Chapter 16

Evolution of Cooperation in Adaptive Social Networks

Sven Van Segbroeck
COMO, Vrije Universiteit Brussel (VUB), B-1050 Brussels, Belgium

Francisco C. Santos
IRIDIA, Université Libre de Bruxelles (ULB), B-1050 Brussels, Belgium

Arne Traulsen
Max-Planck-Institute for Evolutionary Biology, D-24306 Plön, Germany

Tom Lenaerts
SWITCH, VIB and Vrije Universiteit Brussel (VUB),
B-1050 Brussels, Belgium

Jorge M. Pacheco
ATP-Group and CFTC,
Departamento de Física da Faculdade de Ciências,
P-1649-003 Lisboa Codex, Portugal

Humans are organized in societies, a phenomenon that would never have been possible without the evolution of cooperative behavior. Several mechanisms that foster this evolution have been unraveled over the years, with population structure as a prominent promoter of cooperation. Modern networks of exchange and cooperation are, however, becoming increasingly volatile, and less and less based on long-term stable structure. Here, we address how this change of paradigm affects the evolution of cooperation. We discuss analytical and numerical models in which individuals can break social ties and create new ones. Interactions are modeled as two-player dilemmas of cooperation. Once a link between two individuals has formed, the productivity of this link is evaluated. Links can be broken off at different rates. This individual capacity of forming new links or severing inconvenient ones can effectively change the nature of the game. We address random formation of new links and local linking rules as well as different individual capacities to maintain social interactions. We conclude by discussing how adaptive social networks can become an important step towards more realistic models of cultural dynamics.

16.1. Introduction

From human societies to the simplest biological systems, cooperative interactions thrive at all levels of organization. A cooperative act typically involves a cost (c) to the provider while conferring a benefit (b) to the recipient (with $b > c$) [Hamilton (1996); Trivers (1985); Wilson (1975); Axelrod and Hamilton (1981)]. Individuals try to maximize their own resources and are therefore expected to avoid paying any costs while gladly accepting all the benefits offered by others. This ubiquitous paradox is often analyzed in the framework of (evolutionary) game theory. Game theory describes systems in which the success of an individual depends on the action of others. The classical approach focused on the determination of optimal strategic behavior of rational individuals in such a static setting [von Neumann and Morgenstern (1944)]. Evolutionary game theory places this framework into a dynamical context by looking at the evolutionary dynamics in populations of players [Maynard Smith (1982)]. The expected payoff from the game is a function of the frequencies of all strategies. Successful behaviors spread in such a population. There are two interpretations of evolutionary game theory: In the conventional setting, the payoff is interpreted as biological fitness. Individuals reproduce proportional to their fitness and successful strategies spread by genetic reproduction. A second interpretation is the basis for cultural evolution in social systems: Successful behaviors are imitated with a higher probability. They spread by social learning instead of genetic reproduction. Both frameworks are captured by the same mathematical approach: The generic mathematical description of evolutionary game dynamics is the replicator equation [Taylor and Jonker (1978); Hofbauer and Sigmund (1998); Zeeman (1980)]. This system of nonlinear ordinary differential equations describes how the relative abundances (frequencies) of strategies change over time.

The assumption underlying the replicator equation is that individuals meet each other at random in infinitely large, well-mixed populations. But it also emerges in other cases, e.g. if the interaction rates between individuals are not random [Taylor and Nowak (2006)] or from a large-population approximation of evolutionary game dynamics in finite populations [Traulsen *et al.* (2005)].

However, in reality the probability to interact with someone else is not the same across a population or social community. Interactions occur on social networks which define the underlying topology of such cooperation dynamics. Initially, this line of research has focused on regular lattices [Nowak and May (1992); Herz (1994); Lindgren and Nordahl (1994); Szabó and Tőke (1998); Hauert (2002)]. More recently, more complex topologies and general networks have been considered in great detail [Vainstein and Arenzon (2001); Abramson and Kuperman (2001); Ebel and Bornholdt (2002a); Holme *et al.* (2003); Szabó and Vukov (2004); Santos and Pacheco (2005); Ohtsuki *et al.* (2006); Santos *et al.* (2006b, 2008)]. While the theoretical advances in this field are tremendous, there is so far a lack of experimental data. Designing and implementing such experiments has proven difficult and, so far, only general statements as "the probability to be generous is correlated with the number of social links of an individual" can be made [Branas-Garza *et al.* (2007)].

One important property of social networks that is seldom addressed in theoretical studies is that real world social networks are not static. Instead, we make new friends and lose touch with old ones, depending on the kind of interaction we have with them. This makes social networks an example of an adaptive network [Gross and Blasius (2008)]. The basic idea is that interactions which benefit both partners last longer than interactions where one partner is exploited by the other. Here, we discuss such an approach, which leads to analytical results in certain limits. These serve as important starting points for further developments.

16.2. Active Linking: Random Link Formation

We break down the model into two parts: Evolutionary dynamics of strategies (or behaviors) of the individuals associated with nodes in a network whose links describe social interactions. The adaptive nature of the social interactions leads to a network linking dynamics. We consider two-player games of cooperation in which individuals can choose to give help to the opponent (to cooperate, C), or to refuse to do so (to defect, D). The network is of constant size with N nodes. The number of links, however, is not constant and changes over time. There are N_C individuals that cooperate and $N_D = N - N_C$ individuals that defect.

16.2.1. *Linking dynamics*

An interaction between two players occurs if there is a link between these players. Links are formed at certain rates and have specific life-times. We denote by $X(t)$ the number of CC links at time t. Similarly, $Y(t)$ and $Z(t)$ are the number of CD and DD links at time t. The maximum possible number of CC, CD and DD links is given by $X_m = N_C(N_C - 1)/2$, $Y_m = N_C N_D$, and $Z_m = N_D(N_D - 1)/2$, respectively. Suppose cooperators form new links at rate α_C and defectors form new links at rate α_D. Thus, CC links are formed at a rate α_C^2, CD links are formed at a rate $\alpha_C \alpha_D$ and DD links are formed at a rate α_D^2. The death rates of CC, CD and DD links are given by γ_{CC}, γ_{CD} and γ_{DD}, respectively. If the number of links is large, we can model the dynamics of links by differential equations. We obtain a system of three ordinary differential equations for the number of links

$$\begin{aligned}
\dot{X} &= \alpha_C^2 (X_m - X) - \gamma_{CC} X \,, \\
\dot{Y} &= \alpha_C \alpha_D (Y_m - Y) - \gamma_{CD} Y \,, \\
\dot{Z} &= \alpha_D^2 (Z_m - Z) - \gamma_{DD} Z \,.
\end{aligned} \tag{16.1}$$

For $\alpha^2 \gg \gamma$, the network is almost complete, which recovers the results for well-mixed populations. For $\alpha^2 \ll \gamma$, the network is sparse with few links. The most

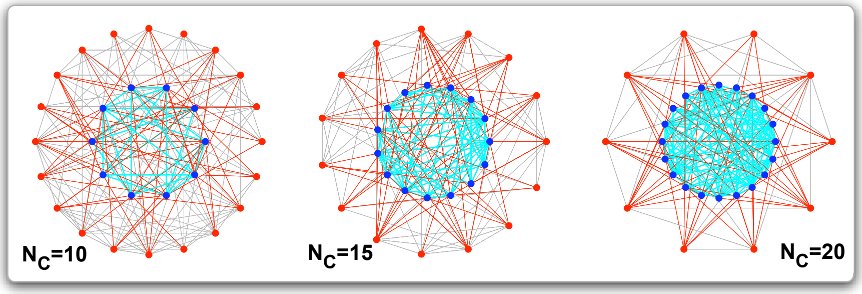

Fig. 16.1. Frequency dependent steady state dynamics. Results of active linking dynamics for a population size of $N = 30$ individuals. Cooperators are located in the "inner-rim", and are represented by blue circles, whereas defectors are located in the "outer-rim", and are represented by red circles. In this way, CC-links (solid cyan lines) live only within the "inner-rim", whereas CD-links (solid red lines) occupy the space between the rims while DD-links (solid grey lines) cross the entire region of the figure. Each panel depicts a snapshot in the steady state of the active-linking dynamics, associated with a different (and fixed) frequency of C and D players. The parameters determining the active linking dynamics are: $\alpha_C = \alpha_D = 0.5$, $\gamma_{CC} = 0.5$, $\gamma_{CD} = 0.25$ and $\gamma_{DD} = 0.5$.

interesting case we discuss below is $\alpha^2 \approx \gamma$, where the system has fixed points with intermediate ranges of X, Y and Z. Rescaling α and γ in an appropriate way (note that the equation contains squares of α and linear terms of γ) does not change the fixed points of the system, but affects the overall timescale of active linking. When this process is coupled with strategy dynamics, such changes can be crucial.

While the above is probably the simplest possibility to model linking dynamics, more sophisticated choices are possible, taking for example the number of existing links of a node into account. However, to address some general properties of the coevolution between links and strategies, we concentrate on the simplest choice first. In the steady state, the number of links of the three different types is given by

$$\begin{aligned} X^* &= X_m \frac{\alpha_C^2}{\alpha_C^2 + \gamma_{CC}} = X_m \phi_{CC} \,, \\ Y^* &= Y_m \frac{\alpha_C \alpha_D}{\alpha_C \alpha_D + \gamma_{CD}} = Y_m \phi_{CD} \,, \\ Z^* &= Z_m \frac{\alpha_D^2}{\alpha_D^2 + \gamma_{DD}} = Z_m \phi_{DD} \,. \end{aligned} \tag{16.2}$$

Here, ϕ_{CC}, ϕ_{CD}, and ϕ_{DD} are the fractions of active CC, CD and DD links in the steady states. Examples of population structures attained under steady-state dynamics for three different combinations of (N_C, N_D) are shown in Fig. 16.1.

16.2.2. *Strategy dynamics*

Next, we address the dynamics of the strategies at the nodes. We consider the stochastic dynamics of a finite population, i.e. we restrict ourselves to finite networks. We consider general two-player games of cooperation given by the payoff matrix

$$\begin{array}{cc} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} R & S \\ T & P \end{pmatrix} \end{array} . \tag{16.3}$$

Thus, a cooperator interacting with another cooperator obtains the *reward* from mutual cooperation R. Cooperating against a defector leads to the *sucker's payoff* S, whereas the defector obtains the *temptation to defect* T in such an interaction. Finally, defectors receive the *punishment* P from interactions with other defectors. A social dilemma arises when individuals are tempted to defect, although mutual cooperation would be the social optimum ($R > P$). We distinguish three generic cases of 2-player social dilemmas:

- Dominance: When $T > R > P > S$, we enter the realm of the *Prisoner's Dilemma* (PD) [Rapoport and Chammah (1965)], where cooperation is dominated by defection. The opposite scenario, when $R > T$ and $S > P$, poses no social dilemma and is referred to as a *Harmony Game* (HG) [Posch *et al.* (1999)].
- Coordination: $R > T$ and $S < P$ leads to what is called coordination or *Stag Hunt* games (SH) [Skyrms (2003)], in which it is always good to follow the strategy of the majority in the population. Except for $R + S = T + P$, one strategy has a larger basin of attraction. This strategy is called a risk dominant strategy. For $R + S > T + P$, cooperation is risk dominant.
- Coexistence: In the case of $R < T$ and $S > P$, known as a Hawk-Dove [Maynard Smith (1982)] or *Snowdrift* game (SG) [Sugden (1986); Doebeli and Hauert (2005); Hauert and Doebeli (2004)], a small minority is favored. This means that the ultimate outcome in a population of players is a mixture of strategies C and D.

From the payoff matrix, we can calculate the payoffs of the individuals, depending on the number of interactions they have with cooperators and defectors. On a complete network, the payoffs are

$$\pi_C = R(N_C - 1) + SN_D \tag{16.4}$$

and

$$\pi_D = TN_C + P(N_D - 1)\,. \tag{16.5}$$

Often, the payoffs are scaled by $1/(N-1)$, such that the payoffs do not increase with the population size. For the strategy update process defined below, this corresponds simply to a rescaling of the intensity of selection, i.e. changing the noise intensity, if all individuals have the same number of interactions. If the number of interactions is not the same for all players, the heterogeneity between players can lead to new effects [Santos *et al.* (2006b); Santos and Pacheco (2006)].

For strategy dynamics, we adopt the pairwise comparison rule [Szabó and Tőke (1998); Blume (1993)], which has been recently shown to provide a convenient framework of game dynamics at all intensities of selection [Traulsen *et al.* (2007, 2006)]. According to this rule, two individuals from the population, A and B are randomly selected for update (only the selection of mixed pairs can change the composition of the population). The strategy of A will replace that of B with a probability given by the Fermi function (from statistical physics)

$$p = \frac{1}{1 + e^{-\beta(\pi_A - \pi_B)}} \, . \tag{16.6}$$

The reverse will happen with probability $1 - p$. The quantity β, which in physics corresponds to an inverse temperature, controls the intensity of selection. For $\beta \ll 1$, we can expand the Fermi function in a Taylor series and recover weak selection, which can be viewed as a high temperature expansion of the dynamics [Nowak *et al.* (2004); Traulsen *et al.* (2007)]. For $\beta \gg 1$, the intensity of selection is high. In the limit $\beta \to \infty$, the Fermi function reduces to a step function: In this case the individual with the lower payoff will adopt the strategy of the other individual regardless of the payoff difference.

The quantity of interest in finite population dynamics is the fixation probability ρ, which is the probability that a single mutant individual of one type takes over a resident population with $N - 1$ individuals of another type.

16.2.3. *Separation of timescales*

The system of coevolving strategies and links is characterized by two timescales: One describing the linking dynamics (τ_a), the second one describing strategy dynamics (τ_e). We can obtain analytical results in two limits, where both timescales are separated. Defining the ratio $W = \tau_e/\tau_a$, separation of time scales will occur for $W \ll 1$ and $W \gg 1$.

16.2.3.1. *Fast strategy dynamics*

If strategies change fast compared to changes of the network structure, active linking does not affect strategy dynamics. Thus, the dynamics is identical to the evolutionary game dynamics on a fixed network. Such systems have been tackled by many authors for a long time [Nowak and May (1992); Herz (1994); Lindgren and Nordahl (1994); Szabó and Tőke (1998); Hauert (2002); Vainstein and Arenzon (2001); Szabó and Vukov (2004); Abramson and Kuperman (2001); Ebel and Bornholdt (2002a); Holme *et al.* (2003); Santos and Pacheco (2005); Ohtsuki *et al.* (2006); Santos *et al.* (2006b, 2008)]. The difficulty of an analytical solution for such systems is determined by the topology of the network, which corresponds to an initial condition in our case. Analytical solutions are feasible only for few topologies. One important limiting case leading to analytical solutions are complete networks corresponding to well-mixed systems. In this case, the fixation probability can be approximated by

$$\rho_C = \frac{\mathrm{erf}[\xi_1] - \mathrm{erf}[\xi_0]}{\mathrm{erf}[\xi_N] - \mathrm{erf}[\xi_0]}\,, \tag{16.7}$$

where $\mathrm{erf}(x)$ is the error function and $\xi_k = \sqrt{\frac{\beta}{u}}(ku + v)$ [Traulsen *et al.* (2006)]. We have $2u = R - S - T + P$ and $2v = -R + SN - TN + T$.

For $u \to 0$, we have $\rho_C = (1 - e^{-2\beta v})/(1 - e^{-2\beta v N})$.

If strategy dynamics is fast, the linking dynamics only becomes relevant in states where the system can no longer evolve from strategy dynamics alone, but changing the topology allows to escape from these states.

16.2.3.2. *Fast linking dynamics*

Whenever $W \gg 1$ linking dynamics is fast enough to ensure that the network will reach a steady state before the next strategy update takes place. At the steady state of the linking dynamics, the average payoffs of C and D individuals are given by

$$\pi_C = R\phi_{CC}(N_C - 1) + S\phi_{CD}N_D \tag{16.8}$$

and

$$\pi_D = T\phi_{CD}N_C + P\phi_{DD}(N_D - 1)\,. \tag{16.9}$$

Note that the effective number of interactions of cooperators and defectors can become very different if $\phi_{CC} \gg \phi_{DD}$ or vice versa. Comparing Eqs. (16.8) and (16.9) to Eqs. (16.4) and (16.5) 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

$$\begin{array}{cc} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} R\phi_{CC} & S\phi_{CD} \\ T\phi_{CD} & d\phi_{DD} \end{pmatrix} \end{array} = \begin{array}{cc} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} R' & S' \\ T' & P' \end{pmatrix} \end{array}. \tag{16.10}$$

Consequently, linking dynamics can change the nature of the game [Pacheco *et al.* (2006b)]. So far, we have only shown this in the limit where linking dynamics is much faster than strategy dynamics ($W \gg 1$). However, the result is expected to hold even when the two time scales are comparable (see below and also Refs. [Pacheco *et al.* (2006)b,a].

In general, all generic transformations are possible, as illustrated in Fig. 16.2. The transition points can be determined as follows: Strategy C is a Nash equilibrium for $R > T$. This property changes to $R' < T'$ when

$$\frac{R}{T} < \frac{\phi_{CD}}{\phi_{CC}} = \frac{\alpha_D}{\alpha_C}\,\frac{\alpha_C^2 + \gamma_{CC}}{\alpha_C\alpha_D + \gamma_{CD}}\,. \tag{16.11}$$

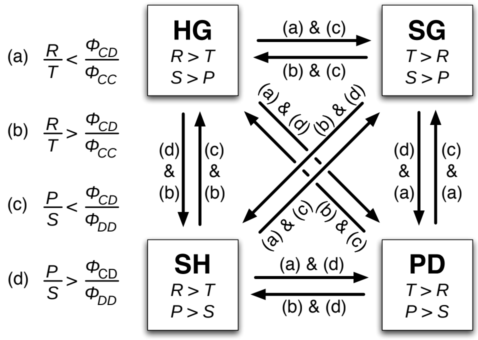

Fig. 16.2. When linking dynamics occurs much faster than strategy dynamics, the nature of the game being played changes. The arrows indicate the conditions under which a game located at the arrow start is transformed into a game located at the arrow end.

For example, ϕ_{CD} can be increased by reducing the death rate of CD links, γ_{CD}. With increasing ϕ_{CD}, the condition is fulfilled at some point. At the transition point, C is either transformed into a Nash equilibrium or loses this property. An equivalent transition for D is given by the condition

$$\frac{P}{S} < \frac{\phi_{CD}}{\phi_{DD}} = \frac{\alpha_C}{\alpha_D} \frac{\alpha_D^2 + \gamma_{DD}}{\alpha_C \alpha_D + \gamma_{CD}} . \tag{16.12}$$

However, the conditions are not entirely independent, since at least two parameters have to be varied. Usually, it is enough to vary the three link-death rates γ and fix the link-birth rates α to observe these transitions. It is also worth mentioning that, in coordination games, the transformation can change risk dominance.

16.2.4. *Comparable timescales*

As we have shown, active linking can lead to a wide range of scenarios that effectively change the character of the game. However, the analytical results have been obtained assuming time scale separation. Figure 16.3 shows the results of numerical simulations for a gradual change of the time scale ratio. Deviations from the analytical predictions are limited to a single order of magnitude. In other words, the time scale separation is not a very strong assumption and remains valid for a much wider range of parameters than expected. Even for moderate active linking, our analytical results are recovered, i.e. they hold when self-organising network structures and the evolutionary game dynamics on the network are intimately entangled. Having identified the relevance of time scale separation in a minimal model of linking dynamics, we now turn to more complex linking dynamics based on local rules.

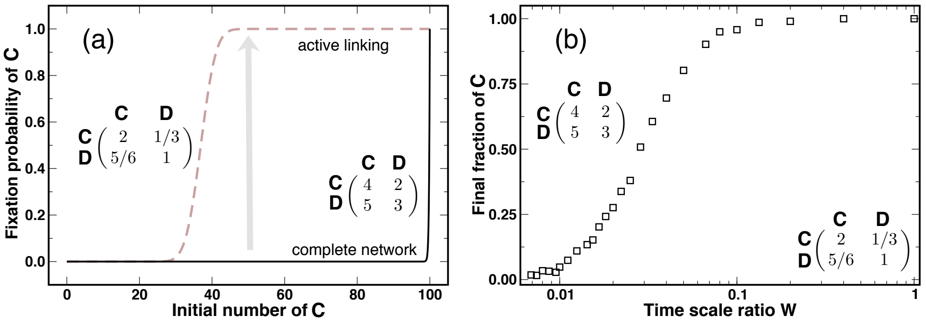

Fig. 16.3. Active linking effectively changes the payoff matrix and the nature of the game. (a) We start from a complete network without structure dynamics ($W = 0$) and a Prisoner's Dilemma game. In this case, the fixation probability of C (full line) is essentially zero for all initial numbers of C. With active linking (dashed line), the game turns into a Stag Hunt game. In this case, C becomes risk dominant and the fixation probability of C exceeds 0.5 if the initial number of C individuals is larger than 36. (b) Numerical simulations reveal the range of validity of our analytical approximations. We start from 50% cooperating individuals. For small W, cooperators never reach fixation. But already for $W = 0.1$, their fixation probability is close to one. Thus, moderate active linking is sufficient to make cooperation the dominant strategy here (averages over 100 realizations, population size $N = 100$, intensity of selection $\beta = 0.05$, $\alpha_C = \alpha_D = 0.4$, $\gamma_{CC} = 0.16$, $\gamma_{CD} = 0.80$ and $\gamma_{DD} = 0.32$.)

16.3. Individual Based Linking Dynamics: Local Link Formation

In the model discussed in Section 16.2, we have a fluctuating number of links and analytical results in the two limits where the time scale of linking dynamics and strategy dynamics are well separated, allowing for the mean-field treatment considered. We now introduce an alternative description in which the number of links is conserved, but in which decision to maintain or rewire a link results both from individual preference in the choice of partners and negotiation between individuals linked [Santos *et al.* (2006a); Van Segbroeck *et al.* (2008)]. Such an individual based decision making cannot be dealt with at a mean-field level and calls for a numerical implementation.

16.3.1. *Specification of the linking dynamics*

To reduce the number of parameters, let us start by restricting the space of possible games by fixing $R = 1$ and $P = 0$, while $-1 \leq S \leq 1$ and $0 \leq T \leq 2$.

$$\begin{array}{cc} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} 1 & S \\ T & 0 \end{pmatrix} \end{array}. \qquad (16.13)$$

This spans the four dynamical outcomes introduced before: a) HG ($S > 0$ and $T < 1$); b) SG ($S > 0$ and $T > 1$); c) SH ($S < 0$ and $T < 1$) and d) PD ($S < 0$ and $T > 1$) (see Section 16.2.2).

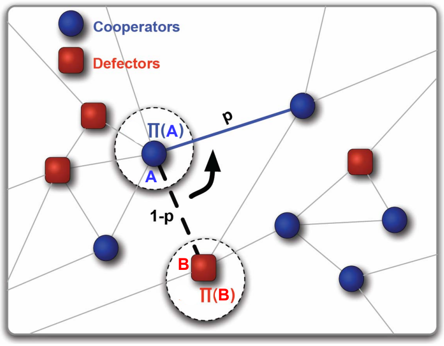

Fig. 16.4. Readjusting social ties. Cooperators and defectors interact via the links of a network. B is satisfied, since A is a cooperator ($T > 0$). On the other hand, A is unsatisfied with this situation ($S < 1$). Therefore, A wants to change the link whereas B does not. The action taken is contingent on the fitness π_A and π_B of A and B, respectively. With probability p (see Eq. (16.6)), A redirects the link to a random neighbor of B. With probability $1 - p$, A stays linked to B. Finally, if both players are dissatisfied, the same methodology is used to decide who keeps the connection.

Because $S \leq 1$ and $T \geq 0$, the payoff against a cooperator is always higher than the payoff against a defector, cf. Eq. (16.13). Thus, interacting with a cooperator is always the best possible option. Consequently, every individual will be satisfied when connected to a C and dissatisfied otherwise. Keeping the total number of links constant, all individuals are now able to decide, on an equal footing, those ties that they want to maintain and those they want to change. The co-evolution between strategy and network structure is therefore shaped by individual preferences towards interacting with one of the two strategies [Santos *et al.* (2006a)]. Figure 16.4 illustrates the process. If A is satisfied, she will decide to maintain the link. If dissatisfied, then she may compete with B to rewire the link (see Fig. 16.4), rewiring being attempted to a random neighbor of B. Thus, the loser in a competition for a link loses an interaction. This paves the way for the evolution of a degree-heterogeneous network. The intuition behind this reasoning relies on the fact that agents, equipped with limited knowledge and scope, look for new social ties by proxy [Kossinets and Watts (2006)]. Such a procedure can only be treated numerically and does no longer lead to a simple rescaling of a payoff matrix as the mechanism discussed in Section 16.2. On the other hand, it introduces some features characteristic of realistic social networks.

The fact that all individuals naturally seek to establish links with cooperating individuals, creates possible conflicts of interests as illustrated in Fig. 16.4. For instance, B is satisfied, because she can profit from A. Obviously, A is not satisfied and would prefer to seek for another cooperator. Decision is contingent on the payoff π_A and π_B of A and B, respectively. With probability $p = [1+e^{-\beta[\pi_A - \pi_B]}]^{-1}$ (also used in the strategy update, cf. Eq. (16.6)), A redirects the link to a random neighbor of B. With probability $1-p$, A stays linked to B. Whenever both A and B

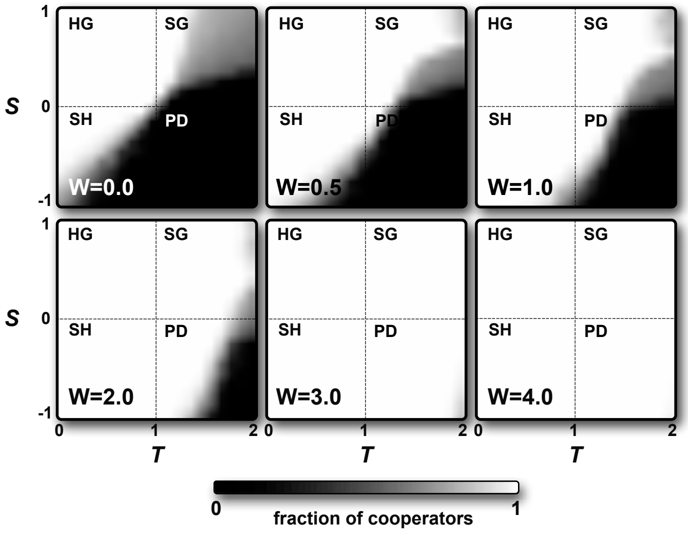

Fig. 16.5. Final frequency of cooperators in all games for different time-scale ratios between strategy and structure dynamics. Results for the fraction of successful evolutionary runs ending in 100% of individuals with strategy C for different values of the time scale ratio W, starting from 50% of each strategy. We study the four different games in the area $2 \geq T \geq 0$ and $1 \geq S \geq -1$: HG, SG, SH and PD (see Section 16.2.2). For $W = 0$ ($N = 10^3$, $z = 30$ and $\beta = 0.005$), the results fit the predictions from well-mixed populations, although individuals only interact with a small subset of the population. With increasing W (faster structure dynamics), the rate at which individuals readjust their ties increases, and so does the viability of cooperators. Above a critical value $W_{critical} \sim 4.0$ (see also Fig. 16.6), cooperators efficiently wipe out defectors. For the strategy evolution dynamics adopted here (pairwise comparison, see Section 16.2.2), and according to [Ohtsuki *et al.* (2006)], cooperators would never be favored in static networks.

are satisfied, nothing happens. When both A and B are unsatisfied, rewiring takes place such that the new link keeps attached to A with probability p and attached to B with probability $1 - p$. Thus, the more successful individual keeps the link with higher probability.

16.3.2. *Numerical results*

As previously, this model establishes a coupling between individual strategy dynamics and population structure dynamics. This leads necessarily to a time scale associated with strategy evolution, τ_e and a second associated with structure evolution, τ_a. When the ratio $W = \tau_e/\tau_a$ approaches 0, the network dynamics is irrelevant and we recover the fast strategy dynamics of Section 16.2.3.1. On the other hand, with increasing W, individuals become apt to adapt their ties and form a degree-heterogeneous network with increasing efficiency.

The contour plots in Fig. 16.5 illustrate the final fraction of cooperators for different values of the ratio W in networks with average connectivity $z = 30$ (this

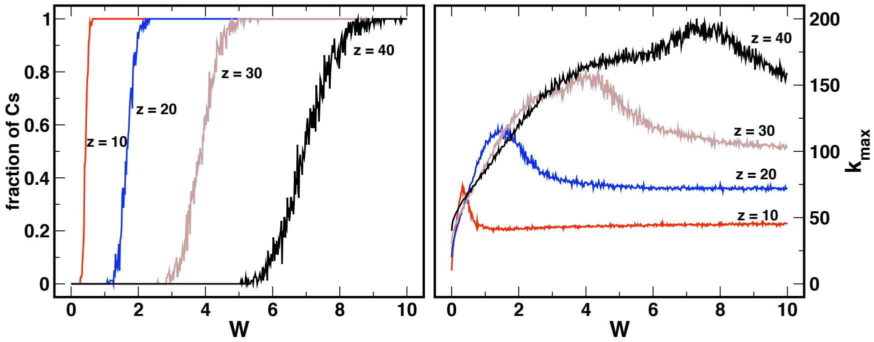

Fig. 16.6. Co-evolution of strategies and links in the game region in which defectors should dominate for different time-scales. Left panel: Final frequency of cooperators at end as a function of W for different average connectivity z. For each average connectivity z, there is a critical value of the time scale ratio W – $W_{critical}$ – above which cooperators wipe out defectors. Right panel: Connectivity k_{max} of the largest hub in the network, as a function of the time scale ratio W. With increasing z, $W_{critical}$ increases. In all cases, the heterogeneity of the associated network becomes maximal at $W_{critical}$. For higher values of W, the heterogeneity decreases again when defectors decrease in frequency. For high values of W, defectors are wiped out and only the heterogeneity generated by the rewiring mechanism in a neutral system prevails (Payoffs $R = 1$, $T = 2$, $S = -1$ and $P = 0$. Intensity of selection $\beta = 0.005$).

value reflects the mean value of the average connectivities reported in [Dorogotsev and Mendes (2003)] for socials networks). We plot the fraction of cooperators who survive evolution, averaged over 100 independent realizations for the same values of the game payoff entries (T, S) and the time scale ratio W. For $W = 0$ the results reproduce, as expected [Santos *et al.* (2006b)], the predictions for finite, well-mixed populations. Yet, with increasing W, cooperators gain an advantage, as they can terminate their undesirable interactions with defectors. Rewiring changes the strategy dynamics and paves the way for a radically distinct evolutionary outcome in which cooperators are now able to dominate for the entire range of games. Under structural dynamics, cooperators can cut their links to defectors, which gives them an advantage compared to the situation on a static network. The swifter the response of individuals to the nature of their ties, the easier it gets for cooperators to wipe out defectors. Note further that cooperators already dominate defectors for $W = 4$, corresponding to a situation far from the time-scale separation conditions defined in Section 16.2.3.

Additional insight is provided in Fig. 16.6 (left panel), where we show how cooperation dominates defection as a function of W when $T = 2$ and $S = -1$ (lower right corner of the panels in Fig. 16.5), which represents the most challenging case for cooperators. Different values of the average connectivity z are shown. For small W, cooperators have no chance. Their fate changes as W approaches a critical value $W_{critical}$ — which increases monotonically with connectivity z — cooperators wiping out defectors above $W_{critical}$ (the increase of $W_{critical}$ with z is expected, since there are more links to be rewired; in practice, $W_{critical}$ is determined as the value of W at which the frequency of cooperators crosses 50%). Thus, the evolutionary outcome and effective game at stake relies on the capacity of individuals to adjust to adverse ties.

Figure 16.6 also provides evidence of the detailed interplay between strategy and structure. On one hand, strategy updating promotes a local assortment of strategies, since Cs *breed* Cs and Ds *breed* Ds. On the other hand, under structural updating, one is promoting local assortative interactions between cooperators (that is, CC-links) and disassortative interactions between defectors and cooperators (that is, CD-links), which constitute *favorable steps* for cooperators, from an individual point of view. Clearly, when simultaneously active, strategy update will reinforce assortativity among Cs, but will inhibit disassortativity between Ds and Cs, which overall will promote the dominance of cooperation over defection.

16.3.3. *Graph structures under individual based linking dynamics*

For any $W > 0$, individual choices lead to heterogeneous graphs in which some individuals interact more and more often than others. The overall onset of increase of heterogeneity qualitatively follows the wave of cooperation dominance shown in Fig. 16.5 [Santos *et al.* (2006a)]. In fact, the overall heterogeneity of the graph increases as W increases reaching a maximum at $W_{critical}$, above which heterogeneity decreases again down to a stationary value determined by neutral dynamics in a system with one strategy only [Santos *et al.* (2006a)]. The results shown suggest that the adaptive dynamics of social ties introduced here coupled with social dilemmas accounts for the heterogeneities observed in realistic social networks [Amaral *et al.* (2000)].

16.4. Local Linking with Individual Linking Time Scales

In the two previous models, the linking dynamics proceeds population-wide at the same speed, determined by W. This implies that all individuals are assumed to react in the same way to adverse social ties. It is commonly observed, however, that different individuals respond differently to the same situation [Rubin (2002); Ridley (2003); Buchan *et al.* (2002)] — some have the tendency to swiftly change partner, whereas others remain connected even though they are dissatisfied with their partners' behavior. Extending the linking dynamics introduced in the previous section allows us to represent this kind of behavioral diversity [Van Segbroeck *et al.* (2008, 2009)].

16.4.1. *Specification of the linking dynamics*

We adopt the same parameterization of 2×2 games as in Section 16.3 and fix the difference between mutual cooperation and mutual defection to 1, making $R = 1$ and $P = 0$. We focus on the PD in which $S < 0$ and $T > 1$, i.e. when defection

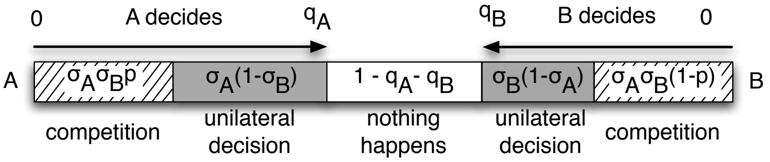

Fig. 16.7. Decision on whose preference (either redirect the link when dissatisfied or maintain the link when satisfied) prevails in case of unilateral or mutual dissatisfaction among the interacting individuals A and B. The different colors indicate the three possible outcomes of the rewiring competition between the two individuals. First, as each individual competes for the link with probability given by her parameter σ, A and B compete both with probability $\sigma_A\sigma_B$ (indicated by the hatched zones). In this case, decision is determined by the payoff-dependent probability p (see Eq. (16.6)). Second, when only one of the individuals competes (indicated by the gray zones), this individual takes a unilateral decision. In total, A's preference prevails with probability $q_A = \sigma_A\sigma_B p + \sigma_A[1 - \sigma_B]$, B's preference with probability $q_B = \sigma_A\sigma_B(1 - p) + \sigma_B[1 - \sigma_A]$. Finally, the white zone indicates the situation in which both individuals refuse to compete, such that the link remains unchanged.

is expected to dominate, although the model could easily be applied to SH and SG games as well. Since $S \leq 1$ and $T \geq 0$, every individual prefers interacting with cooperators to interacting with defectors. Consequently, everyone attempts to maintain links with cooperators, but change links with defectors. However, unlike before, individuals are now not necessarily equally willing to engage in these conflicts. We represent their eagerness to do so by introducing an individual characteristic $\sigma \in [0, 1]$. Individuals with lower values of σ will be more resilient to change, and hence can also be viewed as more loyal towards their interaction partners. In this way, the behavior of each individual is uniquely defined by two parameters: the game strategy (C or D) and the topological strategy (σ). Note that these quantities are both transferred during strategy update. Thus, both aspects of a players strategy are subject to evolution and change over time.

Figure 16.7 illustrates how σ influences the rewiring decisions. Consider two connected individuals A and B, whose topological strategies are given by σ_A and σ_B. A potential conflict about the link arises as soon as at least one of the individuals is dissatisfied about the interaction. If this is the case, both A and B decide independently of each other whether they will compete for the link or not. Each individual competes with probability given by her topological strategy σ. As such, σ_A and σ_B define three possible outcomes for the competition over the link between A and B. First, both A and B compete for the link with probability $\sigma_A\sigma_B$. The individuals' payoffs π_A and π_B ultimately dictate the winner of this conflict. The decision of A prevails with probability $p = [1 + e^{-\beta[\pi_A - \pi_B]}]^{-1}$, the decision of B with probability $1 - p$. If decision is to redirect the link, the new partner is chosen randomly from the immediate neighbors of the former partner. Second, A competes while B does not with probability $\sigma_A[1 - \sigma_B]$. In this case, A decides the fate of the link unilaterally. Similarly, when B competes but A does not (this happens with probability $\sigma_B[1 - \sigma_A]$), B decides the fate of the link unilaterally.

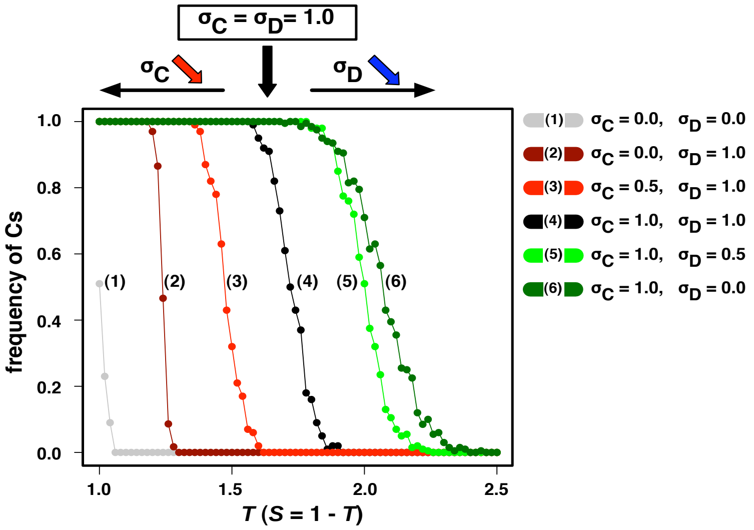

Fig. 16.8. The effect of a strategy-dependent willingness to change σ on the final frequency of cooperators. Results show the fraction of evolutionary runs ending in 100% of cooperating individuals, starting from 50% of each strategy, and this in relation to the game parameter T. The other game parameter S is chosen such that $T + S = 1$ is satisfied, bringing us into the realm of the PD. The situation in which all individuals are equally willing to react to adverse ties ($\sigma_C = \sigma_D = 1.0$) serves as a baseline. Reducing σ_D makes it easier for Cs to wipe out Ds. Reducing σ_C, on the other hand, has the opposite effect ($W = 2.5$, $N = 10^3$, $z = 30$, $\beta = 0.005$).

Hence, both individuals have the opportunity for a unilateral decision. Taken together, A's decision prevails with probability $q_A = \sigma_A \sigma_B p + \sigma_A[1 - \sigma_B]$ and B's decision with probability $q_B = \sigma_A \sigma_B (1 - p) + \sigma_B[1 - \sigma_A]$. Finally, the link remains untouched with probability $(1 - \sigma_A)(1 - \sigma_B)$, since no individual competes for the link. This last possibility encompasses the situation in which the social tie is maintained despite, e.g. mutual dissatisfaction. Overall, σ introduces a simple means to study the evolution of each individual's willingness to sever adverse ties. On the one hand, when all individuals have $\sigma = 0$, no links are rewired, reducing the population to a static society. On the other hand, when σ is maximal ($= 1$), the limits investigated in the previous section are recovered.

16.4.2. *Numerical results*

We start by associating the topological strategy σ of an individual with her strategy in the game. This means that individuals with the same game strategy will also have the same topological strategy. In the active linking model of Section 16.2, this is also included, as we assume that the propensity to form links and the lifetime of links is determined by the strategies.

When Ds are less eager to change partner ($\sigma_D = 0.5$ and $\sigma_D = 0.0$) than Cs ($\sigma_C = 1.0$), cooperators ensure the stability of favorable interactions while avoiding adverse ones more swiftly. This makes local assortment of Cs more effective, enhancing the feasibility of Cs' survival, as shown in Fig. 16.8. When Cs' willingness to change is low or absent ($\sigma_C = 0.5$ and $\sigma_C = 0.0$) compared to Ds ($\sigma_D = 1.0$), Cs' chances decrease with respect to the situation in which Cs and Ds react equally swift to adverse ties ($\sigma_C = \sigma_D = 1.0$). Comparing these results with those in which all social ties remain immutable ($\sigma_C = \sigma_D = 0.0$) does, however, show that the rewiring of DD links alone is already beneficial for cooperation.

The rewiring of links, no matter which ones, creates heterogeneous networks that are known to provide cooperators with an environment in which they may acquire an advantage over defectors. Thus, even when cooperators are resilient to change, their behavior prospers at the expense of defectors' greed.

From these results, one might expect that swift reaction to adverse social ties will evolve when σ is considered as an evolutionary trait. This intuition does, however, not always hold. We start each evolutionary run by selecting each individual's σ from a uniform distribution. We analyze the distribution of σ at the end of the evolutionary process, when the population reaches fixation (i.e., all individuals adopt the same game strategy). The lines in Fig. 16.9 correspond to the cumulative distribution $C(\sigma)$ of σ ($C(\sigma_0)$ being defined as the fraction of individuals with $\sigma > \sigma_0$) for both C (solid lines) and D individuals (dashed lines). The initial distributions of σ lead to the black diagonal line; the final distributions are shown for different values of the game parameter T. In the regime where cooperators dominate

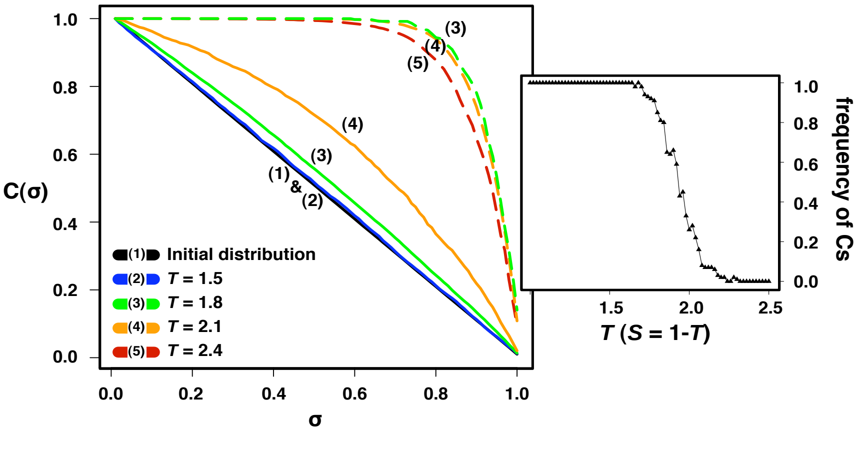

Fig. 16.9. Evolution of σ for cooperators and defectors. The solid (dashed) lines show the fraction of cooperators (defectors) having an eagerness to change links larger than σ, and this for different values of T ($W = 5$, $\beta = 0.005$, $N = 10^3$, $z = 30$). The inset provides the fraction of runs ending in 100% of cooperators as a function of T. The values of σ are uniformly distributed in $[0, 1]$ at the start of each evolution, as indicated in black. Cooperators that react swiftly to adverse ties are only favored by natural selection when defectors start to become competitive ($1.8 \leq T \leq 2.1$). Swift defectors, on the other hand, are always selected, but the strength of this selection pressure drops as T increases. $C(\sigma_0)$ is defined as the fraction of individuals who have $\sigma \geq \sigma_0$.

($T < 1.8$), the incentive to change is low since many social ties rely on mutual satisfaction. Hence, the distribution of σ over all individuals hardly changes. For higher values of T ($1.8 \leq T \leq 2.1$) a transition occurs from cooperator dominance to defector dominance. Competition becomes fierce and it pays to respond swiftly to adverse ties, as evidenced by an increase of $C(\sigma)$ in Fig. 16.9. Ds are, however, subject to a much stronger pressure to change their links than Cs, since they can never establish social ties under mutual agreement. Thus, only Ds with high σ survive. As a consequence, defectors end up to react promptly to adverse ties, whereas cooperators will always be rather resilient to change. For even larger values of T (> 2.1), defection dominates and evolutionary competition of linking dynamics fades away. As a result, the incentive to increase swiftness reduces, a feature which is indeed reflected in the behavior of $C(\sigma)$.

16.5. Discussion

Our analysis has been limited to one-shot games. In other words, individuals interact once during the lifetime of a link as if they have never met before. But in repeated interactions, more possibilities exist. If I only take into account your behavior in the last interaction, there are already $2^2 = 4$ strategies. Since the number of strategies grows rapidly with memory [Lindgren (1991); Ebel and Bornholdt (2002b)], one often considers so called trigger strategies in which individuals keep their behavior unchanged until they are faced with an unsatisfactory partner for the first time. Such strategies can be implemented into our active linking framework, assuming that individuals act repeatedly as long as a link between them is present. This procedure leads to analytical results for evolutionary stability under active linking even in the context of repeated games [Pacheco *et al.* (2008)].

Other studies have shown numerically that network dynamics can significantly help dominated strategies. Even if only the dominant strategy can locally affect the network structure, this can help the dominated strategy under certain linking rules that put restrictions on mutual interactions of the dominant strategy [Zimmermann *et al.* (2005); Zimmermann and Eguíluz (2005); Biely *et al.* (2007)]. A recent study for growing networks has shown that the defectors in the PD have an advantage as long as a network is growing by preferential attachment. Once network growth is stopped, the cooperator strategy increases in frequency [Poncela *et al.* (2008)].

To sum up, by equipping individuals with the capacity to control the number, nature and duration of their interactions with others, we introduce an adaptive network dynamics. This leads to surprising and diverse new game dynamics and realistic social structures. We have presented approaches of how to implement network dynamics. The first one, active linking, allows to define differential equations for the numbers of links, which leads to analytical results. The second approach, individual based linking dynamics, is implemented numerically and leads to network features of empirical social networks. Both cases provide a clear and insightful message: co-evolution of population structure with individual strategy provides an efficient mechanism for the evolution of cooperation in one-shot dilemmas. Moreover, if the willingness to sever undesirable connections is also regarded as part of the individual strategy, the same principles provide an evolutionary basis for the decision of adjusting social ties. For example, in the PD cooperators evolve to maintain their interactions. But defectors are forced to seek new partners frequently, because long term relationships with defectors are undesirable.

The consideration of adaptive social networks is an important step towards more realistic models of social interactions in structured populations. Coupling the dynamics *on* networks with the dynamics *of* networks leads to emergent new phenomena outside the classical considerations of social dynamics on static networks.

References

Abramson, G. and Kuperman, M. (2001). Social games in a social network, *Phys. Rev. E* **63**, p. 030901(R).

Amaral, L. A. N., Scala, A., Barthélémy, M. and Stanley, H. E. (2000). Classes of small-world networks, *Proc. Natl. Acad. Sci. U.S.A.* **97**, 21, pp. 11149–11152.

Axelrod, R. and Hamilton, W. D. (1981). The evolution of cooperation, *Science* **211**, pp. 1390–1396.

Biely, C., Dragosits, K. and Thurner, S. (2007). The prisoner's dilemma on co-evolving networks under perfect rationality, *Phyica D* **228**, pp. 40–48.

Blume, L. E. (1993). The statistical mechanics of strategic interaction, *Games and Economic Behavior* **4**, pp. 387–424.

Branas-Garza, P., Cobo-Reyes, R., Espinosa, M. P., Jiménez, N. and Ponti, G. (2007). Altruism in the (social) network, *working paper, available at EconPapers* .

Buchan, N., Croson, R. and Dawes, R. (2002). Swift neighbors and persistent strangers: A cross-cultural investigation of trust and reciprocity in . . . , *American Journal of Sociology* **108**, 1, pp. 168–206.

Doebeli, M. and Hauert, C. (2005). Models of cooperation based on the prisoner's dilemma and the snowdrift game, *Ecology Letters* **8**, pp. 748–766.

Dorogotsev, S. and Mendes, J. (2003). *Evolution of networks: From biological nets to the Internet and WWW* (Oxford University Press).

Ebel, H. and Bornholdt, S. (2002a). Coevolutionary games on networks, *Phys. Rev. E* **66**, p. 056118.

Ebel, H. and Bornholdt, S. (2002b). Evolutionary games and the emergence of complex networks, *cond-mat/0211666* .

Gross, T. and Blasius, B. (2008). Adaptive coevolutionary networks – a review, *Interface* **5**, pp. 259–271.

Hamilton, W. D. (1996). *Narrow Roads of Gene Land Vol.1* (Freeman, New York).

Hauert, C. (2002). Effects of space in 2x2 games, *Int. J. Bifurcation and Chaos Appl. Sci. Eng.* **12**, pp. 1531–1548.

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

Herz, A. V. M. (1994). Collective phenomena in spatially extended evolutionary games, *J. Theor. Biol.* **169**, pp. 65–87.

Hofbauer, J. and Sigmund, K. (1998). *Evolutionary Games and Population Dynamics* (Cambridge University Press, Cambridge).

Holme, P., Trusina, A., Kim, B. J. and Minnhagen, P. (2003). Prisoner's Dilemma in real-world acquaintance networks: Spikes and quasiequilibria induced by the interplay between structure and dynamics, *Phys. Rev. E* **68**, p. 030901(R).

Kossinets, G. and Watts, D. J. (2006). Empirical analysis of an evolving social network, *Science* **311**.

Lindgren, K. (1991). Evolutionary phenomena in simple dynamics, in C. G. Langton, C. Taylor, J. D. Farmer and S. Rasmussen (eds.), *Artificial Life II. SFI Studies in the Science of Complexity Vol. X* (Addison-Wesley, Redwood City), pp. 295–312.

Lindgren, K. and Nordahl, M. G. (1994). Evolutionary dynamics of spatial games, *Physica D* **75**, pp. 292–309.

Maynard Smith, J. (1982). *Evolution and the Theory of Games* (Cambridge University Press, Cambridge).

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

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

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

Pacheco, J. M., Traulsen, A. and Nowak, M. A. (2006a). Active linking in evolutionary games, *Jour. Theor. Biol.* **243**, pp. 437–443.

Pacheco, J. M., Traulsen, A. and Nowak, M. A. (2006b). Co-evolution of strategy and structure in complex networks with dynamical linking, *Phys. Rev. Lett.* **97**, p. 258103.

Pacheco, J. M., Traulsen, A., Ohtsuki, H. and Nowak, M. A. (2008). Repeated games and direct reciprocity under active linking, *J. Theor. Biol.* **250**, pp. 723–731.

Poncela, J., Gómez-Gardeñes, J., Floría, L. A., Sánchez, A. and Moreno, Y. (2008). Complex cooperative networks from evolutionary preferential attachment, *PLoS One* **3(6)**, p. e2449.

Posch, M., Pichler, A. and Sigmund, K. (1999). The efficiency of adapting aspiration levels, *Proc. Roy. Soc. Lond. B* **266**, pp. 1427–1435.

Rapoport, A. and Chammah, A. M. (1965). *Prisoner's Dilemma* (Univ. of Michigan Press, Ann Arbor).

Ridley, M. (2003). *Nature Via Nurture: Genes, Experience and What Makes Us Human* (HarperCollins Publishers).

Rubin, P. (2002). *Darwinian Politics: The Evolutionary Origin of Freedom* (Rutgers University Press, New Jersey).

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

Santos, F. C. and Pacheco, J. M. (2006). A new route to the evolution of cooperation, *Jour. Evol. Biol.* **19**, pp. 726–733.

Santos, F. C., Pacheco, J. M. and Lenaerts, T. (2006a). Cooperation prevails when individuals adjust their social ties, *PLoS Comput. Biol.* **2**, pp. 1284–1291.

Santos, F. C., Pacheco, J. M. and Lenaerts, T. (2006b). Evolutionary dynamics of social dilemmas in structured heterogeneous populations. *Proc. Natl. Acad. Sci. U.S.A.* **103**, pp. 3490–3494.

Santos, F. C., Santos, M. D. and Pacheco, J. M. (2008). Social diversity promotes the emergence of cooperation in public goods games, *Nature* **454**, pp. 213–216.

Skyrms, B. (2003). *The Stag-Hunt Game and the Evolution of Social Structure* (Cambridge University Press, Cambridge).

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

Szabó, G. and Tőke, C. (1998). Evolutionary Prisoner's Dilemma game on a square lattice, *Phys. Rev. E* **58**, p. 69.

Szabó, G. and Vukov, J. (2004). Cooperation for volunteering and partially random partnerships, *Phys. Rev. E* **69**, p. 036107.

Taylor, C. and Nowak, M. A. (2006). Evolutionary game dynamics with non-uniform interaction rates, *Theoretical Population Biology* **69**, pp. 243–252.

Taylor, P. D. and Jonker, L. (1978). Evolutionary stable strategies and game dynamics, *Math. Biosci.* **40**, pp. 145–156.

Traulsen, A., Claussen, J. C. and Hauert, C. (2005). Coevolutionary dynamics: From finite to infinite populations, *Phys. Rev. Lett.* **95**, p. 238701.

Traulsen, A., Nowak, M. A. and Pacheco, J. M. (2006). Stochastic dynamics of invasion and fixation, *Phys. Rev. E* **74**, p. 11909.

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

Trivers, R. (1985). *Social Evolution* (Benjamin Cummings, Menlon Park).

Vainstein, M. H. and Arenzon, J. J. (2001). Disordered environments in spatial games, *Phys. Rev. E* **64**, p. 051905.

Van Segbroeck, S., Santos, F. C., Nowé A., Pacheco, J. M. and Lenaerts, T. (2008). The evolution of prompt reaction to adverse ties, *BMC Evolutionary Biology*, **8**, p. 287.

Van Segbroeck, S., Santos, F. C., Lenaerts, T. and Pacheco, J. M. (2009). Reacting differently to adverse ties promotes cooperation in social networks, *Phys. Rev. Lett.* **102**, p. 058105.

von Neumann, J. and Morgenstern, O. (1944). *Theory of Games and Economic Behavior* (Princeton University Press, Princeton).

Wilson, E. O. (1975). *Sociobiology* (Harvard University Press, Cambridge, Massachusetts).

Zeeman, E. C. (1980). Population dynamics from game theory, *Lecture Notes in Mathematics*, p. 819.

Zimmermann, M. G. and Eguíluz, V. M. (2005). Cooperation, social networks, and the emergence of leadership in a prisoner's dilemma with adaptive local interactions, *Phys. Rev. E* **72**, p. 056118.

Zimmermann, M. G., Eguíluz, V. M. and San Miguel, M. (2005). Cooperation and emergence of role differentiation in the dynamics of social networks, *Am. J. Soc.* **110**, p. 977.