Available online at www.sciencedirect.com
ScienceDirect
Journal of Theoretical Biology 250 (2008) 723–731
Journal of Theoretical Biology
www.elsevier.com/locate/yjtbi

Repeated games and direct reciprocity under active linking

Jorge M. Pacheco[a,*], Arne Traulsen[b], Hisashi Ohtsuki[b], Martin A. Nowak[b,c]

[a]ATP-Group and CFTC, Departamento de Física da Faculdade de Ciências, P-1649-003 Lisboa Codex, Portugal
[b]Program for Evolutionary Dynamics, Harvard University, Cambridge, MA 02138, USA
[c]Department of Organismic and Evolutionary Biology, Department of Mathematics, Harvard University, Cambridge, MA 02138, USA

Received 17 September 2007; received in revised form 31 October 2007; accepted 31 October 2007
Available online 6 November 2007

Abstract

Direct reciprocity relies on repeated encounters between the same two individuals. Here we examine the evolution of cooperation under direct reciprocity in dynamically structured populations. Individuals occupy the vertices of a graph, undergoing repeated interactions with their partners via the edges of the graph. Unlike the traditional approach to evolutionary game theory, where individuals meet at random and have no control over the frequency or duration of interactions, we consider a model in which individuals differ in the rate at which they seek new interactions. Moreover, once a link between two individuals has formed, the productivity of this link is evaluated. Links can be broken off at different rates. Whenever the active dynamics of links is sufficiently fast, population structure leads to a simple transformation of the payoff matrix, effectively changing the game under consideration, and hence paving the way for reciprocators to dominate defectors. We derive analytical conditions for evolutionary stability.

Keywords: Evolutionary game theory; Structured populations; Coevolution; Dynamically structured populations

1. Introduction

Game theoretic ideas were first introduced to biology by Hamilton (1964) and Trivers (1971), but the field of evolutionary game theory was founded by Maynard Smith and Price (1973) and Maynard Smith (1982). The replicator equation (Taylor and Jonker, 1978; Hofbauer et al., 1979; Zeeman, 1980) constitutes the mathematical foundation of evolutionary game dynamics. It is a system of ordinary differential equations describing how the relative abundances (frequencies) of strategies change over time as a consequence of frequency-dependent selection. The payoff from the game is interpreted as biological fitness. Individuals reproduce proportional to their fitness. Reproduction can be genetic or cultural. The expected payoff of an individual is a linear function of the frequencies of all strategies; the coefficients of this function are the entries of the payoff matrix. For detailed reviews of the replicator equation and other approaches to evolutionary game dynamics, see Fudenberg and Tirole (1991), Weibull (1995), Samuelson (1997), Hofbauer and Sigmund (1998, 2003), Gintis (2000), Bowles (2003), Cressman (2003), Nowak and Sigmund (2004) and Nowak (2006a).

The act of cooperation typically involves a cost c to the provider and a benefit b to the recipient. In the absence of a specific mechanism for the evolution of cooperation, natural selection favors defectors. There are at least five mechanisms that can lead to the evolution of cooperation: kin selection, group selection, direct reciprocity, indirect reciprocity and network reciprocity (= graph selection).

In this paper, we study the interaction between direct and network reciprocity; however, unlike conventional network reciprocity, as defined in Nowak (2006b), here the network is adaptive, as discussed below. The study of the evolution of cooperation under direct reciprocity on dynamical networks deserves special attention, given the recent results which show that co-evolution of population structure with individual strategy provide an efficient mechanism for the evolution of cooperation under simple one-shot games (Pacheco et al., 2006a, b; Santos et al., 2006c).

*Corresponding author. Tel.: +351 217904891; fax: +351 217954288.
E-mail address: pacheco@cii.fc.ul.pt (J.M. Pacheco).

0022-5193/$ - see front matter © 2007 Elsevier Ltd. All rights reserved.
doi:10.1016/j.jtbi.2007.10.040

Direct reciprocity is based on the idea of repeated encounters between two individuals (Trivers, 1971) according to the principle, "*I scratch your back and you scratch mine*". The game theoretic framework of direct reciprocity is the repeated Prisoner's Dilemma (PD), which has been the subject of numerous studies across various disciplines (Rapoport and Chammah, 1965; Axelrod and Hamilton, 1981; Axelrod, 1984; Selten and Hammerstein, 1984; Milinski, 1987; May, 1987; Axelrod and Dion, 1988; Fudenberg and Maskin, 1990; Imhof et al., 2005). A large number of strategies for playing the repeated PD have been analyzed. The most prominent ones are tit-for-tat (Axelrod, 1984), generous-tit-for-tat (Nowak and Sigmund, 1992), contrite-tit-for-tat (Sugden, 1986; Boerlijst et al., 1997) or win-stay, lose-shift (Nowak and Sigmund, 1993).

In general, it is a very difficult task to find successful strategies for playing the repeated PD (Axelrod, 1984; Kraines and Kraines, 1988; Fudenberg and Maskin, 1990; Lindgren, 1991). But if what we want is to investigate if cooperation has any chance to evolve by direct reciprocity at all, then a very simple game can be studied. We only need to consider two strategies: unconditional defectors (D), defect all the time; reciprocators (R) start cooperating and then continue to cooperate as long as the opponent cooperates, but defect if the opponent defects. Such individuals can be thought of as playing a strategy like tit-for-tat or Grim. Tit-for-tat cooperates on the first move and then does whatever the opponent has done on the previous move. Grim cooperates until the opponent defects once and then permanently switches to defection. Despite the difference between these two strategies, when playing against an unconditional defector, tit-for-tat and grim lead to the same sequence of cooperation in the first round and unconditional defection from then on. Only if errors or more complex strategy sets are considered, differences between the strategies arise. Hence, a reciprocator will only cooperate once against a defector and will behave as an unconditional cooperator against another reciprocator.

Let us denote by w the probability of playing another round. The average number of rounds between the same two players is given by $1/(1-w)$. The payoff matrix for reciprocators (R) versus unconditional defectors (D) is given by

$$\begin{array}{cc} & \begin{array}{cc} R & D \end{array} \\ \begin{array}{c} R \\ D \end{array} & \begin{pmatrix} \dfrac{b-c}{1-w} & -c \\ b & 0 \end{pmatrix} \end{array}, \tag{1}$$

that is, reciprocators pay the cost c once, and unconditional defectors receive the benefit b only once.

One-shot and repeated games on spatial lattices have been studied by many authors (Nowak and May, 1992, 1993; Wilson et al., 1992; Nowak et al., 1994; Lindgren and Nordahl, 1994; Killingback and Doebeli, 1996; Nakamaru et al., 1997, 1998; van Baalen and Rand, 1998; Szabó and Tőke, 1998; Hauert et al., 2002; Szabó and Hauert, 2002; Brandt et al., 2003; Hauert and Doebeli, 2004; Hauert and Szabó, 2005; Szabó et al., 2005; Nowak, 2006a; Szabó and Fáth, 2007). Evolutionary graph theory is an extension of this approach to general population structure and networks (Lieberman et al., 2005; Pacheco and Santos, 2005; Santos and Pacheco, 2005; Santos et al., 2005, 2006a, b; Santos and Pacheco, 2006; Ohtsuki and Nowak, 2006a, b, 2007; Ohtsuki et al., 2006, 2007a, b; Pacheco et al., 2006a, b). It is usually assumed that the population structure is constant in the time scale of the evolutionary updating. Recently, Ohtsuki and Nowak (2007) have investigated the evolutionary feasibility of cooperation under direct reciprocity for static networks. The combination of direct reciprocity with (static) network reciprocity was shown to open the way for reciprocators to invade (even when rare) unconditional defectors, which is never possible in a well-mixed population. The effect of network reciprocity is strongest if people have few neighbors (or if most interactions occur only with a subset of "very close friends"). In many real-world social and biological networks (Amaral et al., 2000; Dorogovtsev and Mendes, 2003; May, 2006; Santos et al., 2006c); however, the average connectivity of individuals is not small.

In addition to static networks, one-shot-games on dynamical graphs have also been investigated (Bala and Goyal, 2000; Skyrms and Pemantle, 2000; Zimmermann et al., 2004; Eguíluz et al., 2005; Santos et al., 2006c). It has been recently shown (Pacheco et al., 2006a, b; Santos et al., 2006c) that the limitation to small connectivity may be overcome if one evolves *simultaneously* individual strategy and population structure. Here we investigate the impact of co-evolution of strategy and structure in the evolution of cooperation under direct reciprocity.

In Section 2 we introduce relevant concepts of evolutionary game dynamics in finite and infinite populations, as well as results related to direct reciprocity in well-mixed populations. In Section 3 we introduce the model of active linking dynamics, in which individuals seek new partners and break existing ties at different rates. In Sections 4 and 5 we discuss our results for direct reciprocity on dynamical graphs. In Section 6 we offer conclusions.

2. Evolutionary stability and risk-dominance in well-mixed populations

Consider a game between two strategies, A and B, given by the payoff matrix

$$\begin{array}{cc} & \begin{array}{cc} A & B \end{array} \\ \begin{array}{c} A \\ B \end{array} & \begin{pmatrix} p_{AA} & p_{AB} \\ p_{BA} & p_{BB} \end{pmatrix} \end{array}. \tag{2}$$

An infinitely large population of A players cannot be invaded by B players if $p_{AA} > p_{BA}$, that is, A is both a strict Nash equilibrium and an evolutionarily stable strategy (ESS). In an *infinite* well-mixed population, both strategies are ESS whenever $p_{AA} > p_{BA}$ and $p_{AB} < p_{BB}$. The replicator

equation (Taylor and Jonker, 1978; Hofbauer et al., 1979; Weibull, 1995; Hofbauer and Sigmund, 1998) admits an unstable mixed equilibrium, located at $x^* = (p_{BB} - p_{AB})/(p_{AA} - p_{AB} - p_{BA} + p_{BB})$, where x^* is the equilibrium frequency of A players in the population. Strategy A is risk-dominant (RD) if it has the bigger basin of attraction, that is, whenever $p_{AA} + p_{AB} > p_{BA} + p_{BB}$.

In *finite*, well-mixed populations, a crucial quantity is the fixation probability of a strategy, that is, the probability that the lineage arising from a single mutant of that strategy will take over the entire population (Nowak et al., 2004; Taylor et al., 2004). If $p_{AA} + 2p_{AB} > p_{BA} + 2p_{BB}$ then the fixation probability of strategy A is greater than the fixation probability of a neutral mutant ($1/N$). To be more specific, the product of population size and the intensity of selection has to be small (Traulsen et al., 2006b). This means selection favors the replacement of B by A, and therefore a single A-player in a population of B-players is an advantageous mutant. The condition can be expressed as a $\frac{1}{3}$-rule: if the fitness of the invading A at a frequency of $\frac{1}{3}$ is greater than the fitness of the resident B then the fixation probability of A is greater than $1/N$ (Nowak et al., 2004; Imhof and Nowak, 2006; Ohtsuki et al., 2007c). This condition holds in the limit of weak selection where the payoff from the game is small compared to a constant background fitness (Traulsen et al., 2006a; 2007a,b). Furthermore, if A is RD compared to B, then the fixation probability of A is greater than the fixation probability of B for weak selection and large population size (Nowak et al., 2004; Imhof and Nowak, 2006).

Given the payoff matrix associated with direct reciprocity, Eq. (1), we can immediately write down the following conditions (Ohtsuki and Nowak, 2007):

The reciprocator strategy is an ESS if

$$\frac{b}{c} > \frac{1}{w}. \tag{3a}$$

In this case, a defector in an infinitely large population of cooperators has a lower fitness. The unstable fixed point is located at

$$x^* = \frac{c}{b-c}\frac{1-w}{w}. \tag{3b}$$

In a finite population, however, it is still possible that the fixation probability of a single defector, ρ_D, is greater than that of a neutral mutant ($1/N$). Hence, if we want defectors to be disadvantageous, we must require that $\rho_D < 1/N$. For weak selection and large population size the condition reads (Ohtsuki and Nowak, 2007)

$$\frac{b}{c} > \frac{3-w}{2w}. \tag{3c}$$

In this case, the basin of attraction of reciprocators is greater than $\frac{1}{3}$. Reciprocators become RD when

$$\frac{b}{c} > \frac{2-w}{w}, \tag{3d}$$

that is, $\rho_R > \rho_D$ for large populations and weak selection. Finally, reciprocators become advantageous if $\rho_R > 1/N$; for large populations and weak selection, this is equivalent to (Ohtsuki and Nowak, 2007)

$$\frac{b}{c} > \frac{3-2w}{w}. \tag{3e}$$

3. Basic model and transformation of payoff matrices

Let us study a game between two strategies, A and B, in a population of fixed size, N. There are N_A players who use strategy A, and N_B players who use strategy B.

3.1. Unconditional strategies in finite, well-mixed populations

First consider the case without dynamical linking or conditional strategies. Strategies A and B are unconditional and pure strategies of the 2×2 game with payoff matrix

$$\begin{array}{c} \\ A \\ B \end{array} \begin{array}{c} \begin{array}{cc} A & B \end{array} \\ \begin{pmatrix} p_{AA} & p_{AB} \\ p_{BA} & p_{BB} \end{pmatrix} \end{array}. \tag{4}$$

In each round of the game, A players choose action A, and B players choose action B. Suppose that players keep playing the game with all other players simultaneously. Each A-player interacts with $N_A - 1$ many A-opponents and N_B many B-opponents. Each B-player interacts with N_A many A-opponents and $N_B - 1$ many B-opponents. When it takes an amount of time τ_0 for players to complete a round of game, the payoffs per unit time are calculated as

$$W_A = (N_A - 1)\frac{p_{AA}}{\tau_0} + N_B\frac{p_{AB}}{\tau_0},$$
$$W_B = N_A\frac{p_{BA}}{\tau_0} + (N_B - 1)\frac{p_{BB}}{\tau_0}. \tag{5}$$

If N_A and N_B are large, we can neglect -1 in Eq. (5) and we obtain

$$\begin{pmatrix} W_A \\ W_B \end{pmatrix} = \frac{N}{\tau_0}\begin{pmatrix} p_{AA} & p_{AB} \\ p_{BA} & p_{BB} \end{pmatrix}\begin{pmatrix} x_A \\ x_B \end{pmatrix}. \tag{6}$$

Here x_A and x_B represent relative abundances of strategies, A and B, namely, $x_A = N_A/N$, $x_B = N_B/N$, such that $x_A + x_B = 1$.

3.2. Unconditional strategies in populations with dynamical linking

Next we incorporate the effect of dynamical linking into the payoff matrix. Consider two players in the population. These players are able to play games only when there is a link between them. It is possible for a player to have multiple links and to play games with different partners at the same time. Let ϕ_{ij} represent the average fraction of time a link is present between an $i(= A, B)$-player and a $j(= A, B)$-player. In this case, the payoffs per unit

time become

$$W_A = (N_A - 1)\phi_{AA}\frac{p_{AA}}{\tau_0} + N_B\phi_{AB}\frac{p_{AB}}{\tau_0},$$
$$W_B = N_A\phi_{BA}\frac{p_{BA}}{\tau_0} + N_B\phi_{BB}\frac{p_{BB}}{\tau_0}. \quad (7)$$

We have

$$\begin{pmatrix} W_A \\ W_B \end{pmatrix} = \frac{N}{\tau_0}\begin{pmatrix} \phi_{AA}p_{AA} & \phi_{AB}p_{AB} \\ \phi_{BA}p_{BA} & \phi_{BB}p_{BB} \end{pmatrix}\begin{pmatrix} x_A \\ x_B \end{pmatrix}. \quad (8)$$

Eq. (8) suggests that the linking dynamics introduces a simple transformation of the payoff matrix. We can study standard evolutionary game dynamics using the modified payoff matrix (Pacheco et al., 2006a, b).

The fractions of time that different types of links are active, ϕ, are calculated as follows. Links are formed at certain rates and have specific life-times. Denote by $X(t)$ the number of AA links at time t. Similarly, $Y(t)$ and $Z(t)$ denote the number of AB and BB links at time t. The maximum possible number of AA, AB and BB links is, respectively, given by

$$X_m = N_A(N_A - 1)/2,$$
$$Y_m = N_A N_B,$$
$$Z_m = N_B(N_B - 1)/2. \quad (9)$$

Suppose A and B players have a propensity to form new links denoted by α_A and α_B, such that AA links are formed at a rate α_A^2, AB links are formed at a rate $\alpha_A\alpha_B$ and BB links are formed at a rate α_B^2. Also suppose that the average life-times of links are given by τ_{AA}, τ_{AB} and τ_{BB} ($\gg\tau_0$).

Linking dynamics can then be described by a system of three ordinary differential equations for the number of links (Pacheco et al., 2006a, b):

$$\dot{X} = \alpha_A^2(X_m - X) - \frac{1}{\tau_{AA}}X,$$
$$\dot{Y} = \alpha_A\alpha_B(Y_m - Y) - \frac{1}{\tau_{AB}}Y,$$
$$\dot{Z} = \alpha_B^2(Z_m - Z) - \frac{1}{\tau_{BB}}Z. \quad (10)$$

In the steady state, the number of links of the three different types is given by

$$X^* = \frac{\alpha_A^2\tau_{AA}}{\alpha_A^2\tau_{AA} + 1}X_m,$$
$$Y^* = \frac{\alpha_A\alpha_B\tau_{AB}}{\alpha_A\alpha_B\tau_{AB} + 1}Y_m,$$
$$Z^* = \frac{\alpha_B^2\tau_{BB}}{\alpha_B^2\tau_{BB} + 1}Z_m. \quad (11)$$

Hence we may write

$$\phi_{AA} = \frac{X^*}{X_m} = \frac{\alpha_A^2\tau_{AA}}{\alpha_A^2\tau_{AA} + 1},$$
$$\phi_{AB} = \phi_{BA} = \frac{Y^*}{Y_m} = \frac{\alpha_A\alpha_B\tau_{AB}}{\alpha_A\alpha_B\tau_{AB} + 1},$$
$$\phi_{BB} = \frac{Z^*}{Z_m} = \frac{\alpha_B^2\tau_{BB}}{\alpha_B^2\tau_{BB} + 1}. \quad (12)$$

Examples for cumulative degree distributions of population structures attained under steady-state dynamics for different combinations of the relevant parameters are shown in Fig. 1. Indeed, this simple model of linking dynamics leads to *single-scale* networks as defined by Amaral et al. (2000), with associated cumulative degree distributions exhibiting fast decaying tails (Santos et al., 2006c). Such tails which decay exponentially or faster than exponential, leading to what are known as "broad-scale" and "single-scale" networks, respectively, are features which, together with a large variability in the average connectivity (Dorogovtsev and Mendes, 2003; May, 2006), characterize most real-world social networks. The present model only encompasses single-scale networks. In order to describe the broad-scale networks often encountered in social systems, more refined models should be developed.

The vertical arrows in Fig. 1 indicate the average connectivity of the associated graphs, showing that connectivity values similar to those measured empirically (Dorogovtsev and Mendes, 2003) are easily obtained with the present model. Note, in particular, that the dependence of the stationary networks on the frequency of individuals of a given type will automatically couple network dynamics with the frequency-dependent evolutionary dynamics we introduce in the following.

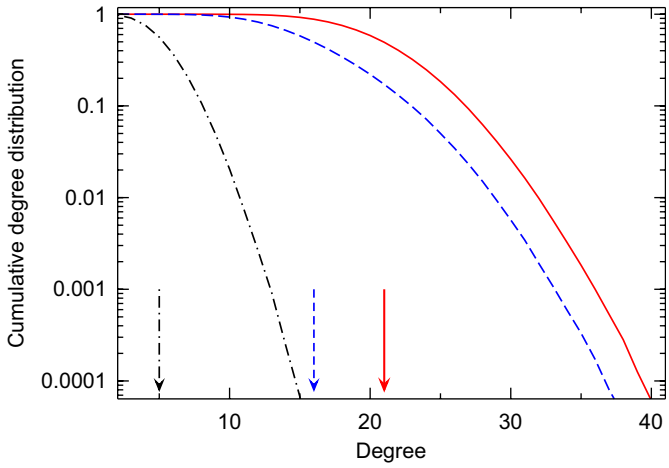

Fig. 1. Cumulative degree distributions (defined as $D(k) = \sum_{j\geqslant k} N_j/N$, with N_j the number of nodes with degree j) for networks generated with the present model, for populations of size $N = 10^3$ and two different types of individuals. The fast decaying tails correlate well with the observed tails of real social networks (Amaral et al., 2000; Dorogovtsev and Mendes, 2003; May, 2006). The present model, however, leads to single-scale networks (Amaral et al., 2000), broad scale networks being out of its scope (for details of the degree distributions, see Pacheco et al., 2006a). On the other hand, the dependence of the final network on the frequency of each type of individuals leads to a natural coupling between network dynamics and frequency-dependent strategy evolution. The vertical arrows indicate the average connectivity of each graph, which is far greater than those typically associated with static graphs where cooperation under direct reciprocity thrives (Ohtsuki and Nowak, 2007). Parameters used: $N_A/N = 0.5$, $\alpha_A = \alpha_B = 1$, $\beta_{AA} = \beta_{AB} = \beta_{BB} = 50$ (red solid curve), $N_A/N = 0.35$, $\alpha_A = 1.1$, $\alpha_B = 0.75$, $\beta_{AA} = \beta_{AB} = \beta_{BB} = 50$ (blue dashed curve) and $N_A/N = 0.5$, $\alpha_A = \alpha_B = 0.2$, $\beta_{AA} = \beta_{AB} = \beta_{BB} = 10$ (black dash–dot curve).

3.3. Conditional strategies in populations with dynamical linking

So far we have assumed that strategies A and B are pure strategies in a single game. What if they are strategies in a repeated game? Consider reciprocators (R) and unconditional defectors (D). Each time a new link is established, a reciprocator cooperates in the first round while an unconditional defector never cooperates. Once a reciprocator faces defection by the opponent, he keeps defecting until the link is broken.

Interactions with two R players last on average for time τ_{RR}. Since it takes time τ_0 to complete a round, they play on average τ_{RR}/τ_0 rounds of Prisoner's Dilemma game within the lifetime of that link. Suppose that the payoff matrix of the single-round Prisoner's Dilemma game is given by

$$\begin{array}{cc} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} p_{CC} & p_{CD} \\ p_{DC} & p_{DD} \end{pmatrix} \end{array}. \tag{13}$$

Both reciprocators gain the payoff of $(\tau_{RR}/\tau_0)\times p_{CC}$ in time τ_{RR}. Therefore, given a link remains established, a payoff per unit time is given by

$$\frac{\tau_{RR}}{\tau_0}\cdot p_{CC}\cdot\frac{1}{\tau_{RR}}=\frac{p_{CC}}{\tau_0}. \tag{14}$$

A similar consideration yields that the payoff per unit time between two unconditional defectors is given by

$$\frac{\tau_{DD}}{\tau_0}\cdot p_{DD}\cdot\frac{1}{\tau_{DD}}=\frac{p_{DD}}{\tau_0}. \tag{15}$$

When a link is established between a reciprocator and a defector, the link lasts for an average time τ_{RD}, so that these players on average play τ_{RD}/τ_0 rounds of Prisoner's Dilemma game. In the first round, the reciprocator cooperates whereas the unconditional defector defects, which yields the payoff of p_{CD} to the reciprocator and p_{DC} to the defector. From the second round on, both keep defecting and gain p_{DD} per round. The average number of rounds of mutual defection is $(\tau_{RD}/\tau_0)-1$. Since the whole repeated game takes time τ_{RD}, the average payoff of reciprocators per unit time is, under the assumption of the link remaining established, given by

$$\left(p_{CD}+\left(\frac{\tau_{RD}}{\tau_0}-1\right)p_{DD}\right)\frac{1}{\tau_{RD}}=\frac{p_{DD}}{\tau_0}+\frac{p_{CD}-p_{DD}}{\tau_{RD}}. \tag{16}$$

Under the same assumption, the average payoff of defectors per unit time is given by

$$\left(p_{DC}+\left(\frac{\tau_{RD}}{\tau_0}-1\right)p_{DD}\right)\frac{1}{\tau_{RD}}=\frac{p_{DD}}{\tau_0}+\frac{p_{DC}-p_{DD}}{\tau_{RD}}. \tag{17}$$

Taking into account the fraction of time when links are absent, we find that the average payoffs per unit time of reciprocators and unconditional defectors are

$$\begin{aligned} W_R &= (N_R-1)\phi_{RR}\frac{p_{CC}}{\tau_0}+N_D\phi_{RD}\left(\frac{p_{DD}}{\tau_0}+\frac{p_{CD}-p_{DD}}{\tau_{RD}}\right), \\ W_D &= N_R\phi_{DR}\left(\frac{p_{DD}}{\tau_0}+\frac{p_{DC}-p_{DD}}{\tau_{RD}}\right) \\ &\quad +(N_D-1)\phi_{DD}\frac{p_{DD}}{\tau_0}. \end{aligned} \tag{18}$$

Therefore, for large populations we obtain

$$\begin{pmatrix} W_R \\ W_D \end{pmatrix}=\frac{N}{\tau_0}\begin{pmatrix} \phi_{RR}p_{CC} & \phi_{RD}\left(p_{DD}+\frac{\tau_0}{\tau_{RD}}(p_{CD}-p_{DD})\right) \\ \phi_{DR}\left(p_{DD}+\frac{\tau_0}{\tau_{RD}}(p_{DC}-p_{DD})\right) & \phi_{DD}p_{DD} \end{pmatrix}\begin{pmatrix} x_R \\ x_D \end{pmatrix}. \tag{19}$$

In the following, we will study the payoff matrix

$$\begin{array}{cc} & \begin{array}{cc} R & D \end{array} \\ \begin{array}{c} R \\ D \end{array} & \begin{pmatrix} \phi_{RR}p_{CC} & \phi_{RD}\left(p_{DD}+\frac{\tau_0}{\tau_{RD}}(p_{CD}-p_{DD})\right) \\ \phi_{DR}\left(p_{DD}+\frac{\tau_0}{\tau_{RD}}(p_{DC}-p_{DD})\right) & \phi_{DD}p_{DD} \end{pmatrix} \end{array} \tag{20}$$

as if associated with the evolutionary dynamics of a well-mixed population. Remember that ϕ's in (20) are determined by Eq. (12). In addition to the entries of the 2×2 payoff matrix, we have six parameters in total, $\alpha_R, \alpha_D, \tau_{RR}, \tau_{RD}, \tau_{DD}$ and τ_0.

4. Results

Let us investigate how the frequencies of strategies R and D change under evolutionary dynamics. The simultaneous evolution of strategy and structure will depend on the time scales associated with strategy evolution (T) and structural evolution (τ_{ij}) (Pacheco et al., 2006a, b; Santos et al., 2006c). Whenever $T\ll\tau_{ij}$ strategies evolve in an immutable network, which leads to the framework investigated by Ohtsuki and Nowak (2007). Whenever $T\gg\tau_{ij}$ graph dynamics always attains a steady state before the next strategy update takes place. This limit, which has been shown to extend to a range of time scales which is wider than expected (Santos et al., 2006c; Pacheco et al., 2006b), is the novel one we shall investigate here. In the following, we always assume that $\tau_0\ll\tau_{ij}\ll T$ holds. Fig. 2 illustrates the magnitudes of the different time scales that appear in the present paper.

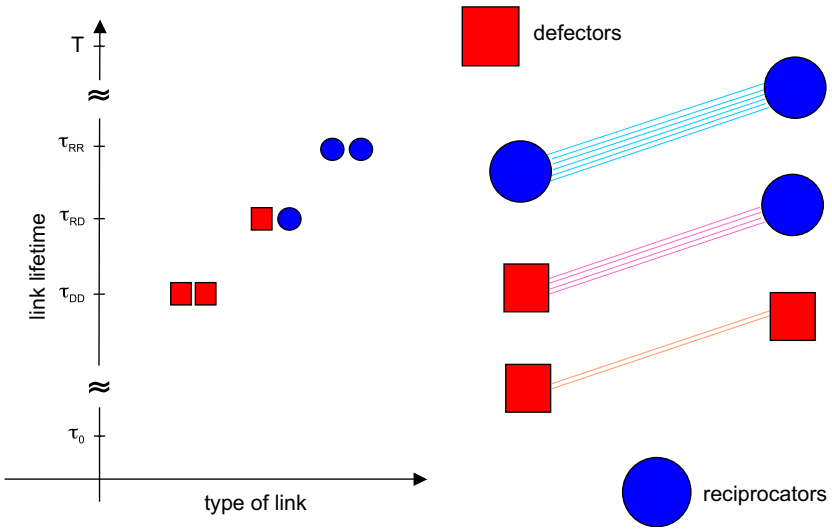

Fig. 2. Characteristic time scales associated with direct reciprocity under active linking dynamics. We assume that a typical interaction between two individuals has an average duration τ_0. For direct reciprocity to be effective, the characteristic duration of links between reciprocators (τ_{RR}), between defectors (τ_{DD}) and between reciprocators and defectors (τ_{RD}) should be larger than τ_0. Nonetheless, each of this type of links may have different characteristic lifetimes, as illustrated in the left panel. Thus, the average number of rounds between pairs of individuals with different strategies may be different, as well as the average number of links between individuals of different types, as illustrated in the right panel. Finally, our analytical results rely on the assumption that the characteristic time scale of active linking—of the order of any of $\{\tau_{RR}, \tau_{RD}, \tau_{DD}\}$—must be much smaller than that associated with strategy evolution (T), as illustrated in the left panel.

Let us study a standard Prisoner's Dilemma game

$$\begin{array}{c} \\ C \\ D \end{array}\!\!\begin{array}{c} \begin{array}{cc} C & D \end{array} \\ \begin{pmatrix} p_{CC} & p_{CD} \\ p_{DC} & p_{DD} \end{pmatrix} \end{array} = \begin{array}{c} \\ C \\ D \end{array}\!\!\begin{array}{c} \begin{array}{cc} C & D \end{array} \\ \begin{pmatrix} b-c & -c \\ b & 0 \end{pmatrix} \end{array} \tag{21}$$

(we provide the general conditions for the case in which $p_{DD} \neq 0$ in Appendix). Suppose, for simplicity, that both reciprocators and unconditional defectors share the same propensity, $\alpha \equiv \alpha_R = \alpha_D$, to form a new link. Matrix (20) simplifies to

$$\begin{array}{c} \\ R \\ D \end{array}\!\!\begin{array}{c} \begin{array}{cc} R & D \end{array} \\ \begin{pmatrix} \dfrac{\tau_{RR}}{\tau_{RR}+\alpha^{-2}}(b-c) & \dfrac{\tau_0}{\tau_{RD}+\alpha^{-2}}(-c) \\ \dfrac{\tau_0}{\tau_{RD}+\alpha^{-2}}b & 0 \end{pmatrix} \end{array}. \tag{22}$$

Multiplying (22) by $(\tau_{RD}+\alpha^{-2})/\tau_0$ gives us

$$\begin{array}{c} \\ R \\ D \end{array}\!\!\begin{array}{c} \begin{array}{cc} R & D \end{array} \\ \begin{pmatrix} s_e(b-c) & -c \\ b & 0 \end{pmatrix} \end{array}, \tag{23}$$

where

$$s_e = \frac{\tau_{RR}}{\tau_0} \cdot \frac{1+\tau_{RD}\alpha^2}{1+\tau_{RR}\alpha^2}. \tag{24}$$

5. Discussion

As seen in (23) (compare with Eq. (1)), the parameter s_e represents *the effective number of rounds of mutual cooperation*. The larger the value of s_e the easier it is for reciprocators to invade the entire population under active linking. For fixed α, τ_0 and τ_{RD}, s_e is an increasing function of τ_{RR}, which conveys the message that the more long-lived the links are between reciprocators, the better for cooperation. On the other hand, for fixed α, τ_0 and τ_{RR}, s_e is also an increasing function of τ_{RD}. In other words, the longer the lifetime of links between reciprocators and defectors, the better for cooperation. This result seems counter-intuitive. However, one may understand it if one considers the type of interaction on this link in detail. Once an *RD* link is established, the reciprocator obtains the sucker's payoff $-c$ once. After that, both individuals receive nothing. For the reciprocator, it is better to keep this link active than breaking it, since otherwise the link might be re-established again and the defector would exploit him once more. Thus, for reciprocators a long lifetime of links is advantageous. If it is an *RR* link, the mutual cooperation leads to a higher payoff. An active *RD* link avoids multiple acts of exploitation by the defector.

We now study how s_e behaves with α. When the propensity to form a new link, α, is very small, s_e becomes

$$s_e \approx \frac{\tau_{RR}}{\tau_0}, \tag{25}$$

which is exactly the same as the average number of rounds played by two reciprocators. On the other hand, when α is very large we obtain

$$s_e \approx \frac{\tau_{RD}}{\tau_0}, \tag{26}$$

which is the average number of rounds played between a reciprocator and an unconditional defector. The feasibility of cooperation relies on the propensity to form new links. When this value is high, s_e is determined by the lifetime of reciprocator–defector links. Since it is often the case in reality that $\tau_{RR} > \tau_{RD}$, we find that the smaller the propensity to establish new links the better for cooperation, given that τ_{RR} contributes more to s_e than τ_{RD}. Indeed, when the propensity to form a new link is high, defectors, who tend to lose a link more frequently than reciprocators, are able to re-establish the link quickly and exploit a reciprocator in a "new" first round, which is unfavorable for cooperation.

When we write s_e in terms of *the effective discounting factor*, w_e

$$s_e = \frac{1}{1-w_e} \quad \text{or} \quad w_e = 1 - \frac{1}{s_e}, \tag{27}$$

all the results from Eq. (3a)–(3e) hold for $w = w_e$, provided the population size N is large such that the underlying mean-field treatment used here remains valid.

For example, the reciprocating strategy is an ESS against unconditional defection whenever

$$\frac{b}{c} > \frac{1}{w_e} = \frac{s_e}{s_e - 1} \tag{28}$$

holds.

In this work we took into account the time scale associated with a single round of a repeated game, as well as the lifetimes of different types of links, together with the possibility that existing links are severed and new links are established. As a result, and in the limit in which link dynamics is faster than evolutionary dynamics of strategies, we have obtained a game-theoretical problem equivalent to a conventional evolutionary game in a well-mixed population, with a rescaled payoff matrix. This equivalence, however, is only mathematical, in the sense that the problem under consideration does not allow us to regain a well-mixed population limit easily. Clearly, the model introduced here captures some of the stylized features of social networks, in which individuals change their social ties in time, and in which rewarding links tend to last longer than unpleasant ones. On the other hand, one may expect that random rewiring does not capture the detailed mechanism(s) underlying social network dynamics (Santos et al., 2006c). While the present model allows one to assess the role of dynamic linking in the evolution of cooperation under direct reciprocity, more elaborate models should be considered in order to describe realistic social dynamics.

Our model shows that, in what concerns the evolution of cooperation under direct reciprocity, the path to cooperation is facilitated by active linking dynamics. Cooperation is most viable when links last long enough and the propensity to form new links is not too high. Certainly this model recovers the message already obtained before that sparse static graphs favor cooperation (Ohtsuki and Nowak, 2007). Yet, dynamic linking enlarges the scope of feasibility of cooperation.

6. Conclusions

Whenever single round interactions of a Prisoner's Dilemma game are swift, and the re-adjustment of different types of links occurs much faster than the re-adjustment of strategies, we find that the role of link rewiring dynamics is to introduce a rescaling of the payoff matrix associated with direct reciprocity. The rescaling obtained widens the scope of feasibility of cooperation already set forward by Ohtsuki and Nowak (2007). Without dynamical linking, reciprocators mutually cooperate in consecutive rounds in a repeated game, whereas unconditional cooperators take advantage of exploiting reciprocators only in the first round. In the traditional framework of studying the iterated Prisoner's Dilemma game, one usually assumes that the number of repeated games that one plays is the same among individuals in the population, and so is the number of the first round of repeated games. When active rewiring and time scales are explicitly taken into consideration; however, this homogeneous assumption is lost, and one must take into consideration the competition between the lifetime of reciprocator–reciprocator links and reciprocator–defector links and the rates of link formation. As shown in Fig. 1, parameter values which ensure the feasibility of cooperation under active linking dynamics lead also to social graphs exhibiting realistic features. Active linking opens a way for cooperation by direct reciprocity to evolve on these realistic networks.

Acknowledgments

Support from FCT, Portugal (J.M.P.), the "Deutsche Akademie der Naturforscher Leopoldina" (A.T., Grant no. BMBF-LPD 9901/8-134), the John Templeton Foundation and the NSF/NIH joint program in mathematical biology (NIH Grant R01GM078986) (M.A.N.) is gratefully acknowledged. The Program for Evolutionary Dynamics at Harvard University is sponsored by Jeffrey Epstein.

Appendix

For the general case in which $p_{DD} \neq 0$, Eq. (23) now reads

$$\begin{array}{c} \\ R \\ D \end{array} \begin{array}{c} \begin{array}{cc} R & D \end{array} \\ \begin{pmatrix} s_e p_{CC} & \eta p_{DD} + (p_{CD} - p_{DD}) \\ \eta p_{DD} + (p_{DC} - p_{DD}) & r_e p_{DD} \end{pmatrix} \end{array}, \tag{A.1}$$

where s_e has been defined before, $r_e = \frac{\tau_{DD}}{\tau_0} \cdot \frac{1+\tau_{RD}\alpha^2}{1+\tau_{DD}\alpha^2}$, and $\eta = \tau_{RD}/\tau_0$.

For Prisoner's Dilemma we know that $p_{DC} > p_{CC} > p_{DD} > p_{CD}$. Hence, direct reciprocity and active linking may

effectively lead to a coordination game whenever

$$s_e p_{CC} > \eta p_{DD} + (p_{DC} - p_{DD}) \quad (A.2)$$

and

$$r_e p_{DD} > \eta p_{DD} + (p_{CD} - p_{DD}). \quad (A.3)$$

References

Amaral, L.A.N., Scala, A., Barthelemy, M., Stanley, H.E., 2000. Classes of small-world networks. Proc. Natl Acad. Sci. USA 97, 11149.

Axelrod, R., 1984. The Evolution of Cooperation. Basic Books, New York, USA.

Axelrod, R., Dion, D., 1988. The further evolution of cooperation. Science 242, 1385–1390.

Axelrod, R., Hamilton, W.D., 1981. The evolution of cooperation. Science 211, 1390–1396.

Bala, V., Goyal, S., 2000. A noncooperative model of network formation. Econometrica 68, 1181–1229.

Boerlijst, M.C., Nowak, M.A., Sigmund, K., 1997. The logic of contrition. J. Theor. Biol. 185, 281–293.

Bowles, S., 2003. Microeconomics: Behavior, Institutions, and Evolution. Princeton University Press, Princeton, NJ.

Brandt, H., Hauert, C., Sigmund, K., 2003. Punishment and reputation in spatial public goods games. Proc. R. Soc. London B 270, 1099–1104.

Cressman, R., 2003. Evolutionary Dynamics and Extensive Form Games. MIT Press, Cambridge, USA.

Dorogovtsev, S.N., Mendes, J.F.F., 2003. Evolution of Networks: From Biological Nets to the Internet and WWW. Oxford University Press, Oxford.

Eguíluz, V., Zimmermann, M.G., Cela-Conde, C.J., Miguel, M.S., 2005. Cooperation and the emergence of role differentiation in the dynamics of social networks. Am. J. Sociol. 110, 977–1008.

Fudenberg, D., Maskin, E., 1990. Evolution and cooperation in noisy repeated games. Am. Econ. Rev. 80, 274–279.

Fudenberg, D., Tirole, J., 1991. Game Theory. MIT Press, Cambridge, USA.

Gintis, H., 2000. Game Theory Evolving. Princeton University Press, Princeton, USA.

Hamilton, W.D., 1964. The genetical evolution of social behavior. J. Theor. Biol. 7, 1–16, 17–52.

Hauert, C., Doebeli, M., 2004. Spatial structure often inhibits the evolution of cooperation in the snowdrift game. Nature 428, 643–646.

Hauert, C., Szabó, G., 2005. Game theory and physics. Am. J. Phys. 73, 405–414.

Hauert, C., De Monte, S., Hofbauer, J., Sigmund, K., 2002. Volunteering as red queen mechanism for cooperation in public goods game. Science 296, 1129–1132.

Hofbauer, J., Sigmund, K., 1998. Evolutionary Games and Population Dynamics. Cambridge University Press, Cambridge, USA.

Hofbauer, J., Sigmund, K., 2003. Evolutionary game dynamics. Bull. Am. Math. Soc. 40, 479–519.

Hofbauer, J., Schuster, P., Sigmund, K., 1979. Evolutionary stable strategies and game dynamics. J. Theor. Biol. 81, 609–612.

Imhof, L.A., Nowak, M.A., 2006. Evolutionary game dynamics in a Wright–Fisher process. J. Math. Biol. 52, 667–681.

Imhof, L.A., Fudenberg, D., Nowak, M.A., 2005. Evolutionary cycles of cooperation and defection. Proc. Natl Acad. Sci. USA 102, 10797–10800.

Killingback, T., Doebeli, M., 1996. Spatial evolutionary game theory: Hawks and Doves revisited. Proc. R. Soc. London B 263, 1135–1144.

Kraines, D., Kraines, V., 1988. Pavlov and the prisoner's dilemma. Theor. Decision 26, 47–79.

Lieberman, E., Hauert, C., Nowak, M.A., 2005. Evolutionary dynamics on graphs. Nature 433, 312–316.

Lindgren, K., 1991. Evolutionary phenomena in simple dynamics. In: Langton, C.G., et al. (Eds.), Artificial Life II.

Lindgren, K., Nordahl, M.G., 1994. Evolutionary dynamics of spatial games. Physica D 75, 292–309.

May, R., 1987. More evolution of cooperation. Nature 327, 15–17.

May, R.M., 2006. Network structure and the biology of populations. Trends Ecol. Evol. 21, 394.

Maynard Smith, J., 1982. Evolution and the Theory of Games. Cambridge University Press, Cambridge, USA.

Maynard Smith, J., Price, G.R., 1973. The logic of animal conflict. Nature 246, 15.

Milinski, M., 1987. Tit for tat in sticklebacks and the evolution of cooperation. Nature 325, 433–435.

Nakamaru, M., Matsuda, H., Iwasa, Y., 1997. The evolution of cooperation in a lattice structured population. J. Theor. Biol. 184, 65–81.

Nakamaru, M., Nogami, H., Iwasa, Y., 1998. Score-dependent fertility model for the evolution of cooperation in a lattice. J. Theor. Biol. 194, 101–124.

Nowak, M.A., 2006a. Evolutionary Dynamics. Harvard University Press, MA.

Nowak, M.A., 2006b. Five rules for the evolution of cooperation. Science 314, 1560–1563.

Nowak, M.A., May, R.M., 1992. Evolutionary games and spatial chaos. Nature 359, 826–829.

Nowak, M.A., May, R.M., 1993. The spatial dilemmas of evolution. Int. J. Bifurcat. Chaos 3, 35–78.

Nowak, M.A., Sigmund, K., 1992. Tit for tat in heterogeneous populations. Nature 355, 250–253.

Nowak, M.A., Sigmund, K., 1993. A strategy of win-stay, lose-shift that outperforms tit for tat in Prisoner's Dilemma. Nature 364, 56–58.

Nowak, M.A., Sigmund, K., 2004. Evolutionary dynamics of biological games. Science 303, 793–799.

Nowak, M.A., Bonhoeffer, S., May, R.M., 1994. More spatial games. Int. J. Bifurcat. Chaos 4, 33–56.

Nowak, M.A., Sasaki, A., Taylor, C., Fudenberg, D., 2004. Emergence of cooperation and evolutionary stability in finite populations. Nature 428, 646–650.

Ohtsuki, H., Nowak, M.A., 2006a. Evolutionary games on cycles. Proc. R. Soc. B 273, 2249–2256.

Ohtsuki, H., Nowak, M.A., 2006b. The replicator equation on graphs. J. Theor. Biol. 243, 86–97.

Ohtsuki, H., Nowak, M.A., 2007. Direct reciprocity on graphs. J. Theor. Biol. 247, 462–470.

Ohtsuki, H., Hauert, C., Lieberman, E., Nowak, M.A., 2006. A simple rule for the evolution of cooperation on graphs and social networks. Nature 441, 502–505.

Ohtsuki, H., Nowak, M.A., Pacheco, J., 2007a. Breaking the symmetry between interaction and replacement in evolutionary dynamics on graphs. Phys. Rev. Lett. 98, 108106.

Ohtsuki, H., Pacheco, J., Nowak, M.A., 2007b. Evolutionary graph theory: breaking the symmetry between interaction and replacement. J. Theor. Biol. 246, 681–694.

Ohtsuki, H., Bordalo, P., Nowak, M.A., 2007c. The one-third law of evolutionary dynamics. J. Theor. Biol. 249 (2007), 289–295.

Pacheco, J.M., Santos, F.C., 2005. Network dependence of the dilemmas of cooperation. In: Mendes, J.F.F. (Ed.), Science of Complex Networks: From Biology to the Internet and WWW, vol. 776. AIP Conference Proceedings, pp. 90–100.

Pacheco, J.M., Traulsen, A., Nowak, M.A., 2006a. Active linking in evolutionary games. J. Theor. Biol. 243, 437–443.

Pacheco, J.M., Traulsen, A., Nowak, M.A., 2006b. Coevolution of strategy and structure in complex networks with dynamical linking. Phys. Rev. Lett. 97, 258103.

Rapoport, A., Chammah, A.M., 1965. Prisoners Dilemma: A Study in Conflict and Cooperation. The University of Michigan Press, Ann Arbor, USA.

Samuelson, L., 1997. Evolutionary Games and Equilibrium Selection. MIT Press, Cambridge, USA.

Santos, F.C., Pacheco, J.M., 2005. Scale-free networks provide a unifying framework for the emergence of cooperation. Phys. Rev. Lett. 95, 098104.

Santos, F.C., Pacheco, J.M., 2006. A new route to the evolution of cooperation. J. Evol. Biol. 19, 726–733.

Santos, F.C., Rodrigues, J.F., Pacheco, J.M., 2005. Epidemic spreading and cooperation dynamics on homogeneous small-world networks. Phys. Rev. E 72, 056128.

Santos, F.C., Rodrigues, J.F., Pacheco, J.M., 2006a. Graph topology plays a determinant role in the evolution of cooperation. Proc. R. Soc. B Biol. Sci. 273, 51–55.

Santos, F.C., Pacheco, J.M., Lenaerts, T., 2006b. Evolutionary dynamics of social dilemmas in structured heterogeneous populations. Proc. Natl Acad. Sci. USA 103, 3490–3494.

Santos, F.C., Pacheco, J.M., Lenaerts, T., 2006c. Cooperation prevails when individuals adjust their social ties. PloS Comput. Biol. 2, 1284.

Selten, R., Hammerstein, P., 1984. Gaps in Harley's argument on evolutionarily stable learning rules and in the logic of tit-for-tat. Behav. Brain Sci. 7, 115–116.

Skyrms, B., Pemantle, R., 2000. A dynamic model of social network formation. Proc. Natl Acad. Sci. USA 97, 9340–9346.

Sugden, R., 1986. The Economics of Rights, Co-operation and Welfare. Blackwell, Oxford.

Szabó, G., Fáth, G., 2007. Evolutionary games on graphs. Phys. Rep. 446, 97–216.

Szabó, G., Hauert, C., 2002. Phase transitions and volunteering in spatial public goods games. Phys. Rev. Lett. 89, 118101.

Szabó, G., Tőke, C., 1998. Evolutionary prisoner's dilemma game on a square lattice. Phys. Rev. E 58, 69–73.

Szabó, G., Vukov, J., Szolnoki, A., 2005. Phase diagrams for an evolutionary prisoner's dilemma game on two-dimensional lattices. Phys. Rev. E 72, 047107.

Taylor, P.D., Jonker, L., 1978. Evolutionary stable strategies and game dynamics. Math. Biosci. 40, 145.

Taylor, C., Fudenberg, D., Sasaki, Nowak, M.A., 2004. Evolutionary game dynamics in finite populations. Bull. Math. Biol. 66, 1621–1644.

Traulsen, A., Nowak, M.A., Pacheco, J.M., 2006a. Stochastic dynamics of invasion and fixation. Phys. Rev. E 74, 011909.

Traulsen, A., Pacheco, J.M., Imhof, L., 2006b. Stochasticity and evolutionary stability. Phys. Rev. E 74, 021905.

Traulsen, A., Nowak, M.A., Pacheco, J.M., 2007a. Stochastic payoff evaluation increases the temperature of selection. J. Theor. Biol. 244, 349–356.

Traulsen, A., Pacheco, J.M., Nowak, M.A., 2007b. Pairwise comparison and selection temperature in evolutionary game dynamics. J. Theor. Biol. 246, 522–529.

Trivers, R.L., 1971. The evolution of reciprocal altruism. Q. Rev. Biol. 46, 35–57.

van Baalen, M., Rand, D.A., 1998. The unit of selection in viscous populations and the evolution of altruism. J. Theor. Biol. 193, 631–648.

Weibull, J., 1995. Evolutionary Game Theory. MIT Press, Cambridge, USA.

Wilson, D.S., Pollock, G.B., Dugatkin, L.A., 1992. Can altruism evolve in purely viscous populations? Evol. Ecol. 6, 331–341.

Zeeman, E.C., 1980. Population dynamics from game theory. In: Lecture Notes in Mathematics, vol. 819. Springer, Berlin.

Zimmermann, M., Eguíluz, V.M., Miguel, M.S., 2004. Coevolution of dynamical states and interactions in dynamic networks. Phys. Rev. E 69, 065102.