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A study of the dynamics of multi-player games on small networks using territorial interactions

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Abstract Recently, the study of structured populations using models of evolutionary processes on graphs has begun to incorporate a more general type of interaction between individuals, allowing multi-player games to be played among the population. In this paper, we develop a birth-death dynamics for use in such models and consider the evolution of populations for special cases of very small graphs where we can easily identify all of the population states and carry out exact analyses. To do so, we study two multi-player games, a Hawk–Dove game and a public goods game. Our focus is on finding the fixation probability of an individual from one type, cooperator or defector in the case of the public goods game, within a population of the other type. We compare this value for both games on several graphs under different parameter values and assumptions, and identify some interesting general features of our model. In particular there is a very close relationship between the fixation probability and the mean temperature, with high temperatures helping fitter individuals and punishing unfit ones and so enhancing selection, whereas low temperatures give a levelling effect which suppresses selection.

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1 Introduction

1.1 Modelling structured populations with multi-player interactions

The modelling of the evolution of a population of individuals where each is located on the vertex of a graph, interacting with their neighbours and potentially replacing them with a direct copy of themselves, is commonly termed evolutionary graph theory (although it is the population and not the graph which evolves), and studies how the structure of this population, i.e. its topology, can affect its evolution (Lieberman et al. 2005; Antal and Scheuring 2006; Nowak 2006; Broom and Rychtář 2008; Voorhees and Murray 2013; Maciejewski et al. 2014). As opposed to traditional evolutionary game theory that mainly considers infinite well-mixed populations, the use of graphs to model population structure on standard games such as the Prisoner's Dilemma and the Hawk–Dove game enables us to work on finite inhomogeneous populations (Ohtsuki et al. 2006; Santos and Pacheco 2006; Hadjichrysanthou et al. 2011). This follows earlier work considering finite and/or spatial populations; for example Nowak and May (1992, 1993) considered the spatial evolution of cooperative behaviour, Schaffer (1988) considered a Hawk–Dove game in a finite population, and Killingback and Doebeli (1996) considered a Hawk–Dove game on a lattice.

This approach, however, is still limited in the sense that it is restricted to pairwise interactions between individuals. Animals of many species live alone or in distinct groups on a certain territory. Although animals generally forage for food within their territory, it can happen that the territory size varies considerably over time. In some cases, it can expand and overlap with other territories, when food becomes rarer, or for the purpose of mating for example. Thus the same place is used by two or more individuals that will interact and sometimes compete when some major items of food are at stake. This kind of situation illustrates the need for models of evolution on structured population to incorporate a more general type of interaction, not only based on pairwise interactions, but also allowing multi-player games to be played among the population.

In general there are many situations where groups of more than two individuals form to cooperate, or to compete. Groups form to fight over food, e.g. in African wild dogs (Ginsberg and Macdonald 1990) or roadrunners (Kelley et al. 2011). Ant colonies are large cooperative enterprises, and similarly primate groups are cooperative structures, containing conflicts related to dominance and resource division. Human society is of course full of examples. Thus it is natural to generalise evolutionary games to more than two individuals. Multi-player games were introduced into biology in Palm (1984) and the theory developed by Broom et al. (1997), see also Bukowski and Miekisz (2004). Such general multi-player games have been studied recently, see for example Gokhale and Traulsen (2010, 2014) and Broom and Rychtář (2013), Chapter 9. A multi-player Hawk–Dove game was considered in Broom and Rychtář (2012), and multi-player public goods games were considered in a number of papers: Hauert et al. (2002), Milinski et al. (2006), Santos et al. (2008), Kurokawa and Ihara (2009), Souza et al. (2009), Santos and Pacheco (2011), Veelen and Nowak (2012), Kurokawa and Ihara (2013).

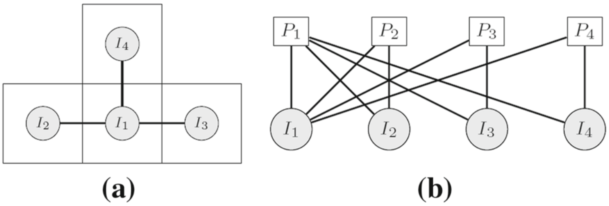
In order to model this more general type of interaction between individuals, Broom and Rychtář (2012) developed a new framework to analyse multi-player games in networks involving groups of different sizes. However, their work is mainly focused on the static analysis of such games. In this study, we are interested in introducing dynamics. We want to analyse this framework on models as simple as possible, and we hope to obtain some general insights by studying the games' dynamics.

1.2 The population and its distribution: the territorial raider model

Broom and Rychtář (2012) used the territorial raider model (see Fig. 1), to represent interactions within a population with overlapping territories. We shall briefly describe it again below. We consider a population of N individuals $I_1, \ldots, I_N$ (see also Sect. 2.2 for an interpretation of I_n in relation to the evolutionary dynamics) who can move and eventually interact in N different places $P_1, \ldots, P_N$, see Fig. 1a. The individual I_n lives in a place P_n and can also move to neighbouring places. We model the population with a graph where vertices represent individuals as well as places of interaction. We assume that individuals move independently of each other and also independently of the population's history (any past movements). The probability of an individual I_n being at place P_m will be denoted by p_{nm}.

2 General framework

Using the general framework described by Broom and Rychtář (2012), we are interested in studying the dynamics of standard games under the territorial raider model, which as we have seen can be represented as a simple graph (see Fig. 1). We wish to see if we can get some insight into the effect of the graph on the evolution of a lone mutant introduced into the population. In (almost) any finite population comprised of two classes of individuals, eventually one type will come to completely dominate the population. The *fixation probability* of a single mutant is the probability that



(a) **(b)**

Fig. 1 The territorial raider model from Broom and Rychtář (2012). **a** Individual I_n lives in place P_n but can visit neighbouring places. The territory of I_1 consists of all places P_1, P_2, P_3 and P_4, the territory of I_2 consists of P_1 and P_2, the territory of I_3 consists of P_1 and P_3, the territory of P_4 consists of P_1 and P_4. **b** An alternative visualization as multi-player interactions on a bi-partite graph where individuals and places are clearly separated. We will call the vertices $I_1, \ldots I_n$ the *I-vertices*

Table 1 The framework notation

Notation	Definition	Description
N	$\in \mathbb{Z}^+\backslash\{0\}$	Population size
A, B		Two types of haploid individuals
I_n		Individual n
S	$= \{n : I_n \text{ is of type } A\}$	State of population
$\mathcal{N}$	$= \{1, 2, \ldots, N\}$	State in which all individuals are of type A
$P_{SS'}$	$\in [0, 1]$	State transition probability
ρ_S^A	$\in [0, 1]$	Probability of fixating in $\mathcal{N}$ when initial state is S
P_m		Place m
p_{nm}	$\in [0, 1]$	Probability of I_n being at P_m
h	$\in [0, \infty)$	Home fidelity, value of h indicates likelihood of individual staying in its home vertex
d	$\in \mathbb{Z}^+\backslash\{0\}$	Number of neighbours
G	$\subset \{1, 2, \ldots, N\}$	Group of indiviuals
$\chi(m, G)$	$\in [0, 1]$	Probability of group G meeting at P_m
F_n	$\in [0, \infty)$	Fitness of individual n
R	$\in [0, \infty)$	Background payoff that individuals start with
$R_{a,b}^A$	$\in [0, \infty)$	Payoff to type A individual in group of a type A's and b type B's
V	$\in [0, \infty)$	Game reward
C	$\in (0, \infty)$	Game cost
R	$\in (0, \infty)$	Background payoff
$R_{i,G}$	$\in [0, \infty)$	Fitness of I_n in group G
v	$= V/C$	Reduced game reward
r	$= R/C$	Reduced background payoff
b_i	$\in [0, 1]$	Probability I_i selected for birth
d_{ij}	$\in [0, 1]$	Probability I_i replaces I_j given I_i selected for birth
T_j	$= \sum_{i \neq j} d_{ij}$	Temperature of I_j

eventually it will completely replace the other type. Some graphs can act as suppressors or amplifiers of evolution (see Lieberman et al. 2005); a graph is a suppressor (amplifier) of evolution if a rare mutant which has fitness higher than the resident population has a smaller (larger) fixation probability on the graph than in the corresponding well-mixed population.

Let us consider a population of individuals of type A and B set on the vertices of a graph. Each individual can move along the edges of this graph and meet one or more other individuals in this process. Each time a group is formed, individuals within this group play a game so that each individual gets a reward according to the outcome of the game for each player. At one point, a dynamic process enables the population to evolve through a birth-death process based on the individuals' fitness, and we are interested in expressing the fixation probability of one individual in this process. The notation used in this paper is summarised in Table 1.

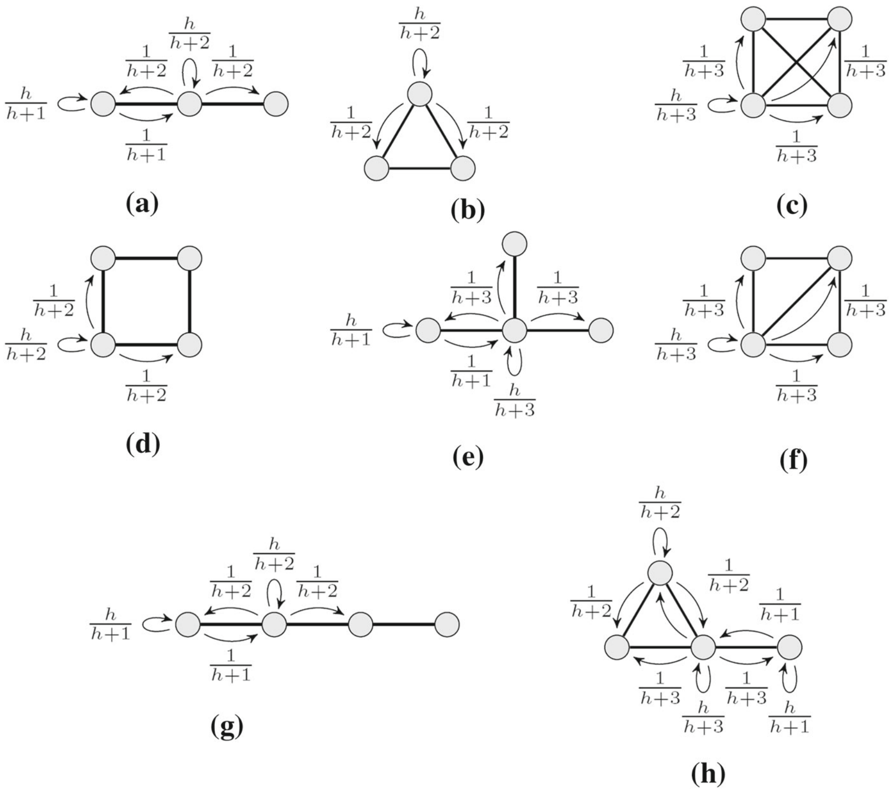


Fig. 2 The population structures and movement probabilities for small graphs on 3 and 4 vertices. An individual moves to a neighbouring vertex with probability $1/(h+d)$ and stays at home with probability $h/(h+d)$ where d is the number of neighbours. **a** The line of 3 vertices, which in this case, is also the star. **b** The triangle. **c** The square with both diagonals, the complete graph for four vertices. **d** The "circle" graph, or a square with no diagonals. **e** The star graph with 4 vertices. **f** The diamond, a square with one diagonal. **g** The line with 4 vertices. **h** The paw

2.1 Spatial structure

The graphs that we will study are representations of territorial raider models. Therefore, it is important to bear in mind that they relate to a more general representation where places and individuals are disconnected as shown in Fig. 1b. In other words, the graphs shown here stand for the kind of models in Fig. 1a. We will consider all of the three and four vertex connected undirected graphs shown in Fig. 2.

In general each individual could have a different probability of movement, but we select a natural model where all movements are governed by a single parameter. We assume that an individual with d neighbours will stay with probability $h/(h+d)$ and move to one of its neighbour with probability $1/(h+d)$. Thus h is a measure of the preference of an individual to stay on its home vertex, and we call this its *home fidelity*. In each case setting $h = 1$ gives the natural parameters of each individual visiting all allowable places (including its home vertex) with equal probability.

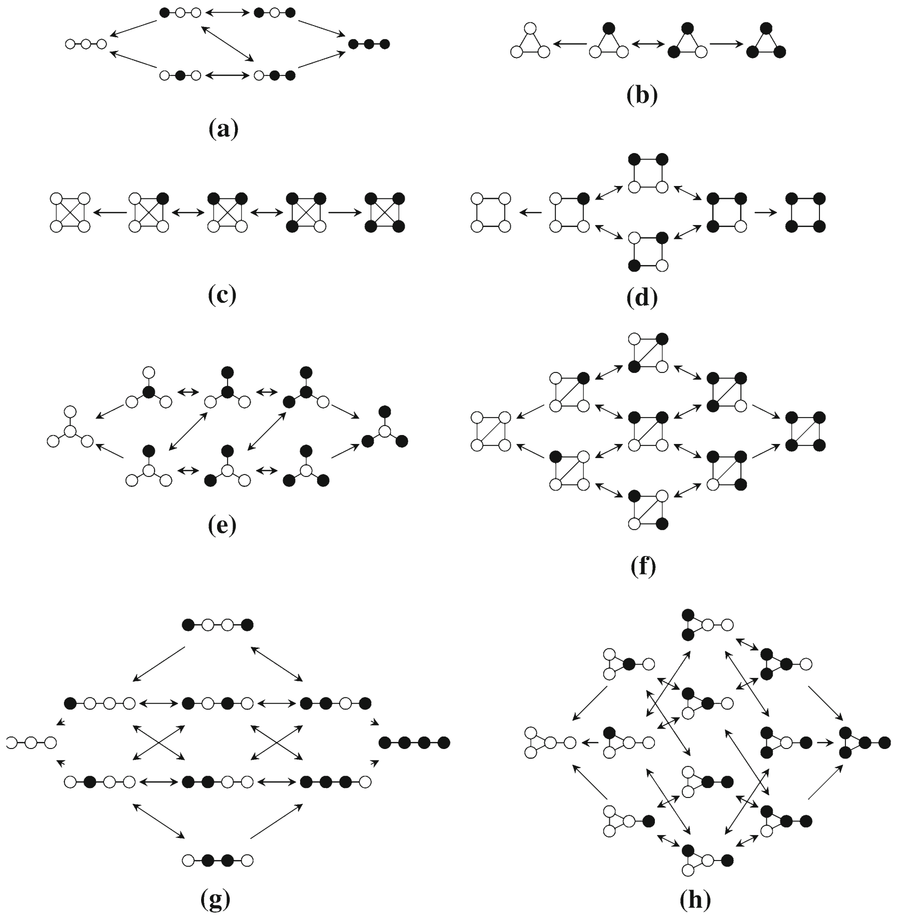


Fig. 3 The transition graphs for small graphs on 3 and 4 vertices. **a** The line of 3 vertices. **b** the triangle. **c** The square with both diagonals, the complete graph for four vertices. **d** The “circle” graph, or a square with no diagonals. **e** The star graph with 4 vertices. **f** The diamond, a square with one diagonal. **g** The line with 4 vertices. **h** The paw

2.2 Evolutionary dynamics

To calculate the fixation probability of A among B individuals at a given spatial structure, the first step is to list all the states that describe all the possible distributions of individuals of both types on the different places throughout the evolutionary process, from the insertion of one individual from type A in a population made up of B individuals until its fixation or elimination.

The evolutionary process then determines if the population can move from one state to another. Here we consider a birth-death dynamics where during each time step, one individual is selected with probability proportional to its fitness to produce a copy of itself, and another individual is selected to be replaced by the copy.

An individual I_j can be replaced by a copy of individual I_i if and only if I_i and I_j could meet in the spatial structure (which here means that P_i and P_j are at most two edges apart from each other). Thus the types of the individuals change through time, and so I_i is more properly thought of as a position in our structure which has a particular relationship to the places $P_1, \ldots, P_N$, rather than an actual individual. The relationship between the position I_i and the potential individuals that can be thought of as similar to that between a gene and its possible alleles. We shall call the positions I_n the *I-vertices* of our structure, but will often simply refer to them as "individuals", unless this distinction needs to be emphasised (see Fig. 1b). Note that while in this paper there is a 1-1 correspondence between places and I-vertices, this is not generally the case, and will not be true for most realistic models. Figure 3 shows the transition graphs (when all graph symmetries are taken into account) for the corresponding graphs from Fig. 2.

Not accounting for the symmetries, a given population structure with N individuals yields a transition graph with 2^N different states that can be indexed by subsets $S \subset \{1, 2, \ldots, N\}$. We will use the convention that state $\emptyset$ represents a population composed entirely of B individuals, and state $\mathcal{N}$ a population of A individuals only. Let $P_{SS'}$ denote the transition probability from state S to state S' in the dynamic process of our game.

Let b_i denote the probability an individual I_i is selected for reproduction and let d_{ij}, for $i \neq j$, denote the probability that I_j is replaced by a copy of I_i given I_i is selected for reproduction. For $S \neq S'$, we have

$$P_{SS'} = \begin{cases} \sum\limits_{i \notin S} b_i d_{ij}; & \text{if } S' = S \backslash \{j\} \text{ for some } j \in S \\ \sum\limits_{i \in S} b_i d_{ij}; & \text{if } S' = S \cup \{j\} \text{ for some } j \notin S \\ 0; & \text{otherwise} \end{cases} \tag{1}$$

and we set

$$P_{SS} = 1 - \sum_{S' \neq S} P_{SS'}. \tag{2}$$

We calculate b_i as being proportional to F_i, the fitness of individual I_i (see (17) in Sect. 3.4 for how we calculate fitness), i.e.

$$b_i = \frac{F_i}{\sum_k F_k}. \tag{3}$$

We calculate d_{ij} by considering all possible places P_m and all possible groups $G \subset \{1, 2, \ldots, N\}$ involving both individuals i and j; weighted by $\chi(m, G)$, the probability of the group G meeting at place P_m, and by a factor $(|G| - 1)^{-1}$ representing the fact that in a group G, an individual I_i could replace any one of $|G| - 1$ other individuals. Thus, we get

$$d_{ij} = \sum_{m=1}^{N} \sum_{\substack{G \\ i,j \in G}} \frac{\chi(m, G)}{|G| - 1}, \text{ where} \tag{4}$$

$$\chi(m, G) = \prod_{k \in G} p_{km} \prod_{k' \notin G} (1 - p_{k'm}); \tag{5}$$

here p_{km} is the probability of I_k moving to P_m, so for example for an individual at the centre of a star the probability that it goes to its ‘home” vertex is $p_{11} = h/(h+3)$ (see Fig. 2e). We note that $d_{ji} = d_{ij}$. Also, the quantity

$$T_j = \sum_{i \neq j} d_{ij} \tag{6}$$

could be regarded as the temperature (Lieberman et al. 2005) of the I-vertex I_j as it is proportional to the frequency of an individual I_j being replaced by another individual (if all individuals are equally likely to produce an offspring). We note that in our setting, the (mean) temperature depends not only on the graph but also on the parameter h, see Fig. 4.

2.3 The fixation probability of A

Finally, let ρ_S^A be the probability that A fixates from state S. We get,

$$\rho_S^A = \sum_{S' \subset \{1,2,\ldots,N\}} P_{SS'} \rho_{S'}^A \tag{7}$$

with boundary conditions

$$\rho_{\emptyset}^A = 0, \tag{8}$$

$$\rho_{\mathcal{N}}^A = 1. \tag{9}$$

The mean fixation probability of A, ρ^A, will be an appropriately weighted average of the fixation probabilities from all states including exactly one individual of type A. Following Allen and Tarnita (2014), we define

$$\rho^A = \sum_i \frac{T_i}{\sum_j T_j} \rho_{\{i\}}^A, \tag{10}$$

which is grounded in the fact that a new type of individual is more likely to appear at a place whose inhabitants are replaced more often (relative to others). We note, however, that the difference between ρ^A and the uniformly weighted average $\sum_i \frac{1}{N} \rho_{\{i\}}^A$ is negligible for all the small graphs we considered. In fact, the latter quantity is never less than ρ^A which is in agreement with results from Allen et al. (2014).

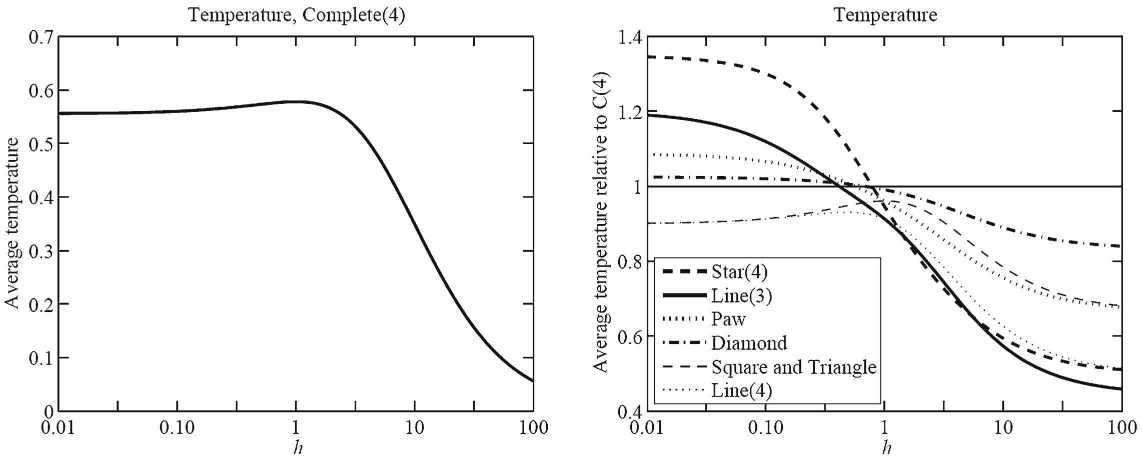


Fig. 4 The average temperatures as given by (6) for small graphs on 3 and 4 vertices. The average temperature for Line(3), Star(4) and paw monotonically decrease with h, the average temperature for other graphs peaks around $h \approx 1$

3 The multi-player games

In this section we summarize two multi-player games, the Hawk–Dove game, and the public goods game. We also introduce the payoffs for the fixed fitness case, which can be seen as a limiting case in our framework.

3.1 The Hawk–Dove game

Let us consider a population of two types of individuals, A stands for a Hawk, and B for a Dove. They both start with a background payoff R, in addition to playing a multi-player Hawk–Dove game, competing for a single reward V that is placed on each vertex of our graph. If all individuals in the group are Doves, they split the reward so that each one gets the same share. If there is at least one Hawk, all the Doves concede and the remaining Hawks fight, so that the winner gets the reward V while the others receive a cost C. Therefore, after one game within a group of a Hawks and b Doves, the average payoffs for the Hawk and the Dove are respectively

$$R^A_{a,b} = R + \frac{V - (a-1)C}{a}, \tag{11}$$

$$R^B_{a,b} = \begin{cases} R, & \text{if } a > 0, \\ R + \frac{V}{b}, & \text{if } a = 0. \end{cases} \tag{12}$$

In what follows, we will be interested in the fixation probability of a single Hawk in a population of Doves as well as in the fixation probability of a single Dove in a population of Hawks.

3.2 The public goods game

Let us consider a population of two types of individuals, A stands for a Cooperator, and B for a Defector. They both start with a background payoff R, representing fitness gained from sources other than the game, in addition to playing a multi-player public goods game. Following for example Veelen and Nowak (2012), a Cooperator (always) pays a cost C so that other individuals in the group share the benefit V. Therefore, after one game within a group of a Cooperators and b Defectors, the average payoffs for the Cooperator and the Defector are respectively

$$R^A_{a,b} = \begin{cases} R - C, & a = 1, b = 0, \\ R - C + \frac{a-1}{a+b-1}V, & \text{otherwise}, \end{cases} \tag{13}$$

$$R^B_{a,b} = R + \frac{a}{a+b-1}V. \tag{14}$$

3.3 Fixed fitness case

In this game, the individuals do not really interact with each other but rather receive a constant payoff depending on their type and irrespective of the groups size or types of the other group members. Specifically, if a group consists of a individuals of type A and b individuals of type B, we define

$$R^A_{a,b} = R + V, \tag{15}$$

$$R^B_{a,b} = R. \tag{16}$$

3.4 Fitness

For simplicity, we assume that the fitness of an individual is the average (equivalently total, since all individuals play the same number of games) payoff from the games. This corresponds to the scenario where individuals first undergo a large number of independent movements, acquiring the average (or total) payoff from the games that are played during this process, and then move one more time to form groups, but in this case, no game is played, only the reproduction (proportional to the acquired payoff) and replacement processes take place.

The fitness of an individual I_i is thus given by

$$F_i = \sum_m \sum_{\substack{G \\ i \in G}} \chi(m, G) R_{i,G}, \tag{17}$$

where $R_{i,G}$ is the fitness of individual I_i in group G. $R_{i,G}$ depends on the state S (in particular on the type of individual I_i and the types of individuals in G). Note that a group can be of size 1, and so include only the individual in question.

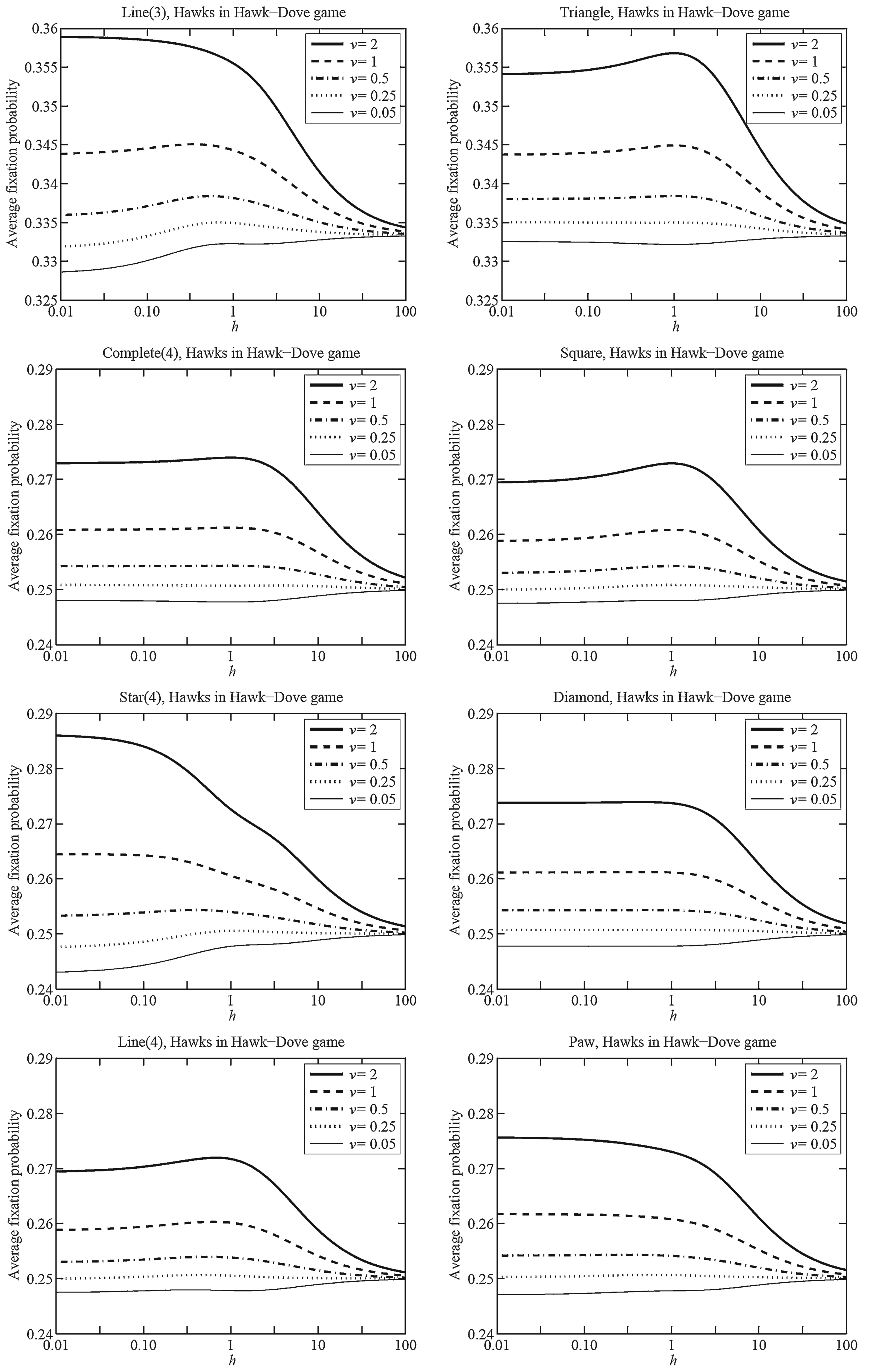
At one point (after a number of games), one individual is chosen for reproduction with probability proportional to its fitness b_i, as given in (3). Next, a copy of individual I_i replaces an individual I_j with probability d_{ij} given in (4).

Note that the background payoff R has no effect in static games, but is important for our dynamics. In general for discrete dynamics, including the one we consider here, the larger the value of R, the weaker the effect of evolution (see e.g. Broom and Rychtář 2013, Chapter 2). Here, we always assume R is sufficiently large that no fitness can ever go negative.

On the other hand, scaling all payoffs by a constant has no effect on the game outcomes, as the numerator and denominator from (3) are both divided by the same constant, and so we only need to consider the reduced parameters $v = V/C$ and $r = R/C$. In the following, we will set the reduced background fitness r equal to 10. Figure 5 shows a series of plots using this model with v varying from 0 to 2.

4 Results

For the Hawk–Dove game, the results for the fixation probabilities of Hawks on small graphs are shown in Fig. 5. The fixation probabilities of Doves on small graphs are shown in Fig. 6. For the public goods game, the results for the fixation probabilities of Cooperators on small graphs are shown in Fig. 7 and the fixation probabilities of Defectors are shown in Fig. 8. The fixation probability ρ^A, depends on the underlying



Line(3), Hawks in Hawk–Dove game

Triangle, Hawks in Hawk–Dove game

Complete(4), Hawks in Hawk–Dove game

Square, Hawks in Hawk–Dove game

Star(4), Hawks in Hawk–Dove game

Diamond, Hawks in Hawk–Dove game

Line(4), Hawks in Hawk–Dove game

Paw, Hawks in Hawk–Dove game

Fig. 5 The fixation probabilities of a single Hawk in a population of Doves for small graphs on 3 and 4 vertices

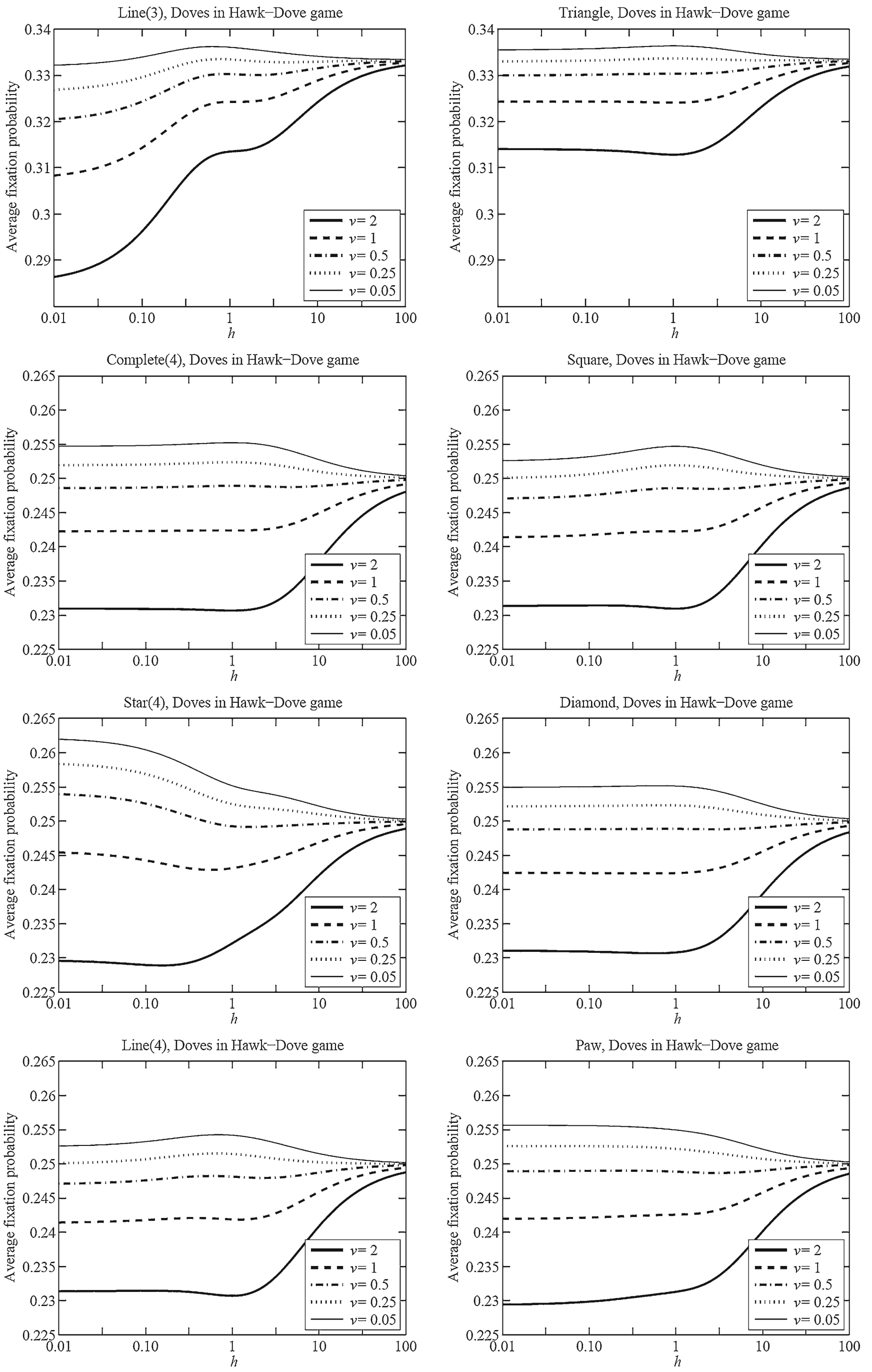


Fig. 6 The fixation probabilities of a single Dove in a population of Hawks for small graphs on 3 and 4 vertices

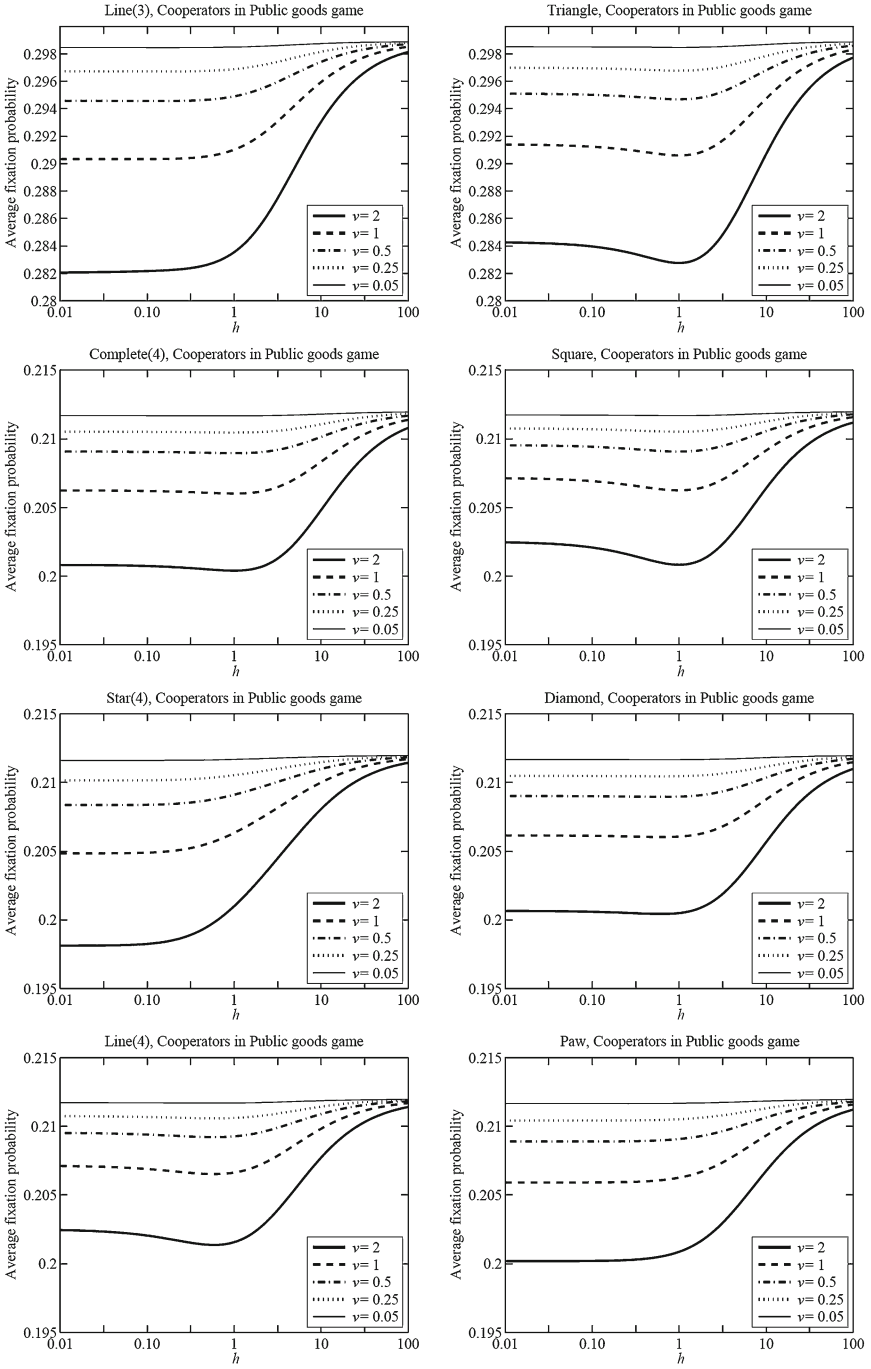


Fig. 7 The fixation probabilities of a single Cooperator in a population of Defectors for small graphs on 3 and 4 vertices

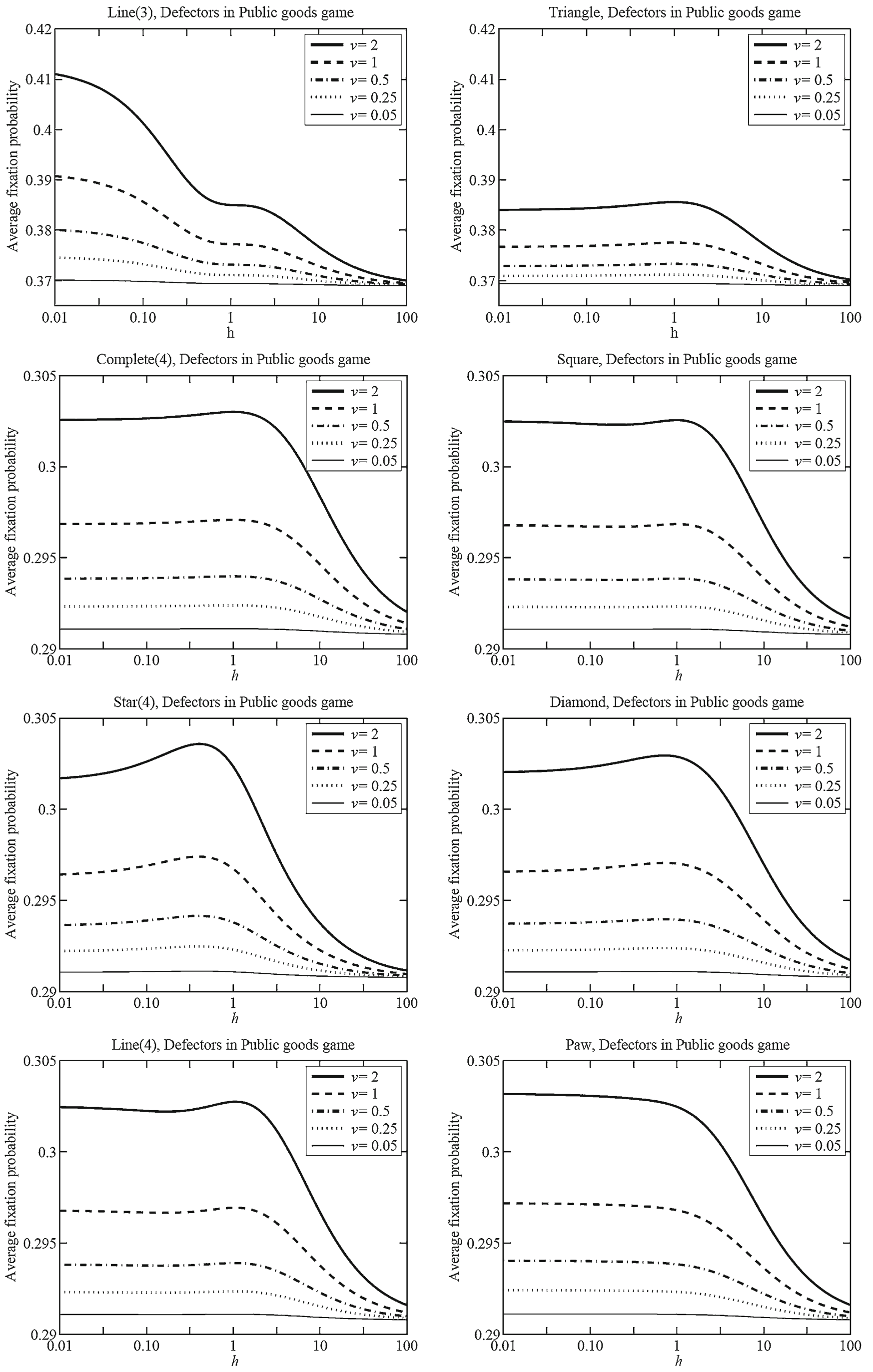


Fig. 8 The fixation probabilities of a single Defector in a population of Cooperators for small graphs on 3 and 4 vertices

graph structure, the home fidelity parameter h, the game and the parameters of the game v (the parameter r was fixed at 10), as well as the type of the invading individual/resident population.

There are a number of features common to both games, and both types of invading mutant within the Hawk–Dove game. The fixation probability in each case naturally depends upon the size of the reward, and the strength of this dependency itself depends upon h. For low values of h, which have a high mean temperature, there is a wide spread of values of fixation probability depending upon the value of v. For high h, corresponding to low mean temperature, the fixation probability depends very little upon v. This can be seen from Fig. 10, where the biggest differences between fixation probabilities are for the highest temperatures. In Hawk–Dove game, a large v is good for Hawks, and a small v is good for Doves (since Hawks still pay costs against other Hawks) and the effect of changing v is most profound when the temperature is highest. In general we see that low temperatures suppress the effect of fitness and thus suppress selection, whereas high temperatures enhance it.

4.1 Fixation probability, temperature and mean group size

In previous work, see for example Broom and Rychtář (2012), Bruni et al. (2014), the authors studied the mean size of an individual's group (the group size from the individual's perspective) defined by

$$\overline{G} = \sum_m \sum_G \frac{\chi(m, G)|G|^2}{\sum_m \sum_G \chi(m, G)|G|}. \tag{18}$$

Note the distinction between (18) and the mean group size from an observer's perspective, as here we weight the groups by the number of individuals within a group. For example, if half of groups are of size 6 and half are of size 12, from the observer's

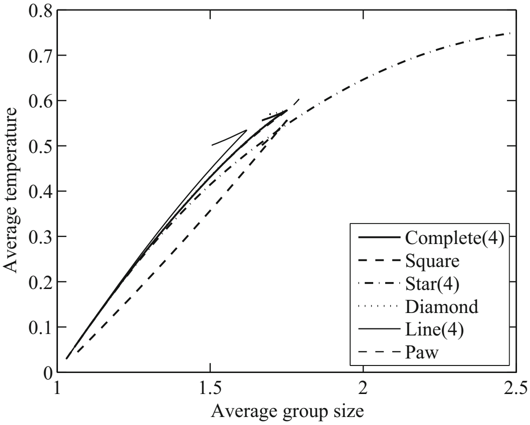


Fig. 9 The mean temperature versus the mean group size for graphs with 4 vertices (as h varies from 0 to 100). For complete graphs, the line with 4 vertices and the diamond, i.e. the graphs where the mean temperature peaks at $h \approx 1$, there is a spike in the correlation figure corresponding to the fact that the mean temperature and the mean group size increase (decrease) at different speeds as $h < 1$ (or $h > 1$). Note that Star(4) has the largest possible mean group size

perspective the mean group size is 9, but from the individual's perspective this is 10, as 2/3 of individuals are in the larger groups.

In Broom and Rychtář (2012) it was observed that the mean group size was an important factor affecting the fitness, and we thus expected that this would be the case for the fixation probability too. In fact this is so, but it turns out that the mean temperature and the mean group size are strongly correlated, see Fig. 9, and the effect of the mean group size on the fixation probability is less strong than that of the mean temperature, and hence we have focused on the mean temperature in the discussion of our results. We can see that ρ^A strongly correlates with the mean temperature for the underlying graphs as shown at Fig. 10. The correlation is negative for the public goods game and ranges from positive to negative as v decreases for Hawks in the Hawk–Dove game or increases for Doves in Hawk–Dove game.

4.2 High home fidelity h

For low temperatures, the relationship between mean temperature and fixation probability is effectively linear, although this linear dependence breaks down for high temperatures, and breaks down fast for larger or more heterogeneous graphs like the star with 7 vertices, see Fig. 10.

For example consider the case of the complete graph, where every I-vertex has the same temperature, which we denote below simply by T. In this case the fixation probability is given by the standard formula (see e.g Karlin and Taylor 1975; Traulsen and Hauert 2009)

$$\rho^A = \frac{1}{1 + \sum_{j=1}^{N-1} \prod_{k=1}^{j} \gamma_k}, \tag{19}$$

where γ_k is the ratio of the probability of a decrease in the number of type A individuals and the probability of an increase in that number (given there are currently k type A individuals). Since $d_{ij} = d_{ji}$, in this case $\gamma_k = b_{A,k}/b_{B,k} = F_{A,k}/F_{B,k}$, where the latter expressions are the ratios of the birth probabilities of types B and A and the fitnesses of types B and A (that depends on k but does not depend on position).

For both games this is the ratio of two terms that are approximately linear in the temperature, when this temperature is low, as we show below. Any individual is only likely to be with at most one other individual, and a payoff above the baseline will only occur if this is a cooperator (each with probability roughly $1/h$). The temperature at each I-vertex is approximately $(N-1)/h$. Recalling that the (reduced) background fitness and reward values are denoted by r and v, respectively, if type A is a Cooperator in the public goods game, we obtain

$$F_{A,k} \approx r - 1 + \frac{(k-1)v}{h} \approx r - 1 + \frac{k-1}{N-1} vT, \tag{20}$$

$$F_{B,k} \approx r + \frac{kv}{h} \approx r + \frac{k}{N-1} vT. \tag{21}$$

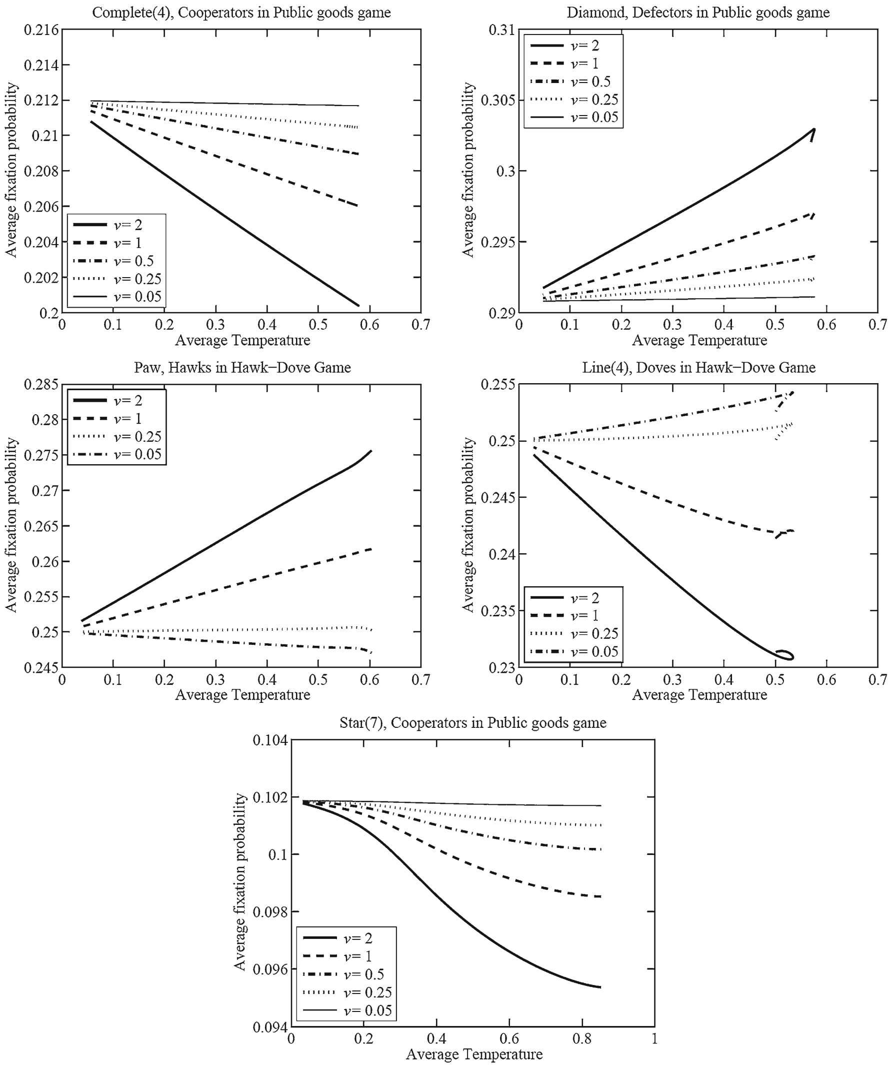


Fig. 10 The fixation probability as a function of the mean temperature for various graphs. For all small graphs, the correlations look similar and depend primarily on the game played

For sufficiently small temperatures, it is thus clear that γ_k is approximately linear in the mean temperature, and so consequently we can see that the fixation probability will also be approximately linear in the mean temperature, although this linearity breaks down as soon as the temperature becomes sufficiently large.

For the fixed fitness case, we can actually see the situation from the point of view of classical evolutionary graph theory (Lieberman et al. 2005). No matter what our underlying population structure, we can construct an evolutionary graph W with the vertices given by the set of I-vertices $\{I_i; i = 1, \dots N\}$ and the edges between I_i and I_j weighted by $w_{ij} = d_{ij}$ corresponding to the fact that I_j is being replaced by I_i with

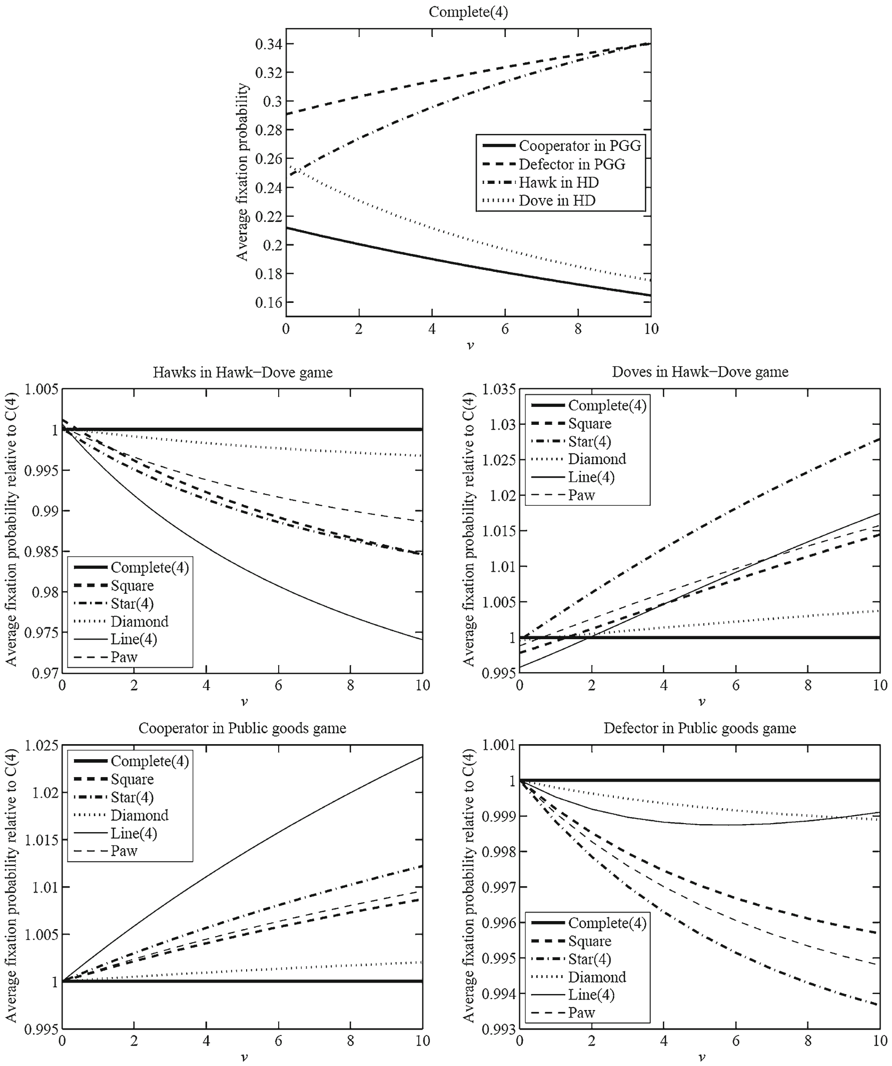


Fig. 11 Dependence of the fixation probability on v for $h = 1$

probability d_{ij}. Since $d_{ij} = d_{ji}$, the resulting evolutionary graph W is a circulation (Lieberman et al. 2005, Appendix). Consequently, type A, having a relative fitness $(r + v)/r$ when compared to type B, will fixate with the Moran probability (Moran 1958)

$$\rho^A = P_{Moran}\left(\frac{r+v}{r}\right) = \frac{1 - \frac{r}{r+v}}{1 - \left(\frac{r}{r+v}\right)^N}. \tag{22}$$

The above results hold for any graph and the fixed fitness case; and it holds approximately for any graph and any game where the payoffs of different types of individuals are nearly constant. Within our framework, this happens if $h \to \infty$ because then the individuals rarely move and thus rarely interact. For the Public Goods game, it also happens if $v \to 0$. In this case, Cooperators receive payoff $r - 1$ while Defectors receive payoffs r, resulting in

$$\rho^A = P_{Moran}\left(\frac{r-1}{r}\right) = \frac{1 - \frac{r}{r-1}}{1 - \left(\frac{r}{r-1}\right)^N}. \tag{23}$$

For $r = 10$ and $N = 4$, we thus get $P_{Moran} \approx 0.2119$ which corresponds to our results for $h \to \infty$ or $v \to 0$ as seen in Fig. 11. For the Hawk–Dove game, as $h \to \infty$, the fitnesses of both the Hawk and the Dove tend to r as the individuals rarely meet. Thus, the fixation probability of either a Hawk or a Dove tends to $1/N$ as $h \to \infty$ as seen in Figs. 5 and 6.

Note that for the Hawk–Dove game, when $v \to 0$ but h is not too large, the fixation probability of Hawks and Doves is *not* $1/N$. This is caused by the fact that Hawks still interact and thus have a disadvantage over Doves. The disadvantage grows with growing mean group size (i.e. with growing mean temperature). Consequently, the fixation probability is not the Moran probability if $h \ll \infty$.

4.3 Effects of the graph and the game

The fixation probability also depends upon the population structure more generally over and above the mean temperature. For low h in particular the heterogenous star graph, and to a lesser extent the paw, have a wider range of fixation probabilities for differing values of v than any of the other graphs. Note, however, that the line is less variable than the homogeneous well-mixed population. This may be the effect of the temperature (note that the star has the highest mean temperature as well as the widest range of fixation probabilities), or the variance in the group size, or possibly both effects working in conjunction.

A second observation that can be made on these graphs is that the ordering of fixation probabilities for different graphs can change as the parameters vary. For example, for the Hawk–Dove game with three vertices, whatever the value of the reduced gain v, the fixation probability of the triangle and the line cross for $h \approx 0.66 \approx 10^{-0.18}$. Note that this approximately corresponds to the point where the mean temperature gets higher on the triangle than on the line. Similar observations are true for some (but not all) of the graphs (and other games considered here), see Fig. 12.

There are some features specific to the particular game in question. For the Hawk–Dove game, the highest fixation probabilities can occur for intermediate values of $\log(h) \approx 0$, both for Dove invaders and for Hawk invaders. This is particularly the case for the square and the line. This occurs when the reward value v is high for Hawk invaders, and the effect disappears for low v. The figures are noticeably different for different graphs, and we can thus say that there is a significant graph effect for the Hawk–Dove game. For the public goods game these features do not appear, and we see eight broadly similar figures. Thus for the public goods game, we can say that there is

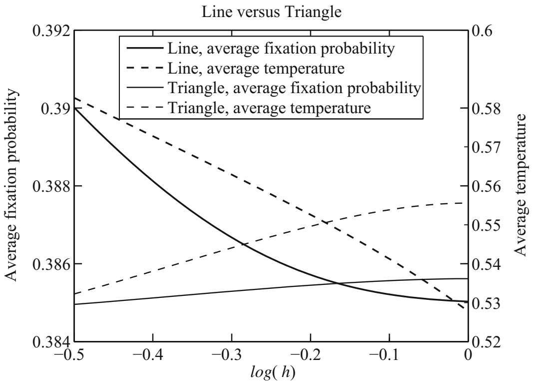


Fig. 12 Dependence of the fixation probability on the graph

not a significant graph effect, at least for the small graphs that we have considered. The main features where the graphs differ is in the broader spread on the star as mentioned above, and the dip in the fixation probability for intermediate values of v.

5 Discussion

In this study we used the modelling framework described by Broom and Rychtář (2012) to consider interactions of individuals in a non-homogeneous environment. We have developed a birth-death dynamics for this framework so that for the first time we can carry out a dynamic analysis. We note that for evolutionary graphs, there is a wide variety of dynamic models considered including a number of common dynamics used, for example the invasion process (Lieberman et al. 2005), BD-D process (Masuda 2009), voter model (Antal et al. 2006), DB-B process (Ohtsuki et al. 2006), and link dynamics (Lieberman et al. 2005), see also Shakarian et al. (2012), Allen and Nowak (2014), Débarre et al. (2014) for recent reviews. In a forthcoming paper we will develop an equivalent range of dynamics for our framework.

We analysed and compared the dynamics of some simple games on different spatial structures and tried to determine some general features. The aim was to look at the simplest possible cases in relation to this framework. There are three key components of the model. One is the dynamics, as mentioned above. A second is the population structure which has a number of key features; home fidelity, temperature, group size. Often conditioning upon one or more of these features, the structure only has a secondary effect. In particular the fixation probability was shown to be strongly correlated with the mean temperature. Within the population, individuals play games, and each game as well as being distinct, has specific features (in our case reward, cost and baseline reward) which govern how well individuals do. The value of the reward v was shown to have a potentially significant effect on the fixation probability; the size of this effect depended upon aspects of the population structure. In particular, a high mean temperature made the effect of this parameter much more critical, and the effect will be stronger when the graph is highly heterogeneous, on the star for example.

The presented framework is set up in a way that given any graph structure and any multi-player game, one can automatically generate a system of linear equations yielding fixation probabilities. The results for graphs on 3 and 4 vertices are shown in this paper. The results for graphs on more vertices can theoretically be obtained in a similar fashion. For some highly symmetrical classes of graphs (such as complete graphs, or stars), the analysis can still be performed even for large graphs, and such cases will be explored in an upcoming paper. However, the system of linear equations grows exponentially with the number of vertices (see Broom et al. 2010, for a similar scenario) and the number of possible graphs grows even faster (Harary and Palmer 1973, p. 240) and the limits of these brute force numerical methods lie at around 9 or 10 vertices.

The two games that we consider, Hawk–Dove and the public goods game, can be said to represent cooperative dilemmas, with the cooperative strategies being Hawk and Cooperate, respectively. In our model, we see that for the cases shown, the cooperative strategies generally do poorly. For the public goods game, the fixation probability of a single Cooperator (Defector) is always less (more) than $1/N$. Similarly, for the Hawk–Dove game, the fixation probability for a single Hawk is often greater than 1/N, although it can fall below this value for small v. The fixation probability of a single Dove is often less than $1/N$, although it can climb above this value for small v. One reason for this is that, in general, birth-death processes do not favour cooperation (see e.g. Ohtsuki et al. 2006). Thus it may be that cooperation is generally disfavoured in the public goods game. For the Hawk–Dove game, an important factor could be the small size of the graphs used, which mean that in turn the groups formed remain small. Large groups will tend to disfavour Hawks, as they generate costs without rewards for all but one Hawk in any group. Thus for larger graphs, we may obtain more cooperative behaviour, in the form of relatively higher fixation probabilities for Doves as opposed to Hawks.

We note that we have made some assumptions about evolution in terms of the dynamics as mentioned above. We have also assumed that in our birth-death process the new offspring cannot replace a parent within the group (e.g. if the parent kills and replaces another individual). If the offspring could replace the parent, then the denominator $|G| - 1$ in Eq. (4) would become $|G|$. This changes the results slightly; most notably, it decreases the temperatures as we would divide by larger numbers. However, the shapes of the curves and the correlations are effectively as before.

The different graphs in our model can be considered to represent different ways in which biological territories overlap. Alternatively our graphs can represent distinct social relationships within a group. While we only considered small graphs, we believe that our results will generalise. As mentioned above, mean temperature seems to be a more important factor than the specific structure. In the biological context, this represents a measure of interaction between the individuals within the population. High mean temperature corresponds to highly mobile individuals which interact potentially in larger groups than when the mean temperature is low. This gives us a natural measure of the strength of the effect of a particular game in a population. What's more, temperatures can be estimated in real populations, as long as the meetings between individuals in groups can be reliably recorded, so that the frequency of the formation of different groups can be estimated. It would be of great interest to work out the temperatures in various real population scenarios, and to ascertain how accurate our general conclusions are.

Finally we note that all of the populations in this paper correspond to graphs, as we see in Fig. 1a. This is for ease of explanation only, and in fact the framework of Broom and Rychtář (2012) allowed for a far greater variety of population types. In subsequent work, we will consider a wider class of populations, and in particular explore cases where there are more individuals than places and so large groups of individuals can form.

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