Evolving cooperation

Martin A. Nowak [a,b,c,]*

[a] *Program for Evolutionary Dynamics, Harvard University, Cambridge, MA 02138, USA*
[b] *Department of Mathematics, Harvard University, Cambridge, MA 02138, USA*
[c] *Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA 02138, USA*

This article is a brief introduction to the special issue 'Evolution of cooperation' published by the Journal of Theoretical Biology to mark its 50th anniversary. Cooperation is a favorite topic among evolutionary biologists because it seems to be at variance with natural selection. Why should one individual help another who is a potential competitor in the struggle for survival? Yet cooperation is abundant in nature and appears to be involved in all great constructive steps of life on earth. Here I propose a definition for games that are cooperative dilemmas. The Prisoner's Dilemma represents the most stringent situation, where natural selection opposes cooperation unless a mechanism for the evolution of cooperation is at work. In relaxed social dilemmas some cooperation can evolve even without a mechanism, but a mechanism would tend to augment the level of cooperation or facilitate its emergence. I discuss five mechanisms: direct reciprocity, indirect reciprocity, spatial selection, multi-level selection and kin selection. These mechanisms can work separately and together to promote evolution of cooperation. I give a short overview of the papers in this issue and provide an outlook of some of the goals that might lie ahead.

Biologists are interested in cooperation, because it seems to be the antithesis to the competition that is fundamental to natural selection. Why should one individual help another who is a competitor in the struggle for survival? Yet cooperation is abundant in nature. It can be seen among viruses, bacteria, other microorganisms, animals, plants and humans. The evolutionary processes which have led to the eukaryotic cell, to multi-cellular organisms, to social insects and to human society are all based to some extent on cooperation.

Cooperation is a key aspect of social evolution, where interactions among individuals affect reproductive success. The standard mathematical approaches for studying social behavior are offered by game theory (Harsanyi and Selten, 1988; Fudenberg and Tirole, 1991; Osborne and Rubinstein, 1994; Samuelson, 1997; Camerer, 2003) and evolutionary game theory (Maynard Smith, 1982; Hofbauer and Sigmund, 1988, 1998, 2003; Weibull, 1995; Skyrms, 1996; Dugatkin and Reeve, 1998; Cressman, 2003; Nowak and Sigmund, 2004; Nowak et al., 2004; Taylor et al.,

2004; Nowak, 2006; Antal et al., 2009a; Sigmund, 2010; Helbing, 2011). Understanding the genetic evolution of behavior requires the interaction between evolutionary game theory and population genetics.

1. What is cooperation?

Consider a game between two strategies, C and D, given by the payoff matrix

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

When does it make sense to call strategy C 'cooperation' and strategy D 'defection'? In other words when is the game a 'cooperative dilemma'?

We can consider the following definition (see also Hauert et al., 2006): the game is a cooperative dilemma if (i) two cooperators get a higher payoff than two defectors, $R > P$, and (ii) yet there is an incentive to defect. This incentive can arise in three different ways: (iia) if $T > R$ then it is better to defect when playing against a cooperator; (iib) if $P > S$ then it is better to defect when playing against a defector; and (iic) if $T > S$ then it is better to be the defector in an encounter between a cooperator and a defector. If at least one of those three conditions hold, then we have a cooperative dilemma. If none hold, then there is no dilemma and C is simply better than D. If all three conditions hold, then we have a Prisoner's Dilemma, which is defined by $T > R > P > S$ (Rapoport and Chammah, 1965).

The Prisoner's Dilemma is the most stringent cooperative dilemma. Here defectors dominate cooperators. Thus, in a well-mixed population natural selection always favors defectors over cooperators. For cooperation to arise in the Prisoner's Dilemma we need a mechanism for the evolution of cooperation (Nowak, 2006).

Cooperative dilemmas which are not the Prisoner's Dilemma could be called 'relaxed cooperative dilemmas'. In these games it is possible to evolve some level of cooperation even if no mechanism is at work. One such example is the snow-drift game, given by $T > R > S > P$. Here we find a stable equilibrium between cooperators and defectors even in a well-mixed population.

* Correspondence address: Program for Evolutionary Dynamics, Harvard University, Cambridge, MA 02138, USA.
E-mail address: martin_nowak@harvard.edu

The above definition can be generalized to n person games. Denote by P_i and Q_i the payoffs for cooperators and defectors, respectively, in groups that contain i cooperators and $n-i$ defectors. For the game to be a cooperative dilemma we require that (i) an all cooperator group gets a higher payoff then an all defector group, $P_n > Q_0$, and (ii) yet there is some incentive to defect. The incentives to defect can take the following form: (iia) $P_i < Q_{i-1}$ for $i = 1 \ldots n$ and (iib) $P_i < Q_i$ for $i = 1 \ldots n-1$. The conditions (iia) mean that an individual can increase its payoff by switching from cooperation to defection. The conditions (iib) mean that in any mixed group defectors have a higher payoff than cooperators. If only some of these incentives (ii) hold than we have a relaxed cooperative dilemma. In this case some evolution of cooperation is possible even without a specific mechanism. But a mechanism would typically enhance the evolution of cooperation by increasing the equilibrium abundance of cooperators, increasing the fixation probability of cooperators or reducing the invasion barrier that needs to be overcome. The volunteer's dilemma is an example for a relaxed situation (Archetti, 2009a,b, Archetti and Scheuring, 2011). If all incentives hold, we have the n person equivalent of a Prisoner's Dilemma, and a mechanism for evolution of cooperation is needed. The 'Public goods game' is an n person Prisoner's Dilemma (Hardin, 1968, Dawes, 1980; Bergstrom et al., 1986).

Optional games (Hauert et al., 2002, 2007) can lead to relaxed social dilemmas. Participation is voluntary, which means besides cooperation and defection there is a third strategy, loners, L. Loners do not participate in the game. If no game occurs, then both individuals receive payoff, P_0. (There can be a cost for entering the game.) We have the following payoff matrix:

$$
\begin{array}{c}
\quad\;\; C \quad D \quad L \\
\begin{array}{c} C \\ D \\ L \end{array}
\left(
\begin{array}{ccc}
R & S & P_0 \\
T & P & P_0 \\
P_0 & P_0 & P_0
\end{array}
\right)
\end{array}
$$

If $R > P_0$ cooperators dominate loners. If $P_0 > P$ loners dominate defectors. If $T > R$ and $P > S$ defectors dominate cooperators. This cyclic domination implies a relaxed social dilemma.

2. Five mechanisms for evolution of cooperation

A mechanism for the evolution of cooperation is an interaction structure, specifying how the individuals of a population interact to accumulate payoff and to compete for reproduction. All proposed interaction structures can be classified into five mechanisms.

2.1. Direct reciprocity

There are repeated encounters between the same two individuals, who can use conditional strategies that depend on previous outcomes. Direct reciprocity is based on the concept of repeated games (Trivers, 1971; Axelrod, 1984; Fudenberg and Maskin, 1986; Milinski, 1987; Binmore, 1994; Mailath and Samuelson, 2006). In a repeated Prisoner's Dilemma, always defect (ALLD) is not necessarily the best strategy. If the chance of another encounter between the same two players is sufficiently high, then cooperative strategies can prevail. Simple strategies for playing the repeated Prisoner's Dilemma include grim-trigger, tit-for-tat, generous-tit-for-tat, contrite tit-for-tat and win-stay, lose-shift (Axelrod, 1984; Molander, 1985; Kraines and Kraines, 1989; Fudenberg and Maskin, 1990; Nowak and Sigmund, 1989, 1992, 1993; Wu and Axelrod, 1995; Boerlijst et al., 1997).

Cooperation via direct reciprocity is never fully stable. Depending on payoff values and the length of the game, tit-for-

tat (TFT) can be robust against invasion by ALLD. But TFT is neutral with always cooperate (ALLC). Random drift can lead from TFT to ALLC. Subsequently ALLC can be invaded by ALLD. Cooperative populations – no matter which strategy they use – are always challenged, undermined and ultimately destroyed. Once cooperation is gone it needs to be rebuilt. Cycles between cooperation and defection are a typical feature of direct reciprocity (Nowak and Sigmund, 1989; Imhof et al., 2005; Imhof and Nowak, 2010).

Another important aspect of direct reciprocity is how to deal with noise (May, 1987). Random mistakes caused by 'trembling hands' or 'fuzzy minds' can lead to destructive vendettas when the players use TFT. Successful strategies for playing repeated cooperative dilemmas need to be able to correct mistakes and repair relationships. Generous tit-for-tat, for example, has a stochastic response to defection: always cooperate when the other person has cooperated and sometimes cooperate even if the other person has defected. Natural selection can therefore promote the evolution of forgiveness (Nowak and Sigmund, 1992).

2.2. Indirect reciprocity

The key aspect of indirect reciprocity is reputation. There are repeated encounters in a population of individuals. Some encounters are observed by others and/or information about those encounters spreads through communication. Individuals can adopt conditional strategies that base their decision on the reputation of the recipient. Direct reciprocity relies on your own experience with someone, while indirect reciprocity uses the experience of others. Cooperation is costly but leads to the reputation of a helpful individual who might receive cooperation from others. Many papers explore empirical (Wedekind and Milinski, 2000; Dufwenberg et al., 2001, Milinski et al., 2002a,b, Wedekind and Braithwaite, 2002; Bolton et al., 2004, 2005; Seinen and Schram, 2005; Bshary and Grutter, 2006; Sommerfeld et al., 2007; Bshary et al., 2008; Engelmann and Fischbacher, 2009; Warneken and Tomasello, 2009) and theoretical aspects of indirect reciprocity (Nowak and Sigmund, 1998a,b, 2005, Suzuki and Akiyama, 2007a,b, Roberts, 2008; Ohtsuki et al., 2009; Uchida, 2010; Uchida and Sigmund, 2010; Berger, 2011).

A strategy for indirect reciprocity consists of a social norm and an action rule. The social norm specifies how to evaluate interactions between individuals. The action rule specifies whether or not to cooperate given the reputation of the other individual. Indirect reciprocity can lead to cooperation if the probability to know someone's reputation is sufficiently high.

Alexander (1987) discusses many important aspects of indirect reciprocity – only some of which have been explored so far – and is perhaps the first person to use this term. Alexander proposed that indirect reciprocity based on reputation is a major factor in the emergence of moral systems in human societies. But Alexander does not provide a formal model and does not delineate the mechanism from group selection. Sugden (1986) points out that defection against an undeserving recipient should not lower one's own reputation. This idea leads to the notion of 'standing' in indirect reciprocity and 'contrite tit-for-tat' in direct reciprocity. Kandori (1992) examines a social norm that gives a bad reputation for cooperating with a defector. This rule is called 'judging' in indirect reciprocity.

David Haig once remarked: 'For direct reciprocity you need a face. For indirect reciprocity you need a name.' Recognizing individual faces and reading their intent can be an important feature for playing repeated games simultaneously with a number of other individuals. For efficient versions of indirect reciprocity, however, it is essential to be able to talk to each other about

others, which necessitates the concept of names. In the absence of names, indirect reciprocity can only work via direct observation of another's action.

Whenever my behavior toward a person depends on the previous interactions between me and that person, we are in the realm of direct reciprocity. Whenever my behavior also depends on what that person has done to others, indirect reciprocity is at work. Thus indirect reciprocity can be seen as a fairly general mechanism that encompasses most human interactions. The essence of indirect reciprocity is conditional behavior that depends on what you have done to me and to others. This mechanism is obviously not limited to games of cooperation and defection.

All theories that study the resolution of multi-player social dilemmas use targeted interactions, such as ostracism, punishment or reward (Yamagishi, 1986; Ostrom, 1990; Sethi and Somanathan, 1996; Fehr and Gächter, 2000; Gürerk et al., 2006; Rockenbach and Milinski, 2006; Milinski and Rockenbach, 2007; Dreber et al., 2008; Jaffe, 2008; Rand et al., 2009; Jacquet et al., 2011). Defectors or cooperators in the multi-player game can be identified and treated differently in subsequent, targeted interactions. The strategies are conditional actions that depend on previous outcomes. Thus, the mechanisms that operate here are either direct or indirect reciprocity. In the first case I respond to what you have done to me. In the second case I respond also to what you have done to others.

Some researchers use the term 'strong reciprocity' to denote the behavior of cooperation in the public goods games and punishment of defectors in the targeted interactions (Bowles and Gintis, 2004). 'Strong reciprocity' describes a behavioral strategy, but not an evolutionary mechanism. For 'strong reciprocity' to evolve the mechanism of indirect reciprocity is implicitly used: I punish you, because you have defected with others.

2.3. Spatial selection

The outcome of evolutionary games can be affected by population structure (Nowak and May, 1992; Lindgren and Nordahl, 1994; Ellison, 1993; Ferriere and Michod, 1996; Killingback and Doebeli, 1996; Nakamaru et al., 1997; Szabó and Tőke, 1998; Van Baalen and Rand, 1998; Szabó and Fath, 2007; Pfeiffer et al., 2001; Hauert and Doebeli, 2004; Yamamura et al., 2004; Santos et al., 2006; Hauert et al., 2008; Helbing and Yu, 2008; Roca et al., 2009; Wakano et al., 2009; Fowler and Christakis, 2010; Li et al., 2010; Rong et al., 2010; Szabó et al., 2010). Strategies that are successful in a well-mixed population, where everyone interacts with everyone else equally likely, may not win in a structured population and vice versa. The population structure specifies who interacts with whom to accumulate payoff and who competes with whom for reproduction. The interaction and replacement structures need not be identical (Ohtsuki et al., 2007).

Population structure can be static or dynamic. Evolutionary graph theory studies evolution on constant graphs (Lieberman et al., 2005; Ohtsuki et al., 2006; Ohtsuki and Nowak, 2006, 2008; Taylor et al., 2007; Fu et al., 2009; Perc, 2009; Liu et al., 2010). In contrast, evolutionary set theory describes individuals moving between sets thereby changing the interaction structure as part of the evolutionary process (Tarnita et al., 2009a). 'Active linking' means that individuals can choose to break unproductive links and establish new ones (Skyrms and Pemantle, 2000; Pacheco et al., 2006; Fu et al., 2008; Perc and Szolnoki, 2010; Fehl et al., 2011; Rand et al., 2011).

Population structure can result from the distribution of individuals in physical space, on social networks or in phenotype space (Antal et al., 2009a,b). Tag based cooperation (Riolo et al., 2001; Traulsen and Claussen, 2004; Jansen and Van Baalen, 2006;

Traulsen and Nowak, 2007) can be interpreted as clustering in phenotype space.

Spatial selection can promote evolution of cooperation, because cooperators from clusters which can prevail against exploitation by defectors. The underlying principle is 'neighbors help each other'. The particular rule that is used for strategic updating (reproduction) is of crucial importance. Cooperation can prevail if the payoff from cooperators inside a cluster influences the movement of the boundary between cooperators and defectors (Nowak and May, 1992; Ohtsuki and Nowak, 2006).

Tarnita et al. (2009b, 2011) provide general results for how any type of population structure affects evolutionary games in the limit of weak selection.

2.4. Multi-level selection

Darwin (1871) wrote: 'There can be no doubt that a tribe including many members who … were always ready to give aid to each other and to sacrifice themselves for the common good, would be victorious over other tribes; and this would be natural selection.' The basic idea is that natural selection does not only act on individuals but also on groups. Just as individuals compete within groups, groups compete with each other. This concept leads to group selection or multi-level selection (Wynne-Edwards, 1962; Wilson, 1975; Wade, 1977; Leigh, 1983; Nunney, 1985; Szathmáry and Demeter, 1987; Goodnight and Stevens, 1997; Sober and Wilson, 1999; Boyd and Richerson, 2002; Kerr and Godfrey-Smith, 2002; Paulsson, 2002; Ono et al., 2003; Killingback et al., 2006; Traulsen et al., 2008; Wilson and Wilson, 2008; Van den Bergh and Gowdy, 2009; Scheuring, 2010; Wang et al., 2011).

Multi-level selection can promote evolution of cooperation. In a simple scenario, defectors dominate cooperators within groups, but groups of cooperators outcompete groups of defectors. Multi-level (or group) selection is a powerful mechanism for the evolution of cooperation especially if there are many small groups and if the migration rate between groups is not too large (Traulsen and Nowak, 2006).

Spatial selection and multi-level selection are distinct mechanisms. In the former case competition (selection) occurs only between individuals. In the second case there is competition between individuals and competition between groups.

The idea of group selection has a long and troubled history, but mostly in terms of verbal arguments on both sides. The mathematical theory of evolution clearly shows that group selection is possible provided certain conditions hold. It requires careful examination to determine whether these conditions are met by a particular empirical situation.

2.5. Kin selection

Kin selection is a mechanism for the evolution of cooperation if properly formulated. Kin selection arises if individuals use conditional strategies based on kin recognition. For example, I will jump into the river to save two brothers, eight cousins, but not a stranger. Therefore the essence of kin selection is kin recognition and conditional behavior. It is a form of nepotism where closer relatives are favored over distant ones and over strangers. The key parameter that arises in kin selection is genetic relatedness (Hamilton, 1964; Grafen, 1979, 1985, 2006; Taylor, 1992; Frank, 1998; Michod, 1999; Rousset, 2004).

Many people equate kin selection with inclusive fitness theory, which is unfortunate in my opinion. Inclusive fitness is a particular method of accounting fitness effects in social situations. Although inclusive fitness is often claimed to be a general approach for studying social evolution, it is in fact a limited

theory that works in some situations but not in others (Nowak et al., 2010). The crucial limitation of the theory is the necessity to split personal fitness into additive components – those that are caused by one's own actions and those that are caused by the actions of others.

The concept of 'stripping' and 'augmenting' personal fitness (as if all effects were additive) is clearly formulated in Hamilton's (1964) definition: 'Inclusive fitness may be imagined as the personal fitness which an individual actually expresses in its production of adult offspring as it becomes after it has been first stripped and then augmented in a certain way. It is stripped of all components which can be considered as due to the individual's social environment, leaving the fitness which he would express if not exposed to any of the harms or benefits of that environment. This quantity is then augmented by certain fractions of the quantities of harm and benefit which the individual himself causes to the fitnesses of his neighbors. The fractions in question are simply the coefficients of relationship appropriate to the neighbors whom he affects; unit for clonal individuals, one-half for sibs, one-quarter for half-sibs, one-eighth for cousins,…and finally zero for all neighbors whose relationship can be considered negligibly small.'

The problem is that most evolutionary processes do not grant such additivity. Therefore, inclusive fitness is a particular method that can be used in some situations but not in others (Nowak et al., 2010). Proponents of inclusive fitness theory do not seem to appreciate this mathematical fact (Abbot et al., 2011; Boomsma et al., 2011; Strassmann et al., 2011; Ferriere and Michod, 2011; Herre and Wcislo, 2011). Gardner et al. (2011) – also avoiding the essential problem – explore whether generalized versions of Hamilton's rule can be formulated as to be 'always true'. The problem here is that 'cost' and 'benefit' become complicated parameters that depend on relatedness and population structure. Such a mathematical formula does not help to solve any particular evolutionary process and has no predictive power for theory or experiment (see also Nowak et al., 2011).

Several authors have pointed out that calculating inclusive fitness, whenever that is possible, provides little or no insight for understanding evolutionary dynamics (Fletcher et al., 2006; Fletcher and Doebeli, 2009; Van Veelen, 2009; Doebeli, 2010; Traulsen, 2010). Gadagkar (2010) discusses the inclusive fitness debate from the perspective of a biologist who has studied social insects for over two decades.

For obtaining a good understanding of kin selection as a mechanism for the evolution of cooperation, it is – in my opinion – essential to develop a theory which is not limited by the concept of inclusive fitness. This is an important task for future research.

3. This issue

Archetti and Scheuring (2012) make the important point that nonlinear public goods games need not be n-person Prisoner's Dilemmas. Instead they can be relaxed social dilemmas, in which some cooperation can arise without the need of a specific mechanism.

Axelrod (2012) gives a brief historical and autobiographical perspective of his highly influential work that launched many studies of direct reciprocity.

Sigmund (2012) gives a state of the art review of indirect reciprocity discussing recent theoretical advances and experimental tests.

Damore and Gore (2012) review social evolution among microbes and discuss the inadequacy of inclusive fitness theory or Hamilton's rule to make meaningful predictions in this area.

They call for a return to rigor in models of microbial social evolution.

Alger and Weibull (2012) study social evolution in a framework where the assortment parameter is an exogenously given constant, which determines the degree to which interactions preferentially occur between individuals that use the same strategy or behavioral rule (Eshel and Cavalli-Sforza, 1982; Alger and Weibull, 2010). They conclude that in their framework Hamilton's rule is generally violated.

Simon et al. (2012) show that Hamilton's rule generally fails to predict the direction of selection in a simple multi-level selection model. They also point out that the relatedness parameter in Hamilton's rule is at best only a description of the current level of assortment, but does not provide an understanding of the mechanism that leads to assortment nor its temporal dynamics.

Van Veelen et al. (2012) argue that group selection and kin selection approaches are not equivalent; they also discuss problems which arise when using the Price equation instead of a specific model for evolutionary dynamics.

Szabó and Szolnoki (2012) study spatial evolutionary game dynamics among players that have some degree of other regarding social preferences. There is a parameter, Q, which scales the utility function from completely selfish, $Q=0$, to fraternal, $Q=1/2$, to totally other regarding, $Q=1$. In the latter case the overstatement of the other regarding preference leads to a social conflict called "lovers' dilemma".

Santos et al. (2012) argue that diversity can promote cooperation in games on graphs. They observe that cooperators in highly connected positions are more able to resist invasion of defectors than vice versa. Defectors in pivotal positions cannot profit there in the long run and become victims of their own success.

Allen et al. (2012) explore how mutation affects evolutionary game dynamics on graphs. They obtain analytical results for weak selection.

Hauert and Imhof (2012) analyze evolutionary game dynamics in deme structured populations with mutation and migration. They find that this population structure does not promote evolution of cooperation except for a pairwise comparison process, which has two parameters for scaling the intensity of selection.

Ellingsen and Robles (2012) study the evolutionary dilemma of parental investment. They challenge the conventional wisdom that early costs are irrelevant for the allocation of subsequent investment. Instead they find that if one parent has substantial early costs, then the other parent should carry a large fraction of later costs.

Traulsen and Reed (2012) compare models of evolutionary game dynamics with those of population genetics (see also Hammerstein, 1996). In particular they show that meiotic drive leads to cooperative dilemmas, while including resistance to meiotic drive leads to rock–paper–scissors games.

Cavaliere et al. (2012) study dynamical graphs where newcomers connect to successful role models and their neighbors. They find that prosperity is associated with instability: the total income of the network increases with the number of connections, but at the same time cooperators become vulnerable to invasion by defectors.

Milinski and Rockenbach (2012) compare the efficiency of reward and punishment in promoting cooperation in public goods games. They argue that the costs of punishment dramatically reduce efficiency in short games, but not necessarily in longer ones (Gächter et al., 2008). Rewarding works well if the public goods game is embedded in a rich social context, where reputation for cooperativeness can pay off independently (Rockenbach and Milinski, 2006).

Cressman et al. (2012) investigate how institutional incentives affect individual rational behavior. They study public goods

games followed by different reward and/or punishment schemes that are carried out by institutions rather than individuals. They argue that full cooperation in the public goods game can be achieved if institutions use both reward and punishment.

Tavoni et al. (2012) study how common-pool resources, to which individuals have open access, lead to multi-person social dilemmas (Hardin, 1968; Ostrom, 1990, Levin, 2009). They suggest that 'equity-driven ostracism', which excludes norm violators from social privileges, is an efficient way to promote cooperation. This approach has a clear advantage over costly punishment, because it is not mutually destructive.

Colman et al. (2012) present an agent based simulation where cooperation evolves because of similarity discrimination. Each agent has two continuously variable genes. One gene specifies the probability to cooperate with similar co-players, while the other gene specifies the probability to cooperate with dissimilar co-players. Similarity is determined by the distance in these two genic values. Similarity judgement could also be based on other phenotypic traits, which would lead to a model similar to Antal et al., (2009b).

Rand (2012) suggests that online labor markets such as Amazon Mechanical Turk provide a useful platform for conducting behavioral experiments. The process is cheap and efficient. The experience is similar to performing computer simulations.

Dasgupta (2012) argues that many empirical studies of human cooperation analyze situations where institutions govern the management of public goods, but the resulting games are not Prisoner's Dilemmas. In some cases exploitation of individuals can masquerade as cooperation.

4. What might lie ahead

Research on cooperation is a highly active field moving into many different directions. Here I give a short list of what seem to be promising open problems.

1. It is often said that cooperation is crucially involved in constructive steps such as the emergence of cells, multi-cellularity and animal societies, but few specific models have been developed. There is a big difference, for example, if multi-cellularity (or eusociality) emerges by coming together of individuals or staying together of individuals after reproduction. Cooperation seems to play a very different role in these two cases.

2. For direct reciprocity it would be important to study the key difference between the simultaneous game (the usual approach) and the alternating game, where the players take turns (Nowak and Sigmund, 1994; Neill, 2001). There is also a continuous range of possibilities between these two extreme forms of conducting a repeated game.

3. For indirect reciprocity the standing and judging strategies seem fragile given the amount of information they need and given their vulnerability to deception. It would be desirable to find variants of indirect reciprocity where simple scoring strategies are more stable.

4. Many models for language evolution tacitly assume cooperation between the players: the common goal is mutual understanding. Vice versa many models of indirect reciprocity assume communication between players. It would be great to develop an approach for the coevolution of language and indirect reciprocity.

5. Let us develop a precise model for kin selection that is not limited *a priori* by an inclusive fitness approach. Individuals recognize kin and behave accordingly. There could be coevolution between cooperation and kin recognition.

6. There is much work on cooperation and defection within a species, but much less theoretical work on cooperation and defection between members of different species (Doebeli and Knowlton, 1998).

7. Evolutionary games are typically studied in populations of equals, where everyone has the same background payoff, same endowment or strength. Breaking this symmetry should have important consequences.

8. Many theoretical and empirical studies of peer punishment (artificially) exclude negative effects such as retaliation or coercion. I expect that the major effect of peer punishment in realistic situations is not promotion of cooperation, but exploitation of individuals.

9. A difficult task is to design field studies that explore cooperative behavior of humans (Bateson et al., 2006; Ernest-Jones et al., 2011). It would be fascinating to quantify payoff and evaluate strategies in natural situations that represent cooperative dilemmas.

10. The interaction between indirect reciprocity and partner choice could be investigated in theory and experiment.

Acknowledgments

References

Abbot, P., et al., 2011. Inclusive fitness theory and eusociality. Nature 471, E1–E4.

Alexander, R.D., 1987. The Biology of Moral Systems. Aldine de Gruyter, New York.

Alger, I., Weibull, J.W., 2010. Kinship, incentives, and evolution. Am. Econ. Rev. 100, 1725–1758.

Alger, I., Weibull, J.W., 2012. A generalization of Hamilton's rule — Love thy sibling how much? J. Theor. Biol. doi:10.1016/j.jtbi.2011.05.008.

Allen, B., Traulsen, A., Tarnita, C.E., Nowak, M.A., 2012. How mutation affects evolutionary games on graphs. J. Theor. Biol. doi:10.1016/j.jtbi.2011.03.034.

Antal, T., Nowak, M.A., Traulsen, A., 2009a. Strategy abundance in 2×2 games for arbitrary mutation rates. J. Theor. Biol. 257, 340–344.

Antal, T., Ohtsuki, H., Wakeley, J., Taylor, P.D., Nowak, M.A., 2009b. Evolutionary game dynamics in phenotype space. Proc. Natl. Acad. Sci. USA 106, 8597–8600.

Archetti, M., 2009a. The volunteer's dilemma and the optimal size of a social group. J. Theor. Biol. 261, 475–480., p. 786.

Archetti, M., 2009b. Cooperation as a volunteer's dilemma and the strategy of conflict in public goods games. J. Evol. Biol. 22, 2192–2200. 788.

Archetti, M., Scheuring, I., 2011. Coexistence of cooperation and defection in public goods games. Evolution 65, 1140–1148.

Archetti, M., Scheuring, I., 2012. Review: game theory of public goods in one-shot social dilemmas without assortment. J. Theor. Biol. doi:10.1016/j.jtbi.2011.06.018.

Axelrod, R., 1984. The Evolution of cooperation.

Axelrod, R., 2012. Launching "The Evolution of Cooperation". J. Theor. Biol. doi:10.1016/j.jtbi.2011.04.015.

Bateson, M., Nettle, D., Roberts, G., 2006. Cues of being watched enhance cooperation in a real-world setting. Biol. Lett. 2, 412–414.

Berger, U., 2011. Learning to cooperate via indirect reciprocity. Games and Economic Behavior 72 (1), 30–37.

Bergstrom, T., Blume, L., Varian, H., 1986. On the private provision of public goods. J. Public Econ. 29, 25–49.

Binmore, K., 1994. Playing Fair: Game Theory and the Social Contract. MIT Press, Cambridge, MA.

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

Bolton, G., Katok, E., Ockenfels, A., 2004. How effective are on-line reputation mechanisms? An experimental investigation. Manage. Sci. 50, 1587–1602.

Bolton, G., Katok, E., Ockenfels, A., 2005. Cooperation among strangers with limited information about reputation. J. Public Econ. 89, 1457–1468.

Boomsma, J.J., Beekman, M., Cornwallis, C.K., Griffin, A.S., Holman, L., Hughes, W.O.H., Keller, L., Oldroyd, B.P., Ratnieks, F.L.W., 2011. Only full-sibling families evolved eusociality. Nature 471, E4–E5.

Bowles, S., Gintis, H., 2004. The evolution of strong reciprocity: cooperation in heterogeneous populations. Theor. Pop. Biol. 65, 17–28.

Boyd, R., Richerson, P.J., 2002. Group beneficial norms spread rapidly in a structured population. J. Theor. Biol. 215, 287–296.

Brandt, H., Sigmund, K., 2004. The logic of reprobation: action and assessment rules in indirect reciprocity. J. Theor. Biol. 231, 475–486.

Brandt, H., Sigmund, K., 2005. Indirect reciprocity, image scoring, and moral hazard. Proc. Nat. Acad. Sci. USA 102, 2666–2670.

Brandt, H., Sigmund, K., 2006. The good, the bad and the discriminator: errors in direct and indirect reciprocity. J. Theor. Biol. 239, 183–194.

Bshary, R., Grutter, A.S., 2006. Image scoring causes cooperation in a cleaning mutualism. Nature 441, 975–978.

Bshary, R., Grutter, A., Willener, A., Leimar, O., 2008. Pairs of cooperating cleaner fish provide better service quality than singletons. Nature 455, 964–967.

Camerer, C.F., 2003. Behavioral Game Theory. Princeton University Press, Princeton, NJ.

Cavaliere, M., Sedwards, S., Tarnita, C.E., Nowak, M.A., Csikász-Nagy, A., 2012. Prosperity is associated with instability in dynamical networks. J. Theor. Biol. doi:10.1016/j.jtbi.2011.09.005.

Colman, A.M., Browning, L., Pulford, B.D., 2012. Spontaneous similarity discrimination in the evolution of cooperation. J. Theor. Biol. doi:10.1016/j.jtbi.2011.05.022.

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

Cressman, R., Song, J.-W., Zhang, B.-Y., Tao, Y., 2012. Cooperation and evolutionary dynamics in the public goods game with institutional incentives. J. Theor. Biol. doi:10.1016/j.jtbi.2011.07.030.

Damore, J.A., Gore, J., 2012. Understanding microbial cooperation. J. Theor. Biol. doi:10.1016/j.jtbi.2011.03.008.

Darwin, C., 1871. The Descent of Man, and Selection in Relation to Sex. John Murray, London.

Dasgupta, P., 2012. Dark matters: exploitation as cooperation. J. Theor. Biol. doi:10.1016/j.jtbi.2011.04.020.

Dawes, R.M., 1980. Social dilemmas. Ann. Rev. Psychol. 31, 169–193.

Doebeli, M., Knowlton, N., 1998. The evolution of interspecific mutualisms. Proc. Natl. Acad. Sci. USA 95, 8676–8680.

Doebeli, M., 2010. Inclusive fitness is just bookkeeping. Nature 467, 661.

Dreber, A., Rand, D., Fudenberg, D., Nowak, M.A., 2008. Winners do not punish. Nature 452, 348–352.

Dufwenberg, M., Gneezy, U., Gueth, W., van Damme, E., 2001. Direct vs indirect reciprocation an experiment. Homo Oecon. 18, 19–30.

Dugatkin, L.A., Reeve, H.K. (Eds.), 1998. Game Theory and Animal Behaviour. Oxford University Press, Oxford, UK.

Ellingsen, T., Robles, J., 2012. The evolution of parental investment: re-examining the anisogamy argument. J. Theor. Biol. doi:10.1016/j.jtbi.2011.09.031.

Ellison, G., 1993. Learning, local interaction, and coordination. Econometrica 61, 1047–1071.

Engelmann, D., Fischbacher, U., 2009. Indirect reciprocity and strategic reputation-building in an experimental helping game. Games Econ. Behav. 67, 399–407.

Ernest-Jones, M., Nettle, D., Bateson, M., 2011. Effects of eye images on everyday cooperative behavior: a field experiment. Evol. Human Behav. 32, 172–178.

Eshel, I., Cavalli-Sforza, L.L., 1982. Assortment of encounters and evolution of cooperativeness. Proc. Natl. Acad. Sci. USA 79, 1331–1335.

Fehl, K., van der Post, D.J., Semmann, D., 2011. Co-evolution of behaviour and social network structure promotes human cooperation. Ecol. Lett. 14, 546–551.

Fehr, E., Gächter, S., 2000. Cooperation and punishment in public goods experiments. Am. Econ. Rev. 90, 980–994.

Ferriere, R., Michod, R.E., 1996. The evolution of cooperation in spatially heterogeneous populations. Am. Nat. 147, 692–717.

Ferriere, R., Michod, R.E., 2011. Inclusive fitness in evolution. Nature 471, E6–E8.

Fishman, M.A., 2003. Indirect reciprocity among imperfect individuals. J. Theor. Biol. 225, 285–292.

Fletcher, J.A., Zwick, M., Doebeli, M., Wilson, D.S., 2006. What is wrong with inclusive fitness? Trends Ecol. Evol. 21, 597–598.

Fletcher, J.A., Doebeli, M., 2009. A simple and general explanation for the evolution of altruism. Proc. Roy. Soc. London B 276, 13–19.

Fowler, J.H., Christakis, N.A., 2010. Cooperative behavior cascades in human social networks. Proc. Natl. Acad. Sci. USA 107, 5334–5338.

Frank, S.A., 1998. Foundations of Social Evolution. Princeton University Press, Princeton, NJ.

Fu, F., Hauert, C., Nowak, M.A., Wang, L., 2008. Reputation-based partner choice promotes cooperation in social networks. Phys. Rev. E 78 (2), 026117.

Fu, F., Wang, L., Nowak, M.A., Hauert, C., 2009. Evolutionary dynamics on graphs: efficient method for weak selection. Phys. Rev. E 79 (4), 046707.

Fudenberg, D., Maskin, E., 1986. The folk theorem in repeated games with discounting or with incomplete information. Econometrica 50, 533–554.

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, MA.

Gächter, S., Renner, E., Sefton, M., 2008. The long-run benefits of punishment. Science 322, 1510.

Gadagkar, R., 2010. Sociobiology in turmoil again. Curr. Sci. 99, 1036–1041.

Gardner, A., West, S.A., Wild, G., 2011. The genetical theory of kin selection. J. Evol. Biol. 24 (5), 1020–1043.

Goodnight, C.J., Stevens, L., 1997. Experimental studies of group selection: what do they tell us about group selection in nature. Am. Nat. 150, S59–S79.

Grafen, A., 1979. The hawk-dove game played between relatives. Anim. Behav. 27, 905–907.

Grafen, A., 1985. A geometric view of relatedness. Oxford Surv. Evol. Biol. 2, 28–89.

Grafen, A., 2006. Optimization of inclusive fitness. J. Theor. Biol. 238, 541–563.

Gürerk, Ö., Irlenbusch, B., Rockenbach, B., 2006. The competitive advantage of sanctioning institutions. Science 312, 108–111.

Hamilton, W.D., 1964. The genetical evolution of social behaviour, I and II. J. Theor. Biol. 7, 1–52.

Hammerstein, P., 1996. Darwinian adaptation, population genetics and the streetcar theory of evolution. J. Math. Biol. 34, 511–532.

Hardin, G., 1968. The tragedy of the commons. Science 3859, 1243–1248.

Harsanyi, J.C., Selten, R., 1988. A General Theory of Equilibrium Selection in Games. MIT Press, Cambridge, MA.

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

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

Hauert, C., Michor, F., Nowak, M.A., Doebeli, M., 2006. Synergy and discounting of cooperation in social dilemmas. J. Theor. Biol. 239, 195–202.

Hauert, C., Traulsen, A., Brandt, H., Nowak, M.A., Sigmund, K., 2007. Via freedom to coercion: the emergence of costly punishment. Science 316, 1905–1907.

Hauert, C., Wakano, J.Y., Doebeli, M., 2008. Ecological public goods games: cooperation and bifurcation. Theor. Pop. Biol. 73, 257–263.

Hauert, C., Imhof, L., 2012. Evolutionary games in deme structured, finite populations. J. Theor. Biol. doi:10.1016/j.jtbi.2011.06.010.

Helbing, D., Yu, W., 2008. Migration as a mechanism to promote cooperation. Adv. Complex Syst. 11, 641–652.

Helbing, D., 2011. Quantitative Sociodynamics. Springer.

Herre, E.A., Wcislo, W.T., 2011. In defence of inclusive fitness theory. Nature 471, E8–E9.

Hofbauer, J., Sigmund, K., 1988. The Theory of Evolution and Dynamical Systems. Cambridge University Press, Cambridge, UK.

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

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

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

Imhof, L.A., Nowak, M.A., 2010. Stochastic evolutionary dynamics of direct reciprocity. Proc. R. Soc. London B 277, 463–468.

Jacquet, J., Hauert, C., Traulsen, A., Milinski, M., 2011. Shame and honour drive cooperation. Biol. Lett. 7, 899–901.

Jaffe, K., 2008. Evolution of shame as an adaptation to social punishment and its contribution to social cohesiveness. Complexity 14, 46–52.

Jansen, V.A.A., Van Baalen, M., 2006. Altruism through beard chromodynamics. Nature 440, 663–666.

Kandori, M., 1992. Social norms and community enforcement. Rev. Econ. Stud. 59, 63–80.

Kerr, B., Godfrey-Smith, P., 2002. Individualist and multi-level perspectives on selection in structured populations. Biol. Philos. 17, 477–517.

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

Killingback, T., Bieri, J., Flatt, T., 2006. Evolution in group-structured populations can resolve the tragedy of the commons. Proc. R. Soc. London B 273, 1477–1481.

Kraines, D., Kraines, V., 1989. Pavlov and the prisoner's dilemma. Theor. Decis. 26, 47–79.

Leigh, E.G., 1983. When does the good of the group override the advantage of the individual? Proc. Natl Acad. Sci. USA 80, 2985–2989.

Leimar, O., Hammerstein, P., 2001. Evolution of cooperation through indirect reciprocation. Proc. R. Soc. London B 268, 745–753.

Levin, S.A. (Ed.), 2009. Games, Groups, and the Global Good. Springer-Verlag, London.

Li, Y., Jin, X., Su, X., Kong, F., Peng, C., 2010. Cooperation and charity in spatial public goods game under different strategy update rules. Physica A 389, 1090–1098.

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

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

Liu, R.-R., Rong, Z., Jia, C.-X., Wang, B.-H., 2010. Effects of diverse inertia on scale-free-networked prisoners dilemma games. Europhys. Lett. 91, 20002.

Mailath, G.J., Samuelson, L., 2006. Repeated Games and Reputations: long-run Relationships. Oxford University Press, New York, NY.

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

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

Michod, R.E., 1999. Darwinian Dynamics: Evolutionary Transitions in Fitness and Individuality. Princeton University Press, Princeton, NJ.

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

Milinski, M., Semmann, D., Krambeck, H.J., 2002a. Donors in charity gain in both indirect reciprocity and political reputation. Proc. R. Soc. London B 269, 881–883.

Milinski, M., Semmann, D., Krambeck, H.J., 2002b. Reputation helps solve the Tragedy of the Commons. Nature 415, 424–426.

Milinski, M., Rockenbach, B., 2007. Spying on others evolves. Science 317, 464–465.

Milinski, M., Rockenbach, B., 2012. On the interaction of the stick and the carrot in social dilemmas. J. Theor. Biol. doi:10.1016/j.jtbi.2011.03.014.

Molander, P., 1985. The optimal level of generosity in a selfish, uncertain environment. J. Conflict Resolut. 29, 611–618.

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

Neill, D.B., 2001. Optimality under noise: Higher memory strategies for the Alternating Prisoner's Dilemma. J. theor. Biol. 211, 159–180.

Nowak, M.A., Sigmund, K., 1989. Oscillations in the evolution of reciprocity. J. Theor. Biol. 137, 21–26.

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

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 the Prisoner's Dilemma game. Nature 364, 56–58.

Nowak, M.A., Sigmund, K., 1994. The alternating prisoner's dilemma. J. Theor. Biol. 168, 219–226.

Nowak, M.A., Sigmund, K., 1998a. Evolution of indirect reciprocity by image scoring. Nature 393, 573–577.

Nowak, M.A., Sigmund, K., 1998b. The dynamics of indirect reciprocity. J. Theor. Biol. 194, 561–574.

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

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

Nowak, M.A., Sigmund, K., 2005. Evolution of indirect reciprocity. Nature 427, 1291–1298.

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

Nowak, M.A., Tarnita, C.E., Wilson, E.O., 2010. The evolution of eusociality. Nature 466, 1057–1062.

Nowak, M.A., Tarnita, C.E., Wilson, E.O., 2011. Nowak et al. reply. Nature 471, E9–E10.

Nunney, L., 1985. Group selection, altruism, and structured-deme models. Am. Nat. 126, 212–230.

Ohtsuki, H., Iwasa, Y., 2004. How should we define goodness? Reputation dynamics in indirect reciprocity. J. Theor. Biol. 231, 107–120.

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., Iwasa, Y., 2006. The leading eight: social norms that can maintain cooperation by indirect reciprocity. J. Theor. Biol. 239, 435–444.

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

Ohtsuki, H., Iwasa, Y., 2007. Global analyses of evolutionary dynamics and exhaustive search for social norms that maintain cooperation by reputation. J. Theor. Biol. 244, 518–531.

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

Ohtsuki, H., Nowak, M.A., 2008. Evolutionary stability on graphs. J. Theor. Biol. 251, 698–707.

Ohtsuki, H., Iwasa, Y., Nowak, M.A., 2009. Indirect reciprocity provides only a narrow margin of efficiency for costly punishment. Nature 457, 79–82.

Ono, S., Misawa, K., Tsuji, K., 2003. Effect of group selection on the evolution of altruistic behavior. J. Theor. Biol. 220, 55–66.

Osborne, M.J., Rubinstein, A., 1994. A Course in Game Theory. MIT Press, Cambridge, MA.

Ostrom, E., 1990. Governing the Commons: The Evolution of Institutions for Collective Action. Cambridge University Press, Cambridge, UK.

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

Panchanathan, K., Boyd, R., 2003. A tale of two defectors: the importance of standing for evolution of indirect reciprocity. J. Theor. Biol. 224, 115–126.

Panchanathan, K., Boyd, R., 2004. Indirect reciprocity can stabilize cooperation without the second-order free-rider problem. Nature 432, 499–502.

Paulsson, J., 2002. Multilevel selection on plasmid replication. Genetics 161, 1373–1384.

Perc, M., 2009. Evolution of cooperation on scale-free networks subject to error and attack. New J. Phys. 11, 033027.

Perc, M., Szolnoki, A., 2010. Coevolutionary games – a mini review. BioSystems 99, 109–125.

Pfeiffer, T., Schuster, S., Bonhoeffer, S., 2001. Cooperation and competition in the evolution of ATP-producing pathways. Science 292, 504–507.

Rand, D.G., Dreber, A., Ellingson, T., Fudenberg, D., Nowak, M.A., 2009. Positive interactions promote public cooperation. Science 325, 1272–1275.

Rand, D.G., Arbesman, S., Christakis, N.A., 2011. Dynamic networks promote cooperation in experiments with humans. Proc. Natl. Acad. Sci. USA 108, 19193–19198.

Rand, D.G., 2012. The promise of Mechanical Turk: how online labor markets can help theorists run behavioral experiments. J. Theor. Biol. doi:10.1016/j.jtbi.2011.03.004.

Rapoport, A., Chammah, A.M., 1965. Prisoner's Dilemma. University of Michigan Press, Ann Arbor, MI.

Riolo, R.L., Cohen, M.D., Axelrod, R., 2001. Evolution of cooperation without reciprocity. Nature 414, 441–443.

Roberts, G., 2008. Evolution of direct and indirect reciprocity. Proc. R. Soc. London B 275, 173–179.

Roca, C.P., Cuesta, J.A., Sanchez, A., 2009. Evolutionary game theory: temporal and spatial effects beyond replicator dynamics. Phys. Life Rev. 6, 208–249.

Rockenbach, B., Milinski, M., 2006. The efficient interaction of indirect reciprocity and costly punishment. Nature 444, 718–723.

Rong, Z., Wu, Z.-X., Wang, W.-X., 2010. Emergence of cooperation through coevolving time scale in spatial prisoners dilemma. Phys. Rev. E 82, 026101.

Rousset, F., 2004. Genetic Structure and Selection in Subdivided Populations. Princeton University Press, Princeton, NJ.

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

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

Santos, F.C., Pinheiro, F.L., Lenearts, T., Pacheco, J.M., 2012. Role of diversity in the evolution of cooperation. J. Theor. Biol. doi:10.1016/j.jtbi.2011.09.003.

Scheuring, I., 2010. Coevolution of honest signaling and cooperative norms by cultural group selection. BioSystems 101, 79–87.

Seinen, I., Schram, A., 2005. Social status and group norms: indirect reciprocity in a repeated helping experiment. Euro. Econ. Rev. 50, 581–602.

Sethi, R., Somanathan, E., 1996. The evolution of social norms in common property resource use. The American Economic Review 86 (4).

Sigmund, K., 2010. The Calculus of Selfishness. Princeton University Press, Princeton, NJ.

Sigmund, K., 2012. Moral assessment in indirect reciprocity. J. Theor. Biol. doi:10.1016/j.jtbi.2011.03.024.

Simon, B., Fletcher, J.A., Doebeli, M., 2012. Hamilton's rule in multi-level selection model. J. Theor. Biol. doi:10.1016/j.jtbi.2011.07.014.

Skyrms, B., 1996. Evolution of the Social Contract. Cambridge University Press, Cambridge, UK.

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

Sober, E., Wilson, D.S., 1999. Unto Others: The Evolution and Psychology of Unselfish Behavior. Harvard University Press.

Sommerfeld, R., Krambeck, H.J., Semmann, D., Milinski, M., 2007. Gossip as an alternative for direct observation in games of indirect reciprocity. Proc. Nat. Acad. Sci. USA 104, 17435–17440.

Strassmann, J.E., Page Jr., R.E., Robinson, G.E., Seeley, T.D., 2011. Kin selection and eusociality. Nature 471, E5–E6.

Sugden, R., 1986. The Economics of Rights, Cooperation and Welfare. Basil Blackwell, Oxford.

Suzuki, S., Akiyama, E., 2007a. Evolution of indirect reciprocity in groups of various sizes and comparison with direct reciprocity. J. Theor. Biol. 245, 539–552.

Suzuki, S., Akiyama, E., 2007b. Three-person game facilitates indirect reciprocity under image scoring. J. Theor. Biol. 249, 93–100.

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

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

Szabó, G., Szolnoki, A., Varga, M., Hanusovszky, L., 2010. Ordering in spatial evolutionary games for pairwise collective strategy updates. Phys. Rev. E 82, 026110.

Szabó, G., Szolnoki, A., 2012. Selfishness, fraternity, and other-regarding preference in spatial evolutionary games. J. Theor. Biol. doi:10.1016/j.jtbi.2011.03.015.

Szathmáry, E., Demeter, L., 1987. Group selection of early replicators and the origin of life. J. Theor. Biol. 128, 463–486.

Takahashi, N., Mashima, R., 2006. The importance of subjectivity in perceptual errors on the emergence of indirect reciprocity. J. Theor. Biol. 243, 418–436.

Tarnita, C.E., Antal, T., Ohtsuki, H., Nowak, M.A., 2009a. Evolutionary dynamics in set structured populations. Proc. Natl. Acad. Sci. USA 106, 8601–8604.

Tarnita, C.E., Ohtsuki, H., Antal, T., Fu, F., Nowak, M.A., 2009b. Strategy selection in structured populations. J. Theor. Biol. 259, 570–581.

Tarnita, C.E., Wage, N., Nowak, M.A., 2011. Multiple strategies in structured populations. Proc. Natl. Acad. Sci. USA 108, 2334–2337.

Tavoni, A., Schlüter, M., Levin, S.A., 2012. The survival of the conformist: social pressure and renewable resource management. J. Theor. Biol. doi:10.1016/j.jtbi.2011.07.003.

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

Taylor, P.D., 1992. Altruism in viscous populations–an inclusive fitness model. Evol. Ecol. 6, 352–353.

Taylor, P.D., Day, T., Wild, G., 2007. Evolution of cooperation in a finite homogeneous graph. Nature 447, 469–472.

Traulsen, A., 2010. Mathematics of kin- and group-selection: formally equivalent? Evolution 64, 316–323.

Traulsen, A., Claussen, J.C., 2004. Similarity-based cooperation and spatial segregation. Phys. Rev. E 70, 046128.

Traulsen, A., Nowak, M.A., 2006. Evolution of cooperation by multi-level selection. Proc. Natl. Acad. Sci. USA 103, 10952–10955.

Traulsen, A., Nowak, M.A., 2007. Chromodynamics of cooperation in finite populations. PLoS ONE 2, e270.

Traulsen, A., Shoresh, N., Nowak, M.A., 2008. Analytical results for individual and group selection of any intensity. Bull. Math. Biol. 70, 1410–1424.

Traulsen, A., Reed, F.A., 2012. From genes to games: cooperation and cyclic dominance in meiotic drive. J. Theor. Biol. doi:10.1016/j.jtbi.2011.04.032.

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

Uchida, S., 2010. Effect of private information on indirect reciprocity. Phys. Rev. E 82, 036111(8).

Uchida, S., Sigmund, K., 2010. The competition of assessment rules for indirect reciprocity. J. Theor. Biol. 263, 13–19.

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.

Van den Bergh, J., Gowdy, J., 2009. A group selection perspective on economic behavior, institutions and organizations. J. Econ. Behav. Organ. 72 (1), 1–20.

Van Veelen, M., 2009. Group selection, kin selection, altruism and cooperation: when inclusive fitness is right and when it can be wrong. J. Theor. Biol. 259, 589–600.

Van Veelen, M., García, J., Sabelis, M.W., Egas, M., 2012. Group selection and inclusive fitness are not equivalent; the Price equation vs. models and statistics. J. Theor. Biol. doi:10.1016/j.jtbi.2011.07.025.

Wade, M.J., 1977. An experimental study of group selection. Evolution 31, 134–153.

Wakano, J.Y., Nowak, M.A., Hauert, C., 2009. Spatial dynamics of ecological public goods. Proc. Natl. Acad. Sci. USA 106, 7910–7914.

Wang, J., Wu, B., Ho, D.W.C., Wang, L., 2011. Evolution of cooperation in multilevel public goods games with community structures. Euro. Phys. Lett. 93, 58001.

Warneken, F., Tomasello, M., 2009. Varieties of altruism in children and chimpanzees. Trends Cogn. Sci. 13 (9), 397–402.

Wedekind, C., Milinski, M., 2000. Cooperation through image scoring in humans. Science 288, 850–852.

Wedekind, C., Braithwaite, V.A., 2002. The long-term benefits of human generosity in indirect reciprocity. Curr. Biol. 12, 1012–1015.

Weibull, J.W., 1995. Evolutionary Game Theory. MIT Press, Cambridge, MA.

Wilson, D.S., 1975. A theory of group selection. Proc. Natl Acad. Sci. USA 72, 143–146.

Wilson, D.S., Wilson, E.O., 2008. Evolution for the good of the group. Am. Sci. 96, 380–389.

Wu, J., Axelrod, R., 1995. How to cope with noise in the iterated Prisoner's Dilemma. J. Conflict Resolut. 39, 183–189.

Wynne-Edwards, V.C., 1962. Animal Dispersion in Relation to Social Behavior. Hafner Publishing Company, Inc., New York, NY.

Yamagishi, T., 1986. The provision of a sanctioning system as a public good. J. Pers. Soc. Psychol. 51, 110–116.

Yamamura, N., Higashi, M., Behera, N., Wakano, J., 2004. Evolution of mutualism through spatial effects. J. Theor. Biol. 226, 421–428.