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# Approximating evolutionary dynamics on networks using a Neighbourhood Configuration model

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## HIGHLIGHTS

- ► Approximation of stochastic evolutionary game dynamics in complex networks.
- ► The model constructed provides an improved accuracy compared to previous models.
- ► The decrease of the average degree of the network might promote the Hawk strategy.
- ► Increasing the heterogeneity of the network facilitates the spread of Hawks.

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## ABSTRACT

Evolutionary dynamics have been traditionally studied on homogeneously mixed and infinitely large populations. However, real populations are finite and characterised by complex interactions among individuals. Recent studies have shown that the outcome of the evolutionary process might be significantly affected by the population structure. Although an analytic investigation of the process is possible when the contact structure of the population has a simple form, this is usually infeasible on complex structures and the use of various assumptions and approximations is necessary. In this paper, we adopt an approximation method which has been recently used for the modelling of infectious disease transmission to model evolutionary game dynamics on complex networks. Comparisons of the predictions of the model constructed with the results of computer simulations reveal the effectiveness of the method and the improved accuracy that it provides when, for example, compared to well-known pair approximation methods. This modelling framework offers a flexible way to carry out a systematic analysis of evolutionary game dynamics on graphs and to establish the link between network topology and potential system behaviours. As an example, we investigate how the Hawk and Dove strategies in a Hawk–Dove game spread in a population represented by a random regular graph, a random graph and a scale-free network, and we examine the features of the graph which affect the evolution of the population in this particular game.

## 1. Introduction

Traditionally, evolutionary dynamics have been studied on infinitely large homogeneous populations. However, many real populations, ranging from ecology and epidemiology to computer science and socio-economics, exhibit complex connectivity structures. These structures can be represented and modelled as a collection of interacting units. At its simplest, a network is a collection of nodes representing well defined units that interact via a set of links that can be directional, weighted and even time dependent. Networks have provided and provide a new modelling paradigm that allows modellers to relax many of the strong implicit assumptions, such as the homogeneously mixing of individuals, and to account for a range of heterogeneities at the level of individuals. A growing amount of research on evolutionary dynamics on networks has shown that the structure of the network might significantly affect the evolutionary process (e.g., Lieberman et al., 2005; Szabó and Fáth, 2007; Nowak et al., 2010; Shakarian et al., 2012).

While the modelling framework offered by networks is a straight-forward and intuitive one, it is often limited to individual-based stochastic simulations that can be difficult to validate, time consuming to run and the results generated can lack generality.

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To tackle this problem, researchers from different areas have developed different techniques that allow us to derive low-dimensional ODE (ordinary differential equation) models that, under certain assumptions about the structure of the network and the dynamics running on it, can approximate well the average outcome from stochastic network simulations. Establishing the clear relation between the exact-stochastic and approximate model is challenging since this requires a mathematical handle on both solutions as well as the formulation of an appropriate limit in which the exact-stochastic model approaches the deterministic limit. One such well known class of approximate models is that of the *pairwise models* (e.g., Matsuda et al., 1992; van Baalen and Rand, 1998; Keeling, 1999; Eames and Keeling, 2002; House and Keeling, 2011) where the dynamics at the node level, in a population with network-like contact structure, is described in terms of the dynamics of pairs of individuals, and the hierarchical dependence on higher order structures is cut off via an appropriately constructed closure. In recent years, other models of similar nature have been derived, for example, the *Probability Generating Function* approach (Volz and Meyers, 2007; Volz, 2008) and more notably the *Effective Degree* model (Lindquist et al., 2011). These models have arisen in the context of epidemiology but their formulation and properties makes them amenable to be used for the modelling of evolutionary game dynamics on networks.

In this paper, we consider the evolutionary dynamics of individuals interacting on different networks playing two strategies, A and B. The game played is described by the payoff matrix

$$\begin{array}{c|cc} & \mathrm{A} & \mathrm{B} \\ \hline \mathrm{A} & a & b, \\ \mathrm{B} & c & d \end{array} \tag{1}$$

whose elements represent the payoffs obtained by the row player when interacting with the column player. The fitness of each individual is assumed to be equal to $f=f_b+wP$, a linear function of the average payoff $P$ obtained by the games played with neighbouring individuals. $f_b$ is a constant background fitness of individuals and $w\in[0,\infty)$ represents the intensity of selection which determines the contribution of $P$ to fitness. When $w\to 0_+$, the payoff $P$ of each individual has a small contribution to the overall fitness and we have so-called weak selection. When $w=0$ all individuals have the same fitness and thus we have the case of neutral drift. Finally, when $w\to\infty$ the contribution of $P$ to the fitness becomes arbitrarily large, and the effect of background fitness $f_b$ becomes negligible. Note that, depending on the nature of the game and the evolutionary process, the individual's payoff, $P$, can be considered in different ways. Alternatively, for example, the total payoff of an individual could be considered as just the sum of the payoffs obtained from each game played with each of its neighbours (accumulated payoff). This, depending on the evolutionary dynamics and the population structure, might yield remarkably different results (see for example, Santos and Pacheco, 2006; Tomassini et al., 2007; Szolnoki et al., 2008). In this work, assuming that at each iteration step individuals interact with neighbouring individuals at the same rate, the total payoff of each individual in each step is considered to be the average of the obtained accumulated payoff. Alternative fitness functions have also been considered. For example, the exponential function of the payoff, $f=\exp(wP)$ (Traulsen et al., 2008). These fitness functions are usually used for modelling the evolution of finite structured populations represented by graphs. Different fitness functions have also been introduced for the modelling of evolutionary dynamics beyond the framework of pairwise interactions between individuals (Broom and Rychtář, 2012).

It is assumed that a number of mutants playing strategy A (A individuals) are introduced into a resident population consisting of individuals playing strategy B (B individuals) by replacing an equivalent number of individuals at random. The population evolves following specific update rules. An analytic approach of the evolutionary process under various update rules is possible when individuals of the population occupy the vertices of simple graphs with a lot of symmetry and lack of complexity. Such graphs are the complete graph (Taylor et al., 2004), the circle (Ohtsuki and Nowak, 2006a; Broom et al., 2010), the star (Broom and Rychtář, 2008; Broom et al., 2010; Hadjichrysanthou et al., 2011) and the line (Broom and Rychtář, 2008). See also Lieberman et al. (2005). However, the analytic investigation of the process in populations with a complex structure is usually impossible, especially when the fitness of individuals depends on the composition of the population, due to the large number of the possible configurations of the population through evolution. In such cases the use of approximation methods is essential. In this paper, using the techniques of the Effective Degree model (Lindquist et al., 2011) we consider evolutionary game dynamics on complex networks under the update rules of the biased voter model as described in Antal et al. (2006). According to this model, at each iteration step an individual dies with probability inversely proportional to its fitness, and thus fitter individuals are more likely to survive, and is replaced by the offspring of a randomly chosen neighbour. During the evolutionary process it is assumed that there is no mutation, just selection, and thus the offspring of each individual is a perfect copy of its parent. Voter model type dynamics is one of the classical interacting particle systems which has been applied to many evolutionary processes, from opinion and culture dynamics to processes in population genetics and kinetics of catalytic reactions (e.g., Liggett, 1985; Frachebourg and Krapivsky, 1996; San Miguel et al., 2005; Castellano et al., 2009), and has received considerable attention. It is noted that since the above process is a stochastic process and the transition probabilities from one state to another are inversely proportional to fitness, the fitness of each individual has to be strictly positive. This is assumed throughout the paper.

We show that for randomly or proportionately mixed networks, with or without degree heterogeneity, the model constructed, called the *Neighbourhood Configuration* model, provides an excellent approximation to output from simulation models, even for relatively small network sizes. Following the same evolutionary dynamics we also construct a pairwise model and highlight its merits and shortcomings when compared to the Neighbourhood Configuration model. As an example, we consider the evolutionary process in a Hawk–Dove game when played in three types of graph which have been widely used; a random regular graph, a random graph and a scale-free network.

## 2. Approximate models of evolutionary game dynamics on networks

### 2.1. Pairwise model

In this section, we first approach the evolutionary process by using the pair approximation method (Matsuda et al., 1992; van Baalen and Rand, 1998; Keeling, 1999; Eames and Keeling, 2002; House and Keeling, 2011). This is a method where the frequency of higher order moments, such as triples composed of three nodes connected in a line, is approximated by the frequency of lower order moments, such as pairs and single nodes. This method works well with graphs with no or little heterogeneity in the number of connections, but can be extended to more heterogeneous graphs with a significant increase in the number of equations. Such methods assume that the underlying graphs have undirected links and that these are either unweighted or uniformly weighted. This approximation method has been used in previous work for the investigation of the evolutionary process in structured populations under different update rules (e.g., Morris, 1997; Hauert and Doebeli, 2004; Ohtsuki et al., 2006; Ohtsuki and Nowak, 2006b; Morita, 2008; Fu et al., 2010). Here, we follow a similar procedure to approach the process when the update rules of the voter model are followed.

Assume a population of $N$ individuals playing either strategy A or strategy B placed on a regular graph of degree $k$. Let $p_A$ ($p_B$) denote the proportion of A (B) individuals in the population and $p_{AB}$ the frequency of AB pairs. Let also $q_{B|A}$ denote the conditional probability that a neighbour of a chosen A individual is a B individual, i.e. $q_{B|A} = p_{AB}/(p_{AA}+p_{AB}) = p_{AB}/p_A$ (thus $1-q_{B|A} = q_{A|A} = p_{AA}/p_A$ denotes the conditional probability that a neighbour of a chosen A individual is another A individual). The equivalent expressions also hold for $q_{A|B}$ and $q_{B|B}$. The links of the networks we consider are assumed to be undirected and therefore $p_{AB} = p_{BA}$.

Since all the vertices of the graph are assumed to be topologically equivalent, every pair of A (B) individuals is equally likely to be connected with probability $q_{A|A}$ ($q_{B|B}$). Thus, the probability that from the $k$ connections of an A individual, $i$ of them are with other As (and thus $k-i$ are with Bs), $l_A(i)$, is approximated by assuming that it follows a binomial distribution. This is given by

$$l_A(i) = \binom{k}{i} q_{A|A}^{i}(1-q_{A|A})^{k-i} = \frac{k!}{i!(k-i)!} q_{A|A}^{i} q_{B|A}^{k-i}. \tag{2}$$

Similarly, the probability that a B individual is connected with $i$ As and $k-i$ Bs is assumed to be given by

$$l_B(i) = \binom{k}{i} (1-q_{B|B})^{i} q_{B|B}^{k-i} = \frac{k!}{i!(k-i)!} q_{A|B}^{i} q_{B|B}^{k-i}. \tag{3}$$

An A individual which is connected with $i$ other A individuals has fitness equal to

$$f_A(i) = f_b + w\left(\frac{ia+(k-i)b}{k}\right). \tag{4}$$

A B individual which is connected with $i$ As has fitness equal to

$$f_B(i) = f_b + w\left(\frac{ic+(k-i)d}{k}\right). \tag{5}$$

Let us denote by $\overline{F}$ the sum of the inverse of the fitnesses of all individuals,

$$\overline{F} = p_A \sum_{i=0}^{k} \frac{l_A(i)}{f_A(i)} + p_B \sum_{i=0}^{k} \frac{l_B(i)}{f_B(i)}. \tag{6}$$

The probability that an A individual dies (with probability inversely proportional to its fitness) and is replaced by a (randomly selected) neighbouring B individual, $P_{A\to B}$, is given by

$$P_{A\to B} = \frac{p_A}{\overline{F}} \sum_{i=0}^{k} \frac{l_A(i)}{f_A(i)} \cdot \frac{k-i}{k}. \tag{7}$$

One of the B individuals dies with probability inversely proportional to its fitness and is replaced by a random neighbouring A individual with probability

$$P_{B\to A} = \frac{p_B}{\overline{F}} \sum_{i=0}^{k} \frac{l_B(i)}{f_B(i)} \cdot \frac{i}{k}. \tag{8}$$

The rate of increase of the frequency of A individuals, $p_A$, (given one transition in each iteration step) is given by the following equation:

$$\begin{aligned}\dot{p}_A &= \frac{1}{N} P_{B\to A} - \frac{1}{N} P_{A\to B} \\ &= \frac{1}{N\overline{F}} \sum_{i=0}^{k} \frac{(k-1)!}{i!(k-i)!} \left( p_B q_{A|B}^{i} q_{B|B}^{k-i} \frac{i}{f_B(i)} - p_A q_{A|A}^{i} q_{B|A}^{k-i} \frac{k-i}{f_A(i)} \right).\end{aligned} \tag{9}$$

When an A individual connected to $i$ other As is replaced by a B individual, the number of AA pairs decreases by $i$ and therefore the frequency of AA pairs, $p_{AA}$, decreases by $i/(kN/2)$ ($kN/2$ is the total number of links). This happens with probability

$$P_{AA\to AB} = \frac{p_A}{\overline{F}} \frac{l_A(i)}{f_A(i)} \cdot \frac{k-i}{k}. \tag{10}$$

Similarly, the number of AA pairs increases by $i$ and therefore $p_{AA}$ increases by $i/(kN/2)$ when a B connected to $i$ As is replaced by an A. This happens with probability

$$P_{AB\to AA} = \frac{p_B}{\overline{F}} \frac{l_B(i)}{f_B(i)} \cdot \frac{i}{k}. \tag{11}$$

According to the above, the rate of increase of the frequency of AA pairs (given one transition in each iteration step) is given by the following equation:

$$\begin{aligned}\dot{p}_{AA} &= \sum_{i=0}^{k} \frac{2i}{kN} P_{AB\to AA} - \sum_{i=0}^{k} \frac{2i}{kN} P_{AA\to AB} \\ &= \frac{2}{kN\overline{F}} \sum_{i=1}^{k} \frac{(k-1)!}{(i-1)!(k-i)!} \left( p_B q_{A|B}^{i} q_{B|B}^{k-i} \frac{i}{f_B(i)} - p_A q_{A|A}^{i} q_{B|A}^{k-i} \frac{k-i}{f_A(i)} \right).\end{aligned} \tag{12}$$

Since, $p_A + p_B = 1$, $p_{AB} = p_{BA} = p_A - p_{AA}$ and $p_{BB} = 1 - p_{AA} - 2p_{AB}$, the system can be described by just two dynamical equations, say (9) and (12). Note that the frequency of larger clusters can be approximated by the frequencies of the pairs. For example, the frequency of the three cluster $XYZ$, $p_{XYZ}$, can be approximated by $p_{XY}p_{YZ}/p_Y$.

### 2.2. Neighbourhood Configuration model

The effective degree model (Lindquist et al., 2011) stems from a model first proposed by Ball and Neal (2008) in the context of an *SIR* type infectious disease transmission model, where nodes in a network are accounted for not only by their disease status but also by their number of susceptible $S$ and infected $I$ neighbours, referred to as the effective degree of the nodes. Keeping track of recovered neighbours $R$ is not important as they play no part in the dynamics. Lindquist et al. (2011) formalised this model by categorising each node according to its disease state as well as the number of its neighbours in the various disease states. Based on heuristic arguments and on the assumption of proportionate mixing, Lindquist et al. (2011) derived a system of ODEs in terms of susceptible and infected nodes with all possible neighbourhood configurations. In this paper, we adopt this method to approach the stochastic evolutionary dynamics of a two-strategy game played on complex networks.

Assume, as above, that a resident population of B individuals placed on an undirected and connected static network is invaded by a number of mutant A individuals. The evolutionary dynamics of the evolutionary process is described by the update rules of the voter model. Each individual in the network is classified according to its strategy and the number of its connected individuals playing each of the strategies. Let us denote by $M_{m,r}$ ($R_{m,r}$) the number of individuals in the class where individuals play the mutant (resident) strategy and each of them is connected to $m$ other mutant individuals and $r$ residents. Consider $m$ and $r$ as the number of links that start from an individual of an $M_{m,r}$ or $R_{m,r}$ class and end at a mutant or a resident, respectively. Assume that the maximum degree of a node on the network is $D_{\max}$ and therefore $m \geq 0$, $r \geq 0$ and $1 \leq m+r \leq D_{\max}$. Hence, the number of different classes is equal to $\sum_{k=1}^{D_{\max}} 2(k+1) = D_{\max}(D_{\max}+3)$.

The sum of the inverse of the fitnesses of all individuals, $\overline{F}$, is given by

$$\overline{F} = \sum_{k=1}^{D_{\max}} \sum_{i+j=k} \left( M_{i,j} \frac{i+j}{i\alpha + j\beta} + R_{i,j} \frac{i+j}{i\gamma + j\delta} \right), \tag{13}$$

where we have set $\alpha = f_b + wa$, $\beta = f_b + wb$, $\gamma = f_b + wc$ and $\delta = f_b + wd$. Let us also define some terms which will be useful in subsequent calculations. Let $L_{xy}$ be the number of links which connect an individual of type $x$ to an individual of type $y$ (with $x$ and $y$ being the start and destination node, respectively), where $x$ and $y$ denotes either a mutant (M) or a resident (R) individual.

$$L_{\mathrm{MR}} = \sum_{k=1}^{D_{\max}} \sum_{i+j=k} jM_{i,j}, \quad L_{\mathrm{RM}} = \sum_{k=1}^{D_{\max}} \sum_{i+j=k} iR_{i,j},$$
$$L_{\mathrm{MM}} = \sum_{k=1}^{D_{\max}} \sum_{i+j=k} iM_{i,j}, \quad L_{\mathrm{RR}} = \sum_{k=1}^{D_{\max}} \sum_{i+j=k} jR_{i,j}. \tag{14}$$

In addition, we use the following notations:

$$H_1 = \sum_{k=1}^{D_{\max}} \sum_{i+j=k} \frac{ij}{i\alpha + j\beta}(M_{i,j} - \delta_{mr}^{ij}),$$
$$H_2 = \sum_{k=1}^{D_{\max}} \sum_{i+j=k} \frac{ij}{i\gamma + j\delta}(R_{i,j} - \delta_{mr}^{ij}),$$
$$H_3 = \sum_{k=1}^{D_{\max}} \sum_{i+j=k} \frac{i^2}{i\gamma + j\delta} R_{i,j},$$
$$H_4 = \sum_{k=1}^{D_{\max}} \sum_{i+j=k} \frac{j^2}{i\alpha + j\beta} M_{i,j}, \tag{15}$$

where $\delta_{mr}^{ij}$ is a function defined as

$$\delta_{mr}^{ij} = \begin{cases} 1 & i = m, j = r \\ 0 & \text{otherwise} \end{cases}. \tag{16}$$

An individual might move from one class to another, either by the change of its strategy or due to the change of a neighbour's strategy. The probability that an A mutant individual of the $M_{m,r}$ class is replaced by a B resident individual and move to the $R_{m,r}$ class is equal to the probability that this individual is selected for death (with probability inversely proportional to its fitness) and is replaced by the offspring of one of its neighbouring residents (which is chosen at random). This probability is equal to

$$\frac{m+r}{\bar{F}(m\alpha + r\beta)} \cdot \frac{r}{m+r} = \frac{r}{\bar{F}(m\alpha + r\beta)}. \tag{17}$$

Similarly, an individual of the $R_{m,r}$ class moves to the $M_{m,r}$ class with probability

$$\frac{m+r}{\bar{F}(m\gamma + r\delta)} \cdot \frac{m}{m+r} = \frac{m}{\bar{F}(m\gamma + r\delta)}. \tag{18}$$

A mutant connected to $m$ other mutants and $r$ residents leaves the $M_{m,r}$ class and enters the $M_{m+1,r-1}$ class when a neighbouring resident is replaced by a mutant. The probability of such a movement is approximated in the following way. The probability that a resident individual from an $R_{i,j}$ class is selected to die and is replaced by an offspring of a mutant neighbour is equal to

$$R_{i,j} \frac{i+j}{\bar{F}(i\gamma + j\delta)} \cdot \frac{i}{i+j} = R_{i,j} \frac{i}{\bar{F}(i\gamma + j\delta)}. \tag{19}$$

We now use an approximation to estimate the probability that a resident individual which is replaced by a mutant is connected to a mutant from the $M_{m,r}$ class. This is assumed to be equal to the probability that a randomly chosen link which connects a resident individual with a mutant (starts from a resident and ends at a mutant), is a link which connects the replaced resident with that mutant individual from the $M_{m,r}$ class ($i$ links connect the replaced resident with a mutant and $r$ links connect an individual of the $M_{m,r}$ with a resident, and so there are $ir$ different ways of having such a connection). This probability is given by

$$\frac{ir}{\sum_{k=1}^{D_{\max}} \sum_{i+j=k} iR_{i,j}}. \tag{20}$$

Hence, the probability that a mutant from the $M_{m,r}$ class moves to the $M_{m+1,r-1}$ class can be approximated by

$$\sum_{k=1}^{D_{\max}} \sum_{i+j=k} R_{i,j} \frac{i+j}{\bar{F}(i\gamma + j\delta)} \cdot \frac{i}{i+j} \cdot \frac{ir}{\sum_{k=1}^{D_{\max}} \sum_{i+j=k} iR_{i,j}} = \frac{H_3 r}{\bar{F} L_{\mathrm{RM}}}. \tag{21}$$

In the same way, the probability that a mutant individual from the $M_{m,r}$ class moves to the $M_{m-1,r+1}$ class is equal to the probability that a neighbouring mutant of that individual is replaced by a resident. The probability of such a transition is approximated by the probability that a mutant individual of the population dies, is then replaced by a neighbouring resident individual, and the replaced individual is connected to the mutant from the $M_{m,r}$ class, i.e. by the probability

$$\sum_{k=1}^{D_{\max}} \sum_{i+j=k} (M_{i,j} - \delta_{mr}^{ij}) \frac{i+j}{\bar{F}(i\alpha + j\beta)} \cdot \frac{j}{i+j} \cdot \frac{im}{\sum_{k=1}^{D_{\max}} \sum_{i+j=k} iM_{i,j} - m}$$
$$= \frac{H_1 m}{\bar{F}(L_{\mathrm{MM}} - m)}. \tag{22}$$

The term $M_{i,j} - \delta_{mr}^{ij}$ represents the number of mutants in an $M_{i,j}$ class that can be replaced by a resident such that the transition of a mutant from the $M_{m,r}$ class to the $M_{m-1,r+1}$ class is possible. When $i = m$ and $j = r$, 1 is subtracted from $M_{m,r}$ because the movement of an individual from the $M_{m,r}$ to the $M_{m-1,r+1}$ cannot be a result of its own replacement. In other words, if a mutant from the $M_{m,r}$ class dies and is replaced by a resident, there are other $M_{m,r} - 1$ mutants from that class that might be connected to it and thus move to the $M_{m-1,r+1}$ class. The term $\sum_{k=1}^{D_{\max}} \sum_{i+j=k} iM_{i,j} - m$ corresponds to the number of links that connect any mutant (starting from it), except the specific one from the $M_{m,r}$ class, to other mutants. The death and replacement events have already happened and we are looking for the probability that a random link that goes from a mutant to another mutant is a link that connects the replaced mutant to a mutant from the $M_{m,r}$ class. This link obviously cannot be any of the $m$ links of that individual.

By symmetric arguments, the probability that an individual leaves the $R_{m,r}$ class and enters the $R_{m+1,r-1}$ class is given by

$$\sum_{k=1}^{D_{\max}} \sum_{i+j=k} (R_{i,j} - \delta_{mr}^{ij}) \frac{i+j}{\bar{F}(i\gamma + j\delta)} \cdot \frac{i}{i+j} \cdot \frac{jr}{\sum_{k=1}^{D_{\max}} \sum_{i+j=k} jR_{i,j} - r}$$
$$= \frac{H_2 r}{\bar{F}(L_{\mathrm{RR}} - r)}, \tag{23}$$

while the probability of leaving the $R_{m,r}$ class and moving to the $R_{m-1,r+1}$ class is given by

$$\sum_{k=1}^{D_{\max}} \sum_{i+j=k} M_{i,j} \frac{i+j}{\bar{F}(i\alpha + j\beta)} \cdot \frac{j}{i+j} \cdot \frac{jm}{\sum_{k=1}^{D_{\max}} \sum_{i+j=k} jM_{i,j}} = \frac{H_4 m}{\bar{F} L_{\mathrm{MR}}}. \tag{24}$$

The transition probabilities of moving from and to the $M_{m,r}$ and $R_{m,r}$ classes are represented schematically in the diagram in Fig. 1.

The dynamics of the $D_{\max}(D_{\max} + 3)$ different classes of the population is described by the following differential equation based compartmental model

$$\dot{M}_{m,r} = -\frac{1}{\bar{F}}\left(\frac{H_3 r}{L_{\mathrm{RM}}} + \frac{H_1 m}{L_{\mathrm{MM}} - m} + \frac{r}{m\alpha + r\beta}\right) M_{m,r} + \frac{H_1(m+1)}{\bar{F}(L_{\mathrm{MM}} - (m+1))} M_{m+1,r-1}$$
$$+ \frac{H_3(r+1)}{\bar{F} L_{\mathrm{RM}}} M_{m-1,r+1} + \frac{m}{\bar{F}(m\gamma + r\delta)} R_{m,r}, \tag{25}$$

$$\dot{R}_{m,r} = -\frac{1}{\bar{F}}\left(\frac{H_2 r}{L_{\mathrm{RR}} - r} + \frac{H_4 m}{L_{\mathrm{MR}}} + \frac{m}{m\gamma + r\delta}\right) R_{m,r} + \frac{H_4(m+1)}{\bar{F} L_{\mathrm{MR}}} R_{m+1,r-1}$$
$$+ \frac{H_2(r+1)}{\bar{F}(L_{\mathrm{RR}} - (r+1))} R_{m-1,r+1} + \frac{r}{\bar{F}(m\alpha + r\beta)} M_{m,r}, \tag{26}$$

for $\{(m,r) : m \geq 0, r \geq 0, 1 \leq m + r \leq D_{\max}\}$.

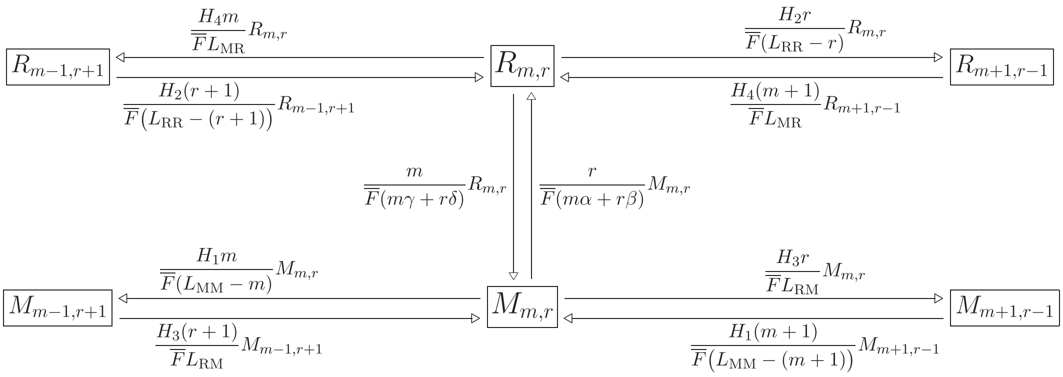

**Fig. 1.** Diagram showing all the probabilities of transition from and to the classes $M_{m,r}$ and $R_{m,r}$.

The density of A individuals in the population is given by $p_A = \sum_{k=1}^{D_{\max}} \sum_{m+r=k} M_{mr}/N$, and the density of B individuals by $p_B = \sum_{k=1}^{D_{\max}} \sum_{m+r=k} R_{mr}/N$.

Note that for very large population sizes, the subtractions of $m$ and $m+1$ from $L_{MM}$, and $r$ and $r+1$ from $L_{RR}$ as well as those of $\delta_{mr}^{ij}$ in the terms $H_1$ and $H_2$, in the model (25)–(26), can be omitted since their effect is negligible (see for example Lindquist et al., 2011 and Gleeson, 2011 where in models of a similar nature such subtractions are avoided). However, this would reduce the accuracy of the solution of the model when the population size is small. Moreover, it should be mentioned that the above subtractions might result in negative values of $M_{m,r}$ and/or $R_{m,r}$ for some values of $m$ and $r$. This is due to the fact that the numerical solution of the system might lead to non-integer values of these quantities which lie between 0 and 1. As a result, the terms $L_{MM}-m$, $L_{MM}-(m+1)$, $L_{RR}-r$ and $L_{RR}-(r+1)$ might become negative. This problem can be solved by setting these terms to be bounded below by 1, which is the minimum natural value that these terms can take.

### 2.3. Numerical examples and comparisons with stochastic simulations

In this section, we examine the effectiveness of the two approximation models described in Sections (2.1) and (2.2); the pairwise model and the Neighbourhood Configuration model. As specific examples we consider the evolution of the population when individuals play Hawk–Dove type games (Maynard Smith and Price, 1973; Maynard Smith, 1982). The Hawk–Dove game is a famous game which has been widely used for the modelling of the aggressive behaviour of animals over food, mates, territories, and other biological resources. According to this game, animals interact with each other over a resource by playing either aggressively using the Hawk strategy (H) or non-aggressively using the Dove strategy (D). When two Hawk players meet, a conflict takes place. The winner takes the resource $V$ while the loser pays a cost $C$. Thus the average payoff obtained by Hawks is $(V-C)/2$. If a Hawk and a Dove meet, the Dove retreats leaving the resource to the Hawk without paying any cost. Thus the Dove obtains nothing while the Hawk receives a payoff $V$. Finally, if two animals playing Dove meet, they either equally share the resource (if divisible) or with equal probability one of the two takes the whole resource with no cost. Thus, in this case Doves obtain an average payoff equal to $V/2$. This game is described by the following payoff matrix:

$$\begin{array}{c|cc} & \text{H} & \text{D} \\ \hline \text{H} & a=\dfrac{V-C}{2} & b=V \\ \text{D} & c=0 & d=\dfrac{V}{2} \end{array}. \qquad (27)$$

In this game, if the value of the resource outweighs the cost of the fight, i.e. if $V>C \Rightarrow a>c$, since $b>d$, an individual always does better by playing the Hawk strategy no matter what the opponent does. Thus, in an infinite homogeneous population the Hawk strategy is the unique Evolutionarily Stable Strategy (ESS). Hawk is also the unique pure ESS when $V=C$, because $b>d$. If $V<C \Rightarrow a<c$, there is a unique ESS where Hawks coexist with Doves at a proportion equal to $(b-d)/(b+c-a-d)=V/C$.

We consider Hawk–Dove type games played on three commonly used families of graphs; the random regular graphs, the random graphs and the scale-free networks. The random graph we consider is an Erdős–Rényi type random graph (Erdős and Rényi, 1959) generated as described in Lindquist et al. (2011). Assume a population of $N$ nodes with no connections between them. Firstly, every (non-connected) node is connected to a random node with degree less than the maximum allowable degree $D_{\max}$. In order to ensure that the graph will be connected (there will be a path between every two nodes of the graph), initially a pair of nodes is connected, and then each of the remaining (non-connected) nodes is connected to a randomly chosen node which is already connected, sequentially. After the connection of all the nodes, two nodes with degree less than $D_{\max}$ are chosen at random and become connected. The last step is iterated until the desired average degree of the graph, $\langle k \rangle$, is reached. The random regular graphs are generated in the same way as the random graph by assuming that $D_{\max}=k$, i.e. with the restriction that every node has the same number of connections. The scale-free networks are networks that have power-law (or scale-free) degree distributions. These are generated following the algorithm of preferential attachment (Barabási and Albert, 1999; Albert and Barabási, 2002). The initial graph consists of a small number of $m_0$ nodes connected with $l_0$ links. A new node of degree equal to $m$ $(\leq m_0)$ is added to the graph and each of its links is connected to one of the existing nodes. The probability that one of the $m$ links is connected to node $i$ with degree $k_i$ is equal to $k_i/\sum_{j=1}^{N} k_j$ (preferential attachment). This process is repeated until the network is composed of $N$ nodes. Given that this happens after $t=N-m_0$ iteration steps, the number of new links that will be added in the graph will be equal to $mt$. Therefore, the network obtained has average degree equal to $\langle k \rangle = 2(mt+l_0)/N$, which for sufficiently large $N$ is well approximated by 2 m. Note that in all the graphs we consider, it is assumed that the links between nodes are undirected and unweighted, every two nodes are connected with at most one link and there are no self-loops, i.e. there is no link which connects a node to itself.

In all the examples, it is assumed that at the initial state of the process the population consists of 50% of individuals playing the Dove strategy and 50% of individuals playing the Hawk strategy randomly distributed among the vertices of the network, so that there is no initial advantage to either of the strategies. The population size, $N$, is relatively small, $N=400$. The results of the pairwise model and the Neighbourhood Configuration model are compared with the average of 100 different network realisations. The equilibrium densities of the strategies have been obtained by averaging the frequency over the last 5000 iteration steps in 40 000 iteration steps (for each graph convergence to an equilibrium state was effectively achieved at a significantly earlier time).

The numerical examples shown in Fig. 2 indicate that, on the three types of network we consider, the prediction of the change in the frequencies of strategies over time given by the solution of the Neighbourhood Configuration model (25) and (26) agrees very well with the results of computer simulations. The numerical results also indicate that the more detailed model provides an approximation with improved accuracy compared to the solution of the pairwise model. Although it is observed that contact structure has little effect on such evolutionary dynamics, the effectiveness of the Neighbourhood Configuration model is clearer on heterogeneous graphs and in general on graphs of low degree, when compared with the pairwise model. As the average degree of the graph increases, i.e. the homogeneity of the graph increases, the predictions of both models are in good agreement with simulation results (see for example, Fig. 4).

One reason that the solution of the Neighbourhood Configuration model is in a better agreement with the solution of the simulation model than that of the pairwise model is that the Neighbourhood Configuration model captures the neighbourhood distribution of an individual better. In the pairwise model it is assumed that the distribution of Y individuals around an X individual, assuming a two-state dynamics, follows a binomial distribution with parameters $\langle k \rangle$ and probability $[XY]/\langle k \rangle [X]$, where $[X]$ is the number of individuals playing strategy X and $[XY]$ the number of pairs between an X and a Y individual ($[X]$ and $[XY]$ are calculated from the simulation model; but they can also be computed from the pairwise model of Section 2.1). The neighbourhood distribution of an X individual can be calculated from the Neighbourhood Configuration model by dividing the number of X individuals connected to $i \in [0, D_{\max}]$ Y individuals by the number of X individuals. We can perform a similar calculation for the simulation model as well. Comparing the neighbourhood distribution of individuals in the three models, the pairwise model, the Neighbourhood Configuration model and the simulation model (see for example Fig. 3), we observe that the solution of the Neighbourhood Configuration model agrees well with the results of simulations. On the other hand, the approximation under the assumption that the neighbourhood of an individual is binomially distributed is not as good.

Although the novelty of this paper is the introduction of this powerful approximation method for the approximation of the evolutionary game dynamics in structured populations, we discuss some main conclusions about the effect of the population structure on the outcome of the evolutionary dynamics in a Hawk–Dove game. Specifically, we discuss how the Hawk and Dove strategies spread in a population represented by a random regular graph, a random graph and a scale-free network. Numerical examples suggest that increasing the heterogeneity of the network favours the emergence of the Hawk strategy. Following the update rules of the voter model, fitter mutants that occupy nodes of high connectivity have an increased chance to survive and reproduce (Sood et al., 2008; Hadjichrysanthou et al., 2011). Therefore, as it is observed in Fig. 2, scale-free networks provide an encouraging environment for the Hawk strategy. However, the most important feature of a graph that affects the evolutionary process is its average degree. The results of our examples indicate that in all types of graph we consider, a decrease of the average number of neighbours that each individual has tends to deviate the equilibrium frequency of Hawks from the equilibrium frequency in the case of the well-mixed population, and this deviation is more pronounced for lower degree graphs. Depending on the values of the payoffs, the decrease of the average degree of the

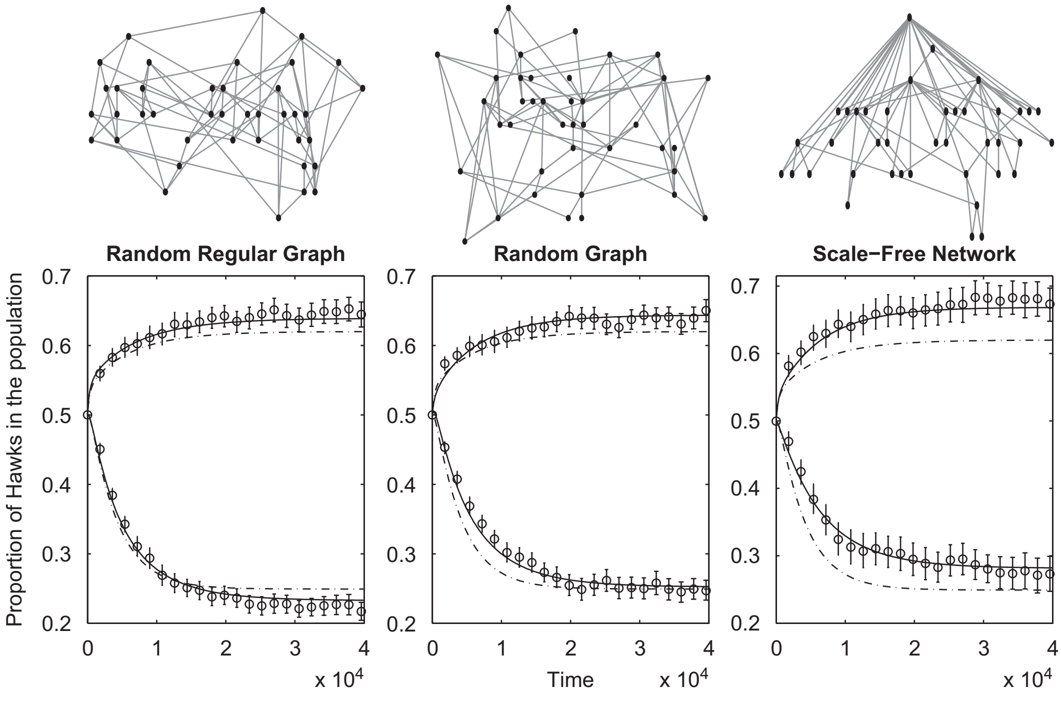

**Fig. 2.** Change over time in the proportion of individuals playing the Hawk strategy in a Hawk–Dove game played on a random regular graph with $k=4$, a random graph with $\langle k \rangle = 4$ and $D_{\max} = 10$, and a scale-free network with $\langle k \rangle = 4$. The solid lines represent the solution of the Neighbourhood Configuration model, the dashed-dotted lines represent the solution of the pairwise model, and the circles represent the average of 100 stochastic simulations. A 95% bootstrap confidence interval for the mean of the simulation results is also presented. The upper curves of each sub-figure represent the case of a game described by the payoff matrix (27) where $V=6$, $C=10$, $f_b=4$ and $w=1$. The lower curves represent the case of a game where $V=4$, $C=10$, $f_b=4$ and $w=1$.

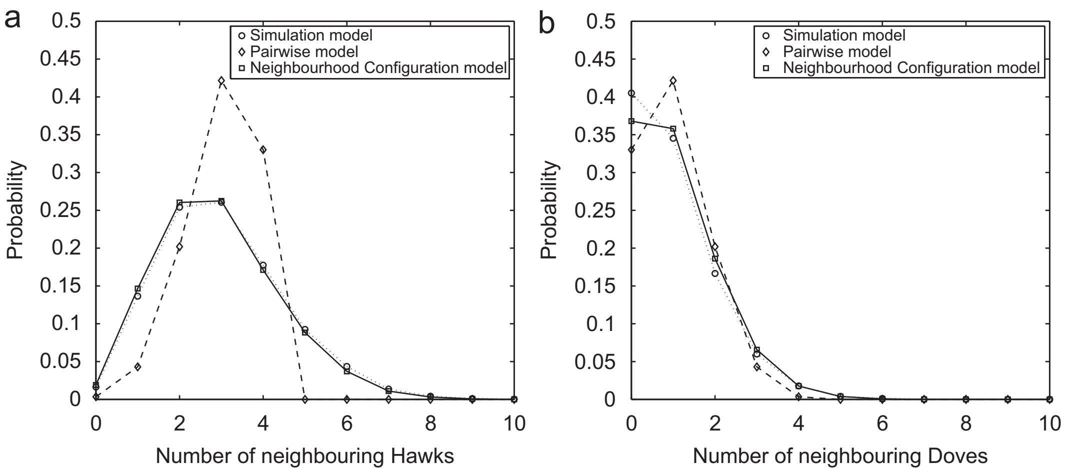

**Fig. 3.** (a) The distribution of Hawks around a Hawk at equilibrium, (b) the distribution of Doves around a Hawk at equilibrium, in a Hawk–Dove game played on a random graph with $\langle k \rangle = 4$ and $D_{\max} = 10$. $V = 6, C = 10, fb = 4$ and $w = 1$.

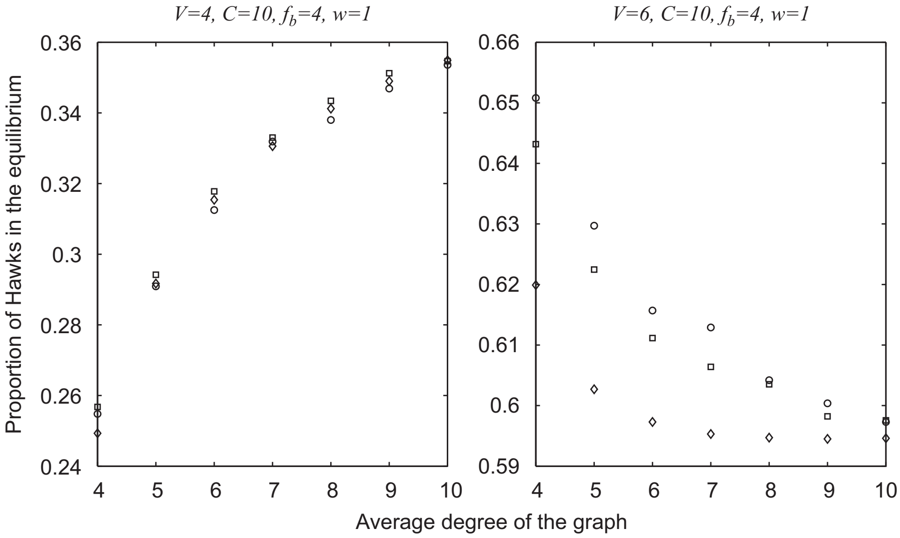

**Fig. 4.** The proportion of Hawks in the equilibrium on random graphs of different average degree, $\langle k \rangle$. The maximum degree of a node, $D_{\max}$, in each of the graphs is equal to $\langle k \rangle + 6$. The squares represent the solution of the Neighbourhood Configuration model, the diamonds represent the solution of the pairwise model, and the circles represent the average of 100 stochastic simulations.

neighbours might enhance or inhibit the use of the Hawk strategy (and thus the Dove strategy). In particular, if the payoffs are such that the equilibrium frequency of Hawks in a well-mixed population is less than half of the population, the decrease of the average number of neighbours decreases their frequency at equilibrium conditions (at least when the average degree is already sufficiently small). If the payoffs are such that the equilibrium frequency in a well-mixed population is higher than half, the equilibrium frequency will tend to increase as the average number of neighbours decreases (see in Fig. 4 the effect of the variation of the average degree of a random graph in two example games). Note that the improved approximation of the Neighbourhood Configuration model when compared to that of the pairwise model is not very clear in our examples presented in Fig. 4, mainly due to the particular example games and the graphs on which the games are played. However, the scope of this figure is to illustrate the effect of the average connectivity of the graph at the equilibrium state of the system.

It should be noted that, due to the nature of the evolutionary dynamics as well as to the nature of the game we consider, the evolution of the population is very slow, especially for networks of low connectivity, and to speed up the evolutionary process and reduce the computation time we reduce the population size and the number of simulations realised. However, small population sizes and small number of realisations of stochastic simulations result in larger oscillations of the simulation results due to the increase of the sensitivity of the process to stochastic effects. Increasing the population size and the number of realisations, this effect is reduced and the difference between the predictions of the computer simulations and the predictions of the Neighbourhood Configuration model decreases.

## 3. Discussion

In this work, we have investigated the stochastic evolutionary game dynamics in structured populations following the update rules of the voter model dynamics, a dynamics which is applied in many models that arise in various fields, such as physics and biology. Whilst analytic investigation of this dynamics is possible when populations have a simple structure, the study of the dynamics in complex structures requires the use of approximation techniques. Here, we propose a Neighbourhood Configuration model for the study of the stochastic evolutionary dynamics of a two-strategy game on complex networks.

As an example, we have considered a Hawk–Dove game played in three widely used types of graph; random regular graphs, random graphs and scale-free networks. The solutions of the model constructed in comparison with the outcome of stochastic simulations imply that the method followed is a powerful and effective method for the approximation of such evolutionary processes. In addition, comparisons with the results of the extensively used pairwise approximation suggest that this method improves the accuracy of the approximation solutions.

Although the aim of this paper is the introduction of the Neighbourhood Configuration model for the approximation of evolutionary game dynamics on graphs, we have considered some important characteristics of the network that might affect the evolution of a population when a Hawk–Dove game is played among individuals. The spatial effects in this evolutionary game have received considerable attention in many previous works, including Killingback and Doebeli (1996), Hauert and Doebeli (2004), Tomassini et al. (2006), Broom et al. (2010), Voelkl (2010) and Hadjichrysanthou et al. (2011). One of the main research questions is whether there are structures and strategy update rules which favour the persistence of the cooperative Dove-like behaviour over the Hawk-like behaviour compared to the evolution in classical evolutionary game theory under the assumption that the population is well-mixed and infinitely large. Killingback and Doebeli (1996) have shown that, for a wide range of parameter values, the square lattice structure may favour the Dove strategy, with respect to the equilibrium frequency of Doves in the population compared to the equilibrium frequency in the classical Hawk–Dove game. On the other hand, in Hauert and Doebeli (2004), extending the investigation of the evolution in this type of game to a broader class of lattices and under different strategy update rules, the authors concluded that spatial structure usually does not promote the spread of the Dove strategy. Santos and Pacheco (2005) showed that among other structures, in Hawk–Dove type games (specifically, in the Snowdrift game), under some specific strategy update rules, the spread of the Dove-like strategies are facilitated particularly on scale-free networks due to the existence of highly connected Doves (see also Santos et al., 2006). Tomassini et al. (2006), based on the results of computer simulations, have considered the game played among individuals on lattices, random graphs and small-world networks and shown that, compared with the case of the well-mixed population, these types of network might enhance or inhibit the use of the Dove strategy (the proportion of Doves at the equilibrium state might be either higher or lower than their proportion given by the theoretical solution of the classical evolutionary game theory), depending on the update rule and the ratio $V/C$. In Broom et al. (2010), Voelkl (2010) and Hadjichrysanthou et al. (2011) it has been shown through an analytical and numerical investigation that the Dove behaviour is favoured on some structures with respect to the probability and time to fixation. In this paper, through numerical examples we have shown that the population structure might significantly influence the evolution of the population. The most important feature of the graph that affects evolution in our examples seems to be average connectivity. Decreasing the average number of connections of each individual increases the difference between the proportion of Hawks from their proportion in the equivalent infinite homogeneous population, in the direction of the nearest absorption state. Hence, depending on the values of the payoffs, the decrease of the average connectivity of the network enhances or inhibits the use of the Hawk strategy. In addition, heterogeneous graphs have been shown to facilitate the spread of Hawks. Particularly, the existence of highly connected nodes promotes the Hawk strategy and scale-free networks appear to be the most hospitable environment among the networks we have considered.

The approximation method presented in this paper is undoubtedly a useful tool which provides an effective way to consider evolutionary dynamics on a wide range of graphs. We believe that its use in future research could give insight into the influence of the population structure on the outcome of such dynamics (see Gleeson, 2011). Future work could involve the application of the Neighbourhood Configuration model in the investigation of other type of dynamics on networks, for example birth–death dynamics where the birth event happens first followed by the death and replacement events. One extension of the model could be the inclusion of a mutation process, a process that usually occurs in natural systems. For example, it could be assumed that with a certain probability the offspring of an $X$ individual is not a copy of its parent but is a $Y$ individual. This would add some complication in the model, because in this case an $X$ individual might be replaced by a $Y$ individual, which is the offspring of a neighbouring $X$ individual. Such an extension would allow us to consider the effect of mutation on evolution on graphs, an important factor that has rarely been studied. This method is also amenable to be extended to dynamic networks and thus offer further potential advantages to modellers (see a modelling framework in this direction in the context of disease propagation in, for example, Marceau et al., 2010 and Taylor et al., 2012).

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