Participation costs can suppress the evolution of upstream reciprocity

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ABSTRACT

Indirect reciprocity, one of the many mechanisms proposed to explain the evolution of cooperation, is the idea that altruistic actions can be rewarded by third parties. Upstream or generalized reciprocity is one type of indirect reciprocity in which individuals help someone if they have been helped by somebody else in the past. Although empirically found to be at work in humans, the evolution of upstream reciprocity is difficult to explain from a theoretical point of view. A recent model of upstream reciprocity, first proposed by Nowak and Roch (2007) and further analyzed by Iwagami and Masuda (2010), shows that while upstream reciprocity alone does not lead to the evolution of cooperation, it can act in tandem with mechanisms such as network reciprocity and increase the total level of cooperativity in the population. We argue, however, that Nowak and Roch's model systematically leads to non-uniform interaction rates, where more cooperative individuals take part in more games than less cooperative ones. As a result, the critical benefit-to-cost ratios derived under this model in previous studies are not invariant with respect to the addition of participation costs. We show that accounting for these costs can hinder and even suppress the evolution of upstream reciprocity, both for populations with non-random encounters and graph-structured populations.

1. Introduction

In addition to kin selection (Hamilton, 1964) and group selection (Wilson, 1975), different types of reciprocity have been proposed for explaining altruistic behavior from an evolutionary perspective (Nowak, 2006). In this paper, we focus on upstream indirect reciprocity and network reciprocity. Contrastingly to direct reciprocity (Trivers, 1971; Axelrod and Hamilton, 1981), which can induce cooperation when individuals base their decision to cooperate on the outcome of previous encounters with the same partner, indirect reciprocity is said to occur when 'the return is expected from someone other than the recipient of the beneficence' (Alexander, 1987). This can happen in one of two ways. In downstream indirect reciprocity (Nowak and Sigmund, 1998a,b; Leimar and Hammerstein, 2001; Panchanathan and Boyd, 2003; Brandt and Sigmund, 2004; Ohtsuki and Iwasa, 2004; Nowak and Sigmund, 2005; Brandt and Sigmund, 2006; Ohtsuki et al., 2006; Ohtsuki and Iwasa, 2007; Uchida and Sigmund, 2010) or vicarious reciprocity (Sigmund, 2010), first individual A helps individual B and then C helps A. Downstream reciprocity is based on reputation: A acquires a good reputation by helping B, thereby increasing its chances of receiving help by C.

In upstream indirect reciprocity (Boyd and Richerson, 1989; Nowak and Sigmund, 2005; Nowak and Roch, 2007; Iwagami and Masuda, 2010), also known as generalized reciprocity (Pfeiffer et al., 2005; Hamilton and Taborsky, 2005; Rutte and Taborsky, 2007; Rankin and Taborsky, 2009) or misguided reciprocity (Sigmund, 2010), first individual A helps individual B and then B helps C. Upstream reciprocity is based on gratitude or moral elevation: individuals who receive help are more inclined to help others in the future. Finally, network reciprocity (Ohtsuki et al., 2006) is at work when the population structure takes the form of a spatial or social network in which clusters of cooperators can help each other and resist invasion from surrounding defectors. Network reciprocity is the generalization of spatial reciprocity (Nowak and May, 1992) to general network models. Under some conditions other mechanisms are also at work in heterogeneous networks, where highly connected individuals can play an important role in promoting cooperation (Santos and Pacheco, 2005, 2006; Szabó and Fáth, 2007; Gómez-Gardeñes et al., 2007; Pacheco et al., 2009).

A simple and general explanation of the evolution of cooperation is the positive assortment between cooperative genotypes and cooperative phenotypes (Fletcher and Doebeli, 2009). In stark contrast with direct, downstream and network reciprocity, upstream reciprocity per se fails to provide such assortment. Thus, strategies based on upstream reciprocity go to extinction in well-mixed populations when competing with defectors

(Nowak and Roch, 2007; Rankin and Taborsky, 2009; Sigmund, 2010). Despite this fact, models of upstream reciprocity are worth studying for several reasons. Firstly, there is ample empirical evidence of upstream reciprocity occurring in humans (Berkowitz and Daniels, 1964; Isen, 1987; Dufwenberg et al., 2001; Güth et al., 2001; Bartlett and DeSteno, 2006; Stanca, 2009) and some evidence in non-human animals such as Norwegian rats (Rutte and Taborsky, 2007). Secondly, it has been theoretically shown that upstream reciprocity can evolve if there is some pre-existent assortment among strategies (Rankin and Taborsky, 2009). Such assortment can be provided, for instance, by the random forma-tion of small groups (Boyd and Richerson, 1989; Pfeiffer et al., 2005), by incorporating group-leaving behavior when experien-cing defection (Hamilton and Taborsky, 2005), or by the simulta-neous presence of another cooperation-promoting mechanism, such as direct reciprocity (Nowak and Roch, 2007) or network reciprocity (Nowak and Roch, 2007; Iwagami and Masuda, 2010). Finally, when acting in tandem with these mechanisms, the presence of upstream reciprocity seems to lead to higher levels of cooperation and/or lower critical cost-to-benefit ratios than those obtained by direct or network reciprocity alone (Nowak and Roch, 2007; Iwagami and Masuda, 2010).

Usually, indirect reciprocity is theoretically studied in the framework of the Donation game. Each round of the game, two players are chosen at random from the population. One is assigned the role of the donor and the other the role of the recipient. The donor has the option of either helping the recipient or not. If the donor chooses to help, the donor will incur a cost c while the recipient obtains a benefit b, with $b > c > 0$. If the donor refuses to help, payoffs are left unchanged. In Nowak and Roch (2007) and Iwagami and Masuda (2010), Donation games are played along 'chains of altruism' leading to random walks in the population of players. Each player can start a chain of altruism by helping a second player in the population, who can in turn help a third player, and so on and so forth. Such sampling of donors and recipients differs from the one normally used in standard models of indirect reciprocity (cf. Nowak and Sigmund, 1998b) in which interaction partners are randomly and independently sampled from the population. In particular, whereas in standard models individuals interact in average the same number of times (half of the times as donors, half of the times as recipients) in Nowak and Roch's model more cooperative players end up interacting more often than less cooperative players.

Whenever an evolutionary game model leads to non-uniform interaction rates, some questions arise regarding the generality of the obtained results. It is not clear, for instance, whether a given strategy is successful because it 'plays well' against competitors or because it plays more often, nor if the assumption of having individuals with no limitations regarding the number of interac-tions they engage in per generation is biologically or socially grounded. It is reasonable to think that a number of extrinsic constraints limit the interacting capacity of individuals or that participation in a game can have a non-negligible cost. This is an issue that has been dealt with in the context of evolutionary games on heterogeneous networks (Santos and Pacheco, 2006; Santos et al., 2006; Masuda, 2007; Tomassini et al., 2007; Tanimoto and Yamauchi, 2010). Different methods have been introduced in order to control for the non-uniformity of interac-tion rates, such as imposing cutoffs in the interaction distribu-tions (Santos et al., 2006), using the average payoff instead of the accumulated payoff when defining fitness (Santos and Pacheco, 2006; Tomassini et al., 2007; see also Taylor and Nowak, 2006) and introducing participation costs (Masuda, 2007; Tanimoto and Yamauchi, 2010). All these studies have shown that adding such limits can hinder and even suppress the evolution of cooperation based on network reciprocity in heterogeneous networks.

In this paper, we re-examine the model of upstream recipro-city first proposed by Nowak and Roch (2007) and further investigated by Iwagami and Masuda (2010). Nowak and Roch (2007) showed that upstream reciprocity is viable when acting in tandem with direct reciprocity or when the population is arranged in a one-dimensional array. Iwagami and Masuda (2010) extended the model to more complex network structures and showed that heterogeneous networks can be important amplifiers of upstream reciprocity. We show that non-uniform interaction rates naturally arise in the original model by Nowak and Roch (2007) and that when population structure favors some assortment of strategies more cooperative players end up playing more often as recipients than less cooperative players, i.e. that interaction rates are strategy-dependent. We find that the evolu-tionary dynamics of upstream reciprocity are modified when controlling for such non-uniformity by introducing participation costs, to the extent that whether or not upstream reciprocity is able to hitch-hike on mechanisms such as direct or network reciprocity depends on the cost of participation in the game.

2. Upstream reciprocity with participation costs

We briefly describe Nowak and Roch's model and its extension to include participation costs. A population V of n individuals plays the upstream reciprocity game. The strategy implemented by player v is denoted by $S_v(p_v, q_v)$, where q_v is the probability to initiate a chain of gratitude and p_v is the probability to pass a chain initiated by another player. Consider the random walk originated in player v. The random walk ends with probability $1 - q_v$ or moves to another player $w \in V - \{v\}$ with probability q_v. Then the walk ends with probability $1 - p_w$ or is passed to another player in $V - \{w\}$ with probability p_w. The process is repeated until the random walk ends. Each time the random walk enters a player it brings a benefit b to that player. Each time the random walk exits a player (without ending) it costs c to that player. In order for the game to be a social dilemma, $b > c > 0$.

Let us denote by N_v^{in} the number of times the random walk started by any player reaches v and by N_v^{out} the number of times such walk exits v without ending. In other words, N_v^{in} and N_v^{out} are, respectively, the number of times player v has acted as recipient and the number of times it has acted as donor. Finally, denote by N_v the total number of participations in a game by player v, i.e. $N_v := N_v^{in} + N_v^{out}$. With these definitions, the accumulated payoff to player v is given by

$$\pi_v = N_v^{in} b - N_v^{out} c. \tag{1}$$

This expression assumes that participation in a game is free. Let us now suppose that both the donor and the recipient pay a fee $d > 0$ for participating in the game. With participation costs, every time the random walk of gratitude reaches a player, it brings a net profit $b - d$ to that player, whereas every time the walk exits a player, it costs $c + d$ to that player. In order to analyze the effects of the introduction of participation costs in the game it thus suffices to make the replacements $b \rightarrow b - d$ and $c \rightarrow c + d$ in Eq. (1). We will make use of this simple fact in the next sections.

Consider now the evolutionary competition between indivi-duals v and w when fitness is equated with the accumulated payoff. The difference in fitness can be expressed as

$$\Delta \pi := \pi_v - \pi_w = (N_v^{in} - N_w^{in})b - (N_v^{out} - N_w^{out})c - (N_v - N_w)d.$$

When $N_v = N_w$, the third term vanishes and the difference in fitness between players v and w is independent of the cost of participation d. When $N_v \neq N_w$, however, the difference in fitness depends on the participation cost d. Evolutionary game dynamics based on the fitness difference, such as the replicator equation

(Taylor and Jonker, 1978; Hofbauer and Sigmund, 1998; Weibull, 1995), are thus influenced by the participation cost d when interaction rates are non-uniform.

Consider a random walk entering and exiting a player (i.e. an individual participating as recipient and immediately as donor), so that the increase in payoff for such player is equal to $\delta\pi := b - c - 2d$. One can identify two regimes in terms of the participation cost d: (i) $d < (b-c)/2$, and (ii) $d > (b-c)/2$. In regime (i), $\delta\pi > 0$. In this case, gratitude-related altruists can prevail by maximizing the number of waves of generosity being initiated and passed, as long as some mechanism of assortment makes such waves return more often to gratitude-related altruists than to other strategists. In regime (ii), $\delta\pi < 0$, and the optimal strategy is now to minimize the number of participations in a game. Defectors never initiate nor pass waves of generosity. Thus, they are expected to perform better than gratitude-related altruists in this regime, and to be evolutionarily stable.

In the following, we confirm these predictions in two models of upstream reciprocity, each one providing assortment of strategies in a different way: (i) by assuming non-random encounters, and (ii) by incorporating network reciprocity. The last model extends the results by Nowak and Roch (2007) and Iwagami and Masuda (2010) to cases when participation is costly.

3. Upstream reciprocity under assortment of encounters

Consider a population of size n and the interaction between strategy $S_1 = S(p_1, q_1)$, of relative frequency x, and strategy $S_2 = S(p_2, q_2)$, of relative frequency $1 - x$. The cooperativity s_i of strategy S_i, defined as 'the expected number of secondary altruistic acts induced by a single player per time-step' (Nowak and Roch, 2007), is given by $s_i = q_i/(1 - p_i)$. The expected fitnesses of S_1 and S_2 are given by their expected accumulated payoffs $\pi_1(x)$ and $\pi_2(x)$, and the evolutionary dynamics by the replicator equation, so that the frequency of S_1 in an infinite population evolves according to

$$\dot{x} = x(1-x)\Delta\pi(x), \qquad (2)$$

where $\Delta\pi(x) := \pi_1(x) - \pi_2(x)$.

We introduce assortment of strategies in a simple manner (Eshel and Cavalli-Sforza, 1982; Boyd and Richerson, 1989; Rankin and Taborsky, 2009). We suppose that, once a player of type S_i has decided to initiate or pass a random walk of gratitude, the probability that the recipient of type S_j is given by $\sigma_{ij} = \sigma_{ij}(x)$, with

$$\sigma_{11} = \sigma + x(1-\sigma),$$

$$\sigma_{22} = \sigma + (1-x)(1-\sigma),$$

and $\sigma_{i1} + \sigma_{i2} = 1$, for $i = 1, 2$. The parameter $\sigma \in [0,1]$ is the degree of assortment: when $\sigma = 0$ interactions are random and we recover the well-mixed limit; when $\sigma > 0$ strategies help their own type more often than what is expected by chance.

In this section we investigate the number of participations in a game by a player, and show that this quantity depends on the cooperativity of its strategy and on the degree of assortment. We also derive the conditions under which a given strategy is favored by natural selection in the framework of the replicator dynamics.

3.1. Number of participations

In order to calculate N_v^{in} and N_v^{out} for each $v \in V$, we follow closely the derivation presented in the supplementary material of Nowak and Roch (2007). For the sake of clarity, we also try to adopt their notation as much as possible. Notice, however, that

the following results are for the general case of upstream reciprocity under assortment of encounters imposed by population structure, whereas Nowak and Roch targeted the link between direct and upstream reciprocity.

By a slight abuse of notation, let us denote by N_i^{out} (resp. N_i^{in}) the average number of times that an individual of type S_i acts as donor (resp. recipient) in a Donation game. Let us also denote by V_i the set of S_i players, so that $V = V_1 \cup V_2$. It is possible to compute N_2^{out} by counting the number of donations originating in V_2 and dividing by the total number of individuals of type S_2. Likewise to compute the number of times a player of type S_2 has acted as recipient. Finally, one can get N_1^{out} and N_1^{in} from N_2^{out} and N_2^{in} by permuting the strategy parameters and the proportions of the two strategies.

Let us first calculate N_2^{in}. In order to calculate this quantity we consider the Markov chain model shown in Fig. 1. With a probability x the random walk starts in a player belonging to V_1; with a probability $1 - x$, in a player belonging to V_2. If we define M_{ij} as the number of times the walk enters any S_2 player when the walk starts on V_i and is conditioned to move to V_j at the first step, we can write

$$
\begin{aligned}
N_2^{in} &= \frac{\sum_{v \in V_2} N_v^{in}}{n(1-x)} \\
&= \frac{nx(\sigma_{11}q_1 M_{11} + \sigma_{12}q_1 M_{12}) + n(1-x)(\sigma_{21}q_2 M_{21} + \sigma_{22}q_2 M_{22})}{n(1-x)} \\
&= \frac{q_1 x(\sigma_{11}M_{11} + \sigma_{12}M_{12}) + q_2(1-x)(\sigma_{21}M_{21} + \sigma_{22}M_{22})}{1-x}. \qquad (3)
\end{aligned}
$$

In order to calculate M_{ij}, and for mathematical convenience, we expand the state space and consider all pairs of consecutive states, such that

$$U = \{u_1 = (V_1, V_1), u_2 = (V_1, V_2), u_3 = (V_2, V_1), u_4 = (V_2, V_2)\}$$

is the new extended space state, where the state (V_i, V_j) denotes the transition between the previous state V_i to the present state V_j. Thus, the substochastic transition matrix of the Markov chain excluding the first step (i.e. describing the transitions between the two lowest states in Fig. 1) is given by

$$
\mathbf{P} = \begin{pmatrix}
p_1\sigma_{11} & p_1\sigma_{12} & 0 & 0 \\
0 & 0 & p_2\sigma_{21} & p_2\sigma_{22} \\
p_1\sigma_{11} & p_1\sigma_{12} & 0 & 0 \\
0 & 0 & p_2\sigma_{21} & p_2\sigma_{22}
\end{pmatrix}.
$$

Now, defining

$$m_{11} = m_{21} = 0, \quad m_{12} = m_{22} = 1,$$
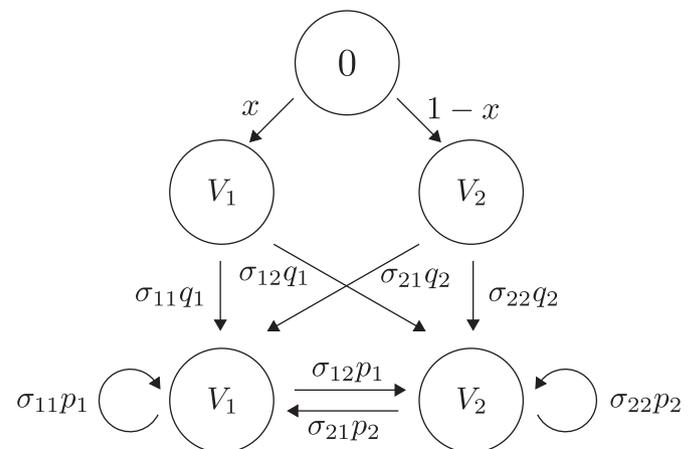
Fig. 1. Transition graph of the Markov chain describing random walks of upstream reciprocity in the population of players. 0 is the initial state.

so that m_{ij} is 1 if the walk moves from V to V_2 and 0 otherwise, we have, by the Markov property:

$$\begin{pmatrix} M_{11} \\ M_{12} \\ M_{21} \\ M_{22} \end{pmatrix} = \begin{pmatrix} m_{11} \\ m_{12} \\ m_{21} \\ m_{22} \end{pmatrix} + \mathbf{P} \begin{pmatrix} M_{11} \\ M_{12} \\ M_{21} \\ M_{22} \end{pmatrix}.$$

Solving this system of equations, we obtain the values M_{ij}. Plugging them in Eq. (3), we obtain after simplifying

$$N_2^{in} = \frac{x(1-\sigma)(q_1-q_2)+q_2(1-\sigma p_1)}{\omega} \tag{4}$$

with

$$\omega = 1-[\sigma(1-p_2)+x(1-\sigma)]p_1-[1-x(1-\sigma)]p_2. \tag{5}$$

We can use the same procedure to compute N_2^{out}. It suffices to reinterpret M_{ij} as the number of times the walk exits any S_2 player when the walk starts on V_i and is conditioned to move to V_j at the first step. In other words, M_{ij} is now the number of times that a single random walk initiated at V_i and that moves to V_j at the first step exits any S_2 player. Thus, we redefine

$$m_{11} = m_{12} = 0, \quad m_{21} = m_{22} = 1,$$

i.e. m_{ij} is now 1 if the walk moves from V_2 to V and to 0 otherwise. Following the same procedure used before for N_2^{in}, we obtain

$$N_2^{out} = \frac{q_2(1-\sigma p_1)+x(1-\sigma)(p_2q_1-p_1q_2)}{\omega} \tag{6}$$

with ω given by Eq. (5).

Finally, we can get N_1^{in} and N_1^{out} from N_2^{in} and N_2^{out} by permuting the parameters and the proportions of the two strategies, i.e. by taking $p_1 \leftrightarrow p_2$, $q_1 \leftrightarrow q_2$, and $x \leftrightarrow (1-x)$. Thus we obtain

$$N_1^{in} = \frac{(1-x)(1-\sigma)(q_2-q_1)+q_1(1-\sigma p_2)}{\omega}, \tag{7}$$

$$N_1^{out} = \frac{q_1(1-\sigma p_2)+(1-x)(1-\sigma)(p_1q_2-p_2q_1)}{\omega}. \tag{8}$$

When the degree of assortment is zero, it is easy to show that $N_1^{in} = N_2^{in}$ and that the inequality $N_2^{out} > N_1^{out}$ simplifies to $s_2 > s_1$. Thus, when the population is well mixed, all individuals interact the same number of times as recipients, and individuals of the more cooperative strategy interact as donors more times than individuals of the less cooperative strategy. When the degree of assortment is greater than zero, it can be shown that both $N_2^{in} > N_1^{in}$ and $N_2^{out} > N_1^{out}$ simplify to $s_2 > s_1$. This means that if S_2 is more cooperative than S_1, S_2 individuals interact in more Donation games than S_1 individuals and that, by construction, more cooperative players play more rounds of the game than less cooperative players. In summary, for any value of σ, $s_1 > s_2 \Rightarrow N_1 > N_2$, i.e. an individual of the more cooperative strategy takes part in more games. This fact makes the replicator dynamics dependent on the participation cost d.

3.2. Difference in accumulated payoffs

The difference in accumulated payoffs between S_1 and S_2 is given by

$$\Delta\pi(x) = [N_1^{in}(b-d)-N_1^{out}(c+d)]-[N_2^{in}(b-d)-N_2^{out}(c+d)]$$
$$= (N_1^{in}-N_2^{in})(b-d)-(N_1^{out}-N_2^{out})(c+d).$$

Replacing Eqs. (4), (6)–(8) in this formula and simplifying, we obtain

$$\Delta\pi(x) = \chi\psi/\omega,$$

where

$$\chi = (b-d)\sigma-(c+d),$$
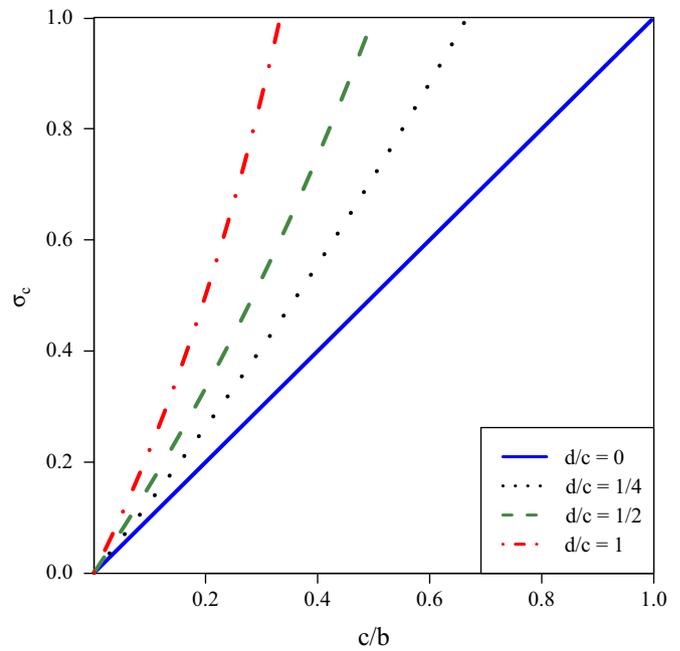
Fig. 2. Critical degree of assortment σ_c as a function of the cost-to-benefit ratio c/b for different values of the ratio between the participation cost and the cost of cooperation d/c. Each curve divides the planeinto two regions. If we assume that strategy S_1 is more cooperative than strategy S_2 and $d < (b-c)/2$, then S_1 dominates S_2 above the curve and S_1 dominates S_2 below the curve. For a fixed cost of cooperation c, increasing the cost of participation d reduces the region of dominance of the more cooperative strategy.

$$\psi = q_1(1-p_2)-q_2(1-p_1),$$

$$\omega = 1-[\sigma(1-p_2)+x(1-\sigma)]p_1-[1-x(1-\sigma)]p_2.$$

Selection favors S_1 over S_2 if $\Delta\pi(x) > 0$. As long as $p_1, p_2 < 1$, ω is always greater than 0. Thus, the condition $\Delta\pi(x) > 0$ only depends on the values of χ and ψ, which are independent of x. Furthermore, $\Delta\pi(x)$ adds no additional equilibria to the replicator equation given by Eq. (2), so that the only equilibria of the replicator equation are given by $x=0$ and 1. If $\chi\psi > 0$, $x=1$ is stable and S_1 dominates S_2. If $\chi\psi < 0$, $x=0$ is stable and S_2 dominates S_1. Let us suppose that S_1 is more cooperative than S_2, i.e. $s_1 > s_2$. Then, ψ is also always greater than 0, and the condition $\Delta\pi(x) > 0$ reduces to $\chi > 0$. If $d < (b-c)/2$ selection favors the more cooperative strategy S_1 if $\sigma > \sigma_c$ and the less cooperative strategy if $\sigma < \sigma_c$, where

$$\sigma_c = \frac{c+d}{b-d} = \frac{1+d/c}{(c/b)^{-1}-d/c} \tag{9}$$

is the critical degree of assortment. σ_c is a monotonically increasing function of the cost of participation d, as we illustrate in Fig. 2 with some numerical examples. If $d > (b-c)/2$ selection always favors the less cooperative strategy S_2 irrespective of the degree of assortment and upstream reciprocity is doomed to extinction.

4. Upstream and network reciprocity

As a second model, we consider the evolution of upstream reciprocity when network reciprocity is also at work. Individuals are embedded in a social network of contacts represented by a simple graph. Interaction and competition are constrained to nearest neighbors in the network. The link between upstream and network reciprocity has been investigated analytically by Nowak and Roch (2007) for the case of the one-dimensional array

and numerically by Iwagami and Masuda (2010) for the cases of regular lattices, random graphs and scale-free networks. Both studies report a synergistic interaction between upstream and network reciprocity. In the following, we show that participation costs can suppress such synergy.

4.1. Analytical results

Let us first consider the analytical treatment reported by Nowak and Roch (2007). Strategies are still denoted by $S(p, q)$, where p is the probability of passing on and q the probability of initiating altruistic acts. Strategists with $p=0$ do not implement upstream reciprocity, since they do not pass chains of gratitude. In particular, $S(0,0)$ gives classical defectors (CDs) and $S(0,1)$ gives classical cooperators (CCs). In contrast, when $p>0$ we obtain strategies such as $S(p, 0)$, passers-on (POs), that pass but not initiate and $S(p, 1)$, generous cooperators (GCs), that both pass and initiate. Players are arranged in a one-dimensional array and 'imitation updating' (Ohtsuki et al., 2006) is used as evolutionary dynamics. For this evolutionary dynamics, a player is randomly chosen from the entire population. Then it will either keep its strategy or imitate one of its neighbors' strategies proportional to fitness.

As shown by Nowak and Roch (2007) for the case of costless participation, GCs win against both CDs and CCs when

$$b/c > h(p) = \frac{8 + 2p + 8\sqrt{1-p^2}}{3 + 4p + \sqrt{1-p^2}}. \tag{10}$$

The function h is monotonically decreasing with the probability to pass p, so that the larger the probability of passing p the lower the benefit-to-cost ratio b/c necessary for GCs to prevail in the population. With $p=1$, $h(p)$ attains its minimum, $h(1)=10/7$. The condition $b/c > 10/7$ is less stringent than the condition $b/c > 4$, obtained when only network reciprocity is at work (Ohtsuki and Nowak, 2006; Ohtsuki et al., 2006). Thus, upstream reciprocity makes the evolution of cooperation by network reciprocity easier when participation is costless.

Let us consider a population comprising GCs and CDs arranged in a one-dimensional array, with players indexed with integer values, so that $v \in \{0,-1,-2,\ldots\}$ play CD and $v \in \{1,2,\ldots\}$ play GC (Fig. 3). Whether the GC–CD boundary will move to the left or to the right as a result of the evolutionary dynamics depends only on the fitnesses of players -1, 0, 1 and 2, which depend in turn on the number of games played by those players. Fig. 4 plots the number of participations in a game by players -1, 0, 1 and 2 as functions of the probability p that a GC passes on a chain of gratitude (see Appendix A for the mathematical expressions). As in the model with assortment of encounters presented in Section 3, interaction rates are non-uniform such that more cooperative players tend to play more games than less cooperative players. The number of games played by an individual also depends on its position in the array. Thus, GCs farther from the GC–CD boundary interact more often than GCs closer to the boundary. Player 0 interacts exclusively as recipient, receiving but not passing random walks arriving from player 1. Players $-1,-2,\ldots$ do not

Fig. 4. Number of participations in a game N_v by a player v as a function of the probability to pass p in the one-dimensional array. The GC–CD boundary is located between players 0 and 1, so that $v \in \{0,-1,-2,\ldots\}$ play CD and $v \in \{1,2,\ldots\}$ play GC (see Fig. 3).
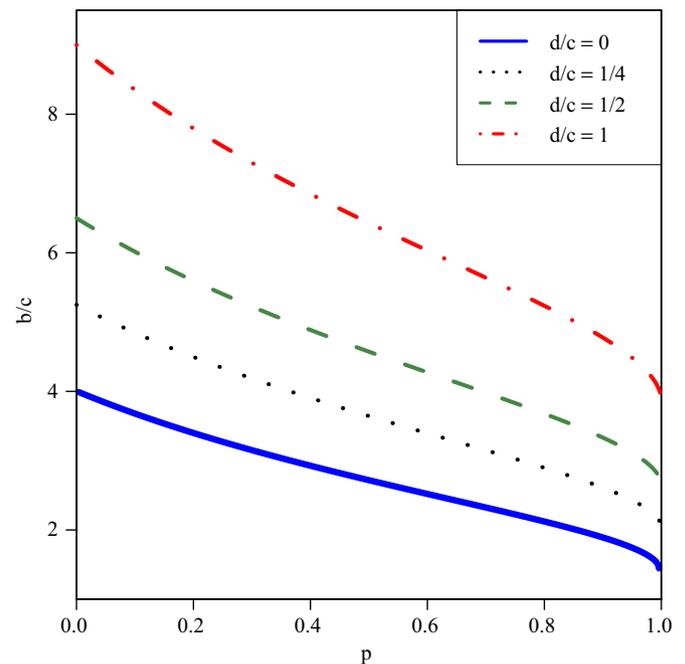
Fig. 5. Critical benefit-to-cost ratio b/c for different values of the ratio between the participation cost and the cost of cooperation d/c in the one-dimensional array. Each curve divides the plane into two regions. Above the curve, GCs win against CDs; below the curve, GCs lose against CDs. For a fixed cost of cooperation c, increasing the cost of participation d reduces the region of dominance of GCs.

interact at all and can actually be considered as loners that do not take part in any social interaction (Hauert et al., 2002).

Since interaction rates are non-uniform, evolutionary dynamics are modified when participation in the game has a cost d. The new results are obtained by making the replacements $b \to b-d$ and $c \to c+d$. The condition for the establishment of altruism thus

Fig. 3. Classical defectors (CDs) and generous cooperators (GCs) arranged in a one-dimensional array.

changes to $(b-d)/(c+d) > h(p)$ or, equivalently, to

$$b/c > d/c + (1 + d/c) \times h(p) \qquad (11)$$

with $h(p)$ as given in Eq. (10). Eq. (11) is harder to fulfill than Eq. (10) for any $d > 0$. This is shown in Fig. 5 for some numerical examples.

4.1.1. Simulation results

We now turn to the interaction between upstream and network reciprocity in less simple graph-structured populations. Such investigation has been recently pioneered by Iwagami and Masuda (2010), who in addition to confirm the synergistic interaction between upstream and network reciprocity, also point out the importance of heterogeneous networks as amplifiers of cooperation when fitness is given by the accumulated payoff and participation in the game is costless. Here, we study the cases when participation has some non-negligible cost.

We use different types of networks as population structures: rings (one-dimensional lattices), random regular networks, and Barabási–Albert scale-free networks (Barabási and Albert, 1999) (see Appendix B for more details on the construction of the random and scale-free networks). All the networks are of size $n = 10^4$. We use rings of degree $k = 2$ and 8, regular random networks with $k = 8$, and scale-free networks of average degree $\langle k \rangle = 8$. For the sake of comparison, we follow the setup considered by Iwagami and Masuda (2010) and described in the following. A simulation step comprises two phases. During the first phase each player in turn attempts to start an independent random walk. Players are assigned a payoff as a result of the interactions with neighboring players along the trajectories of the random walks. In the second phase, when all the random walks have ended, individuals update their strategies according to the obtained payoff. The evolutionary dynamics is the one suggested by Iwagami and Masuda (2010): n_u out of the n players are randomly selected each generation for strategy updating. They synchronously adopt the strategy of the individual with the highest payoff in their neighborhoods (including themselves). We consider the four strategies previously introduced: CDs, CCs, POs and GCs. For the strategies based on upstream reciprocity (POs and GCs) we set $p = 0.8$, and $n_u = 200$ for the evolutionary dynamics. Without loss of generality, we assume $c = 1$. We set the maximum number of rounds to 50 000 for the scale-free networks, regular random graphs and the rings with $k = 2$, and to 150 000 rounds for the rings with $k = 8$.

We found no qualitative differences in the results when we run simulations for other values of n_u (20 and 2000), p (0.7 and 0.9) and $\langle k \rangle$ (6 and 14). For reasons of space, we stick to the baseline model and show the results only for $n_u = 200$, $p = 0.8$ and $\langle k \rangle = 8$.

4.1.2. Populations comprising GCs and CDs

Before considering the competition among the four strategies, we first investigate the outcome of the evolutionary dynamics when only GCs and CDs are present in the population, for random initial configurations of 50% GCs. We found essentially the same results as those reported by Iwagami and Masuda (2010), namely, that network reciprocity can favor GCs over CDs, that degree-heterogeneous topologies are strong amplifiers of cooperation under both upstream and network reciprocity, and that CDs prevail in random regular structures, presumably because of the low clustering coefficient of this topology. Results are, however, dependent on the participation cost d. Fig. 6 shows the final fraction of GCs for different values of the benefit b and the participation cost d. The results for regular random graphs are not shown as defection always prevails in these structures for the region of parameters we considered. For the other population
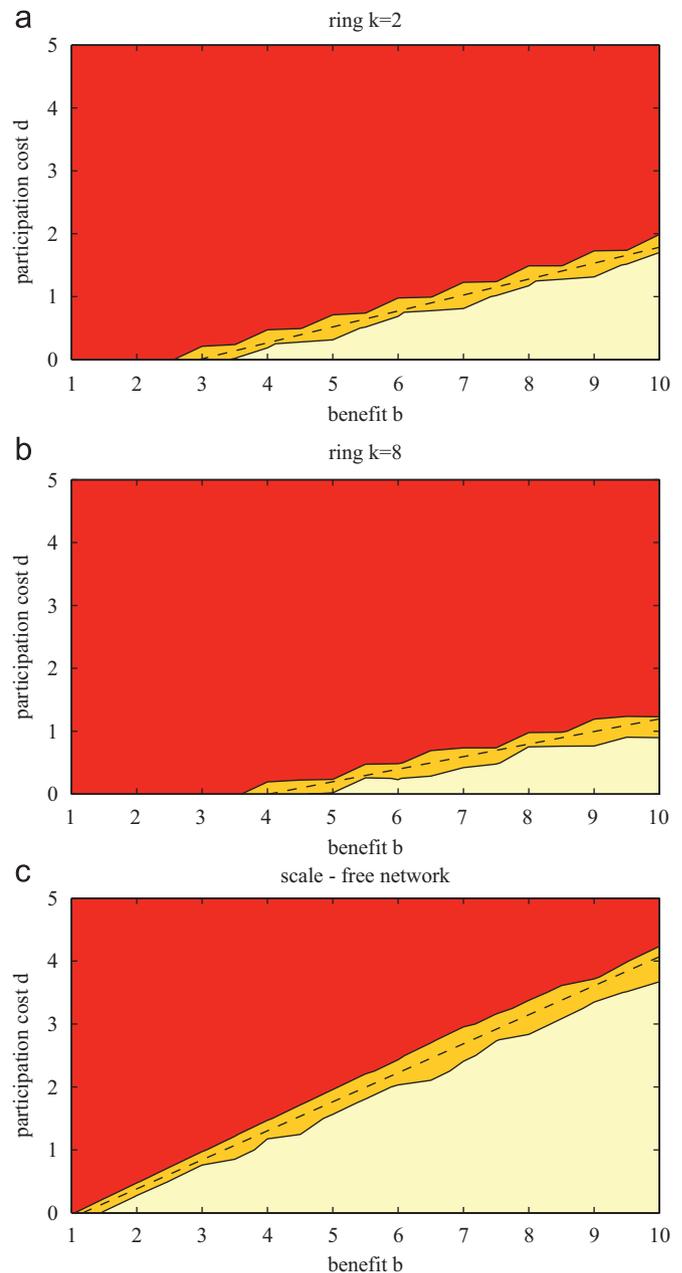
Fig. 6. Average final fraction of GCs ρ for different networks when players initially adopt either GC or CD. We distinguish three zones: $\rho \leq 0.1$, $0.1 < \rho < 0.9$ and $\rho \geq 0.9$. Regions with smaller ρ are shown in darker tones. The dashed lines give the estimated critical values of d for the transition between evolutionary dynamics favoring GCs and evolutionary dynamics favoring CDs. We set $c = 1$ and, for GCs, $p = 0.8$.

topologies, the higher the participation cost, the more difficult for gratitude-related altruists to be selected against pure defectors. In particular, GCs completely vanish if $d > (b-c)/2$ for all population structures. If $d < (b-c)/2$ the detrimental effect of participation costs in the evolution of upstream reciprocity is far less pronounced for scale-free networks than for the other population topologies.

The exact threshold value of the participation cost d above which CDs prevail can be approximated by making use of Eq. (11). In this case, it is reasonable to expect that h depends not only on p, but also on the network topology, the updating rule and the population size. In the absence of theoretical results, h can be numerically approximated by the value of the critical benefit-to-cost ratio when $d = 0$, which can be found by linearly interpolating

the average final fraction of GCs resulting from the simulations. Following this procedure we obtained $h=2.95$ for the rings with $k=2$, $h=4.01$ for the rings with $k=8$, and $h=1.17$ for the scale-free networks. We show the approximated critical values of d for each network with dashed lines in Fig. 6.

4.1.3. Populations comprising CDs, CCs, POs and GCs

Fig. 7 shows the final fraction of the four strategies for different networks when fitness is given by the accumulated payoff and participation is free or when it has a cost $d=1$. The costless case is included for the sake of comparison and completeness, since the results are essentially the same as those found by Iwagami and Masuda (2010).

When participation is free, GCs are able to invade all population structures for sufficiently high values of b, except for the regular random graphs, in which CDs dominate for all the tested values of b. In the rings, the steady state makes a transition between a population dominated by CDs or POs to a population dominated by GCs at a given threshold value of b. Such threshold

is higher for $k=8$ than for $k=2$. Scale-free networks are even more favorable to cooperation in general. In this case neither CDs nor POs go to extinction for all values of b. There is a coexistence of CCs and GCs, with the fraction of GCs increasing with b. With the addition of a participation cost $d=1$ the point at which GCs statistically dominate the outcome of the simulations establishes at sensibly higher values of b. Additionally, CDs can now prevail in the scale-free networks for very low values of b.

5. Discussion

The main conclusion of Nowak and Roch (2007) is that 'upstream reciprocity alone does not select for cooperation, but can promote cooperation if it is linked to a mechanism for the evolution of cooperation', that is, a mechanism providing positive assortment of strategies. Such promotion seems to be a consequence of specific modeling choices, particularly the sampling of donor–recipient pairs along random walks in the population of individuals, and the fact that such sampling leads to non-uniform interaction rates in which
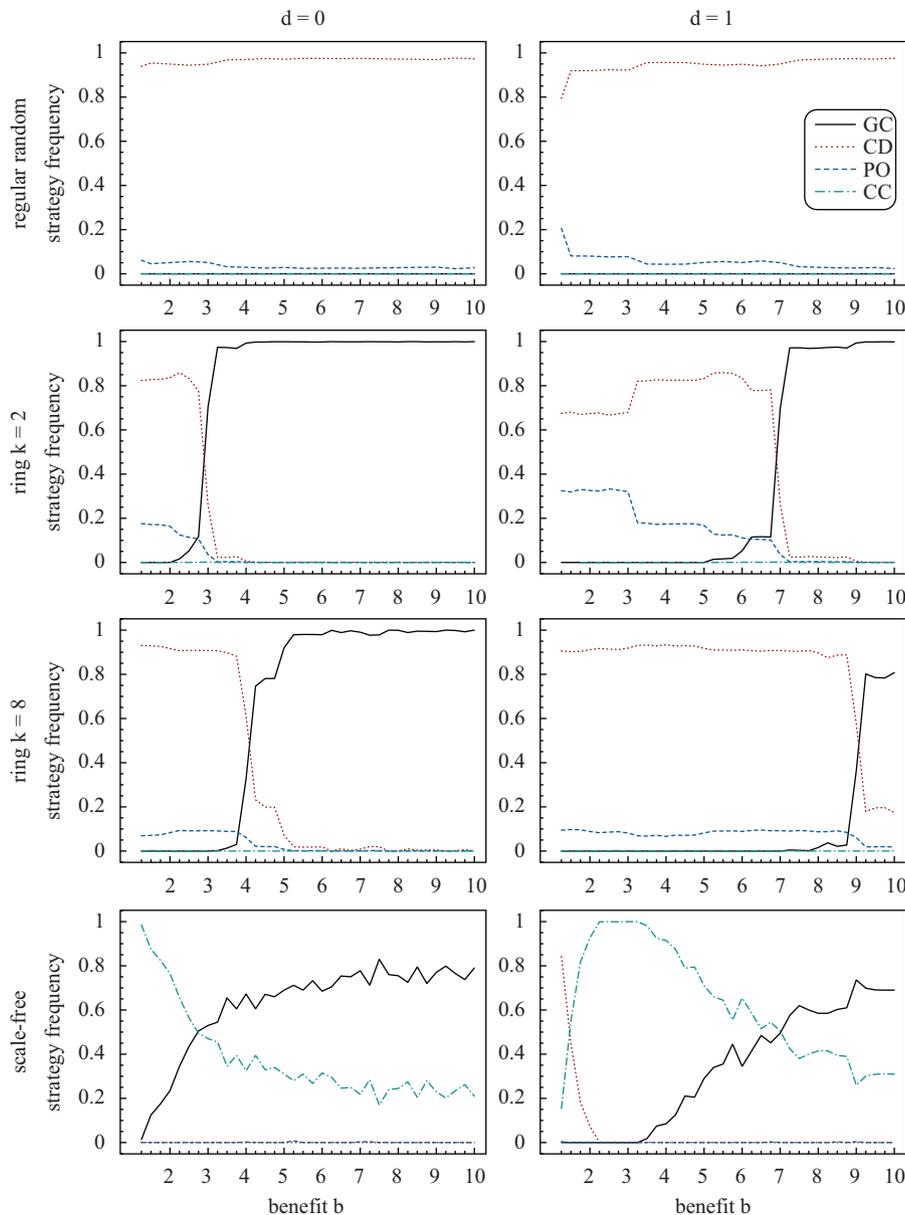
Fig. 7. Final fractions of CDs, CCs, POs and GCs when the four strategies are initially present in the population. We set $c=1$ and, for POs and GCs, $p=0.8$.

more cooperative strategies engage in more rounds of the game per generation than less cooperative strategies. Hence, in Nowak and Roch's model, upstream reciprocity plays a role analogous to that of degree-heterogeneity in network reciprocity. In this sense upstream reciprocity does not constitute an independent mechanism for the evolution of cooperation, but can further enhance the levels of cooperation by inducing non-uniform interaction rates. However, while in evolutionary games on networks such non-uniformity in interaction rates is *strategy-independent* (e.g. some individuals interact more because they are placed in the hubs of a network of contacts), in Nowak and Roch (2007) it is *strategy-dependent*, which implies that more cooperative players end up interacting more times than less cooperative ones.

In this paper, we investigated one way of controlling such non-uniformity in the interaction rates of the players: the introduction of participation costs. Participation costs implement the idea that there is often no free lunch when it comes to social interaction. Even players in the role of recipients have to be available to eager donors in order to get the benefit of altruistic acts directed towards them, and this availability may have a cost. We found that participation costs can have an important effect on the the evolution of upstream reciprocity. Gratitude-related altruism can be unbeatable with respect to defection when participation is free and there is some degree of assortment of strategies, provided for instance by population structure. However, defection can turn out to be the dominant strategy when participation is expensive. Specifically, the higher the participation cost, the higher the degree of assortment and/or the benefit-to-cost ratio needed for upstream reciprocity to evolve. Finally, when participation is so costly that $d > (b-c)/2$, the evolution of upstream reciprocity is totally suppressed. Similar results can be readily obtained if we consider direct reciprocity instead of network reciprocity as the mechanism responsible for building up assortment (see Appendix C).

These results bear resemblance to those obtained by Masuda (2007), who found that participation costs influence the outcome of evolutionary games on degree-heterogeneous networks. In the case studied in this paper, the evolutionary dynamics under Nowak and Roch's model are found to be dependent on the participation cost not only for heterogeneous graphs, but also for any population structure, including well-mixed populations. In the case of networked games of upstream reciprocity, and contrastingly to the results obtained by Masuda (2007) regarding participation costs in network reciprocity alone, heterogeneous networks are more successful than homogeneous networks at promoting upstream reciprocity. Furthermore, scale-free networks were found to promote gratitude-based cooperation for practically all of the region out of the costly regime, i.e. for $d < (b-c)/2$. These highly heterogeneous networks greatly amplify even small positive payoffs resulting from passing along chains of gratitude.

A different but related way to control for the non-uniformity of interaction rates is by using the average payoff instead of the accumulated payoff when defining fitness (Santos and Pacheco, 2006; Tomassini et al., 2007). In this case, the fitness of player v is given by the accumulated payoff divided by the total number of interactions, that is

$$\pi_v = (N_v^{in}b - N_v^{out}c)/N_v. \tag{12}$$

Selection based on the average payoff can be justified when evolutionary dynamics emerge from imitation processes, where it is reasonable to think of individuals looking not at the accumulated payoff over many interactions but at typical or average outcomes of social interactions as the appropriate guidelines when targeting cultural models for imitation. It is easy to see that upstream reciprocity cannot evolve in Nowak and Roch's model when selection is based on the average payoff. Indeed, defectors act only as recipients in this model. Their average payoff

(when interacting with a cooperative strategy that initiates and passes chains of gratitude) is thus always equal to b, which is the maximum possible value of Eq. (12). This fact is the direct result of two additional features of Nowak and Roch's model. First, participation in a game as a donor (i.e. initiating or passing chains of altruistic acts) is not compulsory but voluntary, and players can refrain from taking part in a game. Second, once a player has entered the game as donor it never refuses to help the recipient. Thus, defection is never actually experienced by recipients and only helping acts are passed and reciprocated. Hence, defection is interpreted as the refusal to participate in a game. All of this makes defection the obvious outcome of selection when fitness is given by the average payoff. A slightly different definition of the average payoff when the upstream reciprocity game is played on networks is to normalize the accumulated payoff by the degree of each player instead of by the total number of participations in a game (Iwagami and Masuda, 2010). The evolution of upstream reciprocity is also expected to be hampered when selection is based on this alternative definition of the average payoff.

We note that interaction rates are uniform in other models of upstream or generalized reciprocity (Boyd and Richerson, 1989; Pfeiffer et al., 2005; Hamilton and Taborsky, 2005; Rankin and Taborsky, 2009; Sigmund, 2010, p. 82). Thus, the evolutionary dynamics in these models are invariant with respect to the introduction of participation costs (or to the replacement of the accumulated payoff by the average payoff). This means that the invasion conditions and the effective critical cost-to-benefit ratios derived in these papers are, in contrast to those derived by Nowak and Roch (2007) and Iwagami and Masuda (2010), unaffected by the replacements $b \to b-d$ and $c \to c+d$. Additionally, all of these models assume that participation is compulsory and, when considering Donation games that participation as a donor does not equate with Donation. Donors can refrain from giving and recipients can experience defection. Strategists implementing upstream or generalized reciprocity can thus base their actions on whether they have been helped or have been refused help in the past. This last scenario is missing in the model of upstream reciprocity investigated by Nowak and Roch (2007) and Iwagami and Masuda (2010), where only altruistic acts can be passed and reciprocated. We think that this is a fundamental feature that cannot be omitted in models of reciprocity. When participation is compulsory and acts of defection are allowed to be passed and reciprocated, upstream reciprocity seems to be harder to explain from an evolutionary perspective, even in structured populations. This has already been shown for a model of non-random encounters, where it was found that generalized reciprocity is not evolutionarily stable against both unconditional cooperators and unconditional defectors under a Prisoner's dilemma equivalent to the Donation game (Rankin and Taborsky, 2009).

Appendix A. Upstream and spatial reciprocity: number of participations for GCs and CDs

Consider a population comprising GCs and CDs, arranged in a one-dimensional array. Players are indexed with integer values,

so that players $v \in \{0, -1, -2, \ldots\}$ play CD and players $v \in \{1, 2, \ldots\}$ play GC. The number of participations in the game can be found by making the replacements $b \to 1$ and $c \to -1$ in the expression for the fitness of player v (Eq. (8) in the supplementary material of Nowak and Roch (2007)). By plugging the values $p_0 = q_0 = 0$, $p_1 = p$ and $q_1 = 1$ in the formulas given by Nowak and Roch (2007), we obtain the following values for N_v:

$$N_2 = 1 + \frac{(1+p)\{4H + (H-p)[H(2+p) + 2p]\}}{(H-p)[4H - p^2(2+H)]},$$

$$N_1 = 1 + \frac{(1+p)[p(H-p) + 2H]}{(H-p)(2H - p^2)},$$

$$N_0 = \frac{1}{2} + \frac{p[p(H-p) + 2H]}{2(H-p)(2H - p^2)},$$

$$N_{-1} = 0,$$

where

$$H = 1 + \sqrt{1 - p^2}.$$

Appendix B. Network models

Regular random networks. In these networks every node has the same degree k, but its neighbors are randomly scattered in the graph. To build the networks we start from a one-dimensional lattice with degree k and apply the following algorithm, proposed by Szabó et al. (2004). A randomly selected link AB is removed from the network. A new link is then created going from B, which has lost one link, to a randomly selected node C, which has now one excess link. To maintain the same degree in C one of its edges, for example CD, is deleted. This process of creating a random link starting from the new less-connected node and removing an edge starting from the new more-connected node is repeated $2kn$ times to assure that the neighborhood is completely random. At this point a link between the less-connected player and the first player A, which also lacked one link, is created.

Scale-free networks. Among the several available models for constructing scale-free networks (Newman, 2003), we use the one by Barabási and Albert (1999). Barabási–Albert networks are grown starting from a small clique of m_0 nodes. At each successive time-step a new node is added such that its $m \leq m_0$ edges link it to m nodes already present in the graph. It is assumed that the probability p that a new node will be connected to node i depends on the current degree k_i of the latter. This is called the *preferential attachment* rule. The probability $p(k_i)$ of node i to be chosen is given by $p(k_i) = k_i / \sum_j k_j$, where the sum is over all nodes already in the graph. The model evolves into a network with power-law probability distribution for the vertex degree $P(k) \sim k^{-\gamma}$, with $\gamma \sim 3$ and $\langle k \rangle = 2m$. For the simulations, we used $m_0 = m = \langle k \rangle / 2$.

Appendix C. Upstream and direct reciprocity

In addition to spatial reciprocity, Nowak and Roch (2007) also considered allowing some level of direct reciprocity in the strategies of players as means of introducing assortment of strategies and pave the way for the evolution of upstream reciprocity. Strategies are now given by $S(p, q, r)$, where r is the probability that help is immediately returned to the donor. Recipients reciprocate to the donor with probability r and help a random player with probability $(1-r)p$. The cooperativity s_i of strategy S_i is now given by $s_i = q_i / [(1-r_i)(1-p_i)]$.

Consider the competition between strategies $S_1 = S(p_1, q_1, r_1)$ and $S_2 = S(p_2, q_2, r_2)$. If fitness is given by the accumulated payoff with $d = 0$, then the fitness difference is given by

$$\Delta\pi(x) := \pi_1(x) - \pi_2(x) = (N_1^{in} - N_2^{in})b - (N_1^{out} - N_2^{out})c.$$

According to Nowak and Roch (2007), such fitness difference is given by

$$\Delta\pi(x) = \alpha\beta/\gamma$$

with

$$\alpha = q_1(1-r_2)(1-p_2) - q_2(1-r_1)(1-p_1),$$

$$\beta = (br_2 - c)(1-r_1) - x(b-c)(r_2 - r_1),$$

$$\gamma = [x(1-p_1)(1-r_1(p_2(1-r_2) + r_2)) + (1-x) \times (1-p_2)(1-r_2(p_1(1-r_1) + r_1))] \times (1-r_1)(1-r_2).$$

We can easily derive an expression for the difference in the number of times players of the two types have interacted $N(x) := N_1(x) - N_2(x)$, by making $b \to 1$ and $c \to -1$ in the expressions above. We thus obtain

$$N(x) = \alpha\tilde{\beta}/\gamma,$$

where

$$\tilde{\beta} = (1+r_2)(1-r_1) - 2x(r_2 - r_1).$$

As long as $p_1, p_2 < 0$, γ is always greater than zero and as long as $0 < r_1, r_2 < 1$, $\tilde{\beta}$ is always greater than zero. Thus, the condition $N(x) > 0$ reduces to $\alpha > 0$. We conclude that $s_1 > s_2$, with $s_i = q_i / [(1-r_i)(1-p_i)]$, implies $N_1 > N_2$.

Results are similar to those obtained with the model of non-random encounters analyzed in Section 3 of the present paper. If $s_1 > s_2$, then $N_1 > N_2$. Interaction rates are thus non-uniform and strategy-dependent. With non-zero participation costs the results presented by Nowak and Roch (2007) are valid up to the replacements $b \to b - d$ and $c \to c + d$. If $d > (b-c)/2$, selection always favors the strategy with lower cooperativity. If $d < (b-c)/2$, the critical ratio r_c defining phase transitions in the evolutionary dynamics is given by Eq. (9). Thus, for increasing values of the participation cost d, larger values of r are required for more cooperative strategies to win over less cooperative strategies and for upstream reciprocity to hitch-hike on direct reciprocity.

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