



Evolution of generous cooperative norms by cultural group selection

István Scheuring

Department of Plant Taxonomy and Ecology, Research Group of Theoretical Biology and Ecology, Eötvös Loránd University and the Hungarian Academy of Sciences, Budapest H-1117, Pázmány Péter sétány, 1/c, Hungary

ARTICLE INFO

Article history:

Received 27 May 2008

Received in revised form

16 December 2008

Accepted 16 December 2008

Available online 31 December 2008

Keywords:

Human cooperation

Social norm

Group selection

Indirect altruism

Second-order information

ABSTRACT

Evolution of cooperative norms is studied in a population where individual- and group-level selection are both in operation. Individuals play indirect reciprocity game within their group. Individuals are well informed about the previous actions and reputations, and follow second-order norms. Individuals are norm-followers, and imitate their successful group mates. In contrast to previous models where norms classify actions deterministically, we assume that norms determine only the probabilities of actions, and mutants can differ in these probabilities. The central question is how a selective cooperative norm can emerge in a population where initially only non-cooperative norms were present. It is shown that evolution leads to a cooperative state if generous cooperative strategies are dominant, although the “always defecting” and the “always cooperating”-like strategies remain stably present. The characteristics of these generous cooperative strategies and the presence of always defecting and always cooperating strategies are in concordance with experimental observations.

© 2009 Elsevier Ltd. All rights reserved.

1. Introduction

Altruistic behaviour, which is common in human populations, is usually explained by kin or group selection mechanism or direct and indirect reciprocity (Trivers, 1971; Axelrod, 1984; Dugatkin et al., 1992; Bowles and Gintis, 2003; Heinrich and Heinrich, 2006). Direct reciprocity, that is, the mechanism “I help you and you help me in the near future” can be explained by the existence of some memory to store previous actions (Axelrod and Hamilton, 1981; Axelrod, 1984; Sugden, 1986) or by limited dispersal (Nowak and May, 1992; van Baalen and Rand, 1998). However, evolutionary origin and stability of indirect reciprocity, where the return of altruistic aid is expected from someone other than the recipient of the aid, can only be explained if the actions are observed and classified by the members of society with the help of a social norm (Trivers, 1985; Alexander, 1987). Knowing the actual score (reputation) of a potential recipient (and the donor) and the norm followed by the potential donor, she can decide whether her recipient is worthy of donation or not. If free-riders are excluded effectively from the interaction by this norm then indirect reciprocity can be maintained.

Nowak and Sigmund (1998a, b) have investigated this concept mathematically for the first time. They have shown that cooperation by indirect reciprocity is maintained by a norm called image scoring. An individual's score increases by one if she donates to a recipient and decreases by one if she refuses donation. Individuals who follow image scoring help only those individuals whose score

is above a threshold, so individuals that were altruistic enough in the past are favoured.

These seminal papers catalysed a series of studies, including experimental works (e.g. Wedekind and Milinski, 2000; Fehr and Fischbacher, 2003) and a range of analytical and numerical investigations (e.g. Leimar and Hammerstein, 2001; Brandt and Sigmund, 2004; Panchanathan and Boyd, 2003, 2004; Ohtsuki and Iwasa, 2004; Chalub et al., 2006; Pacheco et al., 2006). Leimar and Hammerstein (2001) pointed out that image scoring is not an evolutionary stable strategy if group structure of human populations and inherent decision stochasticity is taken into account. They found that a so-called standing strategy that offers help if its score is below a critical level can overcome image scoring strategy. Interestingly, subjects follow image scoring rather than standing strategy according to empirical studies (Milinski et al., 2001). Milinski et al. (2001) argued that errors in perception and limited working memory lead to the subjects adopting image scoring strategy.

While Nowak and Sigmund's (1998a) paper dealt already with norms that are sensitive to the state of the donor and the recipient as well, comprehensive theoretical investigations on the success of different social norms in the indirect reciprocity game were addressed only some years later (Brandt and Sigmund, 2004; Ohtsuki and Iwasa, 2004, 2006). Ohtsuki and Iwasa (2004, 2006), similarly to most recent studies, assumed that individuals are either in *Good* or in *Bad* reputation, and they are reliably informed about the reputation state of everyone. They considered all the possible third-order norms, that is when an observer makes decision according to the donor and recipient reputation state and the action of the donor. (For first-order norms, only the actions of

E-mail address: shieazsf@ludens.elte.hu

the donor are taken into account; for second-order norms the reputation of either the recipient or the donor and the action also contribute to determine the new reputation value of the donor.) Thus, there are 2^4 different action strategies and 2^8 possible norms. They assumed that except for some small error individuals that are well-informed about the actions, further individuals can make some errors during execution of intended actions. They found eight reputation systems among the possible $2^4 \times 2^8 = 4096$, which are ESS and maintain a high level of cooperation. The common nature of these so-called “leading-eight” reputation systems is that all of them are nice (maintenance of cooperation), retaliatory (detection and punishment of defection, and justification of punishment), apologetic, and forgiving (Ohtsuki and Iwasa, 2006). In a parallel work, Brandt and Sigmund (2004) studied the evolution of only 14 different reputation systems among the possible 4096, but they studied the invasion and coexistence of strategies in a group-structured individual-based model. Their main conclusion is that the standing strategy is generally superior to image scoring strategy, but standing, image scoring, and judging norms (see below) are typically in stable coexistence.

Similar to Leimar and Hammerstein's (2001) and Brandt and Sigmund's (2004) works, most studies emphasised that ancient human populations lived in small interacting groups; thus, cooperative norms and social institutions are evolved through cultural group selection (Bowles et al., 2003; Bowles and Gintis, 2003; Pacheco et al., 2006; Chalub et al., 2006). The group selection mechanism is widely debated by arguing that group (or multilevel) selection can be explained by kin selection mechanism as well (Traulsen and Nowak, 2006; Taylor and Nowak, 2007; Lehmann et al., 2007; Traulsen et al., 2008). However, the group structure of hunter-gatherer societies is obvious (Ember, 1978; Richerson et al., 2001; Soltis et al., 1995); thus, the group selection perspective is natural in our cases.

The model introduced by Pacheco et al. (2006) is closely related to our system; so we present it in more detail. They investigated the evolution of cooperation by indirect reciprocity based on cultural group selection. Individuals follow a common social norm within the group, but they can use different strategies. The reputation of all individuals is public, but individuals may misinterpret the situation and make errors in the actions with a low probability. They considered third-order social norms. Individuals imitate the strategies of the most successful ones within the group. Groups in which cooperation and thus fitness are high on average are successful in a group selection process. Fitter groups outcompete (and assimilate) the less fit ones, and their norms spread in the population by cultural evolution. Pacheco et al. (2006) found that evolution leads to a second-order norm, named “stern-judging”. Giving help to a good individual and refusing help to a bad individual lead to a good reputation, while refusing help to a good and giving help to a bad one lead to bad reputation under stern-judging norm. We note here that Chalub et al. (2006) had the same conclusion by using a similar model framework. Stern-judging is among the leading-eight norms found by Ohtsuki and Iwasa (2004, 2006), although stern-judging is successful in a multilevel selection process while leading-eight norms are only stable against the invasion of rare non-cooperative strategies under individual-level selection.

What is common in Brandt and Sigmund's (2004), Chalub et al.'s (2006) and Pacheco et al.'s (2006) works is that individuals (or groups of individuals) can follow practically any possible norms initially. The problem of how a cooperative norm can emerge from non-cooperative norms remains open in these studies. Thus, we address the following question: can a cooperative norm evolve in a population divided by groups of individuals

following non-cooperative norms initially? We use the cultural group selection model, where our basic assumption is that norms determine the reputation of actions in a probabilistic basis, and similarly, actions are determined on probabilistic manner. Initially, these probabilities describe non-selectively selfish norms and strategies in all groups, but mutation and selection can change both of them step-by-step. We have shown that evolution leads typically to a generous cooperative norm. In the following, we introduce the model and then results of numerical simulations are presented and discussed.

2. The model

2.1. Basic assumptions, the norm system

Individuals play the indirect reciprocity game. The actor can give help to the recipient, which decreases its fitness by c , while the fitness of the recipient increases by b , where $b > c$ (Nowak and Sigmund, 1998b). (For convenience, we fixed $c = 1$.) If a selfish actor does not help the recipient then the fitness of the partners remains unchanged. The altruistic behaviour is not reciprocated directly by the recipient, but this act is observed and valued by other individuals in the population. Thus, altruistic (selfish) individuals can be rewarded or punished indirectly by a third party if the previous actor becomes a recipient in the future.

Since stern-judging, the most successful norm is a second-order norm in a similar situation, we studied a second-order norm system, that is the classification of a potential recipient depends on its previous act and the reputation of their recipient (Ohtsuki and Iwasa, 2004; Pacheco et al., 2006). We use the simplest reputation system; thus, an individual can be “Good” or “Bad”. Thus, four different acts can be classified: “Selfish” act to a “Bad” recipient ($S \rightarrow B$), “Selfish” act to a “Good” recipient ($S \rightarrow G$), “Altruistic” help to “Bad” individual ($A \rightarrow B$) and “Altruistic” act to “Good” recipient ($A \rightarrow G$).

We assume that the norm followed by an individual classifies acts to be “Good” or “Bad” in a probabilistic manner. Thus, the norm of an individual i is determined by four probabilities: $\{p_{S \rightarrow B}^{(i)}, p_{S \rightarrow G}^{(i)}, p_{A \rightarrow B}^{(i)}, p_{A \rightarrow G}^{(i)}\}$, where $p_{X \rightarrow Y}^{(i)}$ describes the probability that an act X to individual in reputation Y is considered to be “Good” by individual i (and considered to be “Bad” with probability $1 - p_{X \rightarrow Y}^{(i)}$). We assume that not only the norm is on probabilistic basis, but the actions as well. Thus, if a potential actor i using her personal norm valued a recipient to be “Good” according to the previous action of the recipient, then the actor supports the recipient by the altruistic act with probability $q_G^{(i)}$. If the recipient is observed to be “Bad”, then it is supported with probability $q_B^{(i)}$. Therefore, an individual i is characterised by six probabilities: $\{p_{S \rightarrow B}^{(i)}, p_{S \rightarrow G}^{(i)}, p_{A \rightarrow B}^{(i)}, p_{A \rightarrow G}^{(i)}, q_G^{(i)}, q_B^{(i)}\}$, which are denoted by the pair of vectors $\mathbf{p}^{(i)}, \mathbf{q}^{(i)}$ in the sequel.

We assume that the interpretation of an action cannot be perfect; thus, $\varepsilon_1 < p_{X \rightarrow Y}^{(i)} < 1 - \varepsilon_1$, where $\varepsilon_1 \ll 1$ is the interpretation error. Similarly, there are no purely deterministic strategies because of execution mistakes, thus $\varepsilon_2 < q_Y^{(i)} < 1 - \varepsilon_2$ (Leimar and Hammerstein, 2001; Pacheco et al., 2006). For simplicity, we assume that $\varepsilon_1 = \varepsilon_2$ in this paper.

The defined norm system is consistent if the previous act (S or A) of every donor and the social status (G or B) of the recipient of this act are known and unambiguous. Thus, we assume that the social status of the recipient is determined by the actual classification of the actor, and all members of the group are informed about this classification (e.g. Ohtsuki and Iwasa, 2004).

Following the general view about the structure of ancient human population, we assume that individuals are distributed into small interacting groups; thus, selection works within and among groups as well (Bowles et al., 2003; Bowles and Gintis, 2003; Pacheco et al., 2006). For simplicity, each group contains N individuals and there are M groups in our model. In addition to the probabilistic norms and actions defined above, there is another generalisation in our model. While most previous models assumed that all individuals follow exactly the same social norm within a group (Nowak and Sigmund, 1998a, b; Leimar and Hammerstein, 2001; Ohtsuki and Iwasa, 2004, 2006; Pacheco et al., 2006), it is not required here (but see Brandt and Sigmund, 2004).

2.2. The evolutionary mechanism

Actors and recipients are selected randomly within the groups, such that every individual is once in the role of the actor and once in the role of the recipient in each round. The sums of the payoffs are considered as fitnesses of individuals. After rN rounds of interactions, there is a selection mutation step among individuals living in the same group. Pairs of randomly selected individuals are compared, and individual i imitates individual j with a probability given by

$$\pi = \frac{1}{1 + e^{-\beta(w_i - w_j)}}, \quad (1)$$

whereas the inverse process occurs with probability $(1 - \pi)$. Here w_i and w_j refer to the fitness of individual i and j , respectively, β determines the strength of selection (Szabó and Tóke, 1998). If $\beta \rightarrow \infty$ then $\pi \rightarrow 1$ if $w_i > w_j$, that is the less fit individual surely adopts the norm system of the fitter individual, whereas in the limit of $\beta \rightarrow 0$ then $\pi \rightarrow \frac{1}{2}$; thus there is no selection (neutral drift). Parameter β is fixed as $\beta = 10$ in the simulations, but the sensitivity of the results on this parameter is studied in the Appendix.

Imitation is not sufficiently perfect; if individual j adopts the norm system of individual i then the adopted norm is $\mathbf{p}^{(j)} = \mathbf{p}^{(i)} + \sigma_p \mathbf{e}$, where the elements of vector \mathbf{e} are random variables with standard normal distribution, and $\sigma_p \in [0, 1]$. Similarly, the adopted action $\mathbf{q}^{(j)} = \mathbf{q}^{(i)} + \sigma_q \mathbf{e}$. Knowing that human individuals are norm-followers, we might assume that σ_p and $\sigma_q \ll 1$ generally. To study the resistance of a norm against any actions, we assume that $\sigma_q = \sigma_q^{(h)}$ is close to one occasionally. To decrease the number of parameters in the model, we fixed $\sigma_q^{(h)} = 0.8$, which is set with probability 0.1 in the simulations, and otherwise $\sigma_p = \sigma_q = \sigma \ll 1$. In pairs of individuals are compared according to Eq. (1) in one selection mutation step, where l is a positive integer set to 10 in the simulations.

After this “within group” selection step, there is selection among groups. We calculated the average fitness of individuals within groups, and compared randomly selected pairs of groups according to their average fitnesses. The fitter group replaces the less fit one by using the update rule (1), except that now π is determined by the average fitnesses of the groups. The loser group disappears, and a new group is formed with individuals following the norms of individuals of the winner group. We assume that assimilation is not complete in the beaten group, that is K individuals keep their norm system in the next generation in the newly formed group. hM randomly selected pair of groups are compared in this selection step, (that is hM must be an integer). Generally, $h = 1$ in the simulations, but we study the sensitivity of the results to this assumption. After this group selection phase, a new cycle is started with indirect reciprocity games among the individuals within groups.

3. Results

Since we are interested in the emergence of a cooperative norm from a non-cooperative one, initially all individuals are almost perfectly selfish, that is $\mathbf{p}^{(i)} = \mathbf{0} + 0.01\mathbf{e}$, $\mathbf{q}^{(i)} = \mathbf{0} + 0.01\mathbf{e}$ for every $i = 1, 2, \dots, NM$. Further, initially every individual has bad (B) social status.

First, we study the case when there is only one group ($M = 1$); thus, selection is an action at the individual level. We made a comprehensive simulation by varying parameters, and we did not find any combination of parameters for which cooperation stably evolved within 5000 generations. We experienced that cooperative norm can emerge only temporally and only if b is extremely high (Fig. 1). To reveal the correlation between the characteristics of norms and the average fitness we calculated the average norm and action as $\bar{\mathbf{p}} = \sum_i \mathbf{p}^{(i)}$, $\bar{\mathbf{q}} = \sum_i \mathbf{q}^{(i)}$ at every time step. As a consequence of selection by imitation dynamics, we found that most individuals differ from each other moderately at every time step, so the average norm informatively describes the norm system followed by the population. With the help of the average norm, we can calculate the average probabilities of altruistic help of individuals being in different social statuses as

$$P_{X \rightarrow Y} = \bar{p}_{X \rightarrow Y} \bar{q}_G + (1 - \bar{p}_{X \rightarrow Y}) \bar{q}_B = \bar{q}_B + (\bar{q}_G - \bar{q}_B) \bar{p}_{X \rightarrow Y}, \quad (2)$$

where $P_{X \rightarrow Y}$ is the average probability of helping an individual that acts $X (= A, S)$ on individual $Y (= G, B)$ in the previous round. Bar denotes the average quantities everywhere. By plotting the average fitness against $P_{X \rightarrow Y}$ we reveal that low fitness values are strongly correlated with unconditionally selfish behaviour: if fitness values are low then $P_{X \rightarrow Y}$ values are low as well for every action X and status Y (Fig. 2). High average fitness, however, can emerge by a more diverse norm: the selfish action towards a bad individual is rewarded from moderate to high probability ($0.4 < P_{S \rightarrow B} < 0.95$) (Fig. 2A), while the selfish action towards a good individual is rewarded by practically any possible probability ($0.05 < P_{S \rightarrow G} < 0.9$) (Fig. 2B). The $A \rightarrow B$ action is either rewarded with a low ($0.05 < P_{A \rightarrow B} < 0.35$) or it is supported with a high probability ($P_{A \rightarrow B} \approx 0.9$) (Fig. 2C). The altruistic help to a good recipient is supported by the altruistic reward with a high probability ($P_{A \rightarrow G} \approx 0.95$) (Fig. 2D).

The situation can be qualitatively very different if individuals are arranged into groups and selection acts among the groups as well. Fig. 3 depicts a typical case when evolution leads to high

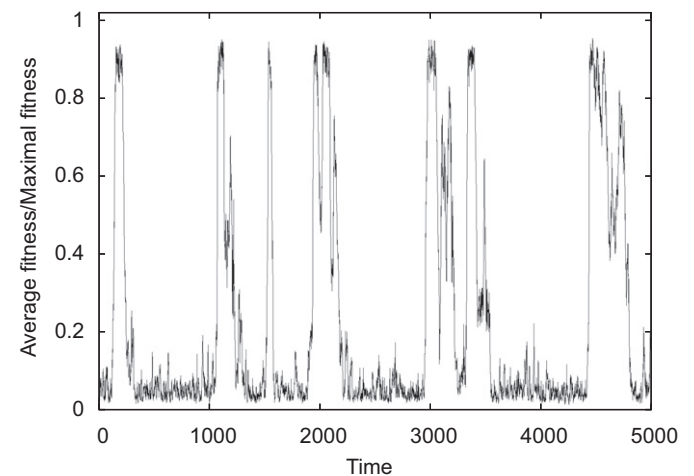


Fig. 1. The actual average fitness per the maximum attainable fitness value in a totally cooperative population in function of generation time. The benefit of receiving aid $b = 20$, while cost of donation is $c = 1$. Other parameters: $N = 100$, $\sigma = 0.3$, $r = 50$, $\varepsilon = 0.01$. Parameter K is not defined in this case.

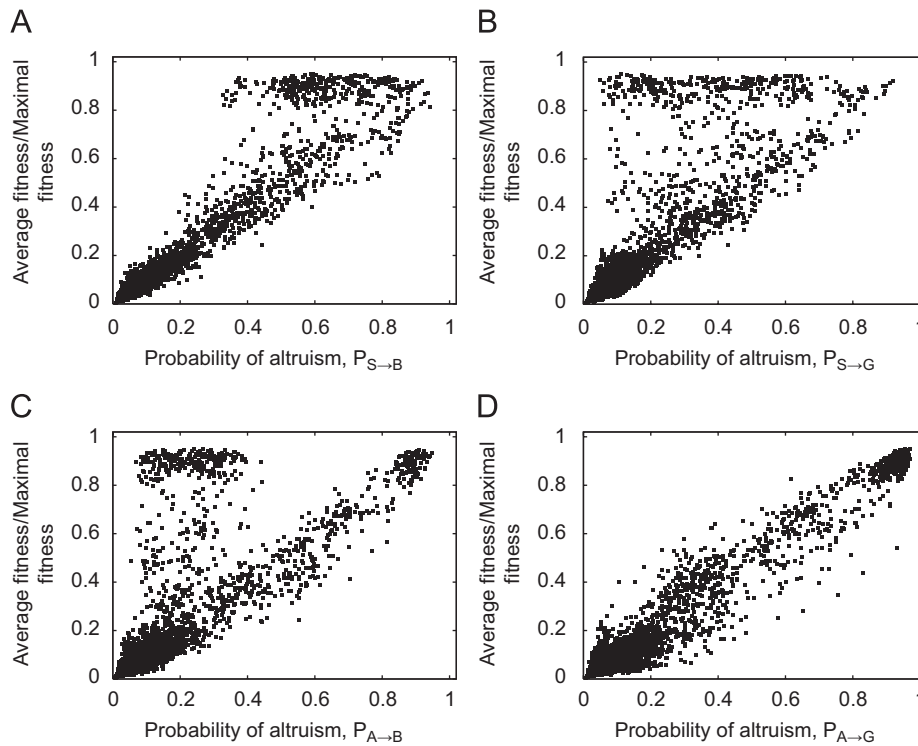


Fig. 2. The correlation among the average fitness and the probabilities of helping individuals being in different social statuses. (A) Average fitness vs. average probability of altruistic help to individual making $S \rightarrow B$ action in the previous round. (B) Average fitness vs. average probability of altruistic help to individual making $S \rightarrow G$ action in the previous round. (C) Average fitness vs. average probability of altruistic help to individual making $A \rightarrow B$ action in the previous round. (D) Average fitness vs. average probability of altruistic help to individual making $A \rightarrow G$ action in the previous round. We analysed the data series that is shown in Fig. 1. To keep the meaning of “good” unambiguous, we plotted the points only where $q_G \geq q_B$. For more details, see the main text.

fitness for every individual in every group because of the emergence of a cooperative norm.

According to Fig. 3B and C the cooperative norm considers the selfish action to a bad individual to be good rather than bad ($0.5 < P_{S \rightarrow B} < 0.7$), while the selfish action to a good individual is considered to be bad, and this recipient is supported only with a low probability ($P_{S \rightarrow G} \approx 0.25$). The $A \rightarrow G$ action is considered to be good and this altruist is supported with a very high probability (generally $P_{A \rightarrow G} \approx 0.85$). The reputation of $A \rightarrow B$ action fluctuates between high and low values in the cooperative state ($0.2 < P_{A \rightarrow B} < 0.8$), indicating that the reputation of this action is practically not under selection. The only exception can be observed at the initial transient state when fitness increases abruptly. Then, before the emergence of a selective norm described above, $P_{A \rightarrow B}$ becomes always almost as high as $P_{A \rightarrow G}$ (see Fig. 3C in time interval 0–800). We note here that “Good” and “Bad” signals are arbitrary in our model. Depending on random events, their role can fit the meanings or can be just the opposite in the cooperative state. For example, while $q_G \approx 1$, $q_B \approx 0$, and $p_{A \rightarrow G} \approx 1$ in Fig. 3B, then in other cases $q_G \approx 0$, $q_B \approx 1$, and $p_{A \rightarrow B} \approx 1$. For convenience we show the cases when “Good” means an individual that is supported with a high probability in a cooperative state ($q_G \approx 1$).

In addition to the characteristics of the average strategies in the cooperative state, it is interesting to know how evolution leads to this state. Similarly, it is important to reveal whether qualitatively different strategies can remain in coexistence in the cooperative state, or not. To study these questions, we made a simple classification for every strategy. As we computed $P_{X \rightarrow Y}$ above, we can determine these quantities for every individual. So

$$P_{X \rightarrow Y}^{(i)} = q_B^{(i)} + (q_G^{(i)} - q_B^{(i)})p_{X \rightarrow Y}^{(i)} \quad (3)$$

is the probability that individual i helps on an individual that acts $X(=A, S)$ to an individual being reputation $Y(=B, G)$ in the previous round. We made the following classification for $P_{X \rightarrow Y}^{(i)}$:

- If $0 \leq P_{X \rightarrow Y}^{(i)} < \frac{1}{3}$, then this probability determines a “defective” strategy and is denoted by D.
- If $\frac{1}{3} \leq P_{X \rightarrow Y}^{(i)} < \frac{2}{3}$, then the probability of altruistic and selfish act is roughly the same; so this strategy is “random”, and is denoted by R.
- If $\frac{2}{3} \leq P_{X \rightarrow Y}^{(i)} \leq 1$, then altruistic act is more probable than the selfish one; so this strategy is considered to be “cooperative” and is denoted by C.

(If we allow more classes then the results become less transparent, and the interpretation becomes more complex.) We order $P_{X \rightarrow Y}^{(i)}$ into a vector as $(P_{S \rightarrow B}^{(i)}, P_{S \rightarrow G}^{(i)}, P_{A \rightarrow B}^{(i)}, P_{A \rightarrow G}^{(i)})$, and the classified probabilities are ordered in a similar manner. For example, strategies based on a “stern-judging-like” norm are denoted by (C,D,D,C), while strategies based on “image scoring-like” norm are denoted by (D,D,C,C).

Similarly, q_G and q_B actions were classified as D, R, or as C type. Thus, we can have nine different types of action pairs from the always defecting (D,D) type to the always cooperating (C,C) type.

Using this three-state classification, we followed the number of individuals in the different strategy and action classes along evolution. For better comparison, we used the same numerical experiment as in Fig. 3. It was found that only four types of actions are present at least temporarily in non-negligible fraction (more than 5%), namely the (D,D), (R,D), (C,D), and (C,C) actions (Fig. 4). We observed that the vast majority of individuals, that is 80–90% of them follow only four or six different strategies among the

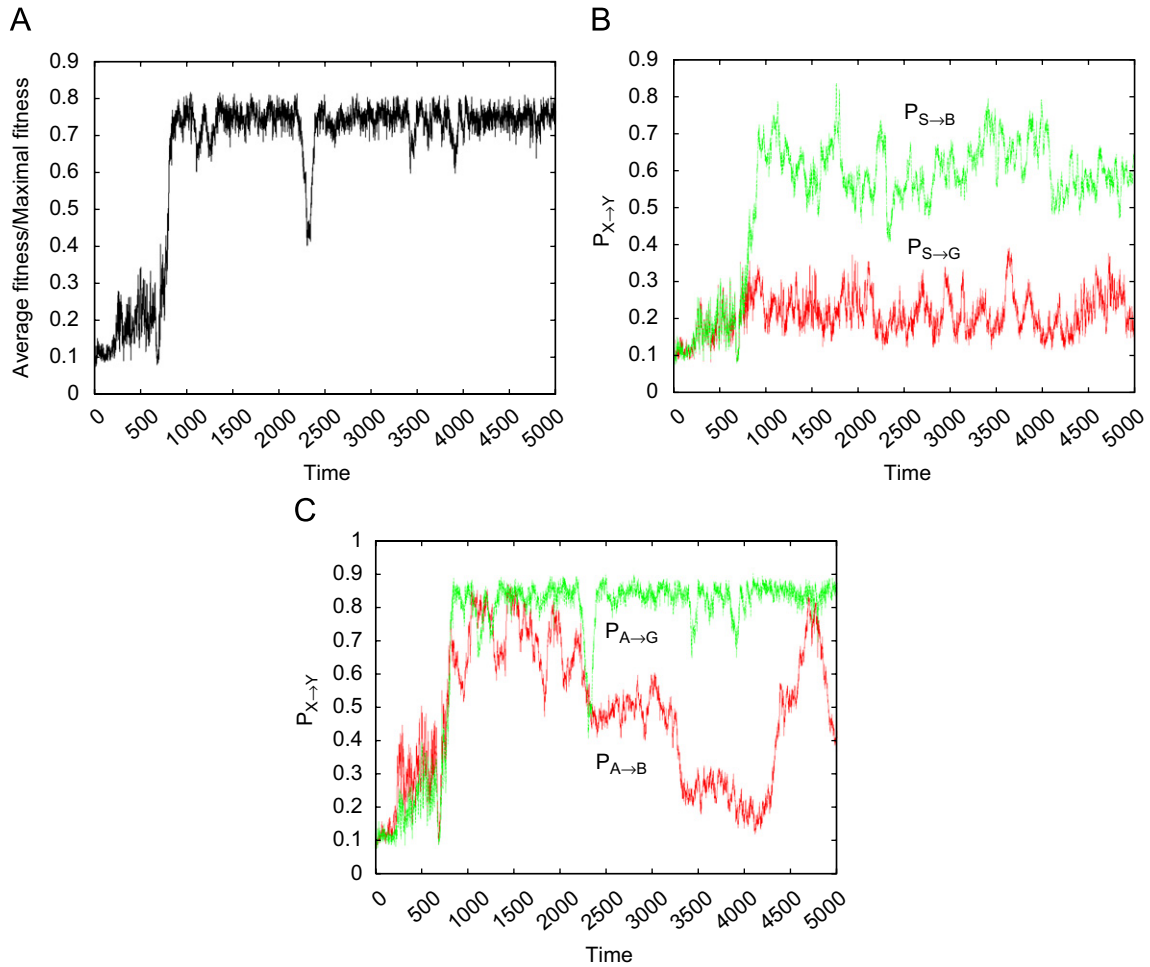


Fig. 3. (color online) Evolution of high average fitness by the emergence of a cooperative norm. (A) The average fitness in function of the generation time. (B) The average probabilities of altruistic help to individuals making selfish action for a bad ($S \rightarrow B$) (green online) or selfish action for a good ($S \rightarrow G$) (red online) individual in the previous round in function of time. (C) The average probabilities of altruistic help to individuals making altruistic action for a good ($A \rightarrow G$) (green online) or altruistic action for a bad ($A \rightarrow B$) (red online) individual in the previous round in function of time. The parameters of the simulation are: $M = 64$, $N = 64$, $K = 5$, $b = 3$, $\sigma = 0.01$, $r = 20$, $\varepsilon = 0.01$.

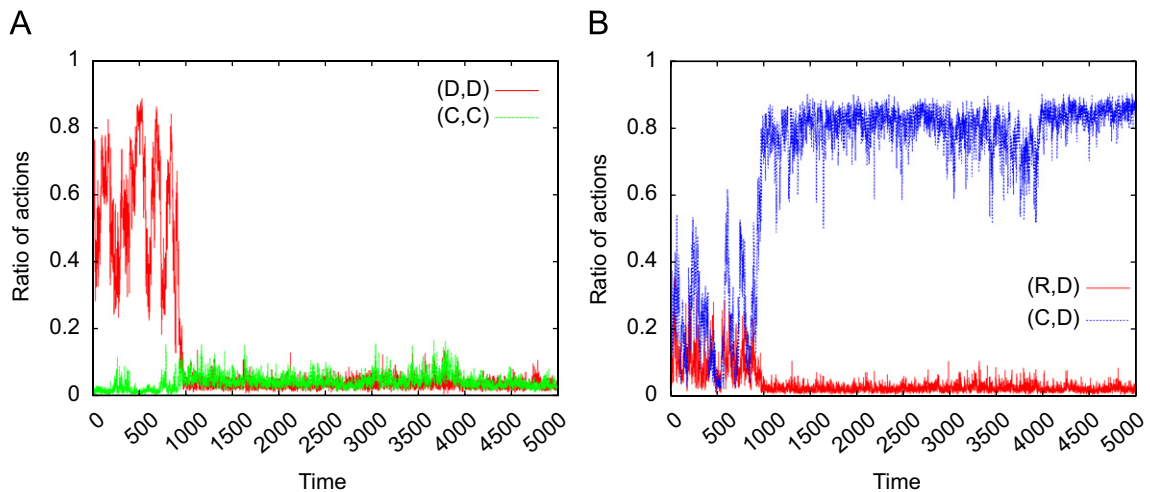


Fig. 4. (color online) The evolution of actions using a “three-state” classification. (A) The percentage of (D,D) (red online) and (C,C) (green online) actions in function of the generation time. (B) The percentage of (C,D) (blue online) and (R,D) (red online) actions in function of generation time. The parameters of the simulation are the same as in Fig. 3.

possible 81. Further, there is a fast exchange of these dominant strategies when the cooperative state emerges in the system (see Fig. 5A and compare to Fig. 3). Since initially all individuals follow

unconditionally defective strategies (ALLD-like or (D,D,D,D)), it is not surprising that their ratio is high for a while, but interesting about 5% of the populations remain stably ALLD-like in the

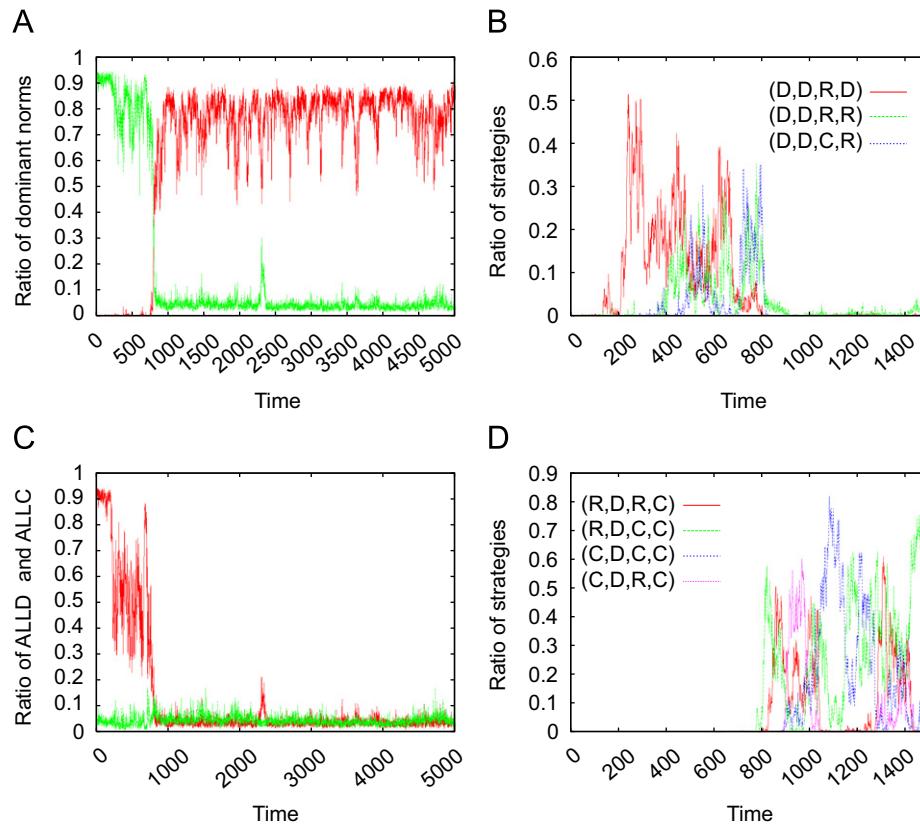


Fig. 5. (color online) The evolution of strategies using a “three-state” classification. (A) The percentage of dominant strategies in function of the generation time. The dominant strategies in the non-cooperative state are (D,D,D,D), (D,D,R,D), (D,D,R,R), (D,D,C,R) (green online), and in the cooperative state are (R,D,D,C), (R,D,R,C), (R,D,C,C), (C,D,D,C), (C,D,R,R), (C,D,C,C), (C,R,D,C) (red online). (B) The ratio of always defecting (ALLD-like) (red online) and always cooperating (ALLC-like) (green online) strategies in the population in function of generation time. (C) The ratio of dominant strategies (except the always defective (D,D,D,D)) in the non-cooperative state. (D) The ratio of cooperative dominant strategies in the neighbourhood of the non-cooperative, cooperative transition. The parameters of the simulation are the same as in Fig. 3.

cooperative state as well (Fig. 5C). The unconditionally cooperative strategies (ALLC-like or (C,C,C,C)) emerge soon after some evolutionary steps, and remain present in the population in about 5%, almost independently from the total level of cooperation in the population (Fig. 5C). We found that increasing inherent error (ε) increases the fraction of ALLD-like strategies, but punishing norms keep their fraction below 10% even at very high level of error. On the other side, increasing benefit (b) of altruistic act leads to a moderately increased level of ALLC-like strategies in the equilibrium, while the fraction of ALLD-like strategies remains practically constant.

The dominant strategies are steadily present neither within the non-cooperative nor within the cooperative state, but emerge abruptly and catalyse the evolution of other strategies. This series of “strategy catalysation” is particularly visible before and after the transition to the cooperative state (Fig. 5B and D). Besides the dominant ALLD-like strategy (which is not shown in Fig. 5B) roughly three strategies follow each other in the non-cooperative state: First the (D,D,R,D), then the (D,D,R,R), and last the (D,D,C,R) strategy spread (Fig. 5B). As the ALLD-like strategy becomes less and less dominant (see Fig. 5C), the other dominant strategies, following each other, become more and more generous for the altruistic act, while they remain defective against the selfish acts. Although the dominant strategies exchange each other in the cooperative state too, they have common characteristics: They are non-defective (R or C) for the $S \rightarrow B$ act, defective for the $S \rightarrow G$ act, and cooperative for the $A \rightarrow G$ act (Fig. 5D). Thus, dominant norms can be described as (C/R,D,*,C/R), where (*) is a wild card, implying that all possible strategies (D,R,C) can be included here. Because of the inherent stochasticity of the system, different

evolutionary pathways can be observed in different numerical experiments even at the same parameter set. However, all these pathways have the same qualitative characteristics described above.

Comparing Fig. 4A to Fig. 5C it is clear that the dominance of ALLD-like strategies is correlated with the dominance of (D,D) action, while the frequency of the ALLC-like strategy is in correlation with the frequency of (C,C) action. Similarly, by comparing Fig. 4B to Fig. 5B, D we can see that the emergence of more cooperative strategies is in correlation with the higher frequency of (R,D) action before the transition, and (C,D) action prevails in the cooperative state where the set of generous judging strategies are dominant.

To reveal the robustness of the result, we made 20 independent numerical experiments with the same parameter set and computed the average strategies ($\langle P_{X \rightarrow Y} \rangle$) and the average relative fitness, together with their variances (Fig. 6). Variance is generally small or moderate indicating that evolution to this cooperative state is a common nature of the model. Higher variance is measured for the $\langle P_{A \rightarrow B} \rangle$ strategy, which is the consequence of its slow fluctuation (see Fig. 3C and its explanation in the Conclusions). The occasional abrupt spread and collapse of defectors are behind the short-term bursts of variance of the average fitness. For higher b -s, the cooperative state is even more stable, and all variances are even smaller.

The relation between the benefit cost ratio and the average strategies and average fitness are studied in the cooperative state. We made ten independent numerical experiments at the same parameter setting, and computed the average behaviour from this as before. To characterise the cooperative state, we computed the time average and its variance of the above-defined $\langle P_{X \rightarrow Y} \rangle$

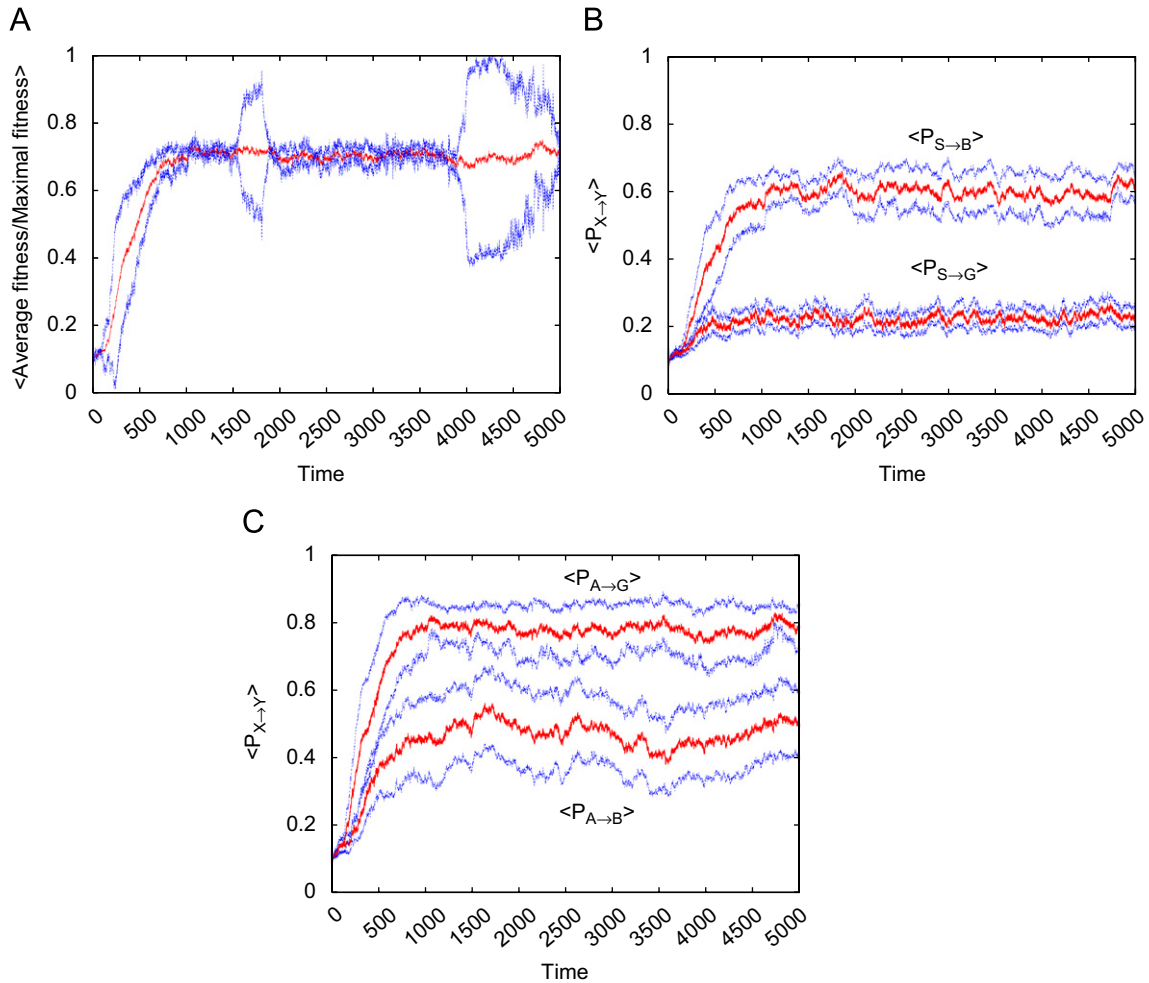


Fig. 6. (color online). The average fitness and average strategies in function of generation time. (A) Average fitness of 20 independent simulations (red online) with its variance (blue online). (B) Average $\langle P_{S \rightarrow B} \rangle$ and $\langle P_{S \rightarrow G} \rangle$ strategies (red online) and their variances (blue online). (C) Average $\langle P_{A \rightarrow B} \rangle$ and $\langle P_{A \rightarrow G} \rangle$ strategies (red online) and their variances (blue online). The parameters are the same as in Fig. 3.

quantities from $t = 4500$ to 5000 . This double average is denoted by $\langle \langle \cdot \rangle \rangle$. We found that the increased benefit cost ratio increases the probability of cooperation for all strategies, except for $A \rightarrow B$ action, where $\langle \langle P_{A \rightarrow B} \rangle \rangle$ does not significantly change as b/c varies (Fig. 7B and C). Since the average level of cooperation increases as b/c increases, the average fitness increases as well (Fig. 7A).

Similarly, we studied how the average strategies and fitness depend on the inherent noise ε . Since cooperative state can evolve only for higher b/c ratio when inherent noise is high, b is set to 9 in the numerical experiments. In concordance with our intuition, average fitness decreases as ε increases (Fig. 8A). This decreasing trend is valid for $\langle \langle P_{A \rightarrow G} \rangle \rangle$ and $\langle \langle P_{S \rightarrow B} \rangle \rangle$ (Fig. 8B), that is probability of cooperation declines with rewarding ($A \rightarrow G$) and with punishing ($S \rightarrow B$) individuals as noise enhances in the system. The opposite trend is found for $\langle \langle P_{A \rightarrow B} \rangle \rangle$ and $\langle \langle P_{S \rightarrow G} \rangle \rangle$ (Fig. 8C), that is individuals become more generous with the nasty action $S \rightarrow G$ and with the altruistic action $A \rightarrow B$ as inherent noise increases. While $\langle \langle P_{A \rightarrow B} \rangle \rangle$ becomes higher at higher inherent noise, the temporal fluctuation of it decreases, as the declining variance of this probability indicates (Fig. 8C). Interestingly, in cases when benefit to cost is relatively high (b is at least four times higher than c) and error is also relatively high, then only $S \rightarrow G$ action is considered as a bad behaviour ($\langle \langle P_{S \rightarrow G} \rangle \rangle < 0.5$), the others (including $A \rightarrow B$) are valued rather to be good, since all of them are rewarded by cooperation with a probability higher than 0.5 (see Fig. 8B and C).

We made a comprehensive study in the parameter space (although the complete scanning of the parameter space would require years of processor time). We found that evolution of the cooperative norm is the typical behaviour of the model in the biologically relevant parameter space. The results of these simulations are summarised in the Appendix.

4. Discussion

We considered groups of individuals following a second-order stochastic norm for evaluating acts of indirect altruism. Individuals are in competition with their group fellows, but there is competition among the groups as well. We have shown that a cooperative norm evolves typically from the state where only non-cooperative norms were present initially. Knowing the general positive effect of group selection on the evolution of cooperation (or altruism) (e.g. Maynard Smith and Szathmáry, 1995; Traulsen and Nowak, 2006; Pacheco et al., 2006), our result is not surprising to some extent. However, the characteristics of the evolutionary dynamics and the evolved state are far from obvious. Before the transition to the cooperative state, a series of strategies change each other. These strategies are willing to help more and more those individuals that were altruist in the previous round (Fig. 5B), that is, before the transition an image scoring-like strategy evolves. After the transition, dominant

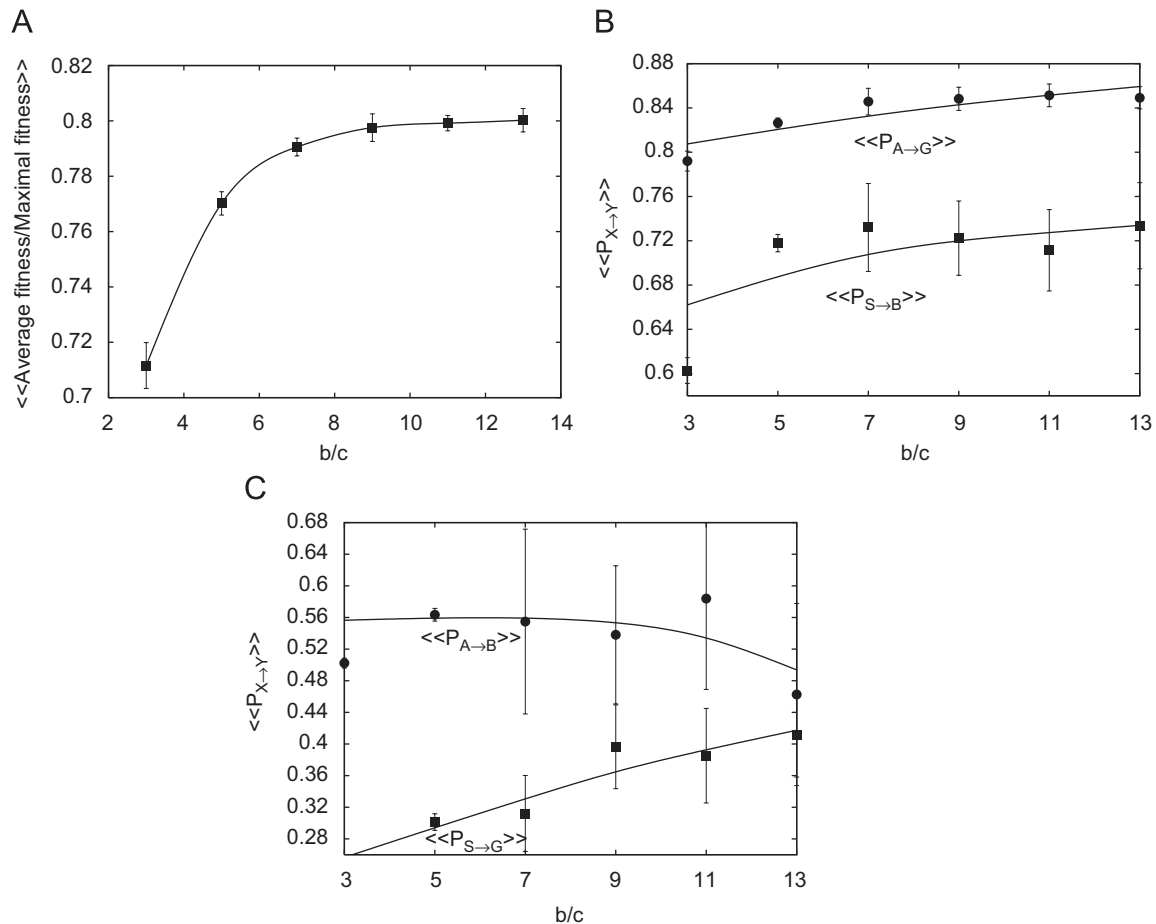


Fig. 7. The average fitness and average strategies in function of benefit cost ratio in the cooperative state. The average time evolution of the fitness and the strategies are computed from 10 independent simulations, and the average and variance of the last 500 values ($t = 4500 - 5000$) are plotted. (A) Average fitness at different b/c . (B) $\langle\langle P_{A \rightarrow G} \rangle\rangle$ and $\langle\langle P_{S \rightarrow B} \rangle\rangle$ strategies and their variances. (C) $\langle\langle P_{A \rightarrow B} \rangle\rangle$ and $\langle\langle P_{S \rightarrow G} \rangle\rangle$ strategies and their variances. (Solid lines are only for visualising the trends.) The other parameters are the same as in Fig. 3.

strategies condone upon those who refuse to help recipient with a bad score and frown upon those who refuse to help a recipient with a good score, which behaviour is the characteristic of the standing strategy (Fig. 5D). The strategies that emerge later are less helpful to those recipients whom previously gave help to a bad individual. Thus, they follow a judging-like strategy, although these so-called “generous judging” strategies are less strict than the “stern-judging” strategies emerged in Pacheco et al.’s (2006) model.

We can summarise the characteristics and reasons of the differences of “generous-judging” and “stern-judging” strategies in three points:

- Generous judging considers $A \rightarrow G$ and $S \rightarrow B$ as good behaviour similar to stern-judging. However, according our comprehensive simulations altruistic act to a good group fellow ($A \rightarrow G$) is rewarded by the generous judging with a higher probability than the punishing selfish act to a bad fellow ($S \rightarrow B$) (see Figs. 7 and 8). The deterministic stern judging could not make such a difference between the rewarding ($A \rightarrow G$) and the punishing ($S \rightarrow B$) acts.
- The selfish act to a good fellow ($S \rightarrow G$) is considered as a bad behaviour for both generous and stern-judging, but generous judging generously rewards it with probability 0.2–0.45 (Figs. 7 and 8). It is clear that in a noisy environment, in which generous judging operates nasty acts can occur as simple misinterpretation of the situation or misbehaviour, so

that some kind of generosity is needed to maintain stable cooperation. We note here that selection in a stochastic version of the iterated prisoners dilemma game leads to a similarly generous strategy (generous tit-for-tat) (Nowak and Sigmund, 1992).

- While altruistic help to a bad fellow is a bad action for stern-judging, this behaviour is practically not under selection for generous judging if interpretation error (ε) is small. Using the parameter set indicated above, we found that this ($A \rightarrow B$) action is present only in less than 5% of the population being in the cooperative state if $\varepsilon \lesssim 0.05$. Because of the inherent noise in this system it is likely that the norm of this action is practically neutral. However, for higher ε values $A \rightarrow B$ actions are present more frequently in the system. Interestingly, altruistic help to the bad fellow is considered rather as a good action if interpretation error is higher (see Fig. 8C). At the same time, decreased variance in $\langle\langle P_{A \rightarrow B} \rangle\rangle$ at higher inherent error indicates that selection increased for this act (Fig. 8C). This characteristic of generous judging—which is in clear contrast with stern judging—is the direct consequence of inherent stochasticity of the system.

Besides the dominant presence of generous judging strategies, ALLC- and ALLD-like strategies can be observed in the evolved state. What is more, ALLC-like strategy evolves early, and its frequency increases only a bit at the non-cooperative to cooperative state transition (Fig. 5C). Intuitively, the emergence

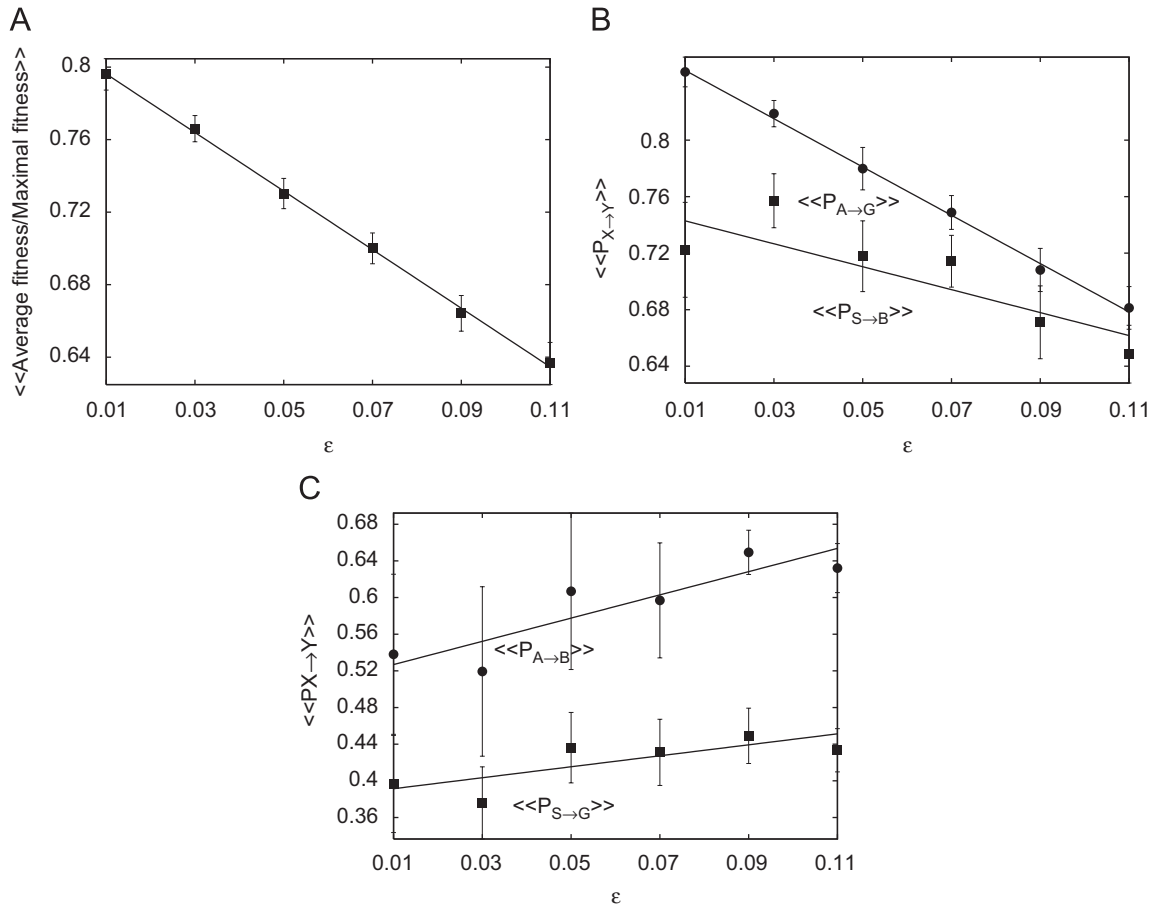


Fig. 8. The average fitness and average strategies in function of inherent error (ε) in the cooperative state. The average time evolution of the fitness and the strategies are computed from 10 independent simulations, and the average and variance of the last 500 values ($t = 4500 - 5000$) are plotted. (A) Average fitness at different ε . (B) $\langle P_{A \rightarrow G} \rangle$ and $\langle P_{S \rightarrow B} \rangle$ strategies and their variances. (C) $\langle P_{A \rightarrow B} \rangle$ and $\langle P_{S \rightarrow G} \rangle$ strategies and their variances. (Solid lines are only for visualising the trends.) $b = 9$ and the other parameters are the same as in Fig. 3.

of ALLC-like strategy besides the ALLD-like strategy at the early phase of evolution is the direct consequence of group selection used in the model. Groups with some altruists have a higher fitness than groups without them, which balances their individual level handicap (e.g. Maynard Smith, 1964). Later, at transition to the cooperative state the frequency of ALLD-like strategy decreases abruptly but it remains successful at a low frequency by parasitising ALLC-like strategy. Since punishing of the ALLD-like strategy is less efficient if the inherent error is more enhanced, it is natural that the frequency of ALLD-like strategies increases in a more noisy system. Generous judging strategies keep the fraction of ALLD-like strategy low in a more noisy system by increasing the probability of cooperation for individuals that were selfish to a bad individual previously (Fig. 8C).

Naturally, cooperative norm can evolve only above a critical level of benefit–cost ratio and below a critical noise level, but it is interesting to see how these parameters ($b/c, \varepsilon$) modify the system's behaviour in the cooperative state. We found that increasing b/c increases the level of generosity by increasing the probability of cooperation for the donor making selfish action to a good recipient (see Fig. 7C). Also, the cooperation to the rewarding $A \rightarrow G$ and punishing the $S \rightarrow B$ donor increase as the benefit–cost ratio increases (Fig. 7B). Cooperation with $A \rightarrow B$ does not change as b/c varies (Fig. 7C), while increased inherent noise makes individuals more generous to this altruistic act (Fig. 8C).

We studied the robustness of our model by changing systematically its parameters (see Appendix). The simulations suggest that evolution leads to the generous judging norm if the number

of groups are high enough, and, if the group size, and the number of non-assimilated individuals are low enough (see Table 1). As it seems to be strange, evolution of this cooperative norm does occur most easily at intermediate levels of group selection strength. However, this result can be explained if we use the contextual approach of multilevel selection (Heisler and Damuth, 1987; Okasha, 2004). According to this approach, the one-generation change of the average of a phenotypic character (denoted by $\Delta \bar{z}$) in a population subdivided into groups of equal size is

$$\Delta \bar{z} = \frac{\omega_1 \text{Var}(z_{ij}) + \omega_2 \text{Var}(Z_j)}{\bar{w}}, \quad (4)$$

where z_{ij} is the phenotypic value of the i th organism in group j , Z_j is the average phenotypic value in the j th group, \bar{w} is the average fitness, Var is the variance of these variables, and ω_1 and ω_2 are the coefficients describing how strongly individual and group average phenotypes determine the fitness of an individual (Heisler and Damuth, 1987; Okasha, 2004). There is a tension between the two levels of selection if signs of the ω -s are different. Naturally, this is the case in our model; thus, the direction of change of \bar{z} (the probabilities of the norm) is determined by group selection if $|\omega_2 \text{Var}(Z_j)| > |\omega_1 \text{Var}(z_{ij})|$. When the left-hand side of this inequality is maximum we may ask the question, when is the group selection effect most pronounced. If group level selection is weak, then ω_2 is small, but $\text{Var}(Z_j)$ is high, if selection is strong, then the situation is reversed: ω_2 is high, but $\text{Var}(Z_j)$ is small. The product of these

quantities is maximum at an intermediate level of selection strength, as we have experienced in the simulations.

Following previous studies, we assumed that more successful individuals are imitated by the less successful ones (e.g. [Boydt et al., 2003](#); [Pacheco et al., 2006](#)). However, to imitate a stochastic norm seems to be a complex task that may need much information about the past actions of the imitated individual. Thus, the conception that the offspring (not a randomly selected group mate) imitates the parents' norms by learning their behaviour is a realistic alternative assumption (e.g. [Nowak and Sigmund, 1998a, b](#); [Leimar and Hammerstein, 2001](#); [Bowles and Gintis, 2004](#)). To check whether our are robust against this modified selection mechanism or not, we made a series of simulations with the following alternative algorithm for the individual level of selection: Since it is an asexual model, we simply assume that offsprings adopt (learn or inherit genetically) the norm of their parent. Naturally, inheritance is not perfect, the variance of deviation is described by σ as before. After the reproduction step, the parents die and there will be exactly N offspring individuals in the next generation, in a way that the reproduction probability of a parent is proportional to its relative fitness. We found qualitatively the same results as in the imitation model, except that a bit higher benefit–cost ratio is needed for the evolution of a cooperative norm.

Our model is based on the assumption that individuals follow inherently stochastic social norms. The question is what do the experiments on indirect reciprocity games suggest about the stochasticity of the subjects' decisions? It is clear (and is not surprising) from experiments that subjects do not give deterministic “yes” or “no” decisions to a given situation in indirect reciprocity or in public goods games ([Wedekind and Milinski, 2000](#); [Milinski et al., 2001](#); [Fehr and Fischbacher, 2003](#); [Bolton et al., 2005](#)). The stochasticity of the decisions may originate from the misinterpretation of the situations, although the simplicity of the experimental settings may cause only a very limited noise in the deterministic choices. However, this is not the case: In [Milinski et al.'s](#) experiment ([Milinski et al., 2001](#)), subjects play the indirect reciprocity game in groups. One of the subjects in each group is secretly instructed to be always selfish. These players are punished almost with 100% after some rounds by doing selfish act, but the few altruistic donors of these selfish individuals are donated consistently with about 70% ($P_{A \rightarrow B} \approx 0.7$). This latter value is hardly the consequence of misinterpretation, it is rather the sign of norm stochasticity and/or norm polymorphism. Norm polymorphism, that is individuals can be classified into qualitatively different groups according to their behaviour, is generally observed in game theoretical conflicts (e.g. [Yamagishi, 1986](#); [Kurzban and Houser, 2005](#); [Shinada and Yamagishi, 2007](#)). [Bolton et al.'s](#) work (2005) serves an even stronger background for our assumption. They focused on the effect of information limitations on the amount of cooperation in a set of indirect reciprocity games. In one series of settings, subjects were informed to build up a second-order norm. [Bolton et al. \(2005\)](#) measured the probabilities of altruistic act on individual following action X ($X = S, A$) to individuals being in state Y ($Y = G, B$) in the previous ground, that is, they measured exactly the $P_{X \rightarrow Y}$ probabilities experimentally. They never found that any $P_{X \rightarrow Y}$ probabilities are close to zero or one implying deterministic norm. Besides the population level of polymorphism, even the same individual typically does not always behave in a completely consistent manner and may sometimes give or not give altruistic aid in comparable situations (Axel Ockenfels personal communication). [Bolton et al. \(2005\)](#) found that $P_{A \rightarrow G} > P_{A \rightarrow B} > P_{S \rightarrow B} > P_{S \rightarrow G}$ in the experiments, although values of these probabilities depend strongly on the b/c ratio. Independently of the other parameters, the same order can be observed in our model in the

cooperative state, if benefit–cost ratio is high as in the experiments, and if interpretation error is high enough (Fig. 8).

Another important conclusion is that in addition to the generous judging strategies ALLC- and ALLD-like strategies are stably present in the population. Interestingly, [Kurzban and Houser \(2005\)](#) found that approximately 20% of individuals are always defecting free-riders, 13% are unconditional cooperators, and 63% are reciprocators in a modified version of the public goods game. Consequently, a very similar type of strategy polymorphism can be observed in an experimental situation, although the social dilemma is different from the one used in our model system.

Acknowledgements

This work was founded by OTKA T049692 and NN71700 (TECT). The author thanks the referees for helpful comments and suggestions.

Appendix

Besides the simulations depicted in [Figs. 7 and 8](#) we made a comprehensive study in the parameter space to reveal the robustness of our results. In the first series of simulations M is varied ($M = 2, \dots, 64$) and the other parameters are fixed ($b = 2$, $r = 20$, $\varepsilon = 0.01$, $\sigma = 0.01$, $l = 10$, $\beta = 10$, $N = 64$, $K = 5$). When M was small (< 10), we did not experience the emergence of cooperative norm within 2000 generations, but if M was roughly above 10 then the cooperative norm was able to evolve in some simulations. When M is roughly above 30, the cooperative norm emerges surely within a few hundred generations. We found that the average fitness in the cooperative state and the qualitative characteristics of cooperative norms do not depend on M if $M > 30$.

In the following experiment, N is varied ($N = 10, \dots, 100$) and M is fixed ($M = 32$), while the other parameters remain the same as in the previous set of simulations. Cooperation emerges after a short time at relatively small group sizes, however, the fitness and the probabilities determining the norm are highly fluctuating. Larger group sizes population alternates between the metastable cooperative and non-cooperative states. In the cooperative state, the norm is qualitatively the same as in [Fig. 3](#).

It is important that the benefit of the altruistic act is relatively small ($b = 2$) in the above mentioned simulations. Repeating the previous simulations with a higher benefit ($b = 4$), we found that cooperative norm stable evolves both at smaller ($N = 10$) and at bigger ($N = 64$) group sizes, albeit the evolved norms remain qualitatively different.

Next, we studied how the ratio of non-assimilated individuals effects norm-evolution. We varied K between 0 and 20 while $N = 64$, $M = 32$ and the other parameters were the same as before. Cooperative norm has evolved within some hundred of generations until $K < 15$, but remains selfish within 2000 generations if the number of non-assimilated individuals is higher than this value. Interestingly, neither the characteristics of the cooperative norm nor the average fitness depend on the number of non-assimilated individuals in the cooperative state.

Another important parameter is σ , which describes how precisely imitators follow the successful norms. It is changed between 0.005 and 0.1 in our simulations, while $K = 0$, $N = 64$, $b = 3$ and $M = 32$, and the other parameters are the same as before. Increasing σ decreases the average fitness in the cooperative state, and increases the fluctuation of fitness and norms at the same time. As σ increases the evolved norms become metastable, and the system jumps between the alternative

Table 1

The effect of parameters on the evolution of a cooperative norm and the average fitness in the cooperative state.

Changing parameter	Prob. of a coop. norm	Fitness in a coop. state
$M = 4, \dots, 64$	+	0
$N = 10, \dots, 100$	–	+
$K = 0, \dots, 20$	–	–
$b = 1.5, \dots, 20$	+	+
$\sigma = 0.005, \dots, 0.1$	0/–	–
$r = 10, \dots, 90$	–	0
$l = 1, \dots, 110$	Optimum	Optimum
$\varepsilon = 0, 0.1, \dots$	–	–
$\beta = 1, \dots, 100$	+	0
$h = 1, 1/2, \dots, 1/16$	Optimum	0

+ Means that the increased parameter has a positive effect, – means negative effect, and 0 denotes that it has a neutral effect on the evolution of a cooperative norm. M is the number of groups, N is the population size within a group, K is the number of non-assimilated individuals, b is the benefit of the recipient (cost of the altruistic act set to 1), σ is the variance of the norm deviation after imitation, rN is the number of interactions between two selection steps, lN pairs of individuals are compared in the individual selection step, ε describes the interpretation and execution error, β determines the strength of the selection, and hM groups are compared in the group selection step.

metastable states (i.e. “Good” is supported or “Bad” is supported with a high probability). Above a critical σ (it is about 0.07 in our simulation) norm imitation will be so inaccurate that norms classify actions practically in a non-selective manner. For example if $\sigma = 0.07$ then $P_{X \rightarrow Y} \approx 0.38$ for every action, and consequently average fitness in the population is about 38% of the possible maximum fitness that would be attained in a perfectly cooperative state.

We studied the effect of r (the number of interactions within two group-selection steps) on the evolution of cooperative norm as well. Parameter r was changed within the interval [10 90], while other parameters were as before. We found that the evolution of a cooperative norm becomes less probable within the studied time interval as r increases. Further, it was found that increasing l (the number of pairwise comparisons among individuals within a group) first increases the probability of evolution of the cooperative norm and the average fitness on this cooperative state ($l = 1$ –40), but this tendency is reversed at higher values of l -s ($l = 50$ –110) ($l = 1, \dots, 110$, $M = 32$, $N = 64$, $K = 0$, $b = 2$, $\sigma = 0.01$, $\beta = 10$, $r = 20$).

In concordance with our intuition, increasing β , that is increasing the strength of selection has a positive effect on the evolution of cooperative norm. For the simulations, we used the same parameter set as in the previous case, except that ε is fixed to 0.01 and β varies between 1 and 100.

The strength of group selection as compared to the individual level of selection can be varied by changing β only in the group selection step, or, similarly, if the number of comparisons among the groups is changed (i.e. parameter h), while the other parameters remain fixed. As we experienced, the cooperative norm evolves most easily at intermediate level of group selection strength. Table 1 summarises the results of the above simulations qualitatively.

References

- Alexander, R.D., 1987. *The Biology of Moral Systems*. Aldine de Gruyter, New York.
 Axelrod, R., 1984. *The Evolution of Cooperation*. Basic Books, New York.
 Axelrod, R., Hamilton, W.D., 1981. The evolution of cooperation. *Science* 211, 1390–1396.

- Bolton, G.E., Katok, E., Ockenfels, A., 2005. Cooperation among strangers with limited information about reputation. *J. Publ. Econ.* 89, 1457–1468.
 Bowles, S., Choi, J.-K., Hopfensitz, A., 2003. The co-evolution of individual behaviors and social institutions. *J. Theor. Biol.* 223, 135–147.
 Bowles, S., Gintis, H., 2003. *Origins of human cooperation*. In: Hammerstein, P. (Ed.), *Genetic and Cultural Evolution of Cooperation*. The MIT Press, Cambridge, England.
 Bowles, S., Gintis, H., 2004. The evolution of strong reciprocity: cooperation in heterogeneous populations. *Theor. Popul. Biol.* 65, 17–28.
 Boyd, R., Gintis, H., Bowles, S., Richerson, P.J., 2003. The evolution of altruistic punishment. *Proc. Natl. Acad. Sci. USA* 100, 3531–3535.
 Brandt, H., Sigmund, K., 2004. The logic of reprobation: assessment and action rules for indirect reciprocity. *J. Theor. Biol.* 231, 475–486.
 Chalub, F.A.C.C., Santos, F.C., Pacheco, J.M., 2006. The evolution of norms. *J. Theor. Biol.* 241, 233–240.
 Dugatkin, L.A., Mesterton-Gibbons, M., Houston, A., 1992. Beyond the prisoner's dilemma: towards models to discriminate among mechanisms of cooperation in nature. *Trends Ecol. Evol.* 7, 202–205.
 Ember, C., 1978. Myths about hunter-gatherers. *Ethnology* 17, 439–449.
 Fehr, E., Fischbacher, U., 2003. The nature of human altruism. *Nature* 425, 785–791.
 Heinrich, J., Heinrich, N., 2006. Culture, evolution and the puzzle of human cooperation. *Cogn. Syst. Res.* 7, 220–245.
 Heisler, I.L., Damuth, J., 1987. A method for analyzing selection in hierarchically structured populations. *Am. Nat.* 130, 582–602.
 Kurzban, R., Houser, D., 2005. Experiments investigating cooperative types in humans: a complement of evolutionary theory and simulations. *Proc. Natl. Acad. Sci. USA* 102, 1803–1807.
 Lehmann, L., Keller, L., West, S., Roze, D., 2007. Group selection and kin selection: two concepts but one process. *Proc. Natl. Acad. Sci. USA* 104, 6736–6739.
 Leimar, O., Hammerstein, P., 2001. Evolution of cooperation through indirect reciprocity. *Proc. Roy. Soc. B* 268, 745–753.
 Maynard Smith, J., 1964. Group selection and kin selection. *Nature* 201, 1145–1147.
 Maynard Smith, J., Szathmáry, E., 1995. *The Major Transitions in Evolution*. Freeman Spektrum.
 Milinski, M., Semmann, D., Bakker, T.C.M., Krambeck, H.J., 2001. Cooperation through indirect reciprocity: image scoring or standing strategy? *Proc. Roy. Soc. B* 268, 2495–2501.
 Nowak, M., May, R., 1992. Evolutionary games and spatial chaos. *Nature* 359, 826–829.
 Nowak, M., Sigmund, K., 1992. Tit for tat in heterogeneous populations. *Nature* 355, 250–252.
 Nowak, M., Sigmund, K., 1998a. The dynamics of indirect reciprocity. *J. Theor. Biol.* 194, 561–574.
 Nowak, M., Sigmund, K., 1998b. Evolution of indirect reciprocity by image scoring. *Nature* 393, 573–577.
 Ohtsuki, H., Iwasa, Y., 2004. How should we define goodness?—reputation dynamics in indirect reciprocity. *J. Theor. Biol.* 231, 107–120.
 Ohtsuki, H., Iwasa, Y., 2006. The leading eight: social norms that can maintain cooperation by indirect reciprocity. *J. Theor. Biol.* 239, 435–444.
 Okasha, S., 2004. Multilevel selection and the partitioning of covariance: a comparison of three approaches. *Evolution* 58, 486–494.
 Pacheco, J.M., Santos, F.C., Chalub, F.A.C.C., 2006. Stern-judging: a simple, successful norm which promotes cooperation under indirect reciprocity. *PLOS Comp. Biol.* 2 (e178), 1634–1638.
 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.
 Richerson, P., Robert, B., Bettinger, R.L., 2001. Was agriculture impossible during the pleistocene but mandatory during the holocene? A climate change hypothesis? *Am. Antiquity* 66, 387–411.
 Shinada, M., Yamagishi, T., 2007. Punishing free riders: direct and indirect proportion of cooperation. *Evol. Hum. Behav.* 28, 330–339.
 Soltis, J., Boyd, R., Richerson, P.J., 1995. Can group-functional behaviours evolve by cultural group selection? An empirical test. *Cur. Anthropol.* 36, 473–494.
 Sugden, R., 1986. *The Evolution of Rights, Co-operation and Welfare*. Blackwell, Oxford.
 Szabó, G., Töke, C., 1998. Evolutionary prisoner's dilemma game on a square lattice. *Phys. Rev. E* 58, 69–73.
 Taylor, C., Nowak, M., 2007. Transforming the dilemma. *Evolution* 61, 2281–2292.
 Traulsen, A., Nowak, M., 2006. Evolution of cooperation by multilevel selection. *Proc. Natl. Acad. Sci. USA* 103, 10952–10955.
 Traulsen, A., Shores, N., Nowak, M., 2008. Analytical results for individual and group selection of any intensity. *Bull. Math. Biol.* 70, 1410–1424.
 Trivers, R., 1971. The evolution of reciprocal altruism. *Q. Rev. Biol.* 46, 35–57.
 Trivers, R., 1985. *Social Evolution*. Benjamin Cummings, Menlo Park, CA.
 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.
 Wedekind, C., Milinski, M., 2000. Cooperation through image scoring in humans. *Science* 288, 850–852.
 Yamagishi, T., 1986. The provision of sanctioning system as a public good. *J. Pers. Soc. Psychol.* 51, 110–116.