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Good predictors for the fixation probability on complex networks of multi-player games using territorial interactions

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Abstract

In 2012 Broom and Rychtar developed a new framework to consider the evolution of a population over a non-homogeneous underlying structure, where fitness depends upon multiplayer interactions amongst the individuals within the population played in groups of various sizes (including one). This included the independent model, and as a special case the territorial raider model, which has been considered in a series of subsequent papers. Here individuals are based upon the vertex of a graph but move to interact with their neighbours, sometimes meeting in large groups. The most important single property of such populations is the fixation probability, the probability of a single mutant completely replacing the existing population. In a recent paper we considered the fixation probability for the Birth Death Birth (BDB) dynamics for three games, a Public Goods game, the Hawk-Dove game and for fixed fitnesses for a large number of randomly generated graphs, in particular seeing if important underlying graph properties could be used as predictors. We found two good predictors, temperature and mean group size, but some interesting and unusual features for one type of graph, Barabasi-Albert graphs. In this paper we use a regression analysis to investigate (the usual) three alternative evolutionary dynamics (BDD, DBB, DBD) in addition to the original BDB. In particular, we find that the dynamics split into two pairs, BDB/DBD and BDD/DBB, each of which give essentially the same results and found a good fit to the data using a quadratic regression involving the above two variables. Further we find that temperature is the most important predictor for the Hawk-Dove game, whilst for the Public Goods game the group size also plays a key role, and is more important than the temperature for the BDD/DBB dynamics.

Keywords: complex networks, evolutionary graph theory, fixation probability, game theory, territory.

I. INTRODUCTION

Evolutionary graph theory considers a population where the structure is not homogeneous and affects its evolution and dynamics [1–7]. An inhomogeneous population is a better choice when geographical proximity and social status produce different number of connections

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between individuals. For many species like African wild dogs [8] and roadrunners [9], more than one individual may use the same territory, and groups may be formed. For these situations, multiplayer games are suitable for modelling the complex behaviour of individuals on cooperative, competition, dominance and resource division situation, for instance [10–14]. Usually, pairwise interactions between individuals are considered, using classical games, such as the Prisoner’s Dilemma and the Hawk-Dove game [15–17].

Such models of multiplayer games on structured populations can be applied to situations where variably sized groups of individuals meet and interact. In [18] a new framework for modelling structured populations involving multiplayer games was developed [see also 19, 20]. The model presented in [21] considered three classical games (hawk-dove, prisoner’s dilemma, and fixed fitness) using the “territorial raider” model [22], and the invasion process dynamics for some small graphs. In [23], this was expanded by considering a larger population and more complex types of graphs. By using a large range of different population structures, the authors found that the graph temperature and the average group size are good predictors of fixation probability. Some topological parameters of the graph have been tested, but they were considered poor predictors, although the clustering coefficient may be helpful as a secondary predictor.

In this paper, the objective is to expand the study presented in [23] by considering three other replacement dynamics and using regression tools to verify the variables that are good predictors for the fixation probability. In [23], four complex graph models had been tested with a wide range for creating different types of graphs. From Erdős-Renyi, small-world, scale-free, and Barábasi-Albert [24], the topological parameters, average group size, temperature, and fixation probability analysis showed that the Barábasi-Albert model simulation contained the whole range of variables and results found in the paper. Therefore, only Barábasi-Albert graphs will be considered here.

The population structure, territorial raider model, evolutionary dynamics, and evolutionary game are presented in the next section. The methodology for selecting the underlying population structures, based upon graphs (as described in Section II) for the simulations is then described in Section III. In The results are presented in Section IV and discussed in Section V.

II. THE MODEL

The model that we consider is a special case of the independent model introduced in [18]. In that model, a population contains N individuals (I_1, \dots, I_N) allowed to move to M places (P_1, \dots, P_M). The probability of individual I_n being at place P_m is denoted by p_{nm} . Letting \mathcal{G} denote any group of individuals, the probability $\chi(m, \mathcal{G})$ that group \mathcal{G} forms in place P_m is given by

$$\chi(m, \mathcal{G}) = \prod_{i \in \mathcal{G}} p_{im} \prod_{j \notin \mathcal{G}} (1 - p_{jm}). \quad (1)$$

For a group \mathcal{G} formed in place m , each individual I_n receives a payoff $R_{n,m,\mathcal{G}}$ from the multiplayer game of that group. The fitness of I_n is found by averaging its payoff over all possible groups and places and is given by

$$F_n = \sum_m \sum_{\substack{\mathcal{G} \\ n \in \mathcal{G}}} \chi(m, \mathcal{G}) R_{n,m,\mathcal{G}}. \quad (2)$$

In the territorial raider model also developed in [18], and used in [21] and [23], one individual is living at each place ($N = M$). For each iteration, individuals move to neighbouring places, returning to their original place at the end of the iteration. This could represent, for example, a population of territorial diurnal (nocturnal) individuals who forage during the day (night), but return to their nest during the night (day). From now on we shall use the alternative term “network” instead in place of “graph” for modelling such a population, where nodes represent the places and individuals, also characterizing the territorial raider model as described here. The term “graph” will be reserved for the underlying individual replacement weights in the evolutionary process as described below (the *evolutionary graph*).

Concerning the individuals’ movements, as in [21] and [23] we use the single parameter h that governs every movement. Therefore, an individual with d neighbours stays at its original node with probability $h/(h+d)$ and moves to any given one of its neighbours’ node with probability $1/(h+d)$. The parameter h was termed the *home fidelity* parameter since it is a likelihood of an individual to stay at its original node. Note that high values of h mean that individuals will often be alone at home, and low values will make the whole population move and interact more. For $h = 1$, all allowable places, including the home node, will be visited with equal probability.

The evolutionary graph, as used in [1], is a graph with a weighted adjacency matrix $\mathbf{W} = (w_{ij})$ where $w_{ij} \geq 0$ are the replacement weights, usually right-stochastic, i.e. $\sum_j w_{ij} = 1$. Every node v_i of the evolutionary graph is occupied by precisely one individual and if $w_{ij} > 0$ then the individual on v_i can replace the individual on v_j with a copy of itself. Here, w_{ij} represents the probability of an offspring of individual I_i to replace another individual I_j proportional to the time I_i and I_j spend together, as described below. The probability that I_i and I_j meet is given by summing $\chi(m, \mathcal{G})$ over all m such that $i, j \in \mathcal{G}$, using appropriate weights. In this meeting, I_i will spend an equal amount of time with each other individual in group \mathcal{G} and, therefore, we weight $\chi(m, \mathcal{G})$ with $1/(|\mathcal{G}| - 1)$ since there are $|\mathcal{G}| - 1$ other individuals. For $i = j$, we can sum $\chi(m, \mathcal{G})$ over all m such that $\mathcal{G} = \{i\}$ (note that here there is no need to weight $\chi(m, \mathcal{G})$ because I_i is alone). The replacement weights are therefore calculated as follows

$$w_{ij} = \begin{cases} \sum_m \sum_{i,j \in \mathcal{G}} \frac{\chi(m, \mathcal{G})}{|\mathcal{G}| - 1} & i \neq j, \\ \sum_m \chi(m, \{i\}) & i = j. \end{cases} \quad (3)$$

In the previous work [23], the evolution of the population was ruled by an adaptation for the current model [21] of the Invasion Process [1, 25], a birth-death process in which the selection happens in the birth event. Here, we also consider an adaptation of the Voter Model, a death-birth process with selection in the death event [26, 27]. There will be four replacement dynamics: BD-B (another name for the Invasion Process), BD-D [28], DB-B [15], and DB-D (the Voter Model), with the first letter indicating which process happens first (Death or Birth), and the last letter represents the moment the selection is made.

For the BD-B process, for example, an individual is chosen to give birth to an offspring with probability

$$b_i = \frac{F_i}{\sum_{n=1}^N F_n} \quad (4)$$

who then replaces one of its neighbours with probability

$$d_{ij} = \frac{w_{ij}}{\sum_{n=1}^N w_{in}}. \quad (5)$$

A summary of the four dynamics is shown in Table I. Note that the first event is related to one individual (b_i in BD-B and DD-B, and d_j in DB-B and DB-D), and the second event is related to the probability of i replaces j (d_{ij} in BD-B and DD-B, and b_{ij} in DB-B and DB-D).

	<i>birth</i>	<i>death</i>
BD-B	$b_i = \frac{F_i}{\sum_n F_n}$	$d_{ij} = \frac{w_{ij}}{\sum_n w_{in}}$
BD-D	$b_i = \frac{1}{N}$	$d_{ij} = \frac{w_{ij} F_j^{-1}}{\sum_n w_{in} F_n^{-1}}$
DB-B	$b_{ij} = \frac{w_{ij} F_i}{\sum_n w_{nj} F_n}$	$d_j = \frac{1}{N}$
DB-D	$b_{ij} = \frac{w_{ij}}{\sum_n w_{nj}}$	$d_j = \frac{F_j^{-1}}{\sum_n F_n^{-1}}$

TABLE I. Dynamics defined using the replacement weight as in [29]. In each case, B (D) is appended to the name of the dynamics if selection happens in the birth (death) event.

We use two important concepts from evolutionary graphs adapted to the current model: the *fixation probability* and the *temperature* [21, 23]. Assume that we start with a population where all individuals are of type B and we randomly select one of these and replace it with an individual of type A . We then follow our evolutionary dynamics until the population is either all of type A or all of type B (as long as our underlying network is connected, which we assume, one of these two states is reached with probability 1). The fixation probability is the probability that this population evolves to the state where all individuals are of type A . The temperature of an individual is given by

$$T_j = \sum_{i=1, i \neq j}^N w_{ij}. \quad (6)$$

This definition is as in [23]. The temperature was defined in this way for our framework in [21] (where the term strict temperature was used) but follows a similar definition introduced for evolutionary graph theory in [1]. The higher the temperature of an individual, the

more likely that that individual will be replaced in any given timestep. For completely neutral evolution, where every individual has the same fitness, then the temperature is simply proportional (with a factor $1/n$) to the probability that the individual at that site is replaced by a different one (rather than a copy of itself). As we want the temperature to be a property of the structure and not on a specific game and population composition, this is then the natural interpretation. It should also be noted that for many of the models, including this one, following how the weights are calculated we have that $\sum_i^N w_{ij} = 1$. This has the consequence that $T_j = 1 - w_{jj}$, so that the size of self-weights is particularly important, and also that for the BD-B dynamics $b_{ij} = d_{ij}$ and for the DB-D dynamics $b_{ij} = w_{ij}$.

We will consider two types of individuals in the population, A and B , evaluating the fixation probability for one single individual A invading a population of B s, as well as the fixation probability of a single B in a population of A s. The games considered in the contests are multiplayer versions of the Public Goods game, the Hawk-Dove game and the “game” with fixed fitnesses. The payoff of an individual A in a group with a individuals A and b individuals B is denoted by $R_A(a, b)$, and the payoff of an individual B is $R_B(a, b)$.

For the Public Goods game, the population consists of Cooperators, labelled A , and Defectors, labelled B . Individuals start with a background payoff R and then play a game amongst all of the individuals on a given place. A cooperator pays a cost C (even if the Cooperator is alone), and the other individuals share a benefit V [30]. As lone (cooperating) individuals pay the cost with no benefit, this makes the evolution of cooperation harder to achieve than if this was not the case [21, 23]. The payoff expressions for Public Goods game are in Table II, first column.

For the Hawk-Dove game, the population consists of Hawks, labelled A , and Doves, labelled B . Individuals meeting on a place compete for a single reward V . If all of them are Doves, they divide the reward equally. If there are any number of Hawks, Doves concede, and all of the Hawks fight, with the winner getting the reward V , while the others pay a cost C . Moreover, all individuals receive R as a background reward. The payoff expressions for the Hawk-Dove game are in Table II, second column.

For the Fixed Fitness game, individuals do not interact with each other but receive a constant payoff depending only upon their type, independently of the group composition. The payoff expressions for the Fixed Fitness game are in Table II, third column.

	Public Goods	Hawk-Dove	Fixed Fitness
$R_A(a, b) =$	$\begin{cases} R - C, & a = 1, b = 0. \\ R - C + \frac{a - 1}{a + b - 1}V, & \text{otherwise.} \end{cases}$	$R + \frac{V - (a - 1)C}{a}$	$R + V$
$R_B(a, b) =$	$R + \frac{a}{a + b - 1}V$	$\begin{cases} R, & \text{if } a > 0. \\ R + \frac{V}{b}, & \text{if } a = 0. \end{cases}$	R
Types of individuals	$A = \text{Cooperator}, B = \text{Defector}.$	$A = \text{Hawk}, B = \text{Dove}.$	

TABLE II. Payoffs $R_A(a, b)$ and $R_B(a, b)$ for individuals A and B , respectively, considering a group with a individuals of type A , and b individuals of type b , for the three games.

As discussed previously, the territorial raider model used is based upon an underlying network structure. In [23], Erdős-Renyi, small-world, scale-free, and Barábasi-Albert networks have been analyzed, but the Barábasi-Albert networks represented the whole variation of network formation (verified by the topological parameters) and results, in the sense that all fixation probabilities, temperatures and group sizes that occurred for the other types of network also occurred for Barábasi-Albert networks. In particular, the most interesting and unusual results came from these networks. Barabási and Albert [31] proposed a rule derived from scale-free networks: *preferential attachment*, where the probability π_{ba} that a new node will connect to a node i is proportional to k_i , the degree of i , that is, $\pi_{ba}(k_i) = k_i / \sum_{j=1}^n k_j$, which is a special case of the network selection methodology that we use.

The next section contains the methodology used for the simulations.

III. METHODOLOGY

The Barábasi-Albert networks used here are representations of territorial raider models. The networks are undirected and connected with a fixed size of $N = 20$ nodes. The parameters that create the networks will be varied accordingly in order to provide the broadest topological range. The library iGraph [32] generates the networks and returns the topological

properties.

For creating a network using the Barabási-Albert model, we need two input parameters: m_{ba} is the number of connections generated per node, and γ_{ba} the exponent of the probability of a node i with degree k_i being chosen to get an edge $\pi_{ba}(k_i) = (k_i^{\gamma_{ba}} / \sum_{j=1}^n k_j^{\gamma_{ba}})$ according to non-linear preferential attachment. For $\gamma_{ba} = 1$ we have the linear and traditional form of the Barabási-Albert model [31]. Therefore, these parameters are chosen uniformly at random in the interval $2 \leq m_{ba} \leq 18$ (integer values), and $1 \leq \gamma_{ba} \leq 5$ (real values).

Using the three games with two situations per game (the invasion of a randomly placed individual of each type placed into a population of the other type), with h randomly chosen in the interval $0.01 \leq h \leq 100$ uniformly distributed on the logarithmic scale, we generate 2000 cases per game and situation for the four dynamics, resulting in 48000 cases.

One case is delineated as follows:

- a network is formed using iGraph with random values for input parameters;
- The mutant is randomly put on one of the nodes;
- Individuals move (or not) from their home place according to the model. Every group with one or more individuals plays the multi-player game;
- Individuals move (or not) from its home place according to the model. Run the replacement process for replacing one individual at a randomly formed group; if it is alone, there is no replacement;
- The simulation ends when either all type A or B individuals have been eliminated from the population.
- This process is run 50000 times to minimise the statistical variability of the results (95% confidence intervals of estimates always have width (sometimes much) less than 0.01).

In order to maintain consistency with the previous works [21, 23], we use the typical initial condition called uniform initialization [33], where all nodes have the same probability to receive the initial mutant. Another alternative is temperature initialization, as developed in [34].

IV. RESULTS

The objective of the analysis is to find good predictors for the fixation probability. A complete set of analysis for BD-B dynamic has been done in [23], where a large number of networks were considered to test if the parameters clustering coefficient, shortest path length, density and diameter of the networks could contribute for predicting the fixation probability. Here, we have done the same for the other three dynamics for Barabási-Albert network, and the results were similar, with the average group size from the individual’s perspective and the temperature *together* being the best predictors when using the regression method for the four dynamics.

Note: from here, we shall use the original letters of the game’s strategies; for the Public Goods game, we use C for cooperators and D for defectors, and for the Hawk-Dove game, we use H for Hawks and D for Doves.

The game parameters considered here are the same as those considered in [23]. We use these because these give more meaningful results (there are many parameter combinations where one of the strategies is totally dominant for all networks for example, or there is no appreciable differences across networks). Thus, the parameters are:

- Public Goods: $R = 2$, $C = 1$, and $V = 2$;
- Hawk-Dove: $R = 10$, $C = 1$, and $V = 2$;
- Fixed Fitness: $R = 50$, and $V = 2$;

with networks of fixed size $N = 20$.

In [23], the fixation probability was studied as a function of temperature, average group size (two alternatives, as explained below), clustering coefficient, density, diameter, and shortest path length. There are two distinct ways of measuring the average group size, from the individual’s perspective and from the observer’s perspective. For example, consider a population of six individuals with three groups of one, one and four individuals. The average group size from the observer’s perspective is $(1 + 1 + 4)/3 = 2$, but the average from the individual’s perspective is $(2 \times 1 + 4 \times 4)/6 = 3$.

The average group size from the individual’s perspective was also used in [21]. The conclusions were that temperature and average group size worked as initial predictors for

fixation probability; and the clustering coefficient, to a limited extent, helped to evaluate some properties of the model, mainly related to networks with star characteristics, like the Barábasi-Albert networks (in the cases where $\gamma_{ba} \gtrsim 2$). We note that Barábasi-Albert networks with the input parameters considered were enough to represent the full range of the results and this is the reason we only consider this type of network here.

The supplementary file contains figures of the fixation probability as a function of temperature, average group size, clustering coefficient, density, diameter, and shortest path length for the three games and four dynamics. Each of these twelve combinations has 2000 points for each situation (C/H/A invading D/D/B and D/D/B invading C/H/A). Note that by using the clustering coefficient, density, diameter, and shortest path length independently, it is not possible to make good predictions for the fixation probability.

Moreover, Figures 3 and 4 of the supplementary file compare the results for network sizes $N = 20$ and $N = 50$ for the first two dynamics (BD-B and BD-D). For the network size $N = 50$ the parameters to generate the networks are chosen uniformly at random in the interval $4 \leq m_{ba} \leq 48$ (integer values), and $1 \leq \gamma_{ba} \leq 5$ (real values), with 1000 cases per game and situation. These results show that there is a similar pattern for bigger networks.

We developed a nonlinear regression quadratic model for predicting the fixation probability with multiple predictor variables. We tried an extensive number of models with combinations of temperature, average group size (from the individual's and the observer's perspective, as explained below), clustering coefficient, density, diameter, and shortest path length. The better results (highest values of R^2 and lowest values of Root-mean-square deviation - RMSE) were achieved for two variables: the average temperature \bar{T} and the average group size from the individual's perspective $\bar{\mathcal{G}}$. Involving more parameters or more complex combinations of them provided no real improvement in the results. Therefore, in this regression model, the observed data are modelled as a quadratic function of \bar{T} and $\bar{\mathcal{G}}$:

$$Z \sim f(X, Y, \beta) \tag{7}$$

where X and Y are vectors of independent variables \bar{T} and $\bar{\mathcal{G}}$, respectively, with the corresponding dependent observed values Z , and f is a nonlinear function regarding the vector of parameters β . The function f is defined according to the equation

$$f(X, Y, \beta) = \beta_0 + \beta_1 X + \beta_2 Y + \beta_3 XY + \beta_4 X^2 + \beta_5 Y^2 + \epsilon \tag{8}$$

The best-fitting parameters β are estimated iteratively by the least squares method, which proceeds by minimizing the sum of squares S of the residuals r_i of a set of m data points, as defined respectively in the following equations:

$$r_i = z_i - f(X, Y, \beta), \text{ for } i = 1, \dots, m \quad (9)$$

and,

$$S = \sum_{i=1}^m r_i^2. \quad (10)$$

The results from this regression method are in Table III with the respective R^2 , RMSE, and β 's values.

In general, the regression method fits the data well, based on the R^2 and RMSE values for the dynamics, games and situations (the highest values of R^2 and lowest values of RMSE occur in Hawk-Dove game for BD-B and DB-D dynamics), with two exceptional cases.

Firstly, the lowest values of R^2 which are near 0, associated with the lowest values of the RMSE, occur for the Fixed Fitness game, situations 1 and 2, in each case for the BD-B and DB-D dynamics, but not the other two. To understand these cases, Figures 1 and 2 contain the fixation probability as a function of the temperature and the average group size for the three games and four dynamics. Each figure has both situations (C invading D and D invading C for the Public Goods game, for instance). Note that these cases have a constant fixation probability for the whole range of temperature and average group size. This is logical as, since we have symmetric weights, the BDB/DBD dynamics both lead to the relative probability of a pair of individuals replacing each other as just the ratio of their fitnesses. This ratio is constant irrespective of the composition of the population, and we thus have a scenario which leads to the classic Moran fixation probability ([35–37] where the probability of a mutant individual of fitness r invading a resident population all with fitness 1 is given by

$$P_M = \frac{1 - 1/r}{1 - (1/r)^N}. \quad (11)$$

For our fixed fitness game the fitnesses are $R + V = 52$ and $R = 50$ which, together with $N = 20$, yield the Moran probabilities 0.070752 and 0.033582 respectively, which match the values from our graphs (the mean values of our data for BDB are 0.070742 and 0.033566, and the values for DBD are 0.070793 and 0.033573).

Secondly, the next lowest values of R^2 occur for the Public Goods game, situation 1, again for the BD-B and DB-D dynamics only. This is simply due to the real fixation probabilities

Dynamic	Game	Situation	R^2	RMSE	β_0	β_1	β_2	β_3	β_4	β_5
BD-B	PG	1	0.175	0.000018	3.1930E-05	-8.2390E-05	-1.2300E-05	2.7410E-05	7.2820E-05	-1.0100E-06
		2	0.916	0.007782	4.1937E-01	-2.4146E-03	-1.0789E-02	7.2041E-03	-1.5685E-01	5.5554E-04
	HD	1	0.950	0.001466	5.9139E-02	6.3163E-03	-3.8888E-04	-3.4145E-03	5.1647E-02	-2.6836E-04
		2	0.963	0.000952	3.7997E-02	-1.9812E-02	7.0522E-03	2.7200E-03	-1.6318E-02	-2.6571E-04
	FF	1	0.001	0.001126	7.0407E-02	1.1330E-03	5.5320E-05	4.0064E-04	-2.1794E-03	-3.5540E-05
		2	0.001	0.000806	3.3392E-02	-4.0530E-05	6.5300E-05	-1.3849E-04	6.5512E-04	1.0300E-06
BD-D	PG	1	0.909	0.002787	7.8740E-02	-3.0150E-02	-3.9579E-02	5.1814E-02	-8.3888E-02	-5.1119E-04
		2	0.971	0.008075	-1.8423E-01	-9.3183E-02	2.6326E-01	-2.3533E-01	3.7564E-01	-3.3652E-03
	HD	1	0.929	0.001223	4.6754E-02	-2.6275E-02	7.2823E-03	5.6757E-03	2.3631E-02	-1.2964E-03
		2	0.864	0.001076	5.0643E-02	1.0598E-02	-3.0465E-03	3.6042E-03	-2.8580E-02	4.3534E-04
	FF	1	0.904	0.001086	3.9850E-02	-5.8898E-03	1.1600E-02	-6.5217E-03	1.2392E-02	-3.8638E-04
		2	0.889	0.000973	5.7569E-02	6.0558E-03	-9.3708E-03	6.0426E-03	-1.4359E-02	2.6824E-04
DB-B	PG	1	0.922	0.002695	7.7611E-02	-2.4606E-02	-3.8406E-02	5.3031E-02	-9.8119E-02	-6.6958E-04
		2	0.973	0.006954	-1.2601E-01	-7.9224E-02	2.0042E-01	-1.7265E-01	3.1023E-01	-2.9501E-03
	HD	1	0.932	0.001190	4.7936E-02	-2.5928E-02	5.8718E-03	7.7311E-03	2.1017E-02	-1.3303E-03
		2	0.846	0.001070	5.1114E-02	1.1001E-02	-3.5012E-03	4.6395E-03	-3.0926E-02	3.7511E-04
	FF	1	0.903	0.001106	4.1766E-02	-7.4888E-03	9.9529E-03	-4.4989E-03	1.2424E-02	-4.1602E-04
		2	0.893	0.000985	5.7554E-02	6.4771E-03	-9.0891E-03	5.8847E-03	-1.5839E-02	2.6220E-04
DB-D	PG	1	0.231	0.000009	2.1440E-05	9.6000E-07	-2.1330E-05	4.9070E-05	-8.0620E-05	-1.6000E-06
		2	0.948	0.007114	4.1777E-01	1.7531E-01	1.6831E-02	-7.6653E-02	-1.5447E-01	4.1649E-03
	HD	1	0.949	0.001456	5.8722E-02	1.9640E-02	-1.0327E-03	-4.8471E-03	4.1041E-02	-9.1850E-05
		2	0.966	0.000954	3.7686E-02	-2.8853E-02	8.1106E-03	2.2921E-03	-6.1045E-03	-3.3466E-04
	FF	1	0.002	0.001157	7.0638E-02	1.7643E-03	-3.0291E-04	8.8440E-04	-3.3426E-03	-3.6910E-05
		2	0.000	0.000805	3.3533E-02	1.3909E-03	-2.9462E-04	5.8685E-04	-2.3106E-03	-1.6400E-05

TABLE III. Regression data.

being very close to zero for these particular cases, and so any distinction between the values for different graphs is drowned out by the noise.

An obvious feature of the data is that for both varying temperature in Figure 1 and varying group size in Figure 2, the plots for BD-B and DB-D are similar, as are the plots of BD-D and DB-B, although the two pairs are very different from each other. This is what we would expect from evolutionary graph theory, where in the weak selection limit these two pairs are indeed identical [15] and we test the hypothesis of equality between the two dynamics within each pair, as well as discussing this more generally, below. It is also interesting to see that for the four dynamics, the increase in temperature has the same effect for the Hawk-Dove game, but the pairs have opposite tendencies for the Public Goods

game. In general, looking at the relative sizes of the coefficients that are related solely to the temperature (β_1 and β_4) and those that are solely related to the group size (β_2 and β_5) for the Hawk-Dove game it is the temperature that is the most important for all of the dynamics. For the Public Goods game the temperature seems more important for the BDB/DBD dynamics, but the group size is more important for the BDD/DBB. For the fixed fitness game, only the constant term (β_0) is relevant for BDB/DBD (note the flat lines on Figures 1 and 2), and for the pair BDD/DBB, the quadratic term related to average group size (β_5) is the less important on the regression.

For our fitted lines, the value of β_3 indicates the interaction term between the group size and the temperature. This is much larger for the Public Goods game than for the Hawk-Dove game (except for the two cases where fixation probabilities are almost zero), and this is consistent with the greater importance of group size for the Public Goods game mentioned above. Finally, the values of R^2 for the Hawk Dove game are larger for the BDB/DBD dynamics than for the BDD/DBB whereas the reverse is true for the Public Goods game. Whereas the fit for BDD/DBB is equivalently good for the two games, the Hawk-Dove game has a strong fit for BDB/DBD, with the fit for the Public Goods game clearly worse. We thus see that there are some specific interaction factors involving the type of game and the type of dynamics which can have significant effects on our results which warrants further exploration.

As we are interested in the distributional properties of data from the two pairs of dynamics, we carried out a non-parametric two-sample Kolmogorov-Smirnov test (KS). The two-sided KS test evaluates the null hypothesis (H_0) that the groups comes from the same continuous distributions against the alternative hypothesis (H_1) that data are from different distributions [38]. It is defined in terms of the cumulative distribution function, using the maximum absolute difference between the two groups x_1 and x_2 , as defined in equation 12. The test rejects the null hypothesis if its statistic D^* , defined as

$$D^* = \max_x (|\hat{F}_1(x) - \hat{F}_2(x)|) \quad (12)$$

is greater than the critical value $D_{n,1-\alpha}$ from a table of percentage points of Kolmogorov statistics [39].

Results for the two pairs of dynamics BD-B, DB-D and BD-D, DB-B as illustrated in Tables IV and IV, indicate that there is no evidence to reject the null hypothesis with a

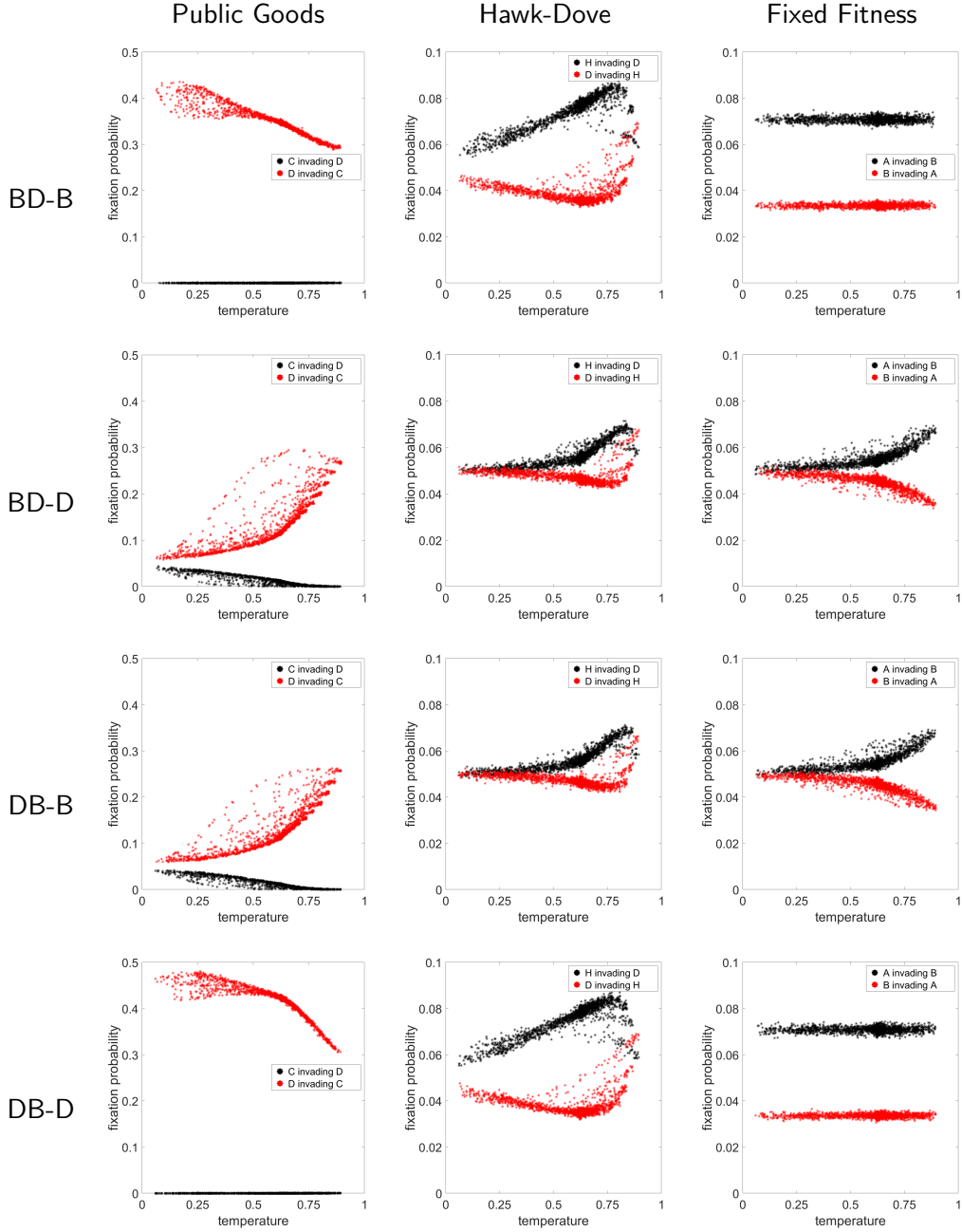


FIG. 1. Fixation probability in function of the temperature for the four dynamics and three games. For the Public Goods game, the black dots represent case of C invading D, the red dots represent the case of D invading C. For the Hawk-Dove game, the black dots represent case of H invading D, the red dots represent the case of D invading H. Finally, for the Fixed Fitness game, the black dots represent case of A invading B, and the red dots represent the case of B invading A. The parameter values are $R = 2$ for Public Goods, $R = 10$ for Hawk-Dove, $R = 50$ for Fixed Fitness, and $C = 1$, $V = 2$ for all the games, and the network size $N = 20$.

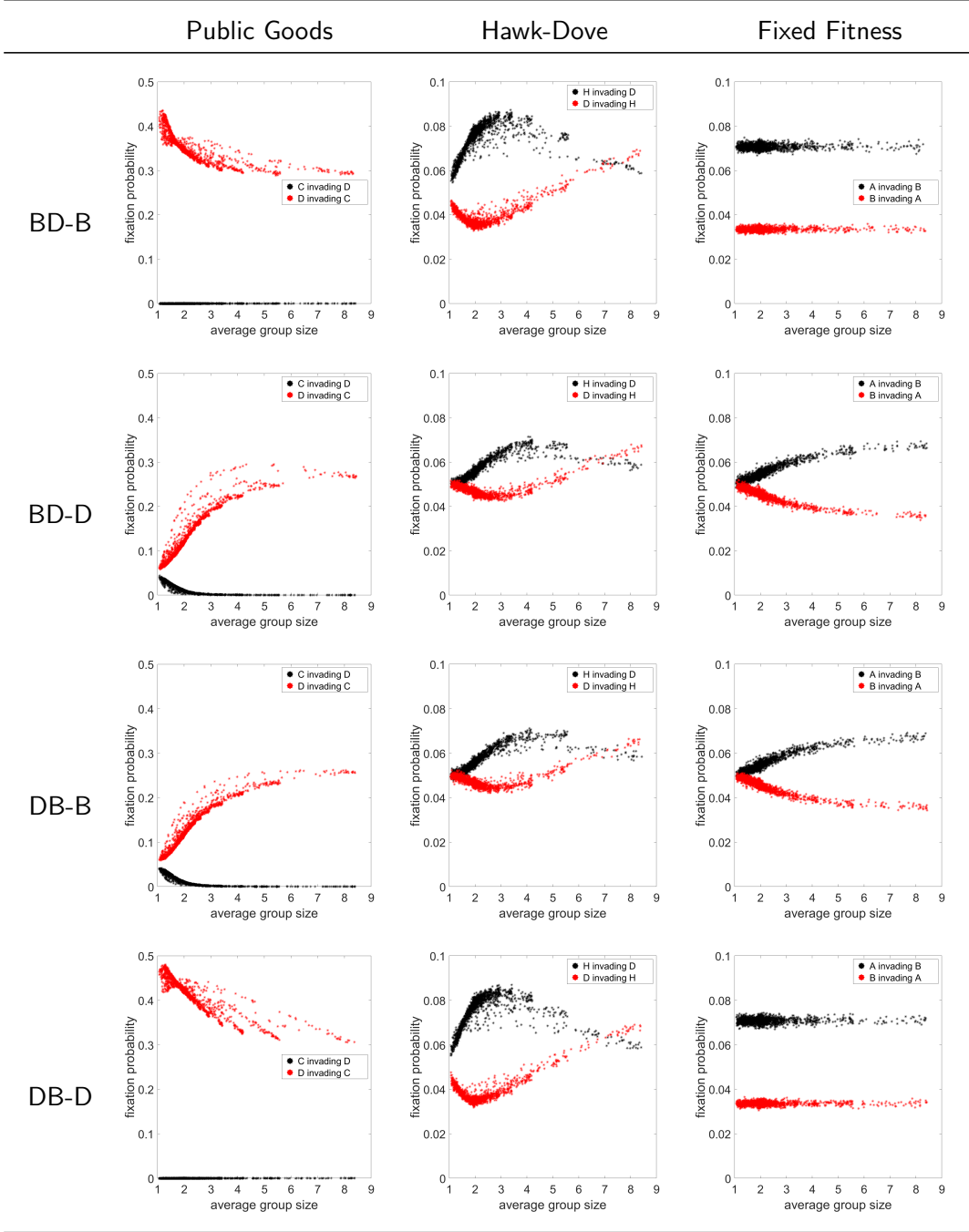


FIG. 2. Fixation probability in function of the average group size for the four dynamics and three games. For the Public Goods game, the black dots represent case of C invading D, the red dots represent the case of D invading C. For the Hawk-Dove game, the black dots represent case of H invading D, the red dots represent the case of D invading H. Finally, for the Fixed Fitness game, the black dots represent case of A invading B, and the red dots represent the case of B invading A. The parameter values are $R = 2$ for Public Goods, $R = 10$ for Hawk-Dove, $R = 50$ for Fixed Fitness, and $C = 1$, $V = 2$ for all the games, and the network size $N = 20$

significance level $1 - \alpha = 0.95$ and $n = 36$, allowing to accept the hypothesis of equivalence.

pairs of dynamics	D^*	$D_{36,0.95}$	Decision
BD-B and DB-D	0.1111	0.2211	accept H_0
BD-D and DB-B	0.0556	0.2211	accept H_0

TABLE IV. Results of the Kolmogorov-Smirnov test.

We are also interested in considering the probability of making a Type II error, i.e. of accepting a false null hypothesis, and in particular are interested in what levels of difference would lead us to reject the null hypothesis. Whereas *post-hoc* power estimates are logically invalid and practically misleading [40–42], we used a nonparametric equivalence test with respect to the confidence interval for the median of the difference between groups of dynamics BD-B, DB-D and BD-D, DB-B. The test consists of calculating the 90% confidence interval (CI) for the median of the difference between the groups and rejecting the hypothesis of non-equivalence if the CI is entirely contained in the equivalence interval $[-\Delta, \Delta]$, in which Δ is an user defined practical equivalence value that set how close is close enough to be considered equivalent [43].

The lower and upper limits for the CI (b_l and b_u , respectively), and a summary of the difference data between groups are presented in Table IV. Equivalence tests allow to identify practically insignificant effects, whenever effects are statistically smaller than an equivalence value. Therefore, if we choose $\Delta \geq 0.0006097$, which is around 2% of the smallest values for fixation probability (when it is non-zero or does not tend to zero) for all the cases analyzed, it is possible to accept the hypothesis of equivalence.

pairs of dynamics	b_l	b_u	Min.	Median	Max.
BD-B and DB-D	-0.0004898	0.0002347	-0.1777	0.0000052	0.0838570
BD-D and DB-B	-0.0006097	0.0005219	-0.0626	-0.0000127	0.0654100

TABLE V. Summary of data for the nonparametric equivalence test.

Therefore, we conclude that the apparent similarity between dynamics BD-D and DB-B, as well as the similarity between dynamics BD-B and DB-D, evident from Figures 1 and 2, is a real feature of the model, and these pairs can be treated essentially as identical. As previously stated, for evolutionary graph theory this is true for weak selection, but here it is true in general.

Note that the word “essentially” above is important, as they are not truly identical. Consider the BDB/DBD dynamics. Since weights are symmetric, the probability of one of a pair of connected individuals replacing the other is just the ratio of the two fitnesses in each case. Thus this is similar to the fixed fitness case, as we previously discussed. However, these fitnesses are not fixed and as individuals in the population change the fitnesses change, and thus it is important in which pair the replacement happens, and that does depend upon the dynamics. The effect is not generally strong, and so results are very similar, as we see, but not identical.

V. DISCUSSION

In this study, we expanded the methodology presented in [23], also described in [21], finding good predictors for the fixation probability in many heterogeneous population structures. The work presented in [21] considered small structured populations of 3-5 individuals, and the work presented in [23] considered populations of twenty individuals structured according to four complex network models (Erdős-Renyi, small-world, scale-free, and Barábasi-Albert), with both works using the BD-B dynamic. Here, we also considered BD-D, DB-B, and DB-D, working only with Barábasi-Albert networks, since it represented the whole variation of topological parameters, as discussed in [23].

Moreover, we carried out a statistical analysis of the data to find good predictors for the fixation probability. A number of variables were taken into consideration, with the temperature and the average group size from the individual’s perspective being the two most relevant. We have presented the regression results based on a nonlinear quadratic model, and due to similarities between the pairs of dynamics BD-B/DB-D and BD-D/DB-B a statistical analysis of the regression coefficients showed consistency with the hypothesis that the dynamics are derived from data sets with equal distributions. Thus we can treat the dynamics within these pairs as if they are the same as each other.

We found a number of interesting features. Firstly for the fixed fitness case, the fixation probability only depended upon the game payoffs for the BDB/DBD dynamics, and thus presented a completely flat line in Figures 1 and 2. This was explained by the fact that our process involves symmetric weights, and so for fixed fitnesses we just have probabilities that come from the classic Moran probability [35, 36]. We note in contrast that this is not

true for the BDD/DBB dynamics, since Moran’s formula does not hold for these dynamics. With the exception of two cases where fixation probabilities were almost zero, we found good predictors in all other cases. In particular we saw that temperature was more important than group size for the Hawk-Dove game, but that group size was also important for the Public Goods game, with the interaction between the two also important in this latter case.

More generally, we have seen that we can obtain good predictors for the fixation probability within Barábasi-Albert graphs, the most problematic class that we have investigated, typically explaining over 90% of the variation in the fixation probabilities. Thus we can potentially predict fixation probabilities from considering a single movement on the graph (which is required to calculate both the temperature and the mean group size for an arbitrary underlying graph) and do not have to wait for the completion of extensive simulations. This would be particularly important when considering very large populations that could require a huge number of iterations before fixation occurs, as the fixation time can increase very quickly with population size, in particular for games like the Hawk-Dove game where there is a mixed evolutionarily stable strategy for the infinite population case. By using the Barábasi-Albert procedure, we generated a wide range of networks with properties similar to other models. Therefore, the methodology could easily be applied to other models of population evolution that consider networks as scale free graphs and lattices [6, 15, 44, 45], random [15] and regular [45, 46].

As we have seen, there are still not completely convincing explanations about some of the observed dependencies in the data, in particular for the Public Goods game and the effect of the specific dynamics and the interaction between group size and temperature. This is a suitable subject for further investigation. We have also considered only three specific games, and there is the potential for applying the methodology for a wider class of multiplayer game, as well as for more complicated populations, for example involving distinct sub-populations, and realistic evolutionary scenarios more generally. With the extensive options provided by our methodology, it could also be applied to more specific real life situations involving the interplay of territoriality and social interaction, for example in chimpanzees [47] or canids [8].

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