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

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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 competing; 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 (implying 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 our results 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.

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., Rousset and Billiard, 2000; Rousset, 2003; 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 and Lehmann, 2014; Tarnita and 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.

Obviously, lowering the fidelity of parent-offspring strategy transmission—e.g., by increasing the probability of mutation—reduces the relative role played by selection. But in a spatially structured population, the fidelity of parent-offspring strategy transmission also affects the spatial clustering of different strategies, and in particular whether individuals that interact with each other have the same strategy or not; this effect takes place even in the absence of selection. Consequently, the impact of imperfect strategy transmission may differ according to how the population is structured.

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

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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 and 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

2.1. 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 (potentially via other nodes). This simply means that there are not completely isolated subpopulations. 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). For instance, dispersal in a subdivided population is represented by a weighted graph (the probability of sending offspring to a site in the same deme as the parent is different from the probability of sending offspring to a site in a different deme.) Finally, we denote by $\mathbf{D}$ and $\mathbf{E}$ the adjacency matrices of the dispersal and interaction graphs, respectively ($\mathbf{D} = \{d_{ij}\}_{1 \leq i,j \leq N}$, $\mathbf{E} = \{e_{ij}\}_{1 \leq i,j \leq N}$).

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 (Figs. 1 and 3) satisfy Eq. (1), and then are regular. 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, 2007b): the graph looks the same from every node. In other words, the dispersal graph is transitive when it is "homogeneous" (*sensu* Taylor et al. (2007a)), i.e., when all nodes have exactly the same properties in terms of dispersal. In Fig. 1, graphs (b)–(e) are transitive. On the other hand, all the nodes of graph (a) are different (for instance, node 9 is in a triangle while node 12 is not), so this regular graph is not transitive.

Transitive undirected dispersal graphs A graph is undirected if for any two nodes i and j, the weight of the edge from i to j is equal to the weight of the edge from j to i (i.e., there is no need to use arrows when drawing the edges of the graph). The dispersal graph is undirected when for all sites i and j, $d_{ij} = d_{ji}$. In Fig. 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
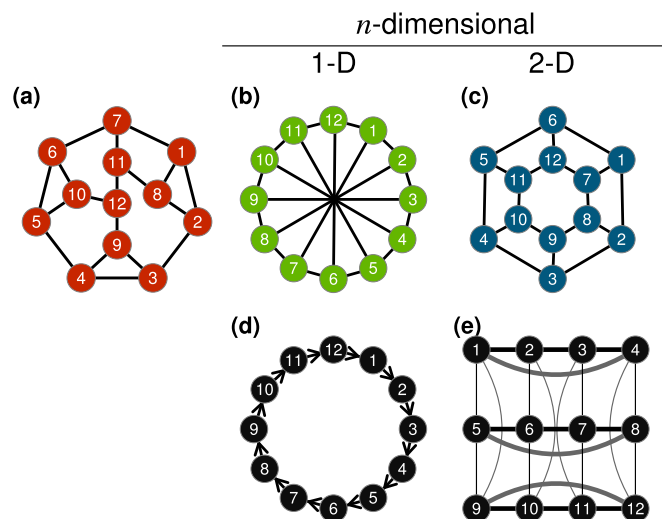
Fig. 1. Examples of regular graphs of size 12. The graphs on the first line are unoriented and unweighted graphs of degree $\nu = 3$, Graph (d) is oriented, graph (e) is weighted. (a) is the Frucht graph, and has no symmetry. Graphs (b) and (d) are one-dimensional, graphs (c) and (e) are two-dimensional (see main text).

indices, such that the graph is unchanged by circular permutation of the indices in each dimension (see Eq. (2)). We denote by $\mathcal{N}$ the ensemble of node indices: $\mathcal{N} = \{0, ..., N_1 - 1\} \times ... \times \{0, ..., N_n - 1\}$, with $\prod_{k=1}^{n} N_n = N$; numbering is done modulo N_k in dimension k. Then for all indices i, j and k of $\mathcal{N}$, node labeling is such that for all edges (modulo the size of each dimension),

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

In Fig. 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 1(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).

2.2. 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 ($\overline{X} = \sum_{i=1}^{N} X_i / N$). The ensemble of all possible states is $\Omega = \{0, 1\}^N$.

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 and Traulsen (2007)).

An individual's fecundity depends on the phenotypes of the individuals it interacts with and on its own phenotype (δX_i for the individual at site i). Without loss of generality, we can write the fecundity of the individual living at site i as