Upstream reciprocity in heterogeneous networks

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ABSTRACT

Many mechanisms for the emergence and maintenance of altruistic behavior in social dilemma situations have been proposed. Indirect reciprocity is one such mechanism, where other-regarding actions of a player are eventually rewarded by other players with whom the original player has not interacted. The upstream reciprocity (also called generalized indirect reciprocity) is a type of indirect reciprocity and represents the concept that those helped by somebody will help other unspecified players. In spite of the evidence for the enhancement of helping behavior by upstream reciprocity in rats and humans, theoretical support for this mechanism is not strong. In the present study, we numerically investigate upstream reciprocity in heterogeneous contact networks, in which the players generally have different number of neighbors. We show that heterogeneous networks considerably enhance cooperation in a game of upstream reciprocity. In heterogeneous networks, the most generous strategy, by which a player helps a neighbor on being helped and in addition initiates helping behavior, first occupies hubs in a network and then disseminates to other players. The scenario to achieve enhanced altruism resembles that seen in the case of the Prisoner's Dilemma game in heterogeneous networks.

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1. Introduction

The mechanism for evolution and maintenance of altruism when egoistic behavior is apparently more advantageous has been a target of intensive studies. Among the many viable mechanisms proposed, we focus on indirect reciprocity, which refers to the concept that a cooperative player is helped by others with whom she/he has not interacted. Cooperative behavior is indirectly rewarded by way of chains of helping behavior of various players. There are two types of indirect reciprocity: downstream reciprocity and upstream reciprocity (Nowak and Sigmund, 2005). In downstream reciprocity, a player witnesses the behavior of other players as a third party. The observing player will assign a good reputation to player X if player X helps others. When a situation arises where this observer interacts with player X in the future, the observer will probably help X if and only if X has a good reputation. A player must establish a good reputation by helping others prior to being helped by other anonymous players. The downstream reciprocity is observed in behavioral experiments (Wedekind and Milinski, 2000; Milinski et al., 2002) and is firmly based on the theory of evolutionary games (Nowak and Sigmund, 1998a,

1998b; Leimar and Hammerstein, 2001; Brandt and Sigmund, 2004; Ohtsuki and Iwasa, 2004, 2006).

In upstream reciprocity, the players first get help from other players. If the recipient complies with upstream reciprocity, then she/he helps another unspecified player. Theoretically, evolution of cooperation based on upstream reciprocity is considered to be difficult. In numerical simulations, cooperation is achieved only when the size of the interaction group is small (Boyd and Richerson, 1989; Pfeiffer et al., 2005). An analytical study showed that upstream reciprocity enables evolution of cooperation only in combination with another mechanism such as direct reciprocity (i.e., repeated interaction between the same players) or spatial reciprocity (i.e., interaction between players on a one-dimensional lattice) (Nowak and Roch, 2007). However, upstream reciprocity has been observed in behavioral experiments conducted on humans. A player that has received a help from another player has increased the propensity to help an anonymous partner in variants of the trust game (Dufwenberg et al., 2001; Greiner and Levati, 2005; Stanca, 2009). Those who are helped by somebody in advance tend to help another partner filling in a tedious survey in laboratory behavioral experiments (Bartlett and DeSteno, 2006). Upstream reciprocity has also been observed in rats. Rats trained to pull a stick to deliver food tend to pull the stick to help another rat after receiving food via a help from a conspecific (Rutte and Taborsky, 2007). Therefore, theoretically assessing the conditions under which upstream reciprocity is

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feasible will help us gain a better understanding of the evolution of cooperation in social dilemma situations.

In this study, we examine the effect of a property of contact networks on upstream reciprocity. A fundamental characteristic of many social networks is that the number of contacts of a node, which we call the degree, has a right-skewed distribution. In particular, scale-free networks, i.e., networks with power-law degree distributions are widely found (e.g., Newman, 2003). In social networks relevant to evolutionary games, scale-free networks have been found in, for example, email social networks (Ebel et al., 2002; Newman et al., 2002). Although other social networks do not exhibit degree distributions that are as right skewed as the power-law distribution, their degree distributions are considerably heterogeneous (Eubank et al., 2004; Lusseau and Newman, 2004; Kossinets and Watts, 2006; Onnela et al., 2007). We investigate the effect of heterogeneous degree distributions on the possible evolution of cooperation based on upstream reciprocity.

We show that upstream reciprocity enhances altruistic behavior of players that are placed in heterogeneous contact networks such as scale-free networks. The mechanism found in our study has resemblance to that for enhanced cooperation shown in the Prisoner's Dilemma in heterogeneous networks (Durán and Mulet, 2005; Santos and Pacheco, 2005, 2006; Santos et al., 2006), which we will discuss in Section 4.

2. Model

2.1. Networks

Consider a contact network with a population of $N = 10\,000$ players. As a model of heterogeneous network, we use the scale-free network generated by the Barabási–Albert (1999) algorithm (Fig. 1A). To generate the scale-free network, we start with the complete graph of $2m+1$ nodes (i.e., each pair of nodes is connected by an edge). Then, we add nodes with degree m one-by-one according to the so-called linear preferential attachment; the probability that an already existing node v_i forms an edge
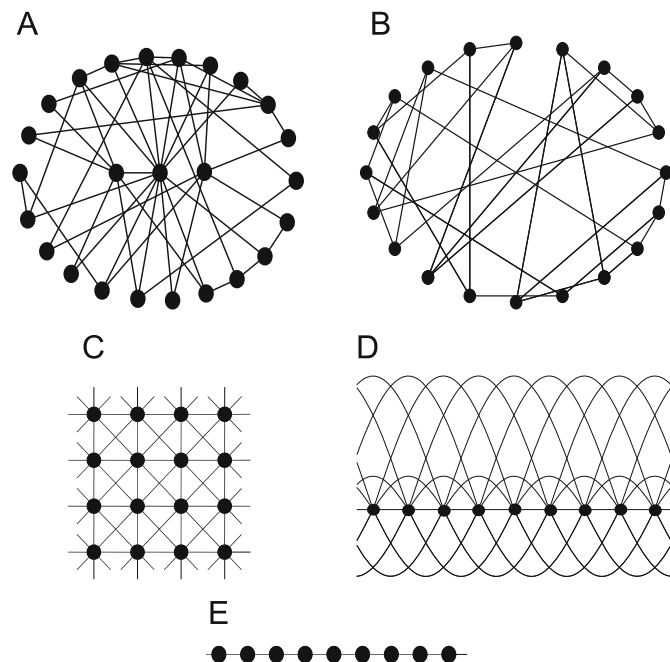
with a newly introduced node is proportional to the degree k_i. Multiple edges (i.e., more than one edge connecting a pair of nodes) are disallowed. In the generated network, the degree follows the power-law distribution $p(k) \propto k^{-3}$ with a lower cutoff at $k = m$ and the mean degree of $\langle k \rangle = 2m$ (Barabási and Albert, 1999). We use $\langle k \rangle = 8$, i.e., $m = 4$, unless otherwise stated.

For comparison, we also use four other types of networks. One is the regular random graph, which is constructed from the configuration model (Newman, 2003) (Fig. 1B). To generate a network, we attach $\langle k \rangle$ stubs, or half edges, to each node. Then, we randomly select two nodes with the equal selection probability and connect them. These two nodes consume one stub each. We repeat this procedure until all stubs are exhausted at all nodes. If the generated network is disconnected or contains self-loops or multiple edges, we discard the network and start the entire procedure all over again. Although its mean degree is small, the regular random graph represents a well-mixed population in which cooperation is not easily enhanced by upstream reciprocity (Boyd and Richerson, 1989; Nowak and Roch, 2007).

In the square lattice, $N = 10\,000$ nodes are placed on the square with a linear length of $\sqrt{N} = 100$. Each node is connected to eight nodes situated in a so-called Moore neighborhood (Fig. 1C). We adopt the periodic boundary condition.

The extended cycle is a one-dimensional network, where the nodes are placed on a ring. Each node is connected to $\langle k \rangle / 2$ nearest nodes on each side, as shown in Fig. 1D.

The scale-free network, the regular random graph, the square lattice, and the extended cycle have $\langle k \rangle = 8$ unless otherwise stated. Therefore, we can compare the effects of different types of networks without having to account for the possible influence of $\langle k \rangle$. We also set $\langle k \rangle = 6$ and 14 in some of the following numerical simulations to confirm the robustness of the results with respect to $\langle k \rangle$.

The final type of network used is the cycle in which each node on a ring is connected to a single nearest node on each side such that $\langle k \rangle = 2$ (Fig. 1E). We use the cycle to compare our numerical results with the previously reported theoretical results (Nowak and Roch, 2007). In contrast to the well-mixed population, the infinite one-dimensional chain network with $\langle k \rangle = 2$ enables upstream reciprocity because it exhibits spatial reciprocity. Spatial reciprocity is a general mechanism for evolution of cooperation in social dilemma games; cooperative players are clustered in a network to help each other and resist the invasion by egoistic players (Axelrod, 1984; Nowak and May, 1992). Such clustering is possible when the size of the boundary of a cluster is small relative to the number of players in the cluster. This situation is expected the most in the cycle and to a certain extent in the extended cycle and the square lattice; however, it is not expected in the Barabási–Albert scale-free network and the regular random graph.

2.2. Game of upstream reciprocity: rule and payoff

A single game of upstream reciprocity (Nowak and Roch, 2007), which is motivated by experimental evidence and previous theoretical work explained in Section 1, is described as follows. First, a player v_i ($1 \le i \le N$) is selected. Player v_i may initiate a chain of helping behavior. If v_i does so, v_i bears the cost c and selects one of its neighbors at an equal selection probability of $1/k_i$, where k_i is the degree of v_i. The selected neighbor, denoted by v_j, receives the payoff b. We assume $b > c > 0$ so that the game represents a social dilemma; a single act of help increases the average payoff of the entire population by $(b-c)/N$, while each player is better off by not helping other players. Without loss of generality, we set $c = 1$.

Fig. 1. Architecture of networks. (A) Scale-free network, (B) regular random graph, (C) square lattice, (D) extended cycle, and (E) cycle.

v_j may not continue the chain of helping behavior. In such a case, the chain of cooperation terminates, and the payoffs for v_i, v_j, and $v_{i'}$ ($i' \neq i, j$) are equal to $-c$, b, and 0, respectively. However, if v_j does pass on the helping action, v_j selects one of its neighbors at a probability of $1/k_j$ and bears the cost c. The selected neighbor receives b. The chain of helping behavior continues until a recipient of help terminates the chain. Note that a chain of cooperation may traverse the same players more than once.

2.3. Strategies

On the basis of a previous study (Nowak and Roch, 2007), we specify the strategy of each player v_i ($1 \leq i \leq N$) using two parameters. The first parameter p_i ($0 \leq p_i \leq 1$) denotes the probability that v_i passes on the helping action to a randomly selected neighbor after receiving it from a neighbor. The second parameter q_i ($0 \leq q_i \leq 1$) denotes the probability that v_i initiates the helping action. A larger p_i or q_i implies that player v_i is more cooperative.

We consider the following four strategies that were introduced by Nowak and Roch (2007):

- Classical defector (CD) is defined by $p_i = 0$ and $q_i = 0$. CD neither initiates nor passes on the help. It is the most egoistic strategy.
- Classical cooperator (CC) is defined by $p_i = 0$ and $q_i = 1$. CC spontaneously initiates the chain of helping behavior but does not react to the cooperation that it receives from a neighbor. CC does not contribute to upstream reciprocity, even though CC is cooperative to some extent.
- Generous cooperator (GC) is defined by $p_i = 0.8$ and $q_i = 1$. GC initiates the helping behavior and passes on the helping action with a high probability. It is the most cooperative strategy. We are concerned with the possibility that heterogeneous networks enhance the fraction of GCs in a population.
- Passer-on (PO) is defined by $p_i = 0.8$ and $q_i = 0$. PO does not initiate the helping behavior but passes on the helping action with a high probability. Although PO is less cooperative than GC, it contributes to the upstream reciprocity.

In the case of GC and PO, we set $p_i = 0.8$ instead of $p_i = 1$. This is to prevent a chain of helping behavior from continuing indefinitely if the population consists of only GC and PO. This choice of p_i is arbitrary. To verify the robustness of our results with respect to the value of p_i, we will carry out some of the following numerical simulations with $p_i = 0.7$ and 0.9.

2.4. Update rule

We principally use the deterministic update rule, which is described in the following. The numerical results do not qualitatively change on using relatively realistic stochastic rules, as shown in Sections 3.1 and 3.4.

We refer to time in the evolutionary dynamics as a round and denote it by t ($= 0, 1, 2, \ldots$). One round consists of N chains of helping behavior, and one chain is initiated by each player. Note that a chain is considered to be empty if the initial player does not help a neighbor, which occurs for CD and PO. The one-round payoff of player v_i is defined as the sum of the payoffs gained by v_i in N chains of cooperation. The payoff that v_i gains in a round is equal to $b \times$ (the frequency at which the chains are brought to v_i) $- c \times$ (the frequency at which the chains are passed from v_i without being terminated).

At the end of each round, the strategies of N_u out of the $N = 10\,000$ players are updated synchronously. Unless otherwise stated, we set $N_u = 200$. We also set $N_u = 20$ and 2000 in some of

the following numerical simulations to examine the robustness of the results with respect to N_u. We randomly and independently select N_u players from the population with equal probability. In the deterministic update rule that we mostly use in this paper, for each selected player v_i, the neighbor with the largest payoff, which is denoted by v_j, is selected. If the payoff of v_j is larger than that of v_i, v_i will copy the strategy of v_j. If there are more than one neighbors with the same largest payoff, we select one of them randomly with equal probability. After tentatively determining N_u copying events, we replace the strategies of the selected nodes simultaneously. We do not assume mutation. This marks the end of one round.

One run lasts until a quasistationary state is attained or the unanimity of one strategy is almost achieved. Specifically, we set the number of rounds to 20 000 in the case of the scale-free network, the regular random graph, and the square lattice. In the case of the extended cycle and the cycle, the number of rounds is equal to 140 000.

3. Results

3.1. GC versus CD

When a player passes on the received help to a neighbor, a neighbor is randomly selected as recipient with equal probability. A chain of helping behavior is equivalent to a simple random walk with random termination. If $p_i = 1$ ($1 \leq i \leq N$), the random walk may continue forever. In this hypothetical situation, the payoff that player i receives is proportional to the stationary density of the random walk. In any undirected network, the stationary density of the simple random walk is proportional to the degree (e.g., Noh and Rieger, 2004). This relation roughly holds true for uncorrelated networks even in the presence of some absorbing nodes at which the random walk terminates (Noh and Rieger, 2004). Therefore, we expect that the number of times that the chain of helping behavior reaches a given node is roughly proportional to the degree. Because a single passage of chain contributes to the payoff $b - c > 0$, the payoff per round for each player is roughly proportional to the degree.

To verify this prediction, we carry out Monte Carlo simulations of the game of upstream reciprocity on the scale-free network with a random mixture of GCs and CDs. We set $b = 1.5$. The probability that each player is initially GC or CD is 0.5. Fig. 2A shows the dependence of the payoff per round on the degree of the player, just before the first update (i.e., $t = 0$). Each data point corresponds to the payoff per round averaged over all players having the same degree and same strategy. For each strategy, the payoff per round is roughly proportional to the degree. CDs generally gain larger payoffs than GCs, because CDs exploit GCs in the neighborhood.

However, from Fig. 2A, it cannot be concluded that CD takes over GC in the evolutionary time course. The same statistics are plotted at $t = 200$ in Fig. 2B. As in the case of Fig. 2A, CD gains more than GC at the same degree. At this stage, however, most hubs are occupied by GCs for the following reason. There are usually some GCs in the neighborhood of a GC hub, which is also the case under random initial condition. Then, the GC hub tends to gain a large payoff because GC neighbors help the GC hub. As a result of evolution, GC will spread from the hub to the neighbors, which further increases the payoff of the GC hub. Suppose a situation where CDs invade neighbors of the GC hub and exploit it. Because the degrees of these CDs are generally not large, the CDs cannot be helped by many players even if the neighborhood is occupied by GCs. Therefore, the CDs would not gain the payoff per round as large as that of the GC hub. Accordingly, GC tends to be stabilized
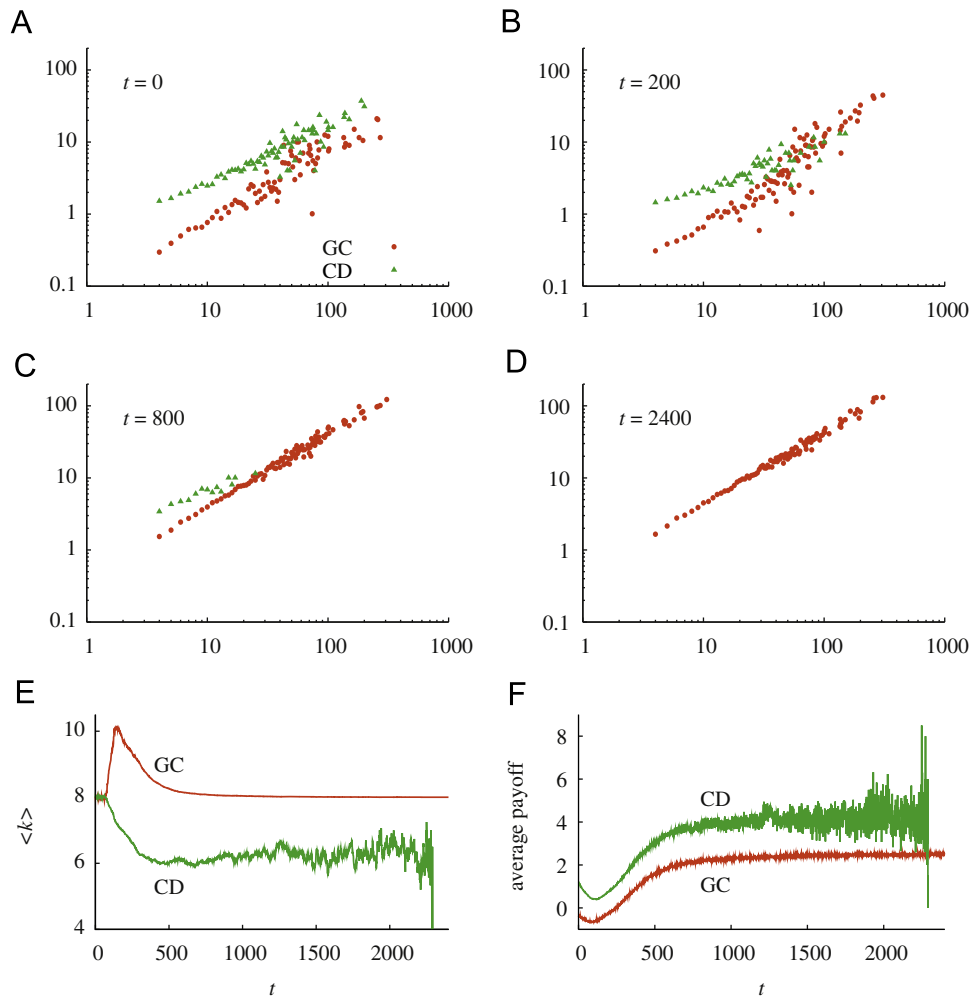
Fig. 2. Payoff per round for each strategy as a function of degree at (A) $t=0$, (B) $t=200$, (C) $t=800$, and (D) $t=2400$. (E) Time course of mean degree for GC and CD. (F) Time course of average payoff for GC and CD. We set $\langle k \rangle = 8$, $p_i = 0.8$, and $N_u = 200$.

at the hub. In contrast, if CD spreads from the hub to the neighbors, the CD hub will obtain a small payoff. Then, a GC in the neighborhood of the CD hub may take over the hub; CDs occupying hubs are not stabilized. GCs gradually spread from hubs to players having small degrees (Fig. 2C), and the entire network is eventually occupied by GCs after sufficient rounds (Fig. 2D).

The time courses of the mean degree of GCs and that of CDs corresponding to the run shown in Fig. 2A–D are plotted in Fig. 2E. First, the mean degree of GCs grows until most hubs are occupied by the GCs. It then relaxes to $\langle k \rangle = 8$. The mean degree of the CDs is considerably smaller than $\langle k \rangle = 8$ throughout the run.

The time courses of the average payoff per round of GCs and that of CDs, corresponding to the same run as above, are shown in Fig. 2F. Initially, the two average payoffs decrease because CDs replace GCs. Then, GCs are stabilized at hubs, and the GCs begin to disseminate to increase the average payoff of both GCs and CDs. At any t, CDs earn more than GCs on an average. However, this does not imply that CD invades GC macroscopically. As shown in Fig. 2B and C, the players with the largest payoffs are GC hubs rather than CDs. A player is chosen as a potential parent to be mimicked by other players with the probability proportional to its degree (Newman, 2003; Noh and Rieger, 2004). In the scale-free network, a neighbor of an arbitrary player tends to be a hub, and then GC hubs are imitated by relatively many players. Therefore, while the average payoff of CDs is maintained at a larger value

than that of GCs, the fraction of CDs gradually decreases until the CD becomes extinct. The relative strength of a strategy in reproduction is determined not by the average payoff of the players using that strategy but by the degree-weighted average payoff of these players.

The scenario of evolution of helping behavior described above requires heterogeneous degree distribution. To compare different networks, at a given value of b, we generate five realizations of the network and carry out 10 runs on each network for the scale-free network and the regular random graph, which are generated from stochastic algorithms. For the other three deterministic networks, we carry out 50 runs on the network. The average of the final fraction of GC, obtained from the 50 runs, is plotted against b in Fig. 3. In all the networks, except the regular random graph, the fraction of GC increases with b. In fact, the fraction jumps from unanimity of CD to that of GC at a threshold value of b. The threshold value of b above which GCs survive is considerably smaller in the scale-free network than in the other networks. Heterogeneous networks promote the evolution of helping behavior. Among the other networks, the threshold value of b is the smallest in the cycle. The next smallest value is the extended cycle and then the square lattice. The threshold value of b in the random graph is greater than the upper limit shown in Fig. 3 (i.e., $b=10$). Unlike the Barabási–Albert scale-free network and the regular random graph, the other three networks, i.e., the cycle, the extended cycle, and the square lattice, are capable of spatial reciprocity. This fact explains

why these three networks accommodate more GCs as compared to the regular random graph. However, the effect of spatial reciprocity is smaller than the effect of the scale-free networks, at least under the present parameter regime.

We confirm that the results are qualitatively the same for some variations of the model. First, we change the mean degree to $\langle k \rangle = 6$ (Fig. 4A) and $\langle k \rangle = 14$ (Fig. 4B). The results are qualitatively the same as those for $\langle k \rangle = 8$. Quantitatively, GC survives more easily for a smaller $\langle k \rangle$, which coincides with the results for the Prisoner's Dilemma on regular random graph (Ohtsuki et al., 2006). Second, we change p_i for GC and PO to 0.7 (Fig. 5A) and 0.9 (Fig. 5B). The results are qualitatively the same as those for $p_i = 0.8$. Quantitatively, a larger value of p_i yields a larger fraction of GC. Third, we change the number of players updated in one round to $N_u = 20$ (Fig. 6A) and $N_u = 2000$ (Fig. 6B). The results are qualitatively the same as those for $N_u = 200$. Fourth, we show the effect of different stochastic update rules. In the imitation rule (Ohtsuki et al., 2006), at the end of each round, potentially updated player v_i selects a potential parent out of the $k_i + 1$ players, i.e., v_i and the k_i neighbors of v_i. The probability that a node is

selected as the parent is proportional to the payoff. When the payoff is negative, we set this probability to zero. In the Fermi rule (e.g., Szabó and Tőke, 1998; Traulsen et al., 2006), v_i selects a potential parent v_j out of the k_i neighbors with equal probability and copies the strategy of v_j with probability $[1 + \exp(\beta((\text{payoff of player } v_i) - (\text{payoff of player } v_j)))]^{-1}$. Otherwise, v_j copies the stragegy of v_i. The results for the imitation rule and those for the Fermi rule with $\beta = 0.2$ are shown in Fig. 7A and B, respectively. The results resemble those for the deterministic update rule. Although the one-dimensional chain allows for GC at small values of b, as comparable or even smaller than the values for the scale-free network, our main result that heterogeneous networks enhances generous cooperators as compared to homogeneous networks is not violated.

In the case of the cycle, the threshold value of b above which the GC survives the invasion by CD has been obtained for a different update rule in the limit of weak selection (Nowak and Roch, 2007). The survival of the GC is possible when $b/c > f(p)$, where $f(p) = [8 + 2p + 8\sqrt{1-p^2}]/[3 + 4p + \sqrt{1-p^2}]$. Because we set $c = 1$ and $p = 0.8$, the theoretical threshold in this case is equal to $f(0.8) = 2.12$. Fig. 3 indicates that the GC survives when b is larger than approximately 2.6 in the numerical simulations; this value is not too far from the theoretical value. The discrepancy between the theoretical and numerical results is probably attributed to the use of different update rules (stochastic versus deterministic), the difference in selection pressure (weak selection versus strong selection), and/or the difference in the boundary condition of the network (open end versus periodic boundary condition).

3.2. GC versus CC

Next, we examine the case in which GCs and CCs are initially present. Although GC and CC are both cooperative in a classical sense, the GC is more cooperative than the CC in a game of upstream reciprocity. Similar to the case considered in Section 3.1, we start each Monte Carlo simulation using an equal
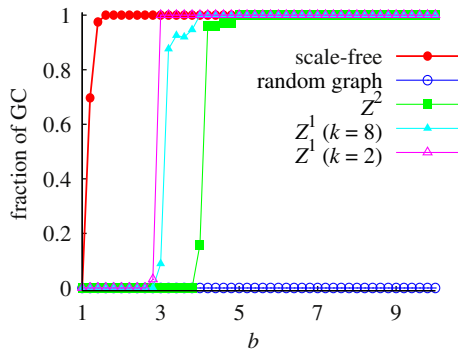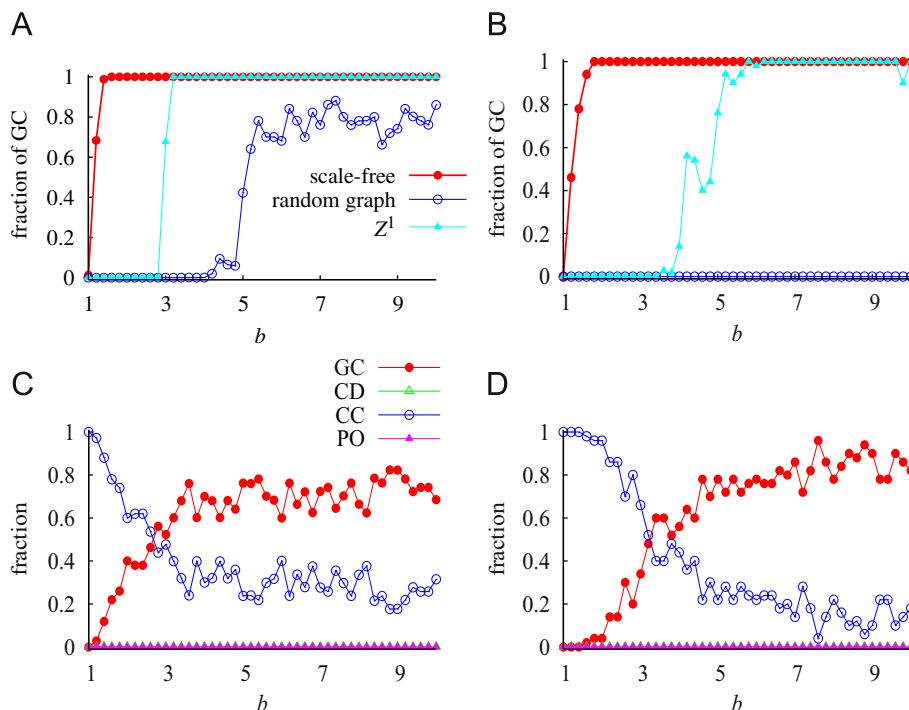

Fig. 3. Final fractions of GC in various networks when players initially adopt either GC or CD. We set $\langle k \rangle = 8$, $p_i = 0.8$, and $N_u = 200$.

Fig. 4. Results for different values of $\langle k \rangle$. (A, B) Final fractions of GC in various networks when players initially adopt either GC or CD. We set (A) $\langle k \rangle = 6$ and (B) $\langle k \rangle = 14$. (C, D) Final fractions of four strategies when players initially adopt either GC, CD, CC, or PO in the scale-free network. We set (C) $\langle k \rangle = 6$ and (D) $\langle k \rangle = 14$.
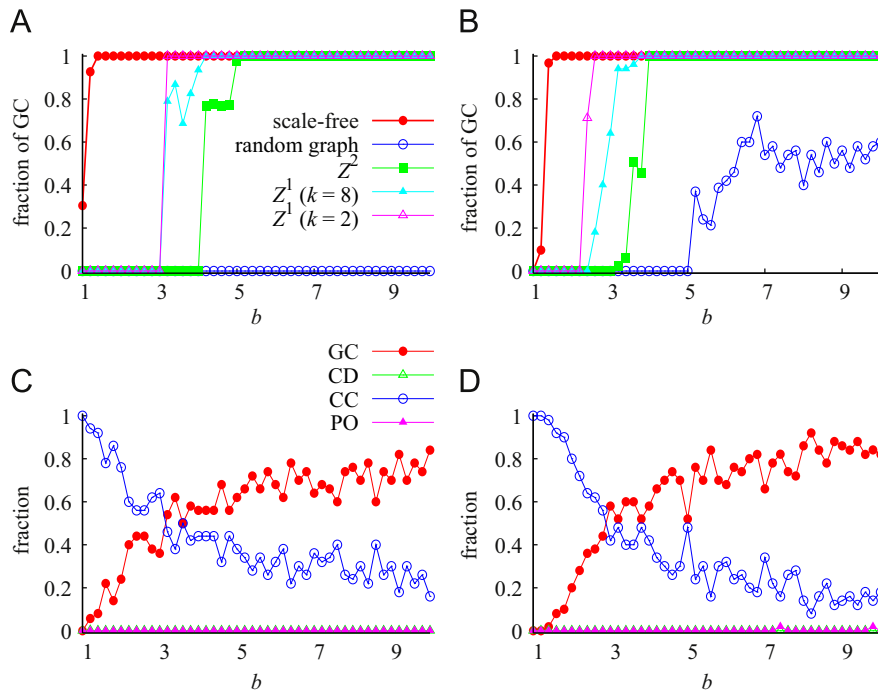
Fig. 5. Results for different values of p_i. (A, B) Final fractions of GC in various networks when players initially adopt either GC or CD. We set p_i for GC to (A) 0.7 and (B) 0.9. (C, D) Final fractions of four strategies when players initially adopt either GC, CD, CC, or PO in the scale-free network. We set p_i for GC and PO to (C) 0.7 and (D) 0.9.
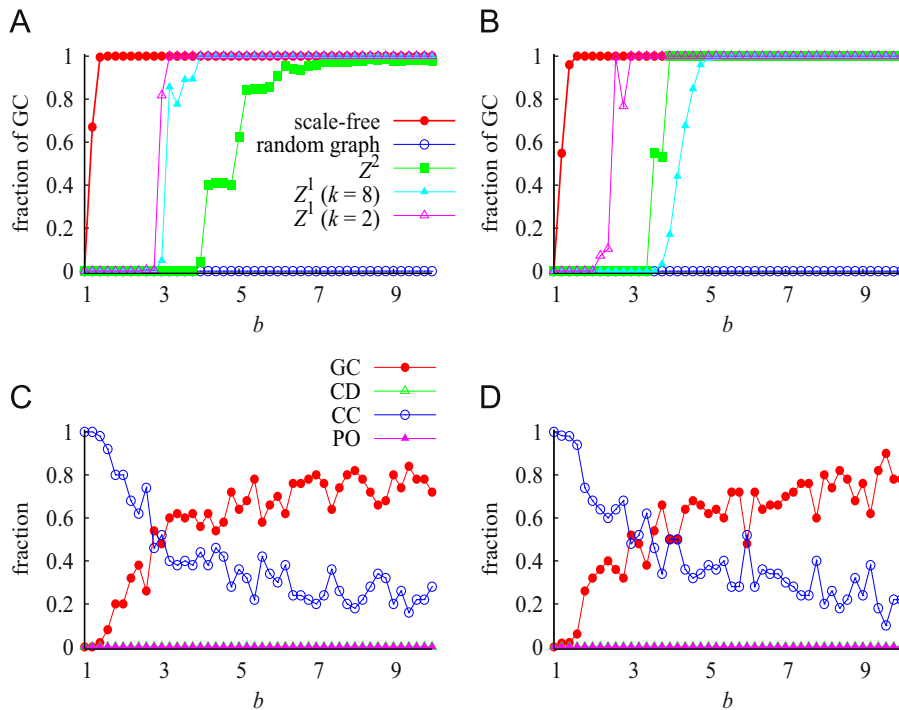

Fig. 6. Results for different numbers of players updated per round. (A, B) Final fractions of GC in various networks when players initially adopt either GC or CD. We set (A) $N_u = 20$ and (B) $N_u = 2000$. (C, D) Final fractions of four strategies when players initially adopt either GC, CD, CC, or PO in the scale-free network. We set (C) $N_u = 20$ and (D) $N_u = 2000$.

fraction of GCs and CCs. In contrast to a population composed of GCs and CDs, in this case, the unanimity of GC or that of CC, instead of a mixture of GC and CC, is reached very often in the final round of runs in the scale-free network and the square lattice. This unanimity is attained even if the number of rounds is set to a small value. If all runs end up at unanimity, the fraction of GC is equal to the fraction of runs in

which unanimity of the GC is reached. This quantity is discretized by the number of runs. Therefore, we carry out 100 runs in the scale-free network and the square lattice to overcome the discretization effect. In the other networks, we carry out 50 runs as in the previous case.

The final fraction of the GC in different networks is shown in Fig. 8. The scale-free network enhances the evolution of the GC to
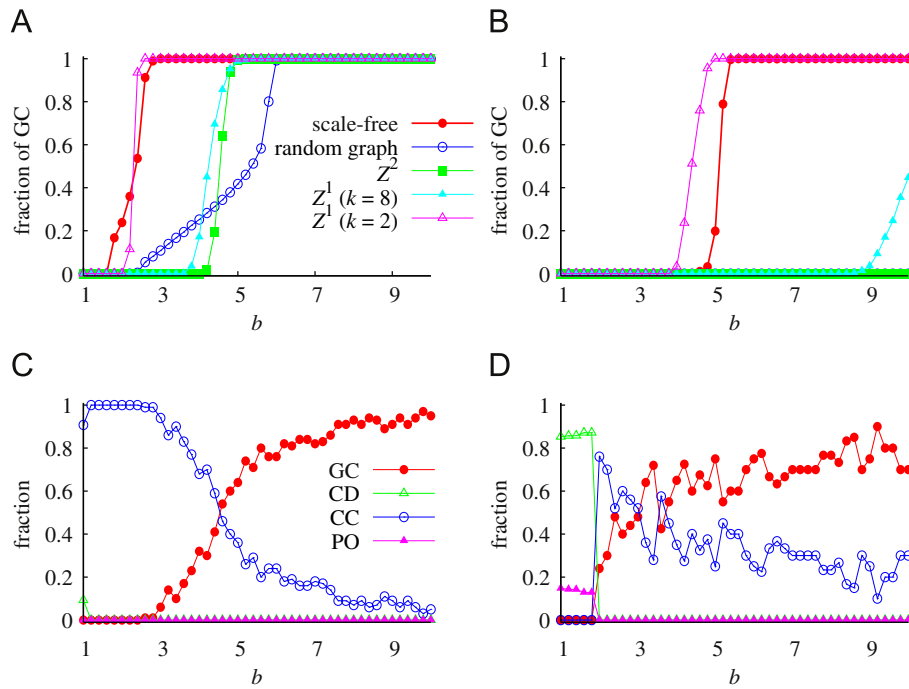
Fig. 7. Results for different update rules. (A, B) Final fractions of GC in various networks when players initially adopt either GC or CD. We use (A) imitation update rule and (B) Fermi update rule. (C, D) Final fractions of four strategies when players initially adopt either GC, CD, CC, or PO in the scale-free network. We use (C) imitation update rule and (D) Fermi update rule.
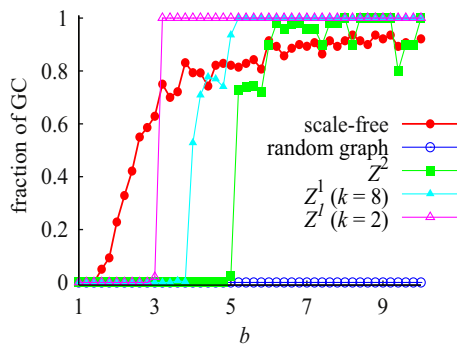

Fig. 8. Final fractions of GC in various networks when players initially adopt either GC or CC.
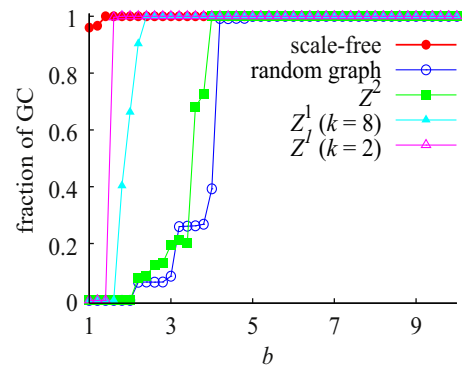

Fig. 9. Final fractions of GC in various networks when players initially adopt either GC or PO.

a greater extent than the other networks, except at large values of b. This result and the ordering of the five networks according to the threshold value of b above which the GC evolves are consistent with those obtained in the case of the population of GCs and CDs (Section 3.1). The threshold value of b in the random graph is greater than the upper limit shown in Fig. 8 (i.e., $b = 10$).

In the case of the cycle, it has been theoretically shown for the original model that the GC survives the invasion by CC when $b/c > f(0.8) = 2.12$ (Nowak and Roch, 2007). In Fig. 8, the GC survives in the cycle when $b/c \geq 3.0$, which is of the same order as the theoretically predicted value for the original model.

3.3. GC versus PO

In this section, we investigate the population composed of GCs and POs. Recall that, even though PO is cooperative in that it passes on helping behavior to a neighbor, the GC is more cooperative in comparison because it initiates a chain of helping behavior and PO does not.

The final fractions of the GC obtained from 50 runs in different networks are compared in Fig. 9. Similar to the results reported in Sections 3.1 and 3.2, the scale-free network yields the largest fraction of the GC. The ordering of the five networks according to the threshold value b is also consistent with those obtained in the population of GCs and CDs (Section 3.1) and that of GCs and CCs (Section 3.2).

Theoretically, GC survives for the original model in the cycle when $b/c > g(p)$, where $g(p) = [p(3 + 3p + \sqrt{1-p^2})]/[(1+2p)(1+p-\sqrt{1-p^2})]$ (Nowak and Roch, 2007). In our simulations, the threshold is estimated to be $g(0.8) = 1.54$. Fig. 9 suggests that the threshold is about 1.5, which is close to the theoretical value for the original model.

3.4. Populations comprising four strategies

We examine the dynamics of a population in which all four strategies are initially present. Each player is assumed to adopt
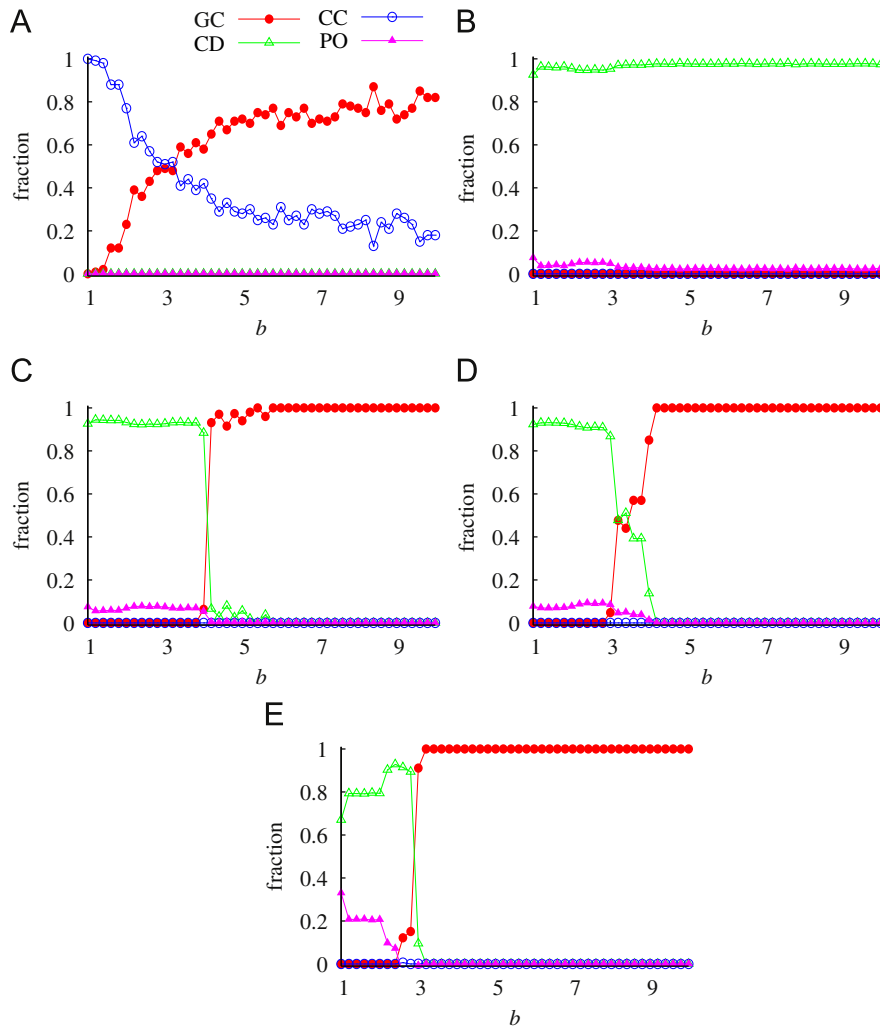
Fig. 10. Final fractions of four strategies when players initially adopt either GC, CD, CC, or PO in (A) scale-free network, (B) regular random graph, (C) square lattice, (D) extended cycle, and (E) cycle. We set $\langle k \rangle = 8$, $p_i = 0.8$, and $N_u = 200$.

either strategy independently with probability 1/4. Similar to the case of the population of GCs and CCs, most runs end up at unanimity of one strategy in the scale-free network and the extended cycle. Therefore, we carry out 100 runs for these two networks to enhance the precision in the computed fraction of different strategies. For the other networks, we carry out 50 runs.

The final fraction of each strategy in the five networks is shown in Fig. 10. In the scale-free network (Fig. 10A), CD and PO do not survive for any value of b. The fraction of GC increases with the value of b. In the regular random graph, the GC does not survive, and the network is almost entirely inhabited by the least cooperative players, i.e., CDs (Fig. 10B). For GC to survive, the value of b larger than 10, which is the upper limit of b examined in Fig. 10B, is required. In the square lattice (Fig. 10C), the extended cycle (Fig. 10D), and the cycle (Fig. 10E), GC takes over CD at a sufficiently large value of b. The lowest to highest threshold value of b above which the GC survives follows the order of the scale-free network, the cycle, the extended cycle, the square lattice, and the regular random graph.

The results are robust against various changes of the model, such as the value of $\langle k \rangle$ (Fig. 4C and D), the value of p_i (Fig. 5C and D), the value of N_u (Fig. 6C and D), and the update rule (Fig. 7C and D). The results in this section including the robustness results are consistent with those obtained for the populations that comprise two strategies (Sections 3.1–3.3).

4. Discussion

We have shown that heterogeneous networks enhance cooperative behavior in a game of upstream reciprocity. Based on the property of the simple random walk on networks, chains of helping behavior traverse hub players more often than players having small degrees. Then, hubs tend to gain a larger payoff. The most cooperative strategy (i.e., GC) is stable once it inhabits hubs, from where it spreads to the entire network. From a quantitative point of view, the impact of heterogeneous networks on enhancing altruism can be much more than that of spatial reciprocity in most cases. Our results are robust against variation in some parameters of the model ($\langle k \rangle$, p_i, and N_u) and variation in update rules.

The route to altruism in the game of upstream reciprocity proposed in this study is similar to that in the Prisoner's Dilemma on heterogeneous networks (Santos and Pacheco, 2005, 2006; Durán and Mulet, 2005; Santos et al., 2006). In this framework, each player is assumed to either cooperate with or defect against all neighbors in a round. Once a cooperator occupies a hub and some surrounding nodes, the hub gains a large payoff and is likely to disseminate its offspring (i.e., cooperators) to the neighbors. This event further increases the payoff of the hub, and the cooperation on the hub is stabilized. In contrast, defection on a hub is not stable because the hub does not gain a large payoff if the defector hub disseminates its offspring to the neighbors.

Cooperators are propagated from hubs to the entire network. In the game of upstream reciprocity in networks, suppose that a GC hub disseminates its offspring to the neighbors. This hub will gain a larger payoff in the subsequent rounds because the neighbors will tend to pass on the chains of helping behavior. Then, the GC hub will receive helping behavior more often than typical players such that its payoff increases, and the GC is stabilized on the hub. This positive feedback is weaker in the case of the PO and absent in the case of the CD and CC.

When player X with a small degree copies the strategy of a successful hub neighbor Y, X may not gain a large payoff because X is not a hub. In the Prisoner's Dilemma on networks, many previous studies assumed that selection is based on the summed payoff; in this, each player sums up the payoff obtained by playing against all neighbors to determine the payoff per round (Santos and Pacheco, 2005, 2006; Durán and Mulet, 2005; Santos et al., 2006). However, it may be advantageous for X not to copy the strategy of Y, because X is not as connected as Y. It may be more profitable for X to copy the strategy of a neighbor that earns a larger payoff per edge. This update rule corresponds to the selection based on the average payoff, i.e., the summed payoff divided by the degree. The average payoff scheme does not enhance cooperation in the Prisoner's Dilemma on heterogeneous networks (Santos and Pacheco, 2006; Tomassini et al., 2007). This argument is also applicable to the game of upstream reciprocity in scale-free networks. The evolution of helping behavior is likely to be hampered if the selection is based on average payoff. This is a major limitation of the present study. The update rule that we have adopted, as well as the rule based on additive payoff used in the Prisoner's Dilemma, may represent a situation in which players are unaware of the degree of their neighbors.

In the game of upstream reciprocity, hubs gain relatively large payoffs because a simple random walker visits hubs relatively often. This is true for an eternally lasting random walk on arbitrary undirected networks (Noh and Rieger, 2004). However, in our model, the random walk terminates in finite time. Then, the random walker may visit specific non-hub nodes more frequently than it visits hubs, as in the case of the random walk in networks with an absorbing boundary (Noh and Rieger, 2004; Newman, 2005). For heterogeneous networks in which populations are not well mixed, perhaps with degree correlation between adjacent nodes or global structure of networks, our results may be modified. The GC may spread from specific non-hub players. In directed networks, the frequency of visit of the random walker to nodes can also deviate from the predicted value based on the degree (Donato et al., 2004; Masuda and Ohtsuki, 2009). Roughly speaking, however, the random walk tends to visit more connected players under all discussed cases. Therefore, we expect that our results qualitatively hold true for general heterogeneous networks.

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