

Evolutionary Games on Star Graphs Under Various Updating Rules

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Abstract Evolutionary game dynamics have been traditionally studied in well-mixed populations where each individual is equally likely to interact with every other individual. Recent studies have shown that the outcome of the evolutionary process might be significantly affected if the population has a non-homogeneous structure. In this paper we study analytically an evolutionary game between two strategies interacting on an extreme heterogeneous graph, the star graph. We find explicit expressions for the fixation probability of mutants, and the time to absorption (elimination or fixation of mutants) and fixation (absorption conditional on fixation occurring). We investigate the evolutionary process considering four important update rules. For each of the update rules, we find appropriate conditions under which one strategy is favoured over the other. The process is considered in four different scenarios: the fixed fitness case, the Hawk–Dove game, the Prisoner’s dilemma and a coordination game. It is shown that in contrast with homogeneous populations, the choice of the update rule might be crucial for the evolution of a non-homogeneous population.

Keywords Fixation probability · Absorption time · Fixation time · Structured populations · Star graph

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1 Introduction

Evolutionary models can be applied in a vast number of biological situations. It is generally assumed that populations are homogeneous, where all individuals are equally likely to meet all others. Heterogeneous populations are often studied by the interactions of pairs of individuals on a graph, starting with Lieberman et al. [8]. There are a number of update rules (evolutionary dynamics) that can be applied to such processes. This has not been of great importance historically, since the evolutionary process on homogeneous populations is not significantly affected by the update rule. However, recent studies suggest that different update rules might result in significant differences in the evolutionary process in populations with a non-homogeneous structure (for example, [2, 10, 14]). In this paper we consider analytically the stochastic evolutionary process following four commonly used update rules on the simplest heterogeneous graph, the star graph.

The star graph is an irregular graph where n vertices, the leaves, are connected to only one vertex, the centre. Evolution on a star-structured population has been commonly studied (for example, [3, 5, 6, 8, 10, 11, 16]). The fixation probability of a single mutant individual with relative fitness r introduced into a resident population structured as a star was first considered in [8] following the rules of the invasion process and assuming a large population size. An exact formula of the fixation probability was given later in [3] (see also [10]). This has been extended in [5] to the more complicated case of frequency dependent fitness by applying evolutionary game theory. In the same paper, the absorption and fixation time of a mutant under the invasion process have also been considered. In [4], it is shown that at least for small graphs, under the invasion process the star is the structure in which a randomly placed mutant has the highest chance of fixation. On the other hand, in [5] it is shown that in this process, the average time needed for the fixation of a mutant on a star is especially long.

In this paper, we investigate an evolutionary game involving two strategies, A and B, played among individuals on a star graph. The game played has a general payoff matrix

$$\begin{array}{c|cc} & A & B \\ \hline A & a & b \\ B & c & d \end{array} \tag{1.1}$$

whose elements represent the payoffs obtained by the row player when interacting with the column player.

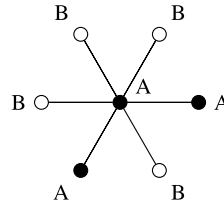
The fitness of each individual, f , is assumed to be $f = f_b + wP$, where f_b is a constant background fitness and P is the average of the payoffs obtained from the games played against all the neighbouring connected individuals. $w \in [0, 1]$ represents the intensity of selection which determines the contribution of P to fitness. When $w \rightarrow 0_+$, we talk about weak selection. In this case the payoff P of each individual has a small effect on its total fitness. In the case where $w = 0$, all individuals have the same fitness ($f = f_b$) and thus we have the case of neutral drift.

Denoting the fitness of an A (B) individual placed in the centre of a star with i As and $n - i$ Bs on the leaves (see Fig. 1) by $f_{Ac}(i)$ ($f_{Bc}(i)$), we obtain

$$f_{Ac}(i) = \frac{i\alpha + (n - i)\beta}{n}, \tag{1.2}$$

$$f_{Bc}(i) = \frac{i\gamma + (n - i)\delta}{n}, \tag{1.3}$$

Fig. 1 A star graph with $n = 6$ leaves. The center node and two of the n leaves ($i = 2$) are occupied by individuals playing strategy A (black nodes) while the rest $n - i = 4$ nodes on the leaves are occupied by individuals playing strategy B (white nodes)



where we have set $\alpha = f_b + wa$, $\beta = f_b + wb$, $\gamma = f_b + wc$ and $\delta = f_b + wd$. The fitness of a player A (B) on the leaves is equal to α (γ) when playing against a player A in the centre and β (δ) when playing against a player B in this position.

Note that here, assuming that at each time step individuals interact with neighbouring individuals at the same rate, we consider each individual’s payoff to be the average payoff obtained from the games it plays, i.e. the sum of the payoffs resulting from the interactions with neighbouring individuals (accumulated payoff) over the total number of interactions. However, the individual’s payoff can be considered in different ways. Alternatively for example, the payoff of an individual could be assumed to be just the accumulated payoff, though it might yield different results (see for example, [9, 13, 15, 17, 18]).

We assume a certain number of individuals playing a strategy X is introduced into a finite population of individuals playing a strategy Y. Due to the finiteness of the population, through evolution the population will eventually reach a state where all individuals play the same strategy. The fixation probability of the strategy X is the probability that at the end of the evolutionary process, the population will consist only of individuals playing X. The mean fixation time (or conditional fixation time) of individuals playing strategy X is the number of time steps required for X individuals to take over the entire population, given that this will happen. The mean absorption time (or unconditional fixation time) is the mean number of time steps needed to reach one of the two absorbing states of the dynamics, i.e. the required time for the process to end up either in the state where all individuals play strategy X or in the state where all individuals play strategy Y.

For four different update rules, we investigate the above quantities when the individuals of the population are placed on a star graph starting from any population composition.

In the next section, we first present the update rules we will consider and the transition probabilities under each of them on the star graph. We then derive the general formulae of the fixation probability and the mean time to absorption and fixation on the star starting from any possible state, the first general formulae for absorption and fixation times on an irregular graph. In Sect. 3, for each of the update rules we derive the appropriate conditions under which one strategy is favoured over the other. Finally, in Sect. 4, we apply our results to two specific cases: the fixed fitness case where individuals have fixed fitness and the frequency dependent fitness case where the fitness of individuals depends on the interactions with the different types of neighbouring individuals. In the latter case, we study three example games: the Hawk–Dove game, the Prisoner’s dilemma and coordination games.

2 Formulae

In this section we present the general exact formulae for the fixation probability and the mean time to absorption and fixation. The derivation of the formulae is shown in Online Appendix A.

2.1 Transition Probabilities

Let $p_{i,j}^{XY}$ denote the transition probability from a state with i A individuals on the leaves and an X individual in the center to the state with j A individuals on the leaves and a Y individual in the center; following the update rules we will consider, only $p_{i,i+1}^{AA}$, $p_{i,i}^{AB}$ and $p_{i,i}^{AA} = 1 - p_{i,i+1}^{AA} - p_{i,i}^{AB}$ ($0 \leq i \leq n - 1$), and $p_{i,i-1}^{BB}$, $p_{i,i}^{BA}$ and $p_{i,i}^{BB} = 1 - p_{i,i-1}^{BB} - p_{i,i}^{BA}$ ($1 \leq i \leq n$) can be nonzero.

We consider four different update rules, called the invasion process (IP) (or birth–death process with selection on the birth), the birth–death process with selection on the death (BD-D), the biased Voter model (VM) (or death–birth process with selection on the death) and the death–birth process with selection on the birth (DB-B).

In the IP [8], each time step consists of an individual being selected for reproduction with probability proportional to its fitness and placing its offspring at a randomly chosen neighbouring vertex. The transition probabilities in this process are given by

$$p_{i,i+1}^{AA} = \frac{f_{Ac}(i)}{f_{Ac}(i) + i\alpha + (n - i)\gamma} \cdot \frac{n - i}{n} = \frac{(n - i)(i\alpha + (n - i)\beta)}{n((n + 1)i\alpha + (n - i)(n\gamma + \beta))}, \tag{2.1}$$

$$p_{i,i}^{AB} = \frac{\gamma}{f_{Ac}(i) + i\alpha + (n - i)\gamma} \cdot (n - i) = \frac{n(n - i)\gamma}{(n + 1)i\alpha + (n - i)(n\gamma + \beta)}, \tag{2.2}$$

$$p_{i,i-1}^{BB} = \frac{f_{Bc}(i)}{f_{Bc}(i) + i\beta + (n - i)\delta} \cdot \frac{i}{n} = \frac{i(i\gamma + (n - i)\delta)}{n(i(n\beta + \gamma) + (n + 1)(n - i)\delta)}, \tag{2.3}$$

$$p_{i,i}^{BA} = \frac{\beta}{f_{Bc}(i) + i\beta + (n - i)\delta} \cdot i = \frac{i n \beta}{i(n\beta + \gamma) + (n + 1)(n - i)\delta}. \tag{2.4}$$

The BD-D process [10] is the process where at each time step an individual is chosen for reproduction at random and then its offspring replaces a neighbouring individual which is chosen with probability inversely proportional to its fitness. The transition probabilities under this process are

$$p_{i,i+1}^{AA} = \frac{1}{n + 1} \cdot \frac{\frac{1}{\gamma}}{i\frac{1}{\alpha} + (n - i)\frac{1}{\gamma}} \cdot (n - i) = \frac{(n - i)\alpha}{(n + 1)(i\gamma + (n - i)\alpha)}, \tag{2.5}$$

$$p_{i,i}^{AB} = \frac{n - i}{n + 1}, \tag{2.6}$$

$$p_{i,i-1}^{BB} = \frac{1}{n + 1} \cdot \frac{\frac{1}{\beta}}{i\frac{1}{\beta} + (n - i)\frac{1}{\delta}} \cdot i = \frac{i\delta}{(n + 1)(i\delta + (n - i)\beta)}, \tag{2.7}$$

$$p_{i,i}^{BA} = \frac{i}{n + 1}. \tag{2.8}$$

In the VM [2], an individual first dies with probability inversely proportional to its fitness and is then replaced by the offspring of a randomly chosen neighbour. Thus, the transition probabilities are

$$p_{i,i+1}^{AA} = \frac{\frac{1}{\gamma}}{\frac{1}{f_{Ac}(i)} + i\frac{1}{\alpha} + (n - i)\frac{1}{\gamma}} \cdot (n - i) = \frac{(n - i)(i\alpha + (n - i)\beta)\alpha}{n\alpha\gamma + (i\alpha + (n - i)\beta)(i\gamma + (n - i)\alpha)}, \tag{2.9}$$

$$p_{i,i}^{AB} = \frac{\frac{1}{f_{Ac}(i)}}{\frac{1}{f_{Ac}(i)} + i\frac{1}{\alpha} + (n-i)\frac{1}{\gamma}} \cdot \frac{n-i}{n} = \frac{(n-i)\alpha\gamma}{n\alpha\gamma + (i\alpha + (n-i)\beta)(i\gamma + (n-i)\alpha)}, \tag{2.10}$$

$$p_{i,i-1}^{BB} = \frac{\frac{1}{\beta}}{\frac{1}{f_{Bc}(i)} + i\frac{1}{\beta} + (n-i)\frac{1}{\delta}} \cdot i = \frac{i\delta(i\gamma + (n-i)\delta)}{n\beta\delta + (i\gamma + (n-i)\delta)(i\delta + (n-i)\beta)}, \tag{2.11}$$

$$p_{i,i}^{BA} = \frac{\frac{1}{f_{Bc}(i)}}{\frac{1}{f_{Bc}(i)} + i\frac{1}{\beta} + (n-i)\frac{1}{\delta}} \cdot \frac{i}{n} = \frac{i\beta\delta}{n\beta\delta + (i\gamma + (n-i)\delta)(i\delta + (n-i)\beta)}. \tag{2.12}$$

Finally, in the DB-B process [12], in each time step an individual dies at random. Then, the gap is occupied by the offspring of a neighbouring individual chosen with probability proportional to its fitness. This process can also be described as follows: a random individual is chosen to update its strategy and chooses one of its neighbours' strategies proportional to their fitness. Thus, the transition probabilities in this process are given by

$$p_{i,i+1}^{AA} = \frac{n-i}{n+1}, \tag{2.13}$$

$$p_{i,i}^{AB} = \frac{1}{n+1} \cdot \frac{\gamma}{i\alpha + (n-i)\gamma} \cdot (n-i) = \frac{(n-i)\gamma}{(n+1)(i\alpha + (n-i)\gamma)}, \tag{2.14}$$

$$p_{i,i-1}^{BB} = \frac{i}{n+1}, \tag{2.15}$$

$$p_{i,i}^{BA} = \frac{1}{n+1} \cdot \frac{\beta}{i\beta + (n-i)\delta} \cdot i = \frac{i\beta}{(n+1)(i\beta + (n-i)\delta)}. \tag{2.16}$$

We observe that in the BD-D and DB-B processes, since the fitness of the individual in the centre is irrelevant, for $a = c$ and $b = d$ these two processes are equivalent to the respective cases of random drift.

In all processes, at every time step an individual gives birth and an individual dies. Thus, the population size remains constant. Note that it is assumed that there is no mutation, just selection, i.e. each offspring is always a perfect copy of its parent. Hence, the evolutionary process lasts until one of the two strategies takes over the population replacing all the individuals playing the other strategy. It should also be noted that to be meaningful in the context of all of the above dynamics, and in discrete dynamics in general, the fitness of the individuals should be positive, and we assume this throughout the paper.

2.2 Fixation Probability

Denote by ${}^X P_i^A$ (${}^X P_i^B$) the probability that individuals playing strategy $X \in \{A, B\}$ fixate in a population originally consisting of i A individuals on the leaves and an A (a B) individual in the centre.

${}^A P_i^A$ and ${}^A P_i^B$ are the solutions of the following system

$${}^A P_i^A = p_{i,i+1}^{AA} {}^A P_{i+1}^A + p_{i,i}^{AB} {}^A P_i^B + (1 - p_{i,i+1}^{AA} - p_{i,i}^{AB}) {}^A P_i^A, \quad 0 \leq i \leq n-1, \tag{2.17}$$

$${}^A P_i^B = p_{i,i}^{BA} {}^A P_i^A + p_{i,i-1}^{BB} {}^A P_{i-1}^B + (1 - p_{i,i}^{BA} - p_{i,i-1}^{BB}) {}^A P_i^B, \quad 1 \leq i \leq n, \tag{2.18}$$

with conditions on the absorbing states ${}^A P_0^B = 0$ and ${}^A P_n^A = 1$.

Rearranging of (2.17)–(2.18) yields

$${}^A P_i^A = \pi_{i,i+1}^{AA} {}^A P_{i+1}^A + \pi_{i,i}^{AB} {}^A P_i^B, \quad 0 \leq i \leq n - 1, \tag{2.19}$$

$${}^A P_i^B = \pi_{i,i}^{BA} {}^A P_i^A + \pi_{i,i-1}^{BB} {}^A P_{i-1}^B, \quad 1 \leq i \leq n, \tag{2.20}$$

where π denotes the transition probability conditional on the system not remaining in the same state, i.e.

$$\pi_{i,i+1}^{AA} = 1 - \pi_{i,i}^{AB} = \frac{p_{i,i+1}^{AA}}{p_{i,i+1}^{AA} + p_{i,i}^{AB}}, \quad 0 \leq i \leq n - 1, \tag{2.21}$$

$$\pi_{i,i}^{BA} = 1 - \pi_{i,i-1}^{BB} = \frac{p_{i,i}^{BA}}{p_{i,i}^{BA} + p_{i,i-1}^{BB}}, \quad 1 \leq i \leq n. \tag{2.22}$$

Solving the system (2.19)–(2.20) inductively (see Online Appendix A.1), we find

$${}^A P_i^A = \frac{A(1, i)}{A(1, n)} \quad (i \neq 0), \tag{2.23}$$

$${}^A P_i^B = \sum_{j=1}^i \pi_{j,j}^{BA} {}^A P_j^A \prod_{k=j+1}^i \pi_{k,k-1}^{BB}, \tag{2.24}$$

where

$$A(l, m) = 1 + \sum_{j=l}^{m-1} \pi_{j,j}^{AB} \prod_{k=l}^j \frac{\pi_{k,k-1}^{BB}}{\pi_{k,k+1}^{AA}}. \tag{2.25}$$

Using (2.19), the condition ${}^A P_0^B = 0$ and (2.23) we find that for $i = 0$,

$${}^A P_0^A = \frac{\pi_{0,1}^{AA}}{A(1, n)}. \tag{2.26}$$

The average fixation probability of a single A individual randomly placed on the star, ${}^A \bar{P}$, is given by

$${}^A \bar{P} = \frac{1}{n + 1} (n {}^A P_1^B + {}^A P_0^A) = \frac{n \pi_{1,1}^{BA} + \pi_{0,1}^{AA}}{n + 1} \frac{1}{A(1, n)} \tag{2.27}$$

(see also [16] for an alternative formula for the fixation probability of a single mutant on the star).

Surprisingly, we observe that for $b = c$, the transition probabilities (2.21)–(2.22) are equal in the VM and the DB-B process. Thus, in this case the fixation probabilities of any number of mutants placed at any position in the two processes are equal, irrespective of what the population size and the elements of the payoff matrix are.

2.3 Mean Time to Absorption

Let us denote by T_i^A (T_i^B) the mean time to absorption starting from i A individuals on the leaves and an A (a B) in the centre. T_i^A and T_i^B are the solutions of the system

$$T_i^A = p_{i,i+1}^{AA} T_{i+1}^A + p_{i,i}^{AB} T_i^B + (1 - p_{i,i+1}^{AA} - p_{i,i}^{AB}) T_i^A + 1, \quad 0 \leq i \leq n - 1, \tag{2.28}$$

$$T_i^B = p_{i,i}^{BA} T_i^A + p_{i,i-1}^{BB} T_{i-1}^B + (1 - p_{i,i}^{BA} - p_{i,i-1}^{BB}) T_i^B + 1, \quad 1 \leq i \leq n, \quad (2.29)$$

with conditions on the absorbing states $T_0^B = 0 = T_n^A$.

Solving the system (2.28)–(2.29) (see Online Appendix A.2), we find that the average time to absorption starting from a single A individual randomly placed on the star, ${}^A T$, is given by

$${}^A T = \frac{1}{n+1} \left(\frac{\pi_{0,1}^{AA} + n\pi_{1,1}^{BA}}{A(1,n)} \sum_{l=2}^n A(l,n) B(l) + 1 + \frac{n}{p_{1,0}^{BB} + p_{1,1}^{BA}} \right), \quad (2.30)$$

where

$$B(l) = \frac{\pi_{l-1,l-1}^{AB}}{\pi_{l-1,l}^{AA}} \sum_{j=1}^{l-1} \left(\frac{\prod_{k=j+1}^{l-1} \pi_{k,k-1}^{BB}}{p_{j,j-1}^{BB} + p_{j,j}^{BA}} \right) + \frac{1}{p_{l-1,l}^{AA}}. \quad (2.31)$$

The derivation of the solution of the mean time to absorption starting from any possible state is shown in Online Appendix A.2.

2.4 Mean Fixation Time

Let ${}^X F_i^A$ (${}^X F_i^B$) denote the mean fixation time of individuals playing strategy $X \in \{A, B\}$ starting from the state with i As on the leaves and an A (a B) in the centre. Following the same method as in [1], ${}^A F_i^A$ and ${}^A F_i^B$ are given by the solution of the system

$${}^A z_i^A = p_{i,i+1}^{AA} {}^A z_{i+1}^A + p_{i,i}^{AB} {}^A z_i^B + (1 - p_{i,i+1}^{AA} - p_{i,i}^{AB}) {}^A z_i^A + {}^A P_i^A, \quad 0 \leq i \leq n-1, \quad (2.32)$$

$${}^A z_i^B = p_{i,i}^{BA} {}^A z_i^A + p_{i,i-1}^{BB} {}^A z_{i-1}^B + (1 - p_{i,i}^{BA} - p_{i,i-1}^{BB}) {}^A z_i^B + {}^A P_i^B, \quad 1 \leq i \leq n, \quad (2.33)$$

where ${}^A z_i^A = {}^A P_i^A$, ${}^A F_i^A$ and ${}^A z_i^B = {}^A P_i^B$, ${}^A F_i^B$. At the absorbing states, ${}^A z_0^B = 0$ (because ${}^A P_0^B = 0$), and ${}^A z_n^A = 0$ (because ${}^A F_n^A = 0$).

Solving the system (2.32)–(2.33) (see Online Appendix A.3), we find that the average fixation time of a single A individual randomly placed on the star, ${}^A \bar{F}$, is given by

$${}^A \bar{F} = \frac{1}{n+1} \left((n+1) \sum_{l=2}^n A(l,n) C(l) + 1 + \frac{n}{p_{1,0}^{BB} + p_{1,1}^{BA}} \right), \quad (2.34)$$

where

$$C(l) = \frac{\pi_{l-1,l-1}^{AB}}{\pi_{l-1,l}^{AA}} \sum_{j=1}^{l-1} \left(\frac{{}^A P_j^B}{p_{j,j-1}^{BB} + p_{j,j}^{BA}} \prod_{k=j+1}^{l-1} \pi_{k,k-1}^{BB} \right) + \frac{{}^A P_{l-1}^A}{p_{l-1,l}^{AA}}. \quad (2.35)$$

The derivation of the solution of the mean time to fixation of As, starting from any possible state, is shown in Online Appendix A.3.

Note that by symmetry, replacing $p_{i,i+1}^{AA}$ by $p_{n-i,n-i-1}^{BB}$, $p_{i,i}^{AB}$ by $p_{n-i,n-i}^{BA}$, $p_{i,i-1}^{BB}$ by $p_{n-i,n-i+1}^{AA}$, $p_{i,i}^{BA}$ by $p_{n-i,n-i}^{AB}$, ${}^A P_i^A$ by $1 - {}^A P_{n-i}^B = {}^B P_{n-i}^B$ and ${}^A P_i^B$ by $1 - {}^A P_{n-i}^A = {}^B P_{n-i}^A$ in the above formulae, we find the respective formulae of the fixation probability and absorption and fixation times of B individuals when they are introduced into a population of As.

3 Favoured Strategies

In evolutionary games, the comparison of the fixation probability of a single mutant playing strategy A, ${}^A\bar{P}$, with that of a mutant playing B, ${}^B\bar{P}$, is of interest. In evolutionary processes where there is no mutation, if ${}^A\bar{P} > {}^B\bar{P}$ then strategy A is favoured over B. The conditions under which one strategy is favoured over the other have been found for several graphs and update rules under the assumption of weak selection (for example, [16]). In this section, we derive the appropriate (general) conditions for strategy A to be favoured over strategy B on the star. We define

$$\rho = \frac{{}^A\bar{P}}{{}^B\bar{P}} \tag{3.1}$$

and seek conditions on $\rho \stackrel{\geq}{\leq} 1$.

Since Bs fixate if and only if As do not, we have

$${}^B\bar{P} = \frac{1}{n+1} (1 - {}^A P_n^B) + \frac{n}{n+1} (1 - {}^A P_{n-1}^A). \tag{3.2}$$

Using (2.19)–(2.20), the fact that $\pi_{i,i+1}^{AA} + \pi_{i,i}^{AB} = 1 = \pi_{i,i}^{BA} + \pi_{i,i-1}^{BB}$ and also (2.23) for $i = n - 1$, (3.2) can be written as

$${}^B\bar{P} = \frac{1}{n+1} (\pi_{n,n-1}^{BB} + n\pi_{n-1,n-1}^{AB}) \left(\prod_{k=1}^{n-1} \frac{\pi_{k,k-1}^{BB}}{\pi_{k,k+1}^{AA}} \right) \frac{1}{A(1,n)}. \tag{3.3}$$

Using (3.3) and (2.27) we obtain

$$\rho = \frac{\pi_{0,1}^{AA} + n\pi_{1,1}^{BA}}{\pi_{n,n-1}^{BB} + n\pi_{n-1,n-1}^{AB}} \prod_{k=1}^{n-1} \frac{\pi_{k,k+1}^{AA}}{\pi_{k,k-1}^{BB}}. \tag{3.4}$$

In the IP, as shown in Online Appendix B.1, for large n we find

$$\rho_{IP} \geq 1 \Leftrightarrow \alpha\beta \left(\frac{\alpha}{\beta} \right)^{\frac{\beta}{\delta-\beta}} \geq \gamma\delta \left(\frac{\delta}{\gamma} \right)^{\frac{\gamma}{\delta-\gamma}}, \quad \alpha \neq \beta, \gamma \neq \delta. \tag{3.5}$$

In the BD-D process, for large n we find (see Online Appendix B.2)

$$\rho_{BD-D} \geq 1 \Leftrightarrow \left(\frac{\delta}{\beta} \right)^{\frac{\beta}{\delta-\beta}} \geq \left(\frac{\alpha}{\gamma} \right)^{\frac{\gamma}{\alpha-\gamma}}, \quad \alpha \neq \gamma, \beta \neq \delta. \tag{3.6}$$

In the VM, for large n we find (see Online Appendix B.3)

$$\rho_{VM} \geq 1 \Leftrightarrow \alpha(\beta + \delta) \left(\frac{\alpha}{\beta} \right)^{\frac{\gamma}{\beta-\alpha}} \geq \delta(\gamma + \alpha) \left(\frac{\delta}{\gamma} \right)^{\frac{\beta}{\gamma-\delta}}, \quad \alpha \neq \beta, \gamma \neq \delta. \tag{3.7}$$

Finally, in the DB-B process for large n we find (see Online Appendix B.4)

$$\rho_{DB-B} \geq 1 \Leftrightarrow \alpha(\beta + \delta) \left(\frac{\alpha}{\gamma} \right)^{\frac{\gamma}{\beta-\alpha}} \geq \delta(\gamma + \alpha) \left(\frac{\delta}{\beta} \right)^{\frac{\beta}{\beta-\delta}}, \quad \alpha \neq \gamma, \beta \neq \delta. \tag{3.8}$$

In the limit of weak selection, i.e. when $w \rightarrow 0_+$, from (3.5), (3.6), (3.7) and (3.8) it follows that on a large star, under all dynamics As are favoured if and only if $a + b > c + d$, which is in agreement with the results of Tarnita et al. [16], where the IP and the DB-B process in this case are considered.

It is shown (see Online Appendix B.5) that in the BD-D and DB-B processes,

$$\rho_{BD-D} \gtrless 1 \Leftrightarrow \rho_{DB-B} \gtrless 1 \Leftrightarrow \alpha\beta \gtrless \gamma\delta, \quad \forall n. \tag{3.9}$$

In the case of weak selection, it follows from (3.9) that under the BD-D and the DB-B processes, As are favoured if and only if $a + b > c + d, \forall n$; this agrees with Tarnita et al. [16] where the DB-B process is considered. In these dynamics, for $\alpha\beta = \gamma\delta, p_{i,i+1}^{AA} = p_{n-i,n-i-1}^{BB}, p_{i,i}^{AB} = p_{n-i,n-i}^{BA}, p_{i,i-1}^{BB} = p_{n-i,n-i+1}^{AA}$ and $p_{i,i}^{BA} = p_{n-i,n-i}^{AB}$. Hence, ${}^A P_i^A = {}^B P_{n-i}^B, {}^A P_i^B = {}^B P_{n-i}^A, T_i^A = T_{n-i}^B, T_i^B = T_{n-i}^A$ and therefore ${}^A \bar{T} = {}^B \bar{T}$, and ${}^A F_i^A = {}^B F_{n-i}^B, {}^A F_i^B = {}^B F_{n-i}^A$ and therefore ${}^A \bar{F} = {}^B \bar{F}, \forall 0 \leq i \leq n$.

Note that for the two birth–death processes (the IP and the BD-D process) there is a step change in ρ going from 0 to infinity in the limiting case of large n , so that for a small change in parameter values there is a huge change in the relative probabilities of fixation of the two strategies, whereas the change is gradual for the death–birth processes (VM and DB-B process).

Following the same procedure on a large complete graph (where every vertex is connected to each other), we find that under the IP

$$\ln(\rho_{CG}) \approx \ln\left(\frac{\alpha\left(\frac{\alpha}{\beta}\right)^{\left(\frac{\beta}{\alpha-\beta}\right)^n}}{\delta\left(\frac{\delta}{\gamma}\right)^{\left(\frac{\gamma}{\delta-\gamma}\right)^n}}\right), \quad \alpha \neq \beta, \gamma \neq \delta \tag{3.10}$$

[1, 7]. This is equivalent to that in the VM. Similarly, we find that ρ in the BD-D and DB-B processes also satisfy (3.10). Hence, As are favoured over Bs if $\alpha\left(\frac{\alpha}{\beta}\right)^{\left(\frac{\beta}{\alpha-\beta}\right)^n} > \delta\left(\frac{\delta}{\gamma}\right)^{\left(\frac{\gamma}{\delta-\gamma}\right)^n}$ and the step change described above occurs, in all processes. Thus, in the two processes where births occur first, evolution on a large star has similar characteristics to that on the complete graph of the same size, with the interaction of the whole population occurring through the central individual, which is continuously replaced. Note that for $\beta = \gamma, \rho_{IP} = \rho_{CG}$ and for $\alpha = \delta, \rho_{BD-D} = \rho_{CG}$. In the other two processes there is a big difference between the star and the complete graph, as a change in the centre individual has a big impact on subsequent evolution on a star.

4 Examples

4.1 The Fixed Fitness Case

In this case we assume that A individuals have fitness equal to r and B individuals fitness equal to 1. This is a special case of an evolutionary game with $a = b = r, c = d = 1, w = 1$ and $f_b = 0$. Here the fitness of each individual remains constant and thus the exact (relative) positions of As and Bs are irrelevant.

4.1.1 The Average Fixation Probability of a Single Mutant

In all dynamics, ${}^A \bar{P} \gtrless 1/(n + 1)$ if and only if $r \gtrless 1$ and thus selection favours (does not favour) the fixation of As when $r > 1$ ($r < 1$). The relationship between fixation probabilities under the different dynamics we consider is shown in Table 1. Note that for $n > 3$, there

is one and only one value of $r > 1$, $r_1(n)$, and one and only one value of $r < 1$, $r_2(n)$ (the exact values of $r_1(n)$ and $r_2(n)$ depend on n), such that ${}^A\bar{P}_{\text{BD-D}} = {}^A\bar{P}_{\text{VM}}$. As n increases, $r_1(n)$ increases rapidly to infinity while $r_2(n)$ decreases rapidly to zero (the behaviour of $r_1(n)$ and $r_2(n)$ as the population size increases is shown in Fig. 4). Thus, except for values of r more extreme than these critical values, as observed from Table 1, the birth–death processes yield a higher chance of fixation for mutants with $r > 1$ and less for mutants with $r < 1$. The average fixation probability in some specific cases is shown in Fig. 2.

When n is large we find that (see Online Appendices C.1 and C.2)

$${}^A\bar{P}_{\text{IP}} \approx \frac{1 - 1/r^2}{1 - 1/r^{2n}}, \quad r \neq 1, \tag{4.1}$$

$${}^A\bar{P}_{\text{BD-D}} \approx \frac{1 - 1/r}{1 - 1/r^n} = {}^A\bar{P}_{\text{Moran}}, \quad r \neq 1, \tag{4.2}$$

where ${}^A\bar{P}_{\text{Moran}}$ is the *Moran probability*, which is equal to the fixation probability of a single mutant on any regular graph [8]. Substituting (2.21)–(2.22) into (2.27) and using (2.9)–(2.16) appropriately, we get (see Online Appendix C.3) that in this case,

$${}^A\bar{P}_{\text{VM}} = \frac{rn(r+1)}{(rn+1)(n+r)} \frac{r^2-1}{r^2 - \left(\frac{rn+1}{r(n+r)}\right)^{n-1}} < \frac{r+1}{n+1}, \tag{4.3}$$

$${}^A\bar{P}_{\text{DB-B}} = \frac{1}{n+1} \left(\frac{1}{n+1} + \frac{r}{n+2r-1} \right) \frac{rn+1}{r+1} < \frac{r+1}{n-1} \tag{4.4}$$

and thus, in contrast to the birth–death processes, for the death–birth processes the increase of the population size decreases the chance of fixation to zero. For $r < 1$ the fixation probability of a mutant decreases with n in all dynamics.

As r decreases, the fixation probability under all dynamics decreases. Moreover, as r approaches 0, the fixation probabilities under all dynamics but DB-B approach 0; ${}^A\bar{P}_{\text{DB-B}}$ converges to $1/(n+1)^2$. Thus, following the DB-B process, even an invader mutant with zero fitness has a small chance to fixate. As r increases to infinity, ${}^A\bar{P}_{\text{IP}}$ and ${}^A\bar{P}_{\text{VM}}$ tend to 1, while ${}^A\bar{P}_{\text{BD-D}}$ converges to $(1/(n+1))(1/(n+1) + n)$ and ${}^A\bar{P}_{\text{DB-B}}$ to $(n/(n+1)) \times (1/(n+1) + 1/2)$. Hence, under the BD-D and the DB-B processes, even for an infinite fitness r , the fixation of a mutant in a finite population is not guaranteed. This case appears even in a homogeneous population of finite size under the DB-B process where the fixation probability of a single mutant tends to $1 - 1/(n+1)$ as r tends to infinity. In its simplest definition, fitness can be thought of as the relative lifetime reproductive success of an individual. Fitter individuals should be more likely to survive and reproduce and an individual with 0 fitness should be certain to be eliminated and one with infinite fitness should be certain to fixate. We note that the IP and VM processes are consistent with this interpretation, but the BD-D and DB-B processes are not.

4.1.2 Mean Time to Absorption Starting from a Single Mutant

Although the fixation of advantageous mutants randomly placed on the star is more likely in the birth–death processes (except some special cases), absorption in these processes is reached slower than in the death–birth processes (except some extreme cases of $n > 4$ and $r \approx 0$). The comparison of the absorption times between the different dynamics is shown in Table 1. Figure 3 represents the absorption times for some specific values of r and n .

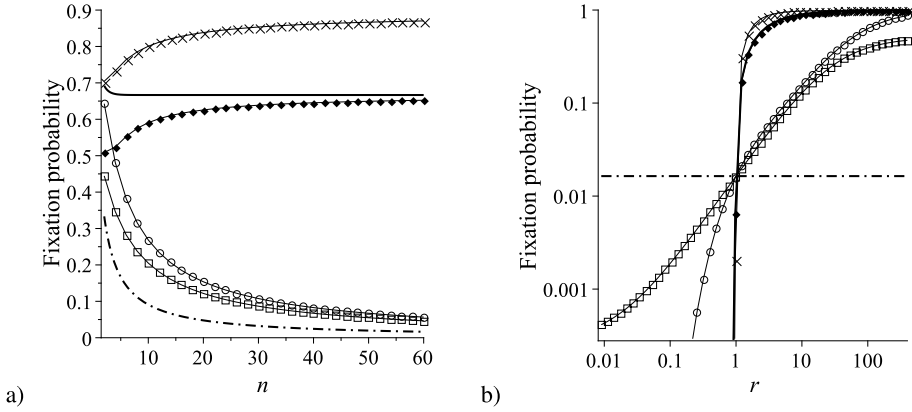


Fig. 2 The average fixation probability of a single mutant on a star graph under the IP (*crosses*), the BD-D process (*diamonds*), the VM (*circles*) and the DB-B process (*boxes*) in the fixed fitness case where **(a)** $r = 3$ and n varies, **(b)** $n = 60$ and r varies. The *solid line* represents the fixation probability in the Moran process and the *dashed-dotted line* represents the fixation probability of a single mutant in the case of neutral drift, $1/(n + 1)$

Here we show explicit approximations of the absorption times starting from a single mutant given by (2.30) for extreme values of r .

For $r \approx 0_+$, in the IP and the VM, $\pi_{i,i}^{AB} \approx \pi_{i,i-1}^{BB} \approx 1$ and $\pi_{i,i+1}^{AA} \approx \pi_{i,i}^{BA} \approx 0$. In the BD-D process, for $i \neq 0$, $\pi_{i,i}^{AB} \approx 1$ and $\pi_{i,i+1}^{AA} \approx 0$. In the DB-B process, for $i \neq n$, $\pi_{i,i-1}^{BB} \approx 1$ and $\pi_{i,i}^{BA} \approx 0$. Given these approximations, following the same procedure as that shown in Online Appendix A.2, we find that for $r \approx 0_+$

$${}^A\bar{T}_{IP} \approx n(n - 1) + 1 > {}^A\bar{T}_{DB-B}, \tag{4.5}$$

$${}^A\bar{T}_{BD-D} \approx \frac{n^2 + 1}{n - 1} + \frac{1}{n + 1} > {}^A\bar{T}_{VM}, \tag{4.6}$$

$${}^A\bar{T}_{VM} \approx 1, \tag{4.7}$$

$${}^A\bar{T}_{DB-B} \approx \frac{n}{n + 1} \sum_{i=1}^{n-1} \left(\frac{1}{i}\right) + \frac{1}{n + 1} + n > {}^A\bar{T}_{BD-D} \quad (\text{for } n > 4). \tag{4.8}$$

For $r \gg 1$, in the IP and the VM, $\pi_{i,i}^{AB} \approx \pi_{i,i-1}^{BB} \approx 0$ and $\pi_{i,i+1}^{AA} \approx \pi_{i,i}^{BA} \approx 1$. In the BD-D process, for $i \neq n$, $\pi_{i,i-1}^{BB} \approx 0$ and $\pi_{i,i}^{BA} \approx 1$. Finally, in the DB-B process, for $i \neq 0$, $\pi_{i,i}^{AB} \approx 0$ and $\pi_{i,i+1}^{AA} \approx 1$. Using these approximations and the formula (2.30), we find that for large $r \gg n$

$${}^A\bar{T}_{IP} \approx \sum_{i=0}^{n-1} \frac{n(i + 1)}{n - i} > {}^A\bar{T}_{VM}, \tag{4.9}$$

$${}^A\bar{T}_{BD-D} \approx n \left(n + \frac{1}{n + 1} \right) \sum_{i=1}^{n-1} \left(\frac{1}{i}\right) + n + \frac{1}{n + 1} > {}^A\bar{T}_{IP}, \tag{4.10}$$

$${}^A\bar{T}_{VM} \approx n^2 > {}^A\bar{T}_{DB-B}, \tag{4.11}$$

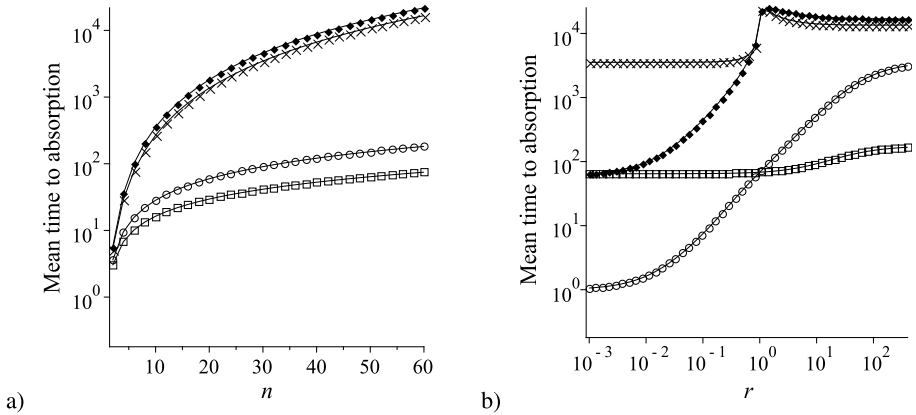


Fig. 3 The mean time to absorption starting from a single mutant on a star graph under the IP (*crosses*), the BD-D process (*diamonds*), the VM (*circles*) and the DB-B process (*boxes*) in the fixed fitness case where (a) $r = 3$ and n varies, (b) $n = 60$ and r varies

$${}^A\bar{T}_{DB-B} \approx \frac{n(n+3)}{2(n+1)} \sum_{i=1}^{n-1} \left(\frac{1}{i}\right) + \frac{n(n+1)+2}{2(n+1)}. \tag{4.12}$$

Note that in the DB-B process once there is an A individual on a leaf and in the centre, then the mean absorption time does not depend on r ; specifically, substituting (2.13)–(2.16) and (2.21)–(2.22) appropriately into the formula giving T_1^A (see Online Appendix A.2), after some calculations it is proved that $T_1^A_{DB-B} = (n+1) \sum_{i=1}^{n-1} 1/i$.

Using the formulae of Sect. 2, we find that in the limit of large population size, in the birth–death processes absorption occurs in a number of time steps that is $O(n^2 \ln n)$. However, in the death–birth processes, absorption is reached much faster, in $O(n)$ time steps.

In a large population, Fig. 3 suggests that following the birth–death processes, absorption is reached slower for a value of r close to 1 (this value tends to 1 as the population size increases). Thus, in large populations neutral mutants yield higher absorption times. However, following the death–birth processes absorption time increases with the increase in r .

4.1.3 Mean Fixation Time of a Single Mutant

As in the case of the absorption time, apart from some special cases of $r \approx 0$ where ${}^A\bar{F}_{VM}$, for example, increases rapidly, the fixation time is generally higher in the birth-first processes than the death-first processes. The comparison of the fixation times for various scenarios is shown in Table 1.

In the limit of large r ($r \rightarrow \infty$), the fixation time of a single mutant in the IP and VM, ${}^A\bar{F}_{IP}$ and ${}^A\bar{F}_{VM}$, are equal to ${}^A\bar{T}_{IP}$ given by (4.9) and ${}^A\bar{T}_{VM}$ given by (4.11), respectively. In the BD-D and DB-B processes we find that

$${}^A\bar{F}_{BD-D} \approx n(n+1) \sum_{i=1}^{n-1} \left(\frac{1}{i}\right) + n + \frac{1}{n+1}, \tag{4.13}$$

$${}^A\bar{F}_{DB-B} \approx (n+1) \sum_{i=1}^{n-1} \left(\frac{1}{i}\right) + \frac{n(n+1)+2}{2(n+1)}. \tag{4.14}$$

Table 1 Comparison of the average fixation probability and the mean times to absorption and fixation of a single mutant on a star graph in the fixed fitness case between the IP, the BD-D process, the VM and the DB-B process. The variation of $r_1(n)$, $r_2(n)$, $r_3(n)$, $r_4(n)$, $r_5(n)$ and $r_6(n)$ with n is shown in Fig. 4. Apart from some extreme cases, the two birth–death processes (IP and BD-D) yield a higher fixation probability for advantageous mutants ($r > 1$) and a lower fixation probability for disadvantageous mutants ($r < 1$) compared to the death–birth processes (VM and DB-B). On the other hand, death–birth processes yield much lower absorption and fixation times than birth–death processes

Comparison of fixation probabilities		
$n = 1$	$r \geq 1$	${}^A\bar{P}_{IP} = {}^A\bar{P}_{VM} = {}^A\bar{P}_{Moran} = r/(r + 1)$ $r/(r + 1) \geq {}^A\bar{P}_{BD-D} = {}^A\bar{P}_{DB-B} = 1/2$
$n = 2, 3$	$r > 1$	${}^A\bar{P}_{IP} > {}^A\bar{P}_{Moran} > {}^A\bar{P}_{VM} > {}^A\bar{P}_{BD-D} > {}^A\bar{P}_{DB-B} > 1/(n + 1)$
	$r < 1$	${}^A\bar{P}_{IP} < {}^A\bar{P}_{Moran} < {}^A\bar{P}_{VM} < {}^A\bar{P}_{BD-D} < {}^A\bar{P}_{DB-B} < 1/(n + 1)$
$n \geq 4$	$1 < r < r_1(n)$	${}^A\bar{P}_{IP} > {}^A\bar{P}_{Moran} > {}^A\bar{P}_{BD-D} > {}^A\bar{P}_{VM} > {}^A\bar{P}_{DB-B} > 1/(n + 1)$
	$1 < r_1(n) < r$	${}^A\bar{P}_{IP} > {}^A\bar{P}_{Moran} > {}^A\bar{P}_{VM} > {}^A\bar{P}_{BD-D} > {}^A\bar{P}_{DB-B} > 1/(n + 1)$
	$r < r_2(n) < 1$	${}^A\bar{P}_{IP} < {}^A\bar{P}_{Moran} < {}^A\bar{P}_{VM} < {}^A\bar{P}_{BD-D} < {}^A\bar{P}_{DB-B} < 1/(n + 1)$
	$r_2(n) < r < 1$	${}^A\bar{P}_{IP} < {}^A\bar{P}_{Moran} < {}^A\bar{P}_{BD-D} < {}^A\bar{P}_{VM} < {}^A\bar{P}_{DB-B} < 1/(n + 1)$
$\forall n$	$r = 1$	${}^A\bar{P}_{IP} = {}^A\bar{P}_{Moran} = {}^A\bar{P}_{BD-D} = {}^A\bar{P}_{VM} = {}^A\bar{P}_{DB-B} = 1/(n + 1)$
Comparison of absorption times		
$n = 1$	$\forall r$	${}^A\bar{T}_{IP} = {}^A\bar{T}_{BD-D} = {}^A\bar{T}_{VM} = {}^A\bar{T}_{DB-B} = 1$
$n = 2$	$1 < r < r_3(n)$	${}^A\bar{T}_{IP} > {}^A\bar{T}_{BD-D} > {}^A\bar{T}_{VM} > {}^A\bar{T}_{DB-B}$
	$1 < r_3(n) < r$	${}^A\bar{T}_{BD-D} > {}^A\bar{T}_{IP} > {}^A\bar{T}_{VM} > {}^A\bar{T}_{DB-B}$
	$r < 1$	${}^A\bar{T}_{BD-D} > {}^A\bar{T}_{IP} > {}^A\bar{T}_{DB-B} > {}^A\bar{T}_{VM}$
$n \geq 3$	$1 < r < r_3(n)$	${}^A\bar{T}_{IP} > {}^A\bar{T}_{BD-D} > {}^A\bar{T}_{VM} > {}^A\bar{T}_{DB-B}$
	$1 < r_3(n) < r$	${}^A\bar{T}_{BD-D} > {}^A\bar{T}_{IP} > {}^A\bar{T}_{VM} > {}^A\bar{T}_{DB-B}$
	$r < r_4(n) < 1^a$	${}^A\bar{T}_{IP} > {}^A\bar{T}_{BD-D} > {}^A\bar{T}_{DB-B} > {}^A\bar{T}_{VM}$
	$r_4(n) < r < 1$	${}^A\bar{T}_{BD-D} > {}^A\bar{T}_{IP} > {}^A\bar{T}_{DB-B} > {}^A\bar{T}_{VM}$
$\forall n$	$r = 1$	${}^A\bar{T}_{IP} = {}^A\bar{T}_{BD-D} > {}^A\bar{T}_{VM} = {}^A\bar{T}_{DB-B}$
Comparison of fixation times		
$n = 1$	$\forall r$	${}^A\bar{F}_{IP} = {}^A\bar{F}_{BD-D} = {}^A\bar{F}_{VM} = {}^A\bar{F}_{DB-B} = 1$
$n = 2$	$1 < r < r_5(n)$	${}^A\bar{F}_{IP} > {}^A\bar{F}_{BD-D} > {}^A\bar{F}_{DB-B} > {}^A\bar{F}_{VM}$
	$1 < r_5(n) < r$	${}^A\bar{F}_{BD-D} > {}^A\bar{F}_{IP} > {}^A\bar{F}_{DB-B} > {}^A\bar{F}_{VM}$
	$r < 1^b$	${}^A\bar{F}_{BD-D} > {}^A\bar{F}_{IP} > {}^A\bar{F}_{VM} > {}^A\bar{F}_{DB-B}$
$n \geq 3$	$1 < r < r_5(n)$	${}^A\bar{F}_{IP} > {}^A\bar{F}_{BD-D}$
	$1 < r_5(n) < r$	${}^A\bar{F}_{BD-D} > {}^A\bar{F}_{IP}$
	$1 < r < r_6(n)$	${}^A\bar{F}_{DB-B} > {}^A\bar{F}_{VM}$
	$1 < r_6(n) < r$	${}^A\bar{F}_{VM} > {}^A\bar{F}_{DB-B}$
$\forall n$	$r < 1^b$	${}^A\bar{F}_{BD-D} > {}^A\bar{F}_{IP} > {}^A\bar{F}_{VM} > {}^A\bar{F}_{DB-B}$
		${}^A\bar{F}_{IP} = {}^A\bar{F}_{BD-D} > {}^A\bar{F}_{VM} = {}^A\bar{F}_{DB-B}$

^aFor $n > 4$ and $r \approx 0$, ${}^A\bar{T}_{IP} > {}^A\bar{T}_{DB-B} > {}^A\bar{T}_{BD-D} > {}^A\bar{T}_{VM}$

^bFor $r \approx 0$, ${}^A\bar{F}_{BD-D} > {}^A\bar{F}_{VM} > {}^A\bar{F}_{IP} > {}^A\bar{F}_{DB-B}$

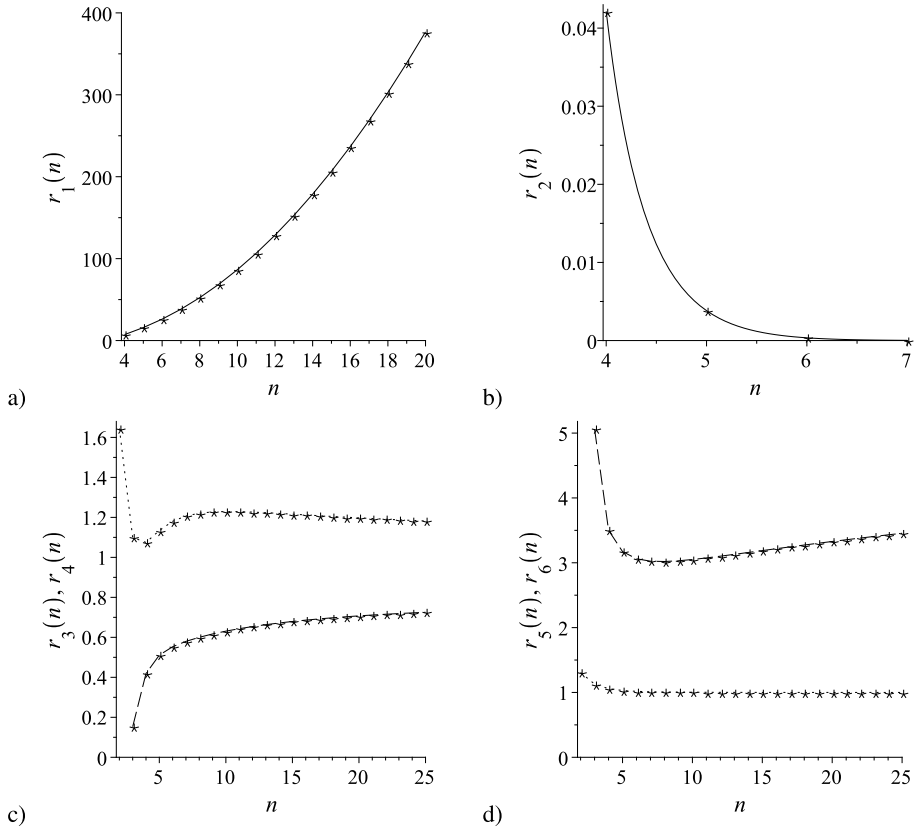


Fig. 4 The behaviour of (a) $r_1(n)$, (b) $r_2(n)$, (c) $r_3(n)$ (dotted line) and $r_4(n)$ (dashed line) and (d) $r_5(n)$ (dotted line) and $r_6(n)$ (dashed line) as n increases

The fixation times in the limiting case of $r \rightarrow 0_+$ are of less interest since in this case the chance of fixation of the mutant individual is very small and we condition on its fixation.

In the limit of large population size, the fixation time in the birth–death processes is $O(n^3)$ while in the death–birth processes the limit is $O(n \ln n)$. Numerical examples suggest that in large populations, following the birth–death processes, as the absorption time, the mean fixation time of a neutral mutant is the highest.

It should be noted that, especially in large populations, ${}^A\overline{F}_{DB-B}$ is affected less by the change in r than the fixation times under other dynamics (as seen for ${}^A\overline{P}_{DB-B}$ and ${}^A\overline{T}_{DB-B}$ above).

4.2 The Frequency Dependent Fitness Case—Example Games on the Star Graph

In this section, we apply the results obtained in the previous sections in cases where the fitness of each individual depends on the composition of the population. We consider various evolutionary games which in an infinite well-mixed population result in different evolutionary outcomes.

4.2.1 A Hawk–Dove Game on the Star Graph

The Hawk–Dove game is a classic game which has been used extensively for the modelling of competition of animals over a food resource. In this game, it is assumed that a pair of individuals contest a resource of value V playing either the aggressive strategy Hawk (H) or the non-aggressive strategy Dove (D). If two individuals playing Hawk meet, a fight take place. At the end of the fight, the two players obtain a payoff on average equal to $(V - C)/2$, where C is the cost of the fight. If two Doves meet, they obtain an average payoff $V/2$. If a Hawk meets a Dove, the Dove retreats leaving the food to the Hawk without any cost, and thus the Hawk obtain the whole food resource, V , while the Dove gets nothing. This game is described by the following payoff matrix.

$$\begin{array}{c|cc}
 & \text{H} & \text{D} \\
 \hline
 \text{H} & a = \frac{V-C}{2} & b = V \\
 \text{D} & c = 0 & d = \frac{V}{2}
 \end{array} \tag{4.15}$$

If the value of the resource outweighs the cost of the fight, i.e. if $V > C$, then an individual always does better by playing Hawk no matter what the opponent does and thus in an infinite homogeneous population the Hawk strategy is the unique Evolutionarily Stable Strategy (ESS). If $V < C$ the unique ESS involves a mixture of V/C Hawks and $1 - V/C$ Doves.

The Average Fixation Probability of a Single Mutant Hawk The illustration of the dependence of ${}^H\bar{P}$ on the population size and the fight cost to the value of the resource ratio, C/V , is shown in Fig. 5 for a Hawk–Dove type of game (4.15). For comparison, in Fig. 5b the respective fixation probabilities of a single Hawk when invading in a complete graph is also presented. Similarly to the fixed fitness case, on the complete graph (see Online Appendix C.4) the updating rules do not much influence the fixation probabilities. Mutants have almost the same probability to fixate under the different dynamics (especially in large populations) with those in the IP and the VM being identical. In our example, we obtain a step change in the fixation probability in all dynamics. If $\rho_{CG} > 1$, mutants fixate with a probability almost independent of C/V ; for $\rho_{CG} < 1$, the fixation probability presents a rapid change and mutants’ elimination becomes almost certain. However, different update rules yield considerably different results on a star graph. Here we can observe two quantitatively different behaviours, one for birth–death processes and another for death–birth processes. In the birth–death processes, for large n , ${}^H\bar{P}$ exhibits a step function behaviour based on ρ ; in fact, for large n we find that (see Online Appendices C.1 and C.2)

$${}^H\bar{P}_{\text{IP}} \approx \begin{cases} \frac{1 - \frac{\gamma\delta}{\beta^2}}{1 - \left(\frac{\gamma\delta}{\beta^2}\right)^n} \approx 1 - \frac{\gamma\delta}{\beta^2}, & \rho_{\text{IP}} > 1, \\ 0, & \rho_{\text{IP}} < 1, \end{cases} \tag{4.16}$$

$${}^H\bar{P}_{\text{BD-D}} \approx \begin{cases} \frac{1 - \frac{\delta}{\beta}}{1 - \left(\frac{\delta}{\beta}\right)^n} \approx 1 - \frac{\delta}{\beta}, & \rho_{\text{BD-D}} > 1, \\ 0, & \rho_{\text{BD-D}} < 1. \end{cases} \tag{4.17}$$

On the other hand, in the death–birth processes, both ${}^H\bar{P}_{\text{VM}}$ and ${}^H\bar{P}_{\text{DB-B}}$ are bounded above by $(\beta + \delta)/\delta(n + 1)$ (see Online Appendix C.3) and thus decrease to 0 as n increases to infinity.

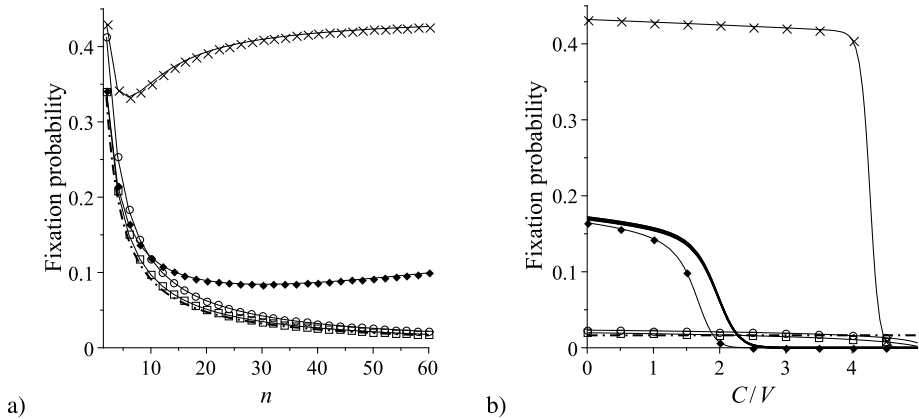


Fig. 5 The average fixation probability of a single mutant Hawk on a star graph under the IP (*crosses*), the BD-D process (*diamonds*), the VM (*circles*) and the DB-B process (*boxes*) in the Hawk–Dove game described by the payoff matrix (4.15) in the case where (a) $C/V = 1.5$ and n varies, (b) $n = 60$ and C/V varies. $f_b = 2$ and $w = 1$. The *thick lines* represent the respective case on the complete graph and the *dashed-dotted line* represents the fixation probability of a single mutant in the case of neutral drift, $1/(n + 1)$

Figure 5b suggests that when Hawks are favoured over Doves in the different update rules, the complete graph promotes the fixation of Hawks compared to the star graph in the BD-D, VM and DB-B process. Moreover, in the IP, favoured Hawks have much higher chance to fixate on a star graph.

Note that in the case of weak selection, in large stars and complete graphs, Hawks are favoured over Doves if the simple condition $C/V < 2$ holds, in all update rules.

In the case where a mutant Dove invades into Hawks, all the above results can be easily obtained by interchanging the two strategies, i.e. by exchanging α and δ , and β and γ .

Mean Time to Absorption and Fixation Starting from a Single Mutant Hawk A comparison of the absorption times for varying population size and varying C/V for the game with payoff matrix (4.15) is shown in Fig. 6. The absorption times on the complete graph as the ratio C/V varies is also shown in Fig. 6b for comparison. On the complete graph, the time needed for mutants to either fixate or die out is almost unaffected by the update rule followed. In large populations, values of the payoffs such that $\rho_{CG} \approx 1$ lead to the highest times before absorption and fixation occur, in all the update rules. However, on the star, as in the fixed fitness case, we observe that the speed to absorption and fixation might significantly vary when following different update rules. There is again a quantitative and qualitative distinction between birth–death and death–birth processes. In most of the cases the birth–death processes yield much higher absorption and fixation times than the death–birth processes. In large populations, both the absorption and fixation times in the two birth–death processes achieve local maxima for parameter values such that $\rho_{IP} \approx 1$ and $\rho_{BD-D} \approx 1$ since then the two strategies coexist for a long time before absorption/fixation occurs. In the VM and DB-B process, although the absorption and fixation times increase as C/V increases, they are affected less by the variation of C/V . In our example, we can see that for the VM as $C/V \rightarrow 5$ (i.e. the fitness of a Hawk individual when playing with just another Hawk tends to 0_+), ${}^H\bar{T}_{VM}$ (and similarly ${}^H\bar{F}_{VM}$) sharply increases. An initial Hawk on a leaf can be eliminated by chance, but if it is not, eventually it will occupy the center. At that moment, a Hawk on the leaves has a very very small fitness, so it will be eliminated and replaced by

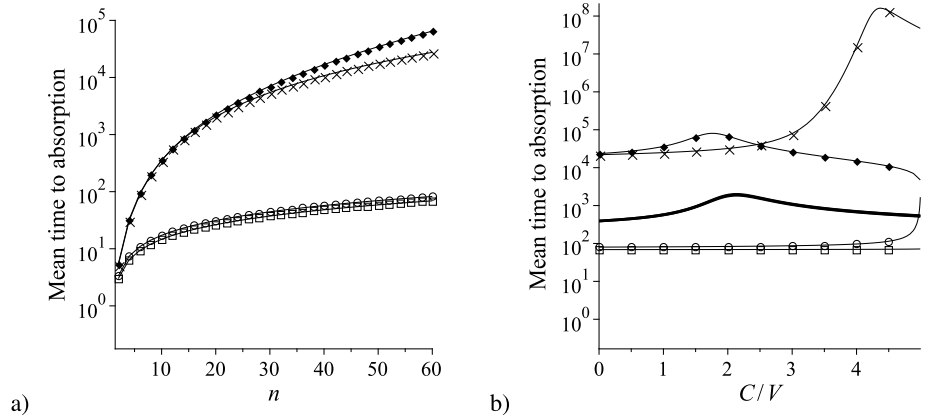


Fig. 6 The mean time to absorption starting from a single mutant Hawk on a star graph under the IP (*crosses*), the BD-D process (*diamonds*), the VM (*circles*) and the DB-B process (*boxes*) in the Hawk–Dove game described by the payoff matrix (4.15) in the case where (a) $C/V = 1.5$ and n varies, (b) $n = 60$ and C/V varies. $f_b = 2$ and $w = 1$. The *thick lines* represent the respective case on the complete graph

an offspring of the individual in the center; this process will be repeated many times before absorption occurs.

Figure 6b suggests that the process on the star might reach one of the two absorbing states much slower than on the complete graph when following the birth–death update rules but much faster when following the death–birth update rules.

4.2.2 Prisoner’s Dilemma on the Star Graph

The Prisoner’s dilemma considers a population where individuals either cooperate (C) or defect (D). In its simplest form, a cooperator pays a cost C and its partner receives a benefit B , and so the payoff matrix is

$$\begin{array}{c|cc} & C & D \\ \hline C & a = B - C & b = -C \\ D & c = B & d = 0 \end{array} \tag{4.18}$$

with $B > C > 0$.

In infinite well-mixed populations defection is the only ESS. On the star, a cooperator and a defector in the centre, respectively, have fitness

$$f_{C_c} = f_b + w \left(\frac{iB}{n} - C \right), \tag{4.19}$$

$$f_{D_c} = f_b + w \frac{iB}{n} \tag{4.20}$$

given i cooperators on the n leaves. A cooperator on a leaf has fitness $f_b + w(B - C)$ against a cooperator in the centre and fitness $f_b - wC$ against a defector in the centre. Similarly, a defector on a leaf has fitness equal to $f_b + wB$ against a cooperator in the centre and fitness equal to f_b against a defector in the centre. Thus, a cooperator always does worse than a defector no matter its position and the composition of the population. By condition (3.9), in the BD-D and DB-B processes, cooperation is never favoured over defection for any

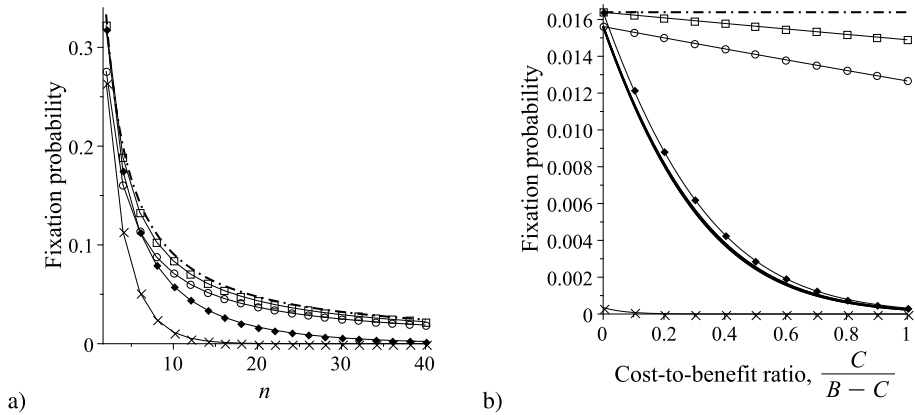


Fig. 7 The average fixation probability of a single mutant cooperator on a star graph under the IP (*crosses*), the BD-D process (*diamonds*), the VM (*circles*) and the DB-B process (*boxes*) in the Prisoner’s Dilemma game described by the payoff matrix (4.18) in the case where (a) $C/(B - C) = 1$ and n varies, (b) $n = 60$ and $C/(B - C)$ varies. $f_b = 10$ and $w = 1$. The *thick lines* represent the respective case on the complete graph and the *dashed-dotted line* represents the fixation probability of a single mutant in the case of neutral drift, $1/(n + 1)$

intensity of selection and any population size. By (3.5) and (3.7) this is true under the IP and the VM as well in large populations. Moreover, by (2.1)–(2.16), the number of cooperators from any state and in any population size increases (decreases) by one with probability less than (greater than) or equal to the respective probability in the case of neutral drift. Thus, the fixation probability of $i \in [1, n]$ cooperators starting from any possible state will always be less than that of neutral mutants, $i/(n + 1)$ (apart from the DB-B process which can be equal to $i/(n + 1)$). Hence, the star graph is not a good graph for the evolution of cooperation.

Numerical examples suggest that a single cooperator almost always has the highest chance of fixation following the two death–birth processes, with that in the DB-B process the highest and that in the IP the smallest one (see Fig. 7). Similarly, the birth–death processes favour the fixation of a single defector into a population of cooperators while in the death–birth processes the cooperators’ population has a higher chance to resist the invasion of a defector, with the fixation probability of the defector close to $1/(n + 1)$, especially for a sufficiently large population. As in the Hawk–Dove game, the absorption and fixation times in the birth–death processes have important quantitative and qualitative differences from those in the death–birth processes. The times to absorption and fixation in the birth–death processes are much higher, mainly due to the large number of defector–defector replacements before their fixation.

Comparisons with the complete graph (see Fig. 7b) indicate that in the IP, the star graph impedes cooperation while in the BD-D, VM and DB-B processes it promotes cooperation (although as we have seen the probability of cooperators fixating is very small in all of these processes).

4.2.3 Coordination Games on the Star Graph

A coordination game is a game with multiple pure strategy Nash Equilibria. In a game played in an infinite homogeneous population between two strategies, A and B, described by the payoff matrix (1.1), strategies A and B are ESSs, and there is an unstable interior

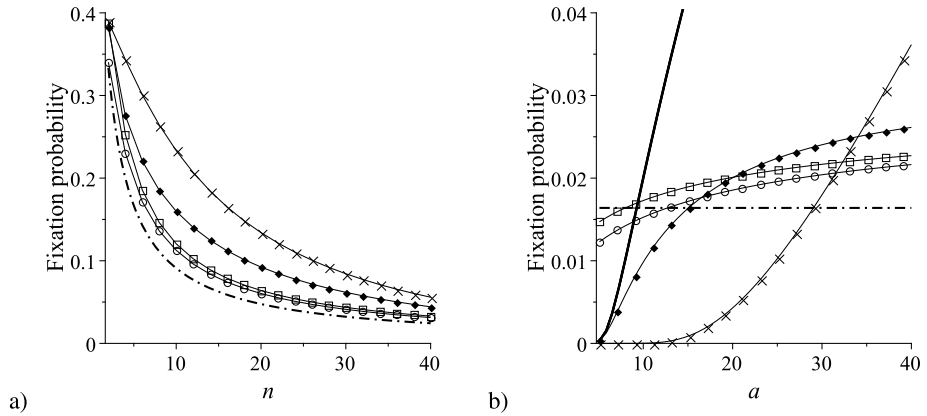


Fig. 8 The average fixation probability of a single mutant playing strategy A on a star graph under the IP (*crosses*), the BD-D process (*diamonds*), the VM (*circles*) and the DB-B process (*boxes*) in a coordination game in the case where **(a)** $a = 35$ and n varies, **(b)** $n = 60$ and a varies. $b = 3, c = 5, d = 4, f_b = 2$ and $w = 1$. The *thick lines* represent the respective case on the complete graph and the *dashed-dotted line* represents the fixation probability of a single mutant in the case of neutral drift, $1/(n + 1)$

equilibrium where the population fraction of A individuals is $A^* = (d - b)/(a + d - b - c)$. Strategy A is called risk dominant if it has the largest basin of attraction, which occurs if $a + b > c + d$, and payoff dominant if it gives the highest payoff compared to the other Nash equilibrium (i.e. if it is Pareto efficient).

Consider a coordination game, for example a Stag Hunt game ($a > c > d > b$), where strategy A is the payoff dominant strategy and strategy B the risk dominant strategy, played on the star graph. On a large star graph, in the case of weak selection the risk dominant strategy is always favoured over the payoff dominant strategy (since $c + d$ is always higher than $a + b$) in all the update rules. For any non-zero intensity of selection, since $a + b < c + d$ and $a > c > d > b$, $\alpha\beta$ is lower than $\gamma\delta$ as well and thus the BD-D and DB-B processes always favour the risk dominant strategy over the payoff dominant strategy on a star graph of any size. It is shown numerically that this holds for the IP and the VM as well. Numerical examples also indicate that in none of the update rules is the fixation of strategy A favoured by selection, i.e. ${}^A\bar{P}$ is always less than $1/(n + 1)$ in all update rules. However, if B is not the risk dominant strategy ($a + b > c + d$), i.e. A is both the payoff dominant and risk dominant strategy, then A might be favoured over B for any non-zero intensity of selection in all the update rules. In addition, it is shown that selection might favour the fixation of A and oppose the fixation of B under any of the update rules, i.e. ${}^A\bar{P} > 1/(n + 1) > {}^B\bar{P}$. Moreover, the chance of A's fixation remains relatively small. Figure 8 shows the average fixation probability of a single A on the star for an example set of parameters, as the population size and the benefit of playing other As, a , vary. The respective probability in the case of the complete graph is also presented in Fig. 8b. We again observe that in large stars, in the two birth–death processes IP and BD-D, values of payoffs such that $\rho_{IP} < 1$ and $\rho_{BD-D} < 1$ result in an almost zero fixation probability while a rapid increase in the fixation probability occurs as ρ_{IP} and ρ_{BD-D} become bigger than 1. The most advantageous update rule for the fixation of strategy A can be either the IP, the BD-D process or the DB-B process. Numerical examples indicate that the fixation probability of A under the VM is always lower than that in the DB-B process. In this game, the speed of the evolutionary process is again much

slower in the birth–death processes with the fixation time of mutants in large populations highest when $\rho_{IP} \approx 1$ and $\rho_{BD-D} \approx 1$.

Comparisons of the results on the star with those on the complete graph suggest that apart from cases where the payoff a is much larger than the other payoffs and the population size is relatively small, in the two birth–death processes the heterogeneity of the star graph inhibits the evolution of strategy A. However, in the two death–birth processes, the star might be a better graph for As to evolve.

5 Discussion

In this paper we have investigated analytically the stochastic process of the evolution of mutants on the simplest irregular graph, the star. We have derived the exact general formulae for the fixation probability and absorption and fixation times starting from any possible state on a star of any size. We have studied the process under different update rules by applying the results obtained in various evolutionary games which result in different evolutionary outcomes in homogeneous populations. It has been shown that although the choice of the update rule of the evolutionary process does not significantly affect the evolution of the invader mutants on homogeneous populations, it might cause considerable differences if these invade in a population with a non-homogeneous structure. However, in most of the cases, these differences are mainly due to the extreme structure of the graph rather than the dynamics themselves.

The IP in combination with the specialness of the star, enhances significantly the selection pressure and outweighs drift. At least for the cases where a mutant always does better (worse) than a resident individual, for example in the fixed fitness case and the Prisoner's Dilemma, the fixation probability of mutants is always higher (lower) than the respective probability on a complete graph of the same size. This happens only in the IP. In the DB-B process the selection pressure is nullified significantly and drift is emphasised partly due to the dynamics itself but mainly due to properties of the star graph. When an individual on a leaf dies randomly, which is the usual event, especially in large populations, it is replaced by the offspring of the individual in the centre without any game played (the fitness of individuals does not contribute to the process). If the individual in the centre dies (with probability $1/(n+1)$) then it is replaced by the offspring of an individual on the leaves which is chosen with probability proportional to fitness, where the fitness of the individual in the centre does not contribute to the process. Thus, especially in large populations, the spread and fixation of mutants happens almost randomly. In the BD-D process, although the first event happens randomly as well, since the increase or decrease of mutants on the leaves depends on the fitness of the individuals in this position, the BD-D process amplifies the contribution of the fitness much more than the DB-B process. Finally, in the VM, although selection operates on $n+1$ individuals (as in the IP), the process on the star is a strong suppressor of fitness. In this process, especially in large populations, the individual in the centre is quite safe and occupying this position at the beginning of the process is highly advantageous. However, the most likely initial position is a leaf, a position from which the role of the fitness decreases. Hence, in most of the cases, birth–death processes yield higher (lower) fixation probabilities of advantageous (disadvantageous) mutants than the death–birth processes. However, these processes usually require exceedingly long times to fixation, which are much larger than the respective times in the death–birth processes.

For the BD-D and DB-B processes where the first event happens randomly, we have seen that even a mutant with infinite fitness might not fixate. On the other hand, in the DB-B

process, even an invader mutant with zero fitness has a small chance to fixate. Hence, both the update rule and the structure of the population might result to the fixation of the less fit individuals and the elimination of the fitter individuals even in these extreme cases.

Most of the previous studies of evolutionary processes on graphs have considered the case of weak selection. It has been shown that in this case, following the rules of the IP and DB-B process, mutants on a large star playing strategy A are favoured over residents playing strategy B if $a + b > c + d$ [16]. We have shown that this condition holds for the BD-D process and the VM as well. In addition, for each of the dynamics we have found appropriate conditions for strategy A to be favoured over strategy B for any intensity of selection. Especially in the BD-D and DB-B processes, we have shown that mutant individuals playing strategy A on a star of any size are favoured over Bs if the simple condition $\alpha\beta > \gamma\delta$ holds. In the case where $\alpha\beta = \gamma\delta$ it has been shown that the fixation probability and the absorption and fixation time of a number of individuals of either type in a population of the other type are identical for any population size.

When a strategy A loses the advantage it has over strategy B and Bs become favoured, the average fixation probability of a mutant individual playing strategy A on a large star tends rapidly to zero when following the two birth–death processes. At this point, the fixation time takes the highest value. This also happens in the well-mixed population. Birth–death dynamics on a star effectively act like a well-mixed population when the population size is large, as the middle node is continuously replaced and all the others have the same relationship to each other through it. For death–birth dynamics this does not happen since the dynamics are very different. The central node is highly important and occupying it is a great advantage. In both processes, the increase of the population size results in an important decrease of the contribution of the payoffs obtained from the games in the evolutionary process and the probability of fixation is close to $1/(n + 1)$, as occupying the centre or not at the start is the key event. In particular, in the DB-B process, a single random event can cause big changes in the evolutionary process on the star irrespective of the values of the payoffs.

Considering the evolution of cooperation in the Prisoner’s Dilemma we have seen that the heterogeneity of the star is an inhospitable environment for cooperation to evolve. It is proved that cooperation is never favoured by selection while defection is always favoured by this, in all update rules. However, it has been shown that there are update rules under which cooperation is encouraged more on the star than on the complete graph. In a similar way, in a Stag Hunt type of game it is difficult for the payoff dominant strategy to evolve on the star. In particular, it is shown that in all update rules the risk dominant strategy is always favoured over the payoff dominant strategy and selection never favours the payoff dominant strategy.

The investigation of the evolutionary process on the star graph under four update rules has demonstrated that both the structure of the population and the update rule when applied in a non-homogeneous structure might have an important influence on the outcome of the evolutionary dynamics. However, it is not clear to what extent the reported characteristics depend upon the unique character of the star. So far, almost all the other analytical investigations have involved regular graphs where the differences of the evolutionary process under different updating rules are relatively minor. On the other hand, it is likely that whilst other irregular graphs may display properties of the star, behaviour will in general not be as extreme as that observed on the star (see [4]). Thus, it would be of interest to investigate whether, and to what extent, some of the observed phenomena hold for larger classes of graphs.

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