\imath \frac{2\pi q l}{N}\right). \tag{B.16b}$$

and in particular (ν being the degree of the dispersal graph)

$$\mathscr{D}_0 = \sum_l \tilde{d}_l = \nu. \tag{B.16c}$$

We obtain

$$\mathscr{Q}_q = \lambda_M + \sum_{l=0}^{N-1} \left[\frac{1-\mu}{2\nu} \left(\sum_k \tilde{d}_k \tilde{Q}_{l-k} + \tilde{d}_k \tilde{Q}_{l+k} \right) \right] \exp\left(-\imath \frac{2\pi q l}{N}\right), \tag{B.17a}$$

$$= \lambda_M + \frac{1-\mu}{2\nu} \left(\mathscr{D}_q \mathscr{Q}_q + \mathscr{D}_{-q} \mathscr{Q}_q \right). \tag{B.17b}$$

Solving for $\mathscr{Q}_q$, we obtain

$$\mathscr{Q}_q = \frac{\lambda_M}{1 - \frac{1-\mu}{2\nu} \left(\mathscr{D}_q + \mathscr{D}_{-q} \right)}. \tag{B.17c}$$

To recover $\tilde{Q}$, we now use an Inverse Discrete Fourier Transform

$$\tilde{Q}_r = \frac{1}{N}\sum_{q=0}^{N-1} \mathscr{Q}_q \exp\left(\imath\frac{2\pi q r}{N}\right); \tag{B.18}$$

combining eq. (B.17c) and eq. (B.18), we obtain

$$\tilde{Q}_r = \frac{1}{N}\sum_{q=0}^{N-1} \frac{\lambda_M}{1-\frac{1-\mu}{2\nu}\left(\mathscr{D}_q+\mathscr{D}_{-q}\right)} \exp\left(\imath\frac{2\pi q r}{N}\right). \tag{B.19a}$$

When $r = 0$, we have $\tilde{Q}_0 = 1$, so combining this with eq. (B.19a), we can now evaluate λ:

$$\lambda_M = \frac{N}{\sum_{q=0}^{N-1}\frac{1}{1-\frac{1-\mu}{2\nu}\left(\mathscr{D}_q+\mathscr{D}_{-q}\right)}}. \tag{B.19b}$$

Finally, when the graph is not oriented, $\mathscr{D}_q = \mathscr{D}_{-q}$.

Two-dimensional graphs

Similar calculations are done with two-dimensional graphs. Numbering is done modulo N_1 for the first dimension, and modulo N_2 for the second dimension ($N_1 N_2 = N$). The 2-D equivalent of eq. (B.14) is

$$\tilde{Q}_{\substack{l_1\\l_2}} = \frac{1-\mu}{2\nu}\sum_{k_1=0}^{N_1-1}\sum_{k_2=0}^{N_2-1}\left(\tilde{d}_{\substack{k_1\\k_2}}\tilde{Q}_{\substack{l_1-k_1\\l_2-k_2}} + \tilde{d}_{\substack{k_1\\k_2}}\tilde{Q}_{\substack{l_1+k_1\\l_2+k_2}}\right) + \delta_{\substack{l_1\\l_2}}\lambda_M, \tag{B.20}$$

where $\delta_{\substack{k_1\\k_2}} = 1$ when $(k_1, k_2) \equiv (0,0)$ (modulo N_1 and N_2), and $\delta_{\substack{k_1\\k_2}} = 0$ otherwise, and

$$\lambda_M = 1 - \frac{1-\mu}{\nu}\sum_{l_1=0}^{N_1-1}\sum_{l_2=0}^{N_2-1}\tilde{d}_{\substack{k_1\\k_2}}\tilde{Q}_{\substack{k_1\\k_2}}. \tag{B.21}$$

We then use 2-D Discrete Fourier Transforms:

$$\mathscr{Q}_{\substack{q_1\\q_2}} = \sum_{l_1=0}^{N_1-1}\sum_{l_2=0}^{N_2-1} \tilde{Q}_{\substack{l_1\\l_2}} \exp\left(-\imath\frac{2\pi q_1 l_1}{N_1}\right)\exp\left(-\imath\frac{2\pi q_2 l_2}{N_2}\right), \tag{B.22a}$$

$$\mathscr{D}_{\substack{q_1\\q_2}} = \sum_{l_1=0}^{N_1-1}\sum_{l_2=0}^{N_2-1} \tilde{d}_{\substack{l_1\\l_2}} \exp\left(-\imath\frac{2\pi q_1 l_1}{N_1}\right)\exp\left(-\imath\frac{2\pi q_2 l_2}{N_2}\right), \tag{B.22b}$$

and obtain

$$\mathscr{Q}_{\substack{q_1\\q_2}} = \lambda_M + \frac{1-\mu}{2\nu}\left(\mathscr{D}_{\substack{q_1\\q_2}} + \mathscr{D}_{\substack{-q_1\\-q_2}}\right)\mathscr{P}_{\substack{q_1\\q_2}}. \tag{B.23a}$$

Solving for $\mathscr{Q}_{\substack{q_1\\q_2}}$,

$$\mathscr{Q}_{\substack{q_1\\q_2}} = \frac{\lambda_M}{1-\frac{1-\mu}{2\nu}\left(\mathscr{D}^{q_1}_{q_2} + \mathscr{D}^{-q_1}_{-q_2}\right)}. \tag{B.23b}$$

Finally, an Inverse Fourier Transform gives us $\tilde{Q}_{\substack{r_1\\r_2}}$:

$$\tilde{Q}_{\substack{r_1\\r_2}} = \frac{1}{N}\sum_{q_1,q_2}\frac{\lambda_M}{1-\frac{1-\mu}{2\nu}\left(\mathscr{D}^{q_1}_{q_2} + \mathscr{D}^{-q_1}_{-q_2}\right)}\exp\left(\imath\frac{2\pi q_1 r_1}{N_1}\right)\exp\left(\imath\frac{2\pi q_2 r_2}{N_2}\right), \tag{B.23c}$$

with C such that $\tilde{P}_{\substack{0\\0}} = p$:

$$\lambda_M = \frac{N}{\sum_{q_1,q_2}\frac{1}{1-\frac{1-\mu}{2\nu}\left(\mathscr{D}^{q_1}_{q_2} + \mathscr{D}^{-q_1}_{-q_2}\right)}}. \tag{B.23d}$$

And when the graph is undirected, $\mathscr{D}^{-q_1}_{-q_2} = \mathscr{D}^{q_1}_{q_2}$.

Illustration: infinite circle

On a circle graph (like in figure 3(a)), the Fourier transform of the dispersal distance is

$$\mathscr{D}_q = 2\cos\left(\frac{2\pi q}{N}\right). \tag{B.24}$$

We can evaluate λ_M using eq. (B.19b),

$$\lambda_M = \frac{N}{\sum_{q=0}^{N-1} \frac{1}{1-(1-\mu)\cos\left(\frac{2\pi q}{N}\right)}}, \tag{B.25a}$$

and when population size is infinite, this becomes

$$\lambda_M = \frac{1}{\int_0^1 \frac{1}{1-(1-\mu)\cos(2\pi x)}\mathrm{d}x} = \sqrt{\mu(2-\mu)}. \tag{B.25b}$$

But we note that the integral does not converge when $\mu \to 0$. Finally, we compute probabilities of identity by descent using eq. (B.19a), and obtain eq. (28b) in the main text for neighbors on the the circle ($q = 1$).

Wright-Fisher model

In a Wright-Fisher model, all individuals are replaced at each time step. Given a state X at time t, for $i \neq j$, probabilities of identity by descent verify

$$\mathbb{E}\left[q_{ij}(t+1)|X(t)\right] = (1-\mu)^2 \sum_{k,l} \frac{d_{ki}d_{lj}}{\nu^2} q_{kl}(t). \tag{B.26}$$

Taking the expectation of this quantity over the stationary distribution of states, we obtain

$$Q_{ij} = \frac{(1-\mu)^2}{\nu^2} \sum_{k,l} \left(d_{ki} d_{lj} Q_{kl} \right) \qquad (i \neq j), \tag{B.27}$$

and $Q_{ij} = 1$ when $i = j$. Eq. (B.27) is valid for any regular graph; all the Q_{ij} terms can be found by solving a system of $N(N-1)/2$ equations (since $Q_{ij} = Q_{ji}$). We can also write eq. (B.5) in matrix form:

$$\mathbf{Q} = \frac{(1-\mu)^2}{\nu^2} (\mathbf{D}^T \mathbf{Q} \mathbf{D}) + \mathbf{L}, \tag{B.28}$$

where $\mathbf{D}$ is the adjacency matrix of the dispersal graph (with elements d_{ij}), ^{T} denotes transposition, and $\mathbf{L}$ is a diagonal matrix whose ith diagonal element is such that $Q_{ii} = 1$.

Transitive undirected graphs

When the dispersal graph is transitive, then all the elements on the diagonal of $\mathbf{L}$ are equal, so we can write $\mathbf{L} = \lambda_{WF} \mathbf{I}_N$, where $\mathbf{I}_N$ is the N by N identity matrix. Like in the case of a Moran updating, when the graph is also undirected, $\mathbf{D} = \mathbf{D}^T$, and we also show by induction that $\mathbf{DQ} = \mathbf{QD}$ (Grafen & Archetti, 2008).

Let us assume without loss of generality that initially ($t = 0$) all individuals are IBD ($q_{ij}(0) = \mathbf{1}_{NN}$, where $\mathbf{1}_{NN}$ is the N-by-N matrix containing only ones) and of type B ($X(0) = \{0, \dots, 0\}$). Also, let us denote by $\zeta_0(X, t)$ the probability that the population is in state X at time t given that it was in state $\{0, \dots, 0\}$ at time 0, and by $\mathbb{E}_t[\,]$ expectations with respect to that distribution, at time t. Then from eq. (B.26), since $q_{ii} = 1$, and given that the graph is regular,

$$\mathbb{E}_1\left[\mathbf{q}\right] = \frac{(1-\mu)^2}{\nu^2}\mathbf{1}_{NN} + \lambda_1 \mathbf{I}_N, \tag{B.29}$$

so

$$\mathbf{D}\cdot\mathbb{E}_1\left[\mathbf{q}\right] = \frac{(1-\mu)^2}{\nu^2}\nu\mathbf{1}_{NN} + \lambda_1 \mathbf{D} = \mathbb{E}_1\left[\mathbf{q}\right]\cdot\mathbf{D}. \tag{B.30}$$

Then, assuming that $\mathbf{D}$ and $\mathbb{E}_t\left[\mathbf{q}\right]$ commute, and given that we assume an undirected dispersal graph ($\mathbf{D} = \mathbf{D}^T$),

$$\mathbb{E}_{t+1}\left[\mathbf{q}\right] = \frac{(1-\mu)^2}{\nu^2}\mathbf{D}\cdot\mathbf{D}\cdot\mathbb{E}_t\left[\mathbf{q}\right] + \lambda_t \mathbf{I}_N, \tag{B.31}$$

so

$$\mathbf{D}\cdot\mathbb{E}_{t+1}\left[\mathbf{q}\right] = \frac{(1-\mu)^2}{\nu^2}\mathbf{D}\cdot\mathbf{D}\cdot\mathbf{D}\cdot\mathbb{E}_t\left[\mathbf{q}\right] + \lambda_t \mathbf{D} = \mathbb{E}_{t+1}\left[\mathbf{q}\right]\cdot\mathbf{D} \tag{B.32}$$

And so, when $t \to \infty$, we have $\mathbf{D}\cdot\mathbf{Q} = \mathbf{Q}\cdot\mathbf{D}$. □

Then with a transitive undirected dispersal graph, eq. (B.28), simplifies into

$$\mathbf{Q} = \frac{(1-\mu)^2}{\nu^2}\mathbf{D}\cdot\mathbf{D}\cdot\mathbf{Q} + \lambda_{WF}\mathbf{I}_N, \tag{B.33}$$

and so (for $\mu > 0$),

$$\mathbf{Q} = \lambda_{WF}\left(\mathbf{I}_N - \frac{(1-\mu)^2}{\nu^2}\mathbf{D}\mathbf{D}\right)^{-1}, \tag{B.34a}$$

with

$$\lambda_{WF} = \frac{1}{\left(\left(\mathbf{I}_N - \frac{(1-\mu)^2}{\nu^2}\mathbf{DD}\right)^{-1}\right)_{1,1}}. \tag{B.34b}$$

It is possible to find more explicit formulae when the graphs are transitive and when they are n-dimensional, and we do so for 1-D and 2-D graphs.

One-dimensional graphs

In a 1D graph, we can rewrite eq. (B.27) as follows, were $\tilde{Q}_m = Q_{0m}$ (numbering being done modulo N):

$$\tilde{Q}_m = \begin{cases} \sum_{k,l} \frac{\tilde{d}_k \tilde{d}_l}{\nu^2} \tilde{Q}_{m-l+k} & (m \neq 0) \\ 1 & (m = 0). \end{cases} \tag{B.35}$$

Using a Discrete Fourier Transform (see eq. (B.16)), we obtain,

$$\mathscr{Q}_q = \frac{(1-\mu)^2}{\nu^2} \mathscr{D}_q \mathscr{D}_{-q} \mathscr{Q}_q + \lambda_{WF}, \tag{B.36a}$$

with

$$\lambda_{WF} = 1 - \sum_{k,l} \frac{\tilde{d}_k \tilde{d}_l}{\nu^2} \tilde{Q}_{-l+k}. \tag{B.36b}$$

Solving for $\mathscr{Q}_q$, we obtain

$$\mathscr{P}_q = \frac{\lambda_{WF}}{1 - \frac{(1-\mu)^2}{\nu^2} \mathscr{D}_q \mathscr{D}_{-q}}. \tag{B.36c}$$

Then using an Inverse Fourier Transform to recover $\tilde{Q}$ (see eq. (B.18)), we obtain

$$\tilde{Q}_r = \frac{1}{N}\sum_{q=0}^{N-1} \frac{\lambda_{WF}}{1-\frac{(1-\mu)^2}{\nu^2}\mathscr{D}_q\mathscr{D}_{-q}} \exp\left(\imath\frac{2\pi q r}{N}\right) \tag{B.37}$$

Noting that $\tilde{Q}_0 = 1$, we can evaluate λ:

$$\lambda_{WF} = \frac{N}{\sum_{q=0}^{N-1}\frac{1}{1-\frac{(1-\mu)^2}{\nu^2}\mathscr{D}_q\mathscr{D}_{-q}}}. \tag{B.38}$$

Two-dimensional graphs

Following the same method as previously, we obtain

$$\tilde{Q}_{r_1 \atop r_2} = \frac{1}{N}\sum_{q_1,q_2} \frac{\lambda_{WF}}{1-\frac{(1-\mu)^2}{\nu^2}\left(\mathscr{D}^{q_1}_{q_2}\mathscr{D}^{-q_1}_{-q_2}\right)} \exp\left(\imath\frac{2\pi q_1 r_1}{N_1}\right)\exp\left(\imath\frac{2\pi q_2 r_2}{N_2}\right), \tag{B.39a}$$

with

$$\lambda_{WF} = \frac{N}{\sum_{q_1,q_2}\frac{1}{1-\frac{(1-\mu)^2}{\nu^2}\left(\mathscr{D}^{q_1}_{q_2}\mathscr{D}^{-q_1}_{-q_2}\right)}}. \tag{B.39b}$$

Illustration: Circle graph with self-loops

On a circle graph with self-loops (like in figure 3(b)), the Fourier transform of the dispersal distance is

$$\mathscr{D}_q = (1-m) + m\cos\left(\frac{2\pi q}{N}\right). \tag{B.40}$$

(Here $\nu = 1$, while with the circle graph we had $\nu = 2$; this does not matter for IBD). We can evaluate λ_{WF} using eq. (B.38),

$$\lambda_{WF} = \frac{N}{\sum_{q=0}^{N-1} \frac{1}{1-(1-\mu)^2\left((1-m)+m\cos\left(\frac{2\pi q}{N}\right)\right)^2}}, \tag{B.41a}$$

and when population size is infinite, this becomes

$$\begin{aligned} \lambda_{WF} &= \frac{1}{\int_0^1 \frac{1}{1-(1-\mu)^2((1-m)+m\cos(2\pi x))^2}\mathrm{d}x}, \\ &= \frac{2\sqrt{(2-\mu)\mu(-\mu-2(1-\mu)m+2)(\mu+2(1-\mu)m)}}{\sqrt{(2-\mu)(-\mu-2(1-\mu)m+2)}+\sqrt{\mu(\mu+2(1-\mu)m)}}, \end{aligned} \tag{B.41b}$$

according to Mathematica (Wolfram Research, Inc., 2015) (isn’t this amazing?). Here as well, the integral does not converge when $\mu \to 0$. Finally, we compute probabilities of identity by descent using eq. (B.39a), and obtain eq. (29) in the main text for neighbors on the the circle ($q = 1$).

C Derivatives of B_{ij} and D_j for specific life-cycles

Birth-Death updating

With a Moran Birth-Death updating rule (see eq. (14)), the derivatives of B_{ij} and D_j with respect to f_k are

$$\left.\frac{\partial B_{ij}}{\partial f_k}\right|_{\delta=0} = \frac{d_{ji}}{\nu}\frac{\delta_{j,k}N-1}{N^2}, \tag{C.1a}$$

$$\left.\frac{\partial D_j}{\partial f_k}\right|_{\delta=0} = \frac{d_{kj}}{N\nu} - \frac{1}{N^2}, \tag{C.1b}$$

with

$$\delta_{j,k} = \begin{cases} 1 & \text{when } j = k, \\ 0 & \text{otherwise.} \end{cases} \tag{C.2}$$

Consequently,

$$\left.\frac{\partial W_j}{\partial f_k}\right|_{\delta=0} = \frac{\delta_{j,k}}{N} - \frac{d_{kj}}{N\nu}. \tag{C.3}$$

Death-Birth updating

With a Moran Death-Birth updating rule (see eq. (19)), the derivatives of B_{ij} and D_j with respect to f_k are given by the following equations:

$$\left.\frac{\partial B_{ij}}{\partial f_k}\right|_{\delta=0} = \frac{\delta_{k,j}d_{ki}\nu - d_{ji}d_{ki}}{N\nu^2}, \tag{C.4a}$$

$$\left.\frac{\partial D_j}{\partial f_k}\right|_{\delta=0} = 0, \tag{C.4b}$$

with $\delta_{k,j}$ as defined in eq. (C.2). As a result,

$$\left.\frac{\partial W_j}{\partial f_k}\right|_{\delta=0} = \frac{\delta_{k,j}}{N} - \sum_{i=1}^{N} \frac{d_{ji} d_{ki}}{N \nu^2}. \tag{C.5}$$

Wright-Fisher updating

With a Wright-Fisher updating rule (see eq. (22)), the derivatives of B_{ij} and D_j with respect to f_k are

$$\left.\frac{\partial B_{ij}}{\partial f_k}\right|_{\delta=0} = \frac{\delta_{k,j} d_{ki} \nu - d_{ji} d_{ki}}{\nu^2}, \tag{C.6a}$$

$$\left.\frac{\partial D_j}{\partial f_k}\right|_{\delta=0} = 0. \tag{C.6b}$$

with $\delta_{k,j}$ as defined in eq. (C.2). Finally,

$$\left.\frac{\partial W_j}{\partial f_k}\right|_{\delta=0} = \delta_{k,j} - \sum_{i=1}^{N} \frac{d_{ji} d_{ki}}{\nu^2}. \tag{C.7}$$

Figures

Figure 1

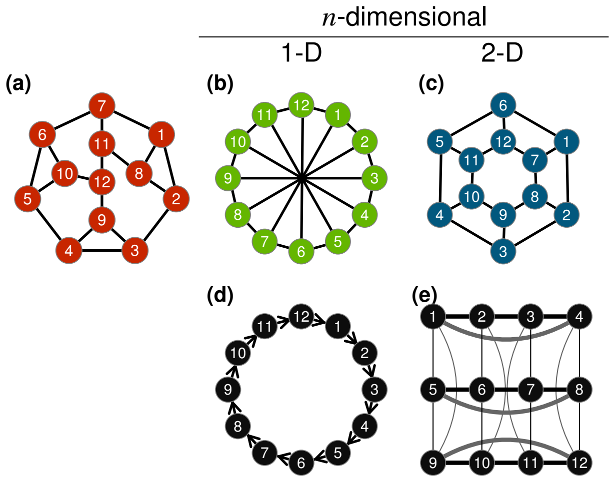

Figure 1: Examples of regular graphs of size 12. The graphs on the first line are unoriented and unweighted graphs of degree $v = 3$; Graph (d) is oriented, graph (e) is weighted. (a) is the Frucht graph, and has no symmetry. Graphs (b) and (d) are one-dimensional, graphs (c) and (e) are two-dimensional (see main text).

878 Figure 2

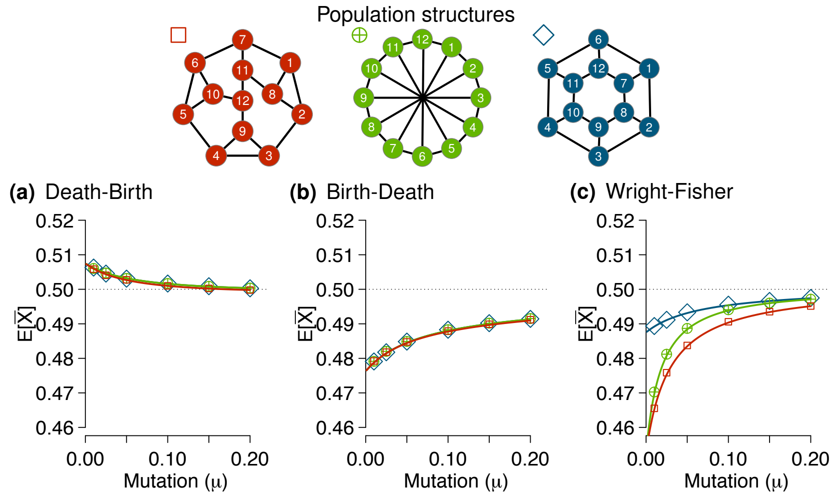

Figure 2: Expected frequency of type-A individuals $\mathbb{E}[\overline{X}]$, depending on population structure (legend on the first line), updating rule ((a): Moran Death-Birth, (b): Moran Birth-Death, (c): Wright-Fisher), and mutation probability μ (horizontal axis): Comparison between the theoretical prediction (curves) and the outcomes of numerical simulations (points). The horizontal dotted gray line corresponds to p, the expected frequency of type-A individuals when there is no selection (*i.e.*, when $\delta = 0$). Other parameters: δ=0.005, $p = 1/2$.

Appendix C

879 **Figure 3**

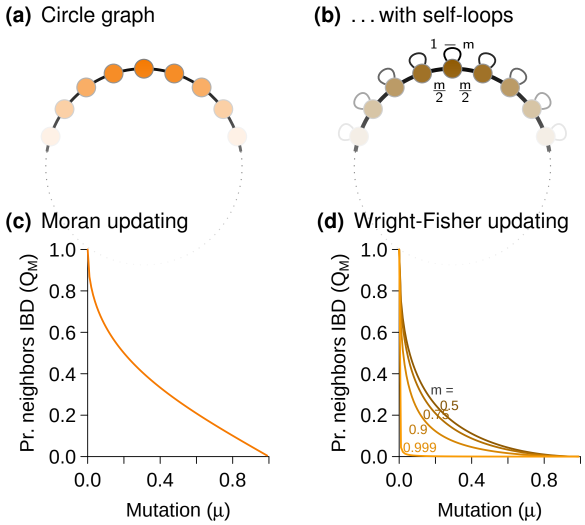

Figure 3: Circle graphs, without (a) or with self-loops ((b); the weight of the self-loop is $1-m$), and Probability that two neighbors on the graph are identical by descent, as function of the mutation probability μ, for the Moran updating on an infinite circle graph (c), and for the Wright-Fisher updating on an infinite circle graph with self loops (d). In (d), emigration probabilities m take values 0.5, 0.75, 0.9, 0.999 (increasingly lighted curves).