Revisiting "The Evolution of Reciprocity in Sizable Groups": Continuous reciprocity in the repeated *n*-person prisoner's dilemma

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ABSTRACT

For many years in evolutionary science, the consensus view has been that while reciprocal altruism can evolve in dyadic interactions, it is unlikely to evolve in sizable groups. This view had been based on studies which have assumed cooperation to be discrete rather than continuous (i.e., individuals can either fully cooperate or else fully defect, but they cannot continuously vary their level of cooperation). In real world cooperation, however, cooperation is often continuous. In this paper, we re-examine the evolution of reciprocity in sizable groups by presenting a model of the *n*-person prisoner's dilemma that assumes continuous rather than discrete cooperation. This model shows that continuous reciprocity has a dramatically wider basin of attraction than discrete reciprocity, and that this basin's size increases with efficiency of cooperation (marginal per capita return). Further, we find that assortative interaction interacts synergistically with continuous reciprocity to a much greater extent than it does with discrete reciprocity. These results suggest that previous models may have underestimated reciprocity's adaptiveness in groups. However, we also find that the invasion of continuous reciprocators into a population of unconditional defectors becomes realistic only within a narrow parameter space in which the efficiency of cooperation is close to its maximum bound. Therefore our model suggests that continuous reciprocity can evolve in large groups more easily than discrete reciprocity only under unusual circumstances.

1. Introduction

Direct reciprocity has long been regarded as a plausible route for the evolution of cooperation in genetically unrelated dyads (Axelrod and Hamilton, 1981; Trivers, 1971), particularly in humans. However, human sociality extends far beyond dyadic cooperation, and is characterized by collective action (Olson, 1965), i.e., a large group of unrelated members involved in the joint production of a shared resource. Based on the pessimistic results of models of the evolution of reciprocity in large groups (Bendor and Mookherjee, 1987; Boyd and Richerson, 1988; Joshi, 1987; Taylor, 1976), the standard view in biology has for years been that reciprocity is unlikely to evolve in groups much larger than dyads (e.g. Boyd et al., 2003; Fehr, 2004; Fehr and Fischbacher, 2003; Gächter and Herrmann, 2009; Hagen and Hammerstein, 2006; Hauert et al., 2002; Henrich, 2004, 2006; Kurzban and Houser, 2005; Sigmund and Nowak, 2000; Suzuki

and Akiyama, 2005). This view has led many theorists to suggest alternative routes for the evolution of group cooperation, for example genetic or cultural group selection (Boyd et al., 2003; Gintis, 2000; Henrich, 2004; Wilson and Sober, 1994), costly signalling (Gintis et al., 2001), opting out of a group (Hauert et al., 2007), and indirect reciprocity (Panchanathan and Boyd, 2004).

Reciprocity in dyads is traditionally modelled as the *tit-for-tat* strategy (Axelrod and Hamilton, 1981) that continues cooperating as long as the partner cooperates, but stops cooperating if the partner did not cooperate in the previous round. *Tit-for-tat* is a discrete strategy that contributes either fully or not at all. Models of reciprocity in groups have defined reciprocity as a discrete strategy that continues cooperating as long as all other group members cooperate, but stops cooperating if one or more co-members defect (Bendor and Mookherjee, 1987; Boyd and Richerson, 1988; Joshi, 1987; Taylor, 1976). However, the evidence that people actually engage in a discrete all-or-nothing strategy—also called a trigger strategy—is weak (Ostrom et al., 1994; Watabe, 1992; Watabe and Yamagishi, 1994). Furthermore, many instances of real-world cooperation seem to be better modelled as continuous rather than discrete, because individuals continuously vary their degree of cooperation from full defection to full cooperation. Bshary and Bronstein (2004), for example, review real world examples of

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interspecific mutualism and find many instances of continuous cooperation. Continuous cooperation is also common in human groups: members tend to modulate their contribution levels in order to approximately match the mean co-member contribution (Croson, 2007; Croson et al., 2005; Fischbacher et al., 2001; Kurzban and Houser, 2005; Kurzban et al., 2001).

The representation of reciprocity as a discrete strategy could be regarded as a trivial or inevitable simplification of a complex reality, of the kind that is often required in formal models. However, we found that replacing discrete reciprocity with continuous mean-matching reciprocity effected significant changes in model results. In Section 2 below, we first review a model of discrete reciprocity in the n-person prisoner's dilemma (Boyd and Richerson, 1988) that is widely cited as having shown the difficulty of the evolution of (discrete) reciprocity in large groups. We then compare this model with a new model that replaces discrete reciprocity with continuous reciprocity. We find that like discrete reciprocity, continuous reciprocity can be evolutionarily stable against an unconditional defection strategy, while unconditional defection can also be evolutionarily stable against both reciprocity strategies. The most important finding is that the basin of attraction for continuous reciprocity gets wider as cooperation gets more efficient, while the basin of attraction for discrete reciprocity remains quite small even when cooperation is extremely efficient. We also investigate the influence of assortative interaction and find it to have a strong synergic effect with continuous reciprocity but not with discrete reciprocity. These results hold even when an unconditional cooperation strategy exists in the population.

However, we find that the advantage of continuous reciprocity is strictly constrained by the efficiency of cooperation; the invasion of continuous reciprocity into a population of defectors becomes realistic only when cooperation is extremely efficient, i.e. when a contribution from a single individual produces a very large benefit for the entire group. Because conditions of such efficiency are probably relatively rare, this finding suggests that in a population divided up into large groups, continuous reciprocity could invade only under unusual circumstances. In Section 3, we demonstrate the robustness of continuous reciprocity in highly efficient public goods situations by extending the strategy space from one in which continuous reciprocators can only match the mean partner contribution to one in which they can contribute above or below this mean.

2. Discrete versus continuous reciprocity

2.1. Repeated n-person prisoner's dilemma game

To model the evolution of cooperation in sizable groups, we considered a large population subdivided into randomly-formed groups of size n which play repeated n-person prisoner's dilemma games. Every round, individual members decide whether to contribute c to their group, in order to create the benefit Bc which is divided equally among all n group members. B is assumed to be smaller than n, so a member's private return is always less than that member's contribution ($Bc/n < c$), and groups are thus public good-producing collective actions characterized by social dilemmas. The game is repeated with the probability w.

2.2. The evolution of discrete reciprocity

First, let us consider two classes of strategies: unconditional defector (D) and discrete reciprocator (T_a). D never contributes, while T_a contributes fully ($c=1$) in the first round and continues

contributing fully as long as a or more group co-members also contribute fully. Let $V(x|y)$ be the payoff to an individual with a strategy x in a group with y reciprocators (in this section, T_a). When D is common, the expected payoff to D is $V(D|0)=0$ while the payoff to a rare T_a is $V(T_a|1)=B/n-1$ when $a=n-1$, and $(B/n-1)/(1-w)$ when $a<n-1$. In both cases, the payoff to T_a is smaller than 0 and thus a rare T_a cannot invade a population when D is common. When T_a is common, the expected payoff to T_a is $V(T_a|n)=(B-1)/(1-w)$. The expected payoff to a rare D is $V(D|n-1)=(B(n-1)/n)/(1-w)$ when $a<n-1$. As $V(T_a|n)<V(D|n-1)$ when $n>2$, T_a cannot prevent the intrusion of D. On the other hand, when $a=n-1$, the expected payoff to D is $V(D|n-1)=B(n-1)/n$ and this is smaller than the expected payoff to T_{n-1} when w is sufficiently large (Boyd and Richerson, 1988). Thus, T_{n-1} is an evolutionary stable strategy that prevents the intrusion of rare D when interactions are sufficiently iterated. In the following, we will consider only T_{n-1} (hereafter referred to simply as T).

It is proved that, when T is evolutionarily stable, there is a unique unstable internal equilibrium (Boyd and Richerson, 1988). However, the basin of attraction for a pure T equilibrium gets smaller quickly as group size increases. The proportion of T at an internal equilibrium is

$$p = \left\{ \frac{1-B/n}{w(B-1)/(1-w)} \right\}^{1/n}.$$

Fig. 1a illustrates how this proportion of T changes as a function of the efficiency of cooperation B/n (marginal per capita return) and w when group size is 100.[1] The upper two lines in Fig. 1a show that T cannot increase its share in a population unless it already composes a large majority of that population; if the proportion of T falls below 85–90%, D increases its share.

2.3. The evolution of continuous reciprocity

We now replace the discrete strategy T with a simple continuous reciprocal strategy R. Like T, R contributes fully in the first round. R then matches the average contribution made by the other $n-1$ players in the previous round. When D is common, the expected payoff to D is $V(D|0)=0$. The expected payoff to rare R is $V(R|1)=B/n-1$ because R contributes fully only in the first round and contributes nothing from the second round. As $V(R|1)<V(D|0)$, D is evolutionarily stable. On the other hand, when R is common, it is proved that the expected payoff to R, $V(R|n)=(B-1)/(1-w)$, is larger than D's expected payoff, $V(D|n-1)$, and R is evolutionarily stable when

$$\frac{B-1}{1-w} > \frac{B(n-1)/n}{1-w(n-2)/(n-1)}$$

(see Appendix A). Because the condition for T to be an ESS is $(B-1)/(1-w) > B(n-1)/n$ and $1-w(n-2)/(n-1)$ is always smaller than 1, R can avoid an invasion of D in a narrower range of conditions than can T.

The basin of attraction for R is drastically larger than that for T, however. Fig. 1a shows the minimum proportion of R and T that must exist in a population in order to prevent the intrusion of D (i.e., the proportion of R and T at an unstable internal equilibrium). In contrast to T, the proportion of R is generally small, especially

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[1] Throughout this paper, we manipulate the value of B/n as a model parameter instead of independently varying the values of B and n. B/n is frequently used as an index of efficiency of cooperation; in order for the game to be a public goods dilemma, its value needs to lie between 0 and c (=1 in our model). Differences between the two reciprocal strategies were exhibited mainly when this index's value was close to its upper limit. Note that the value of B, the amount of benefit produced from one unit of contribution, varies with the increase of the group size, n, even when the efficiency of cooperation index remains constant.

Fig. 1. The minimum proportion of discrete (T) and continuous (R) reciprocity strategies necessary to invade a population of unconditional defectors (D). For both (a) and (b) the group size is set to 100; the horizontal axis is the probability w of interaction continuation, and the vertical axis is the proportion of the reciprocity strategy that must compose the population in order to successfully invade; and the two upper lines represent the discrete strategy T, while the two lower lines represent the continuous strategy R. For (a) groups are formed randomly; the two circle-studded lines show that when efficiency of cooperation (B/n) is moderate, T can invade only when very common, while R can invade when less common, especially as w increases; the two triangle-studded lines show that when efficiency is high, T can invade only when very common, while R can invade when much less common. For (b) groups are formed assortatively; triangle-studded lines show R's advantage in invasion ability when assortation (r) is fairly weak and efficiency is very low, while circle-studded lines show this advantage when assortation is very weak and efficiency is fairly low. For both (c) and (d) the horizontal axis is the size B of the benefit to the group, the three dotted lines represent T, and the three solid lines represent R. Group size n is 20, 50 and 100 for each strategy, while continuation probability w is set to 0.99. For (c) groups are formed randomly and B is truncated at the maximum value minus 1 for each group size. For (d) groups are formed assortatively ($r=1/16$) and B is truncated at the integer value that is smaller and closest to $n/\{(n-1)r+1\}$.

when the efficiency of cooperation, B/n, is high. For instance, when $n=100$ and B/n is 0.95 (so 1 unit of cooperation [$c=1$] produces 95 units of benefit [$B=95$]), R can proliferate even when its initial proportion is only 10% or less. This is markedly different from T, which must compose 85–95% of the population in order to evolve. We increased group size in increments of 100 from 100 to 500, and confirmed that this advantage of R over T holds across all these group sizes. Fig. 1c shows how the basin of attraction for T

and R changes in response to the size of benefit of cooperation (B) and group size (n); the basin of attraction for R changes almost linearly as benefit of cooperation approaches the maximum size (i.e., as B approaches n). For all three group sizes ($n=20$, 50 and 100), the proportion of R at internal equilibrium gets lower than 10% when the efficiency of cooperation (B/n) is larger than about 0.9 (i.e., $B \approx 18$, 45 and 90 for $n=25$, 50 and 100, respectively) which indicates that the invasion of R becomes realistic only in a

narrow range of B that is close to B's maximum value. On the other hand, the basin of attraction for T is less sensitive to the size of B as group size increases.

2.4. Synergic effect between continuous reciprocity and assortative interaction

In dyadic cooperation, a strong synergic effect between reciprocity and assortative interaction is known to exist (Axelrod and Hamilton, 1981); rare reciprocators can invade a population of unconditional defectors much more easily if reciprocators can preferentially interact with other reciprocators and thus decrease the risk of being exploited by defectors. On the other hand, a model of discrete group reciprocity (Boyd and Richerson, 1988) found that assortative group formation does not facilitate the invasion of rare reciprocators very much.

Fig. 2 shows the threshold number of interactions that must be exceeded in order for a rare reciprocator strategy, T or R, to invade a population of unconditional defectors given a specific group size and level of assortative interaction (r) (see Appendix B). The figure illustrates that both T and R can invade when group size is very small ($n=3$ or 5) and when groups continue to interact for a very long time. The threshold value for number of interactions is slightly smaller for R than T, implying that R can more readily evolve, although this difference is minor. As group size gets larger, it quickly gets much tougher or even impossible for both T and R to invade (see also Boyd and Richerson, 1988).

We also investigated the synergic effect of reciprocity and assortative interaction by considering the size of the basin of attraction for reciprocators. We did find a strong synergic effect, but only for R: with assortative interaction, the basin of attraction for R remains large even when cooperation is relatively inefficient. Fig. 1b shows the minimum proportion of discrete reciprocators, T, necessary for T to increase its share when assortative interaction is fairly low ($r=1/16$) and very low ($r=1/64$), and suggests that assortation does not help T very much: in both cases, T cannot prevent the invasion of D if its proportion in a population is smaller than around 85–95%. In contrast, a small degree of assortative interaction drastically decreases the value of efficiency of cooperation (B/n) that is necessary for R to evolve.

When $r=1/16$, a small proportion of R can proliferate even when cooperation is relatively inefficient ($B/n=0.13$). Again, similar results are obtained even when group size is increased from 100 to 500, in increments of 100. Fig. 1d shows how the basin of attraction for T and R changes in response to the size of benefit of cooperation (B) and the group size (n) when $r=1/16$. As when there is no assortative interaction existing (i.e., Fig. 1c), the basin of attraction for R changes almost linearly as B increases to its maximum value (i.e., $n/\{(n-1)r+1\}$; if B is larger than this point, even a rare unconditional cooperator can increase its share in the population of unconditional defectors).

Where does the synergic effect between assortative interaction and continuous reciprocity come from? First, T gains the benefits of mutual cooperation only when all of its co-members are also T; the introduction of just one D co-member induces the collapse of cooperation. The introduction of one or more D also results in the collapse of cooperation when D and R coexist in the same group. However, R gains some benefit from mutual cooperation because of its gradual decrease of cooperation. As the number of D co-members increases, R stops cooperating more quickly and thus minimizes the extent of its own exploitation. R is thus able to reduce cooperation when interacting with too many Ds, and to maintain a moderately high level of cooperation with fewer Ds. As a result, payoffs to D and R marginally increase as the number of reciprocators increases, while payoffs to D and T mostly linearly increase. This non-linearity advantages R, especially when assortative interaction exists (see Fig. 3).

2.5. The third strategy: unconditional cooperators

So far we have investigated interactions between only two strategies (D and either R or T) at one time. Do results change when a third strategy—unconditional cooperation (C)—is added? When D is completely absent, C receives the same benefit as T or R, and C can drift into the populations composed of reciprocators (T or R). However, C is easy prey to D, and after drifting onto a population, C may even help D to beat a reciprocal strategy. In order to examine the influence of unconditional cooperators, we extended the model by adding C and examined the evolutionary dynamics of the system. Appendix C discusses the payoffs and
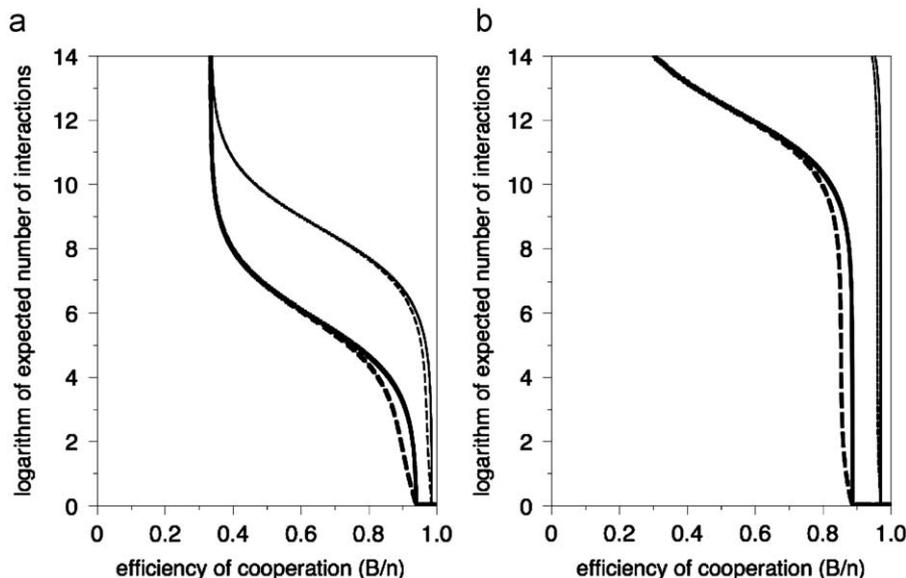
Fig. 2. Minimum number of interactions that must be exceeded for rare reciprocators (T and R) to invade a population of unconditional defectors (D) under assortative group formation. T and R are represented by solid and broken lines, respectively. Thinner lines indicate $r=1/64$ and thicker lines indicate $r=1/16$. Horizontal axis represents efficiency of cooperation (B/n) and vertical axis represents logarithm of expected number of interactions (i.e., $1/1-w$). For (a) $n=3$; (b) $n=5$.
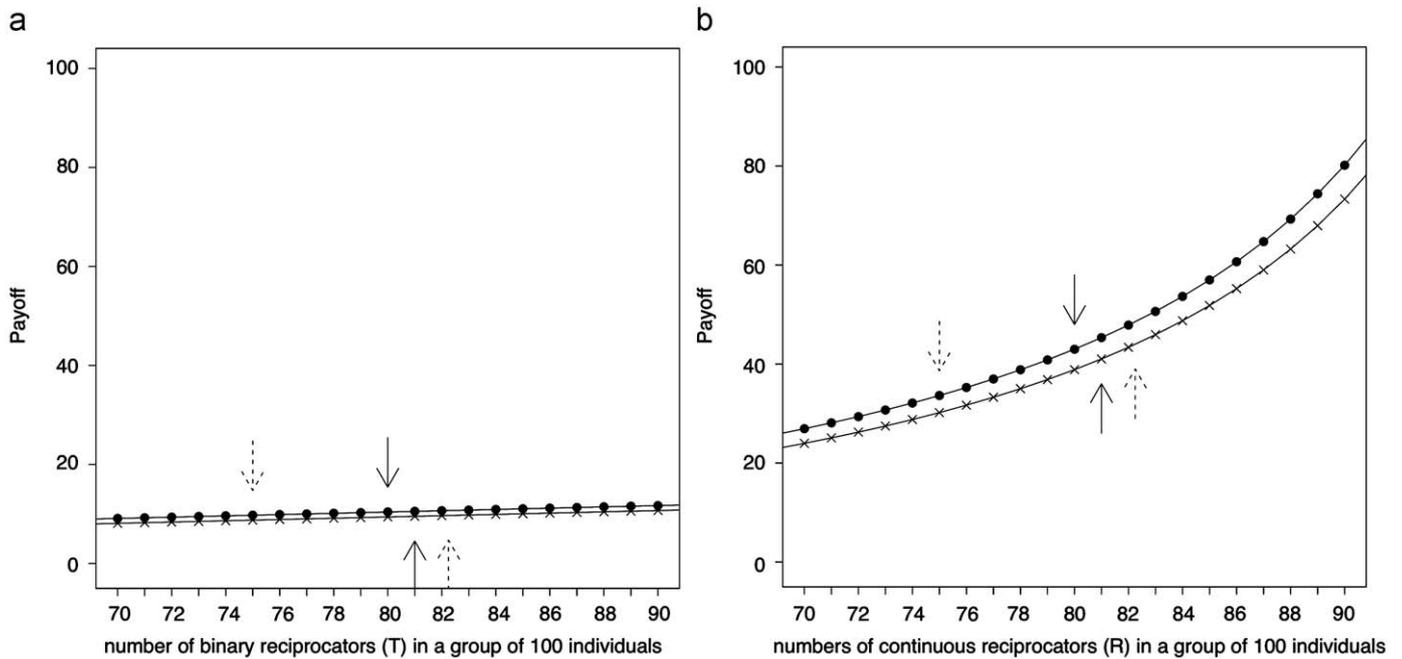
Fig. 3. Payoff to defectors (D) and discrete (T) and continuous (R) reciprocity strategies as a function of the number of reciprocators in the group. For both (a) and (b): parameter values are $n=100$, $B/n=0.50$, and $w=0.95$; the circle-studded and x-studded lines represent payoffs to D and to reciprocators (T in (a) and R in (b)), respectively. Solid arrows in (a) and (b) represent expected numbers of reciprocators in one's group when p is 0.50 and when one is a D (left arrow) or when one is a reciprocator (right arrow). Both (a) and (b) show that a reciprocator's payoff in a group of 50 reciprocators is smaller than a D's payoff in a group of 49 reciprocators, so both (a) and (b) suggest that reciprocity cannot evolve under this parameter setting when there is no assortative interaction. When groups are assortatively formed, reciprocators will find more reciprocators and D will find fewer reciprocators in their groups, so the arrows will move apart from each other. The dotted arrows in (a) and (b) represent expected numbers of reciprocators in one's group when one is a D (left arrow) or a reciprocator (right arrow) and when p is 0.50 and assortation (r) is 1/16. The payoff advantage for reciprocators over D increases at a much greater rate for R (b) then for T (a), indicating that assortative interaction benefits continuous reciprocators more than discrete reciprocators.
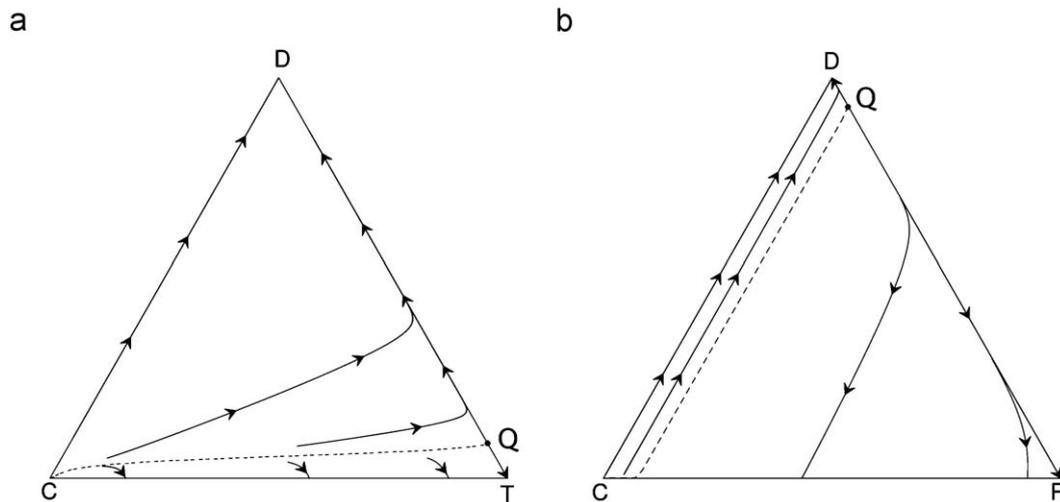
Fig. 4. Evolutionary dynamics of unconditional cooperators (C), unconditional defectors (D) and discrete (T) and continuous (R) reciprocity strategies. An all-D population is evolutionarily stable, and an all-R or all-T population is neutrally stable, as C can receive the same payoff as R or T when D is absent from the population. In both (a) and (b), the line QC separates two regions. Within DQC, the system evolves towards a non-cooperative equilibrium (point D). Within QCR or QCT, the system evolves towards a point on the line CR or CT (i.e., a mix of strategies C and R or T). On the line QR or QT, the system evolves towards an all-reciprocator equilibrium (point R or point T). When R is present in the population (a) the basin of attraction of cooperative strategies C and R is much larger than that of D; however when T is present (b) the basin of attraction of cooperative strategies C and T is much smaller than that of D. For both (a) and (b) the parameter values are $n=100$, $B/n=0.13$, $w=0.95$, and $r=1/16$.

Fig. 4 illustrates the dynamics of three strategies, C, D and either T (Fig. 4a) or R (Fig. 4b), when $n=100$. In both figures, any points on the line QC are unstable internal equilibria and the area above the line QC (including the point C but excluding the point Q) is the basin of attraction for D. Any points on the line TC or RC other than the point C are neutrally stable fixed points, and the area below the line QC is the basin of attraction for a mixture of cooperative strategies. We found that D's basin of attraction composes a large majority of the triangular area when it coexists with C and T, but only a small minority of this area when it coexists with C and R. Again, similar results were obtained when group size was increased incrementally to 500.

3. Extending the strategy space to allow below- and above-mean continuous reciprocity

We next investigated the stability of the continuous mean matching strategy against other variants of continuous reciprocity, such as those who give above or below the mean. Following Le and Boyd (2007), we modelled the strategy space of continuous reciprocal strategies using a parameter, ρ, which ranges from 0 to 2. When $\rho=1$, it is identical with the R mean matching strategy. As ρ gets larger, a player gets more generous than R and contributes more than the mean contribution. When $\rho=2$, it is identical with unconditional cooperation. As ρ gets smaller than 1 it gets less generous, and when $\rho=0$ it is identical with unconditional defection. Contribution at the round t ($\neq 1$) is ρu_{t-1} when $0 \leq \rho \leq 1$ and $u_{t-1}+(\rho-1)(1-u_{t-1})$ when $1 < \rho \leq 2$ where u_{t-1} is the mean contribution made by the other players at round $t-1$. For simplicity, we assumed that all strategies other than D ($\rho=0$) contribute fully in the first round. As we could not find a closed form expression of the payoffs, we conducted a numerical simulation by fixing a number of interactions instead of using a continuation probability of interactions.

3.1. Numerical analysis

We first assumed that the population consists of a single strategy, ρ_k, and checked if a rare single strategy, ρ_r, could invade this population. Fig. 5 is the payoff map of various combinations of ρ_k and ρ_r that shows local dynamics of the system. This system has one non-cooperative attractor, $\rho_k=0$: when the common strategy ρ_k is below the threshold value q, a more generous strategy ($\rho_r > \rho_k$) cannot invade the population. When the common strategy is more generous than this threshold line q but less generous than the mean matching strategy (i.e., $q < \rho_k < 1$), a more generous strategy ($\rho_r > \rho_k$) can invade the population. Remember that strategies $1 \leq \rho_k < q'$ are neutrally stable against any invading strategy $\rho_r \geq 1$, as neither perception nor implementation error exists in the model and both the common and invading strategies receive the same fitness value. If a population becomes too generous ($\rho_k > q'$), any strategy that is less generous than the mean matching strategy ($\rho_k < 1$) can invade the population. We found that the basin of attraction for $\rho_k=0$ is rather small as long as efficiency of cooperation remains high.
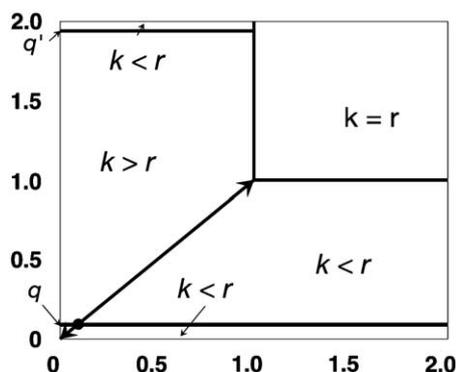
Fig. 5. Comparisons of payoffs of common strategy ρ_k and rare invading strategy ρ_r. Vertical axis represents a common strategy in a population and horizontal axis represents a rare invading strategy. Equality and inequalities inside of the rectangle indicate relative size of payoffs. For instance, in the area denoted $k > r$, common strategies receive higher payoffs than invading strategies. Both strategies receive the same payoffs on the thick lines ($k=r$). Parameter values are set to $n=100$, $B/n=0.95$ and maximum number of rounds $=10$ ($\approx w=0.9$). The parameters q and q' are strongly influenced by the efficiency of cooperation. For instance, when B/n is decreased to 0.65, q increases to 0.36–0.41 and q' decreases to 1.61.

3.2. Agent-based simulations

We then conducted agent-based simulations to further investigate global dynamics of the system and the stability of cooperative states in a heterogeneous population where agents' strategy ρ can take any value ranging from 0 to 2. At the first generation, the entire population was occupied by $\rho=1$. At the end of each generation, each individual produced a number of offspring that was proportional to the payoff that the individual received in that generation, and Gaussian error mutation $\varepsilon \sim N(0, SD)$ was added to each individual's strategy. Fig. 6 shows the results of simulations of 5000 agents that were randomly subdivided into 50 groups of 100 agents at the beginning of each generation and that played 20 rounds ($\approx w=0.95$) of the repeated n-person prisoner's dilemma game with B/n=0.9 for 5000 generations under several mutation sizes (SD of Gaussian mutation: 0.002, 0.02, 0.05 and 0.07).

As the mutation size increased, the system fluctuated more frequently. In general, however, the system exhibited cooperative polymorphism: the average of ρ fluctuated between cooperative ($\rho > 1$) and less cooperative values ($\rho \approx 0.2$–1) across generations but never arrived or stayed at a non-cooperative equilibrium ($\rho=0$).

4. Discussion

This model investigated reciprocity under rather specific conditions, where new groups were formed and dismissed in each generation, in the absence of errors of perception and implementation. We intentionally chose those settings so that our model would be directly comparable to a very influential study (Boyd and Richerson, 1988) that is often cited for suggesting that (discrete) reciprocity is unlikely to have played a very important role in the evolution of group cooperation (e.g. Boyd et al., 2003; Fehr 2004; Fehr and Fischbacher, 2003; Gächter and Herrmann, 2009; Hagen and Hammerstein, 2006; Hauert et al., 2002; Henrich, 2004, 2006; Kurzban and Houser, 2005; Sigmund and Nowak, 2000; Suzuki and Akiyama, 2005). Our results suggest that models which represent reciprocity as discrete rather than continuous may underestimate the adaptiveness of reciprocity in groups.

Although some real world group cooperation surely involves all-or-nothing discrete decisions, continuous cooperation has been observed in numerous species (Bshary and Bronstein, 2004). The disregard of reciprocity's role in the evolution of collective action is surprising, given that (continuous) reciprocity is the most commonly-observed strategy pursued by subjects in n-person cooperation experiments (Croson, 2007; Croson et al., 2005; Fischbacher et al., 2001; Kurzban and Houser, 2005; Kurzban et al., 2001; Yamagishi, 1986; Yamagishi and Sato, 1986). In this study, we pointed out the difference between the discrete reciprocity that has prevailed in past modelling efforts, and the continuous reciprocity that has been observed in these experiments. While the difference between discrete and continuous reciprocity may at first glance seem trivial, it affected model results significantly: compared to discrete reciprocity, the continuous mean matching strategy greatly enlarged the basin of attraction where reciprocity can evolve. However, this advantage of continuous reciprocity was heavily constrained by the size of the benefit from cooperation; the basin of attraction for continuous reciprocators increased almost linearly as the benefit from cooperation (B) increased. In the absence of assortative interaction, when the efficiency of cooperation (B/n) approached around 0.9 (i.e., $B=18$, 45 and 90 for groups of 20, 50 and 100 individuals, respectively), the proportion of continuous reciprocators necessary for invading a population of defectors dropped to below 10% (Fig. 1c). When groups were assortatively formed, the
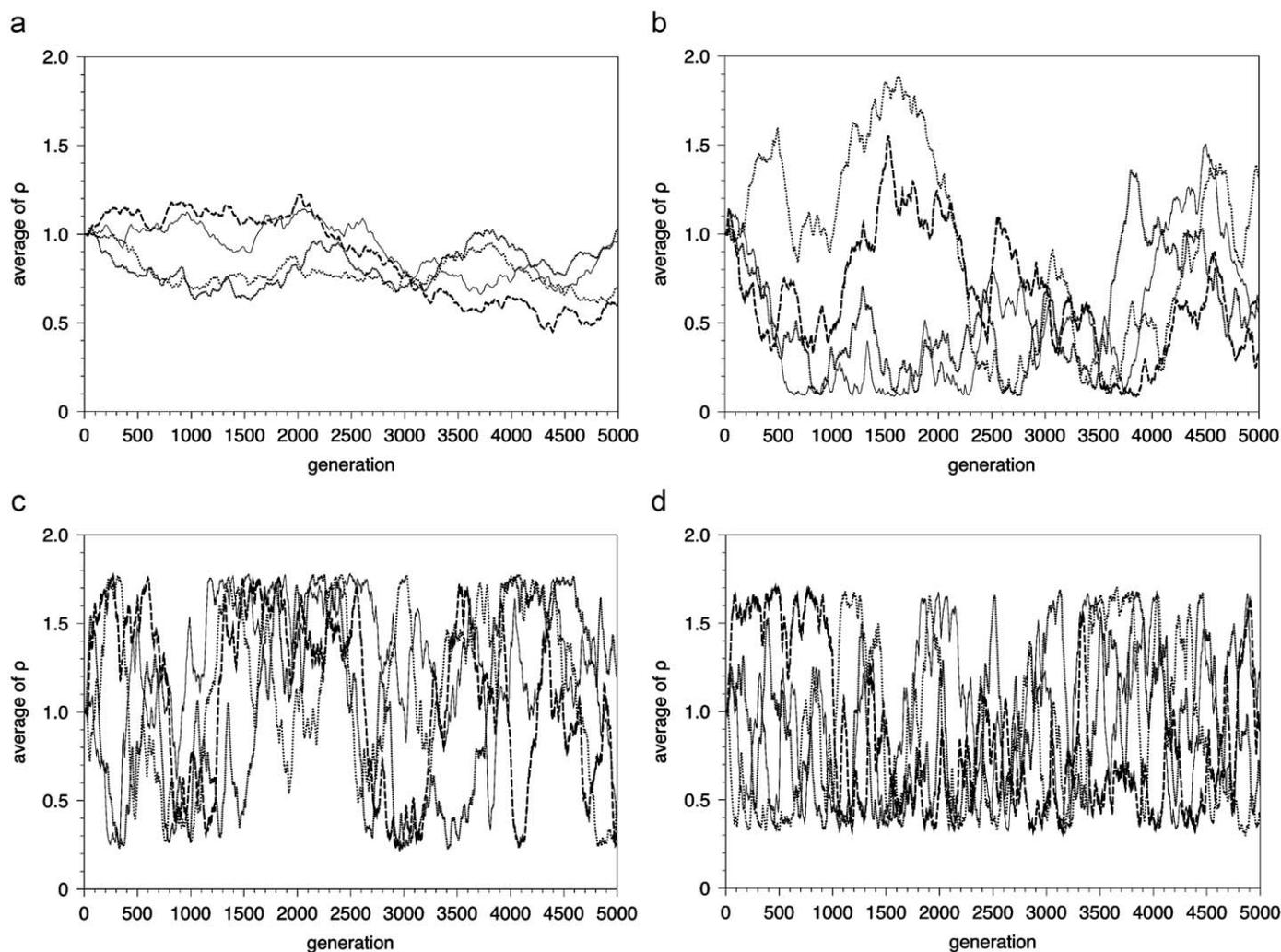
Fig. 6. Evolution of generosity (ρ) in the agent-based computer simulations. For (a) SD=0.002; (b) SD=0.02; (c) SD=0.05; (d) SD=0.07. Each of four lines in the figure represents an independent replication of simulations.

value of B required for continuous reciprocity to invade the population fell significantly (Fig. 1d). For instance, when degree of assortative group formation was fairly weak ($r=1/16$), the proportion of continuous reciprocators necessary for invading the population dropped below 10% when the values of B were around 8, 11, and 12.5 for groups of size 20, 50 and 100, respectively. In both cases with and without assortative interaction, invasion of continuous reciprocity seems to be realistic only in narrow range where the size of the benefit from cooperation comes close to its maximum bound. When the value of the benefit from cooperation was sufficiently large, continuous reciprocity was stable even in a heterogeneous population where strategy space was extended to allow for below- and above-mean reciprocity.

It is important to remember that the value of B indicates the extent to which one unit of contribution by one member benefits the member's entire group. For example, if $B=20$, this means that when one member expends one unit of effort, it produces 20 units of public good for the group. Cooperation may under some extreme circumstances lead to extraordinarily efficient public good provisioning—for example, contributing to the discovery of a new food source during a time of starvation, or helping to build a higher wall in order to defend a village against a large-scale attack. Further, with some public goods, for example public buildings or roads, B tends to increase as n increases, because the total benefit produced often increases with the number of people

who utilize the good. However, it is not clear that such efficient public goods production would have been a realistic aspect of the societies in which human adaptations for reciprocity evolved.

The model presented suggests that continuous reciprocity can evolve in large groups only under a narrow range of circumstances involving unusually high productive efficiency. In this sense, the puzzle of the evolution of large-scale cooperation still remains to be solved. On the other hand, the overall effects of replacing discrete with continuous reciprocity were significant. Future models of the evolution of cooperation should incorporate real-world behavioral regularities that are observed in the context of both cooperation and punishment (e.g., Carpenter, 2007), while still keeping models as simple as possible.

Acknowledgments

Appendix A. When reciprocity is continuous

When more than one R coexists with D in a group, R gradually decreases its contribution because it matches the average contribution made by other group members. When there are m continuous reciprocators and $n-m$ defectors in a group, the contribution made by any R in round i is $z_i = v^{i-1}$ where $v = (m-1)/(n-1)$. Thus in this group, in round i the payoff to R is $B \cdot z_i \cdot m/n - z_i$ and the payoff to D is $B \cdot z_i \cdot m/n$. The expected payoff to D in a group of m R players is $V(D|m) = \sum_{i=1}^{\infty} w^{i-1} \cdot B \cdot z_i \cdot m/n$. $V(R|n)$ is strictly larger than $V(D|n-1)$ when the following condition is satisfied:

$$\frac{B-1}{1-w} > \frac{B(n-1)/n}{1-w(n-2)/(n-1)}$$

because

$$\sum_{i=1}^{\infty} w^{i-1} \cdot z_i = \frac{1}{1-wv}.$$

The expected payoff to R in a group of m R players and $n-m$ D players is

$$V(R|m) = \sum_{i=1}^{\infty} w^{i-1} \cdot B \cdot z_i \cdot m/n - \sum_{i=1}^{\infty} w^{i-1} \cdot z_i.$$

Assuming random group formation, the average payoff to R at the population level is

$$W(R) = W_0 + \sum_{x=0}^{n-1} p(x) \cdot V(R|m = x+1) = W_0 + \sum_{x=0}^{n-1} p(x) \frac{(x+1)B/n - 1}{1 - w \cdot x/(n-1)},$$

where W_0 is the baseline fitness, $p(x)$ is the probability for a focal player to find himself in a group of x other R players and $n-x-1$ other D players given that the proportion of R in a population is p_m;

$$p(x) = \binom{n-1}{x} p_m^x (1-p_m)^{n-1-x}.$$

The average payoff to D is

$$W(D) = W_0 + \sum_{x=0}^{n-1} p(x) \cdot V(D|m = x)$$
$$= W_0 + \sum_{x=0}^{n-1} p(x) \frac{x \cdot B/n}{1 - w(x-1)/(n-1)}.$$

The proportion of R at an internal equilibrium, p_m^* is numerically derived by calculating the value of p_m in the equation, $W(D) = W(R)$. Fig. 1a in the paper illustrates how this value changes as a function of B/n and w when group size is 100.

Appendix B. When groups are assortatively formed

Consider two strategies existing in a population and let $p(x)$ be the probability that a focal player will find himself in a group of x players of the same strategy and $n-x-1$ players of the other strategy. When the proportion of a focal strategy in a population is p,

$$p(x) = \binom{n-1}{x}(r + (1-r)p)^x \{(1-r)(1-p)\}^{n-1-x}.$$

In this equation, r is a parameter, ranging from zero to one, determining the degree of assortative interaction; groups are randomly formed when $r = 0$. Here, r plays the same role as Hamilton's kinship coefficient (Hamilton, 1964) and even unconditional cooperation can evolve when $\{(n-1)r+1\}B/n > c$, which is called the inclusive fitness effect (Hamilton, 1975). When $r > 0$, of particular interest is the situation in which this equation

does not hold, and unconditional cooperation can therefore not evolve.

We analyzed the influence of the assortative interactions in two different ways: invasion analysis and basin of attraction analysis. First, we investigated a situation where an invading strategy is very rare. Assume that p is the proportion of a rare invading strategy in a population. As p approaches 0, the above mentioned probability $p(x)$ approaches to and is approximated by

$$\binom{n-1}{x} r^x (1-r)^{n-1-x}.$$

When D is common in the population, the fitness of a rare invading R is obtained by recalculating $W(R)$ in the Appendix A after replacing $p(x)$ with the new value derived in this section. As the average fitness of the common strategy D is equal to the baseline population fitness W_0, R can invade the population when $W(R) > W_0$. The threshold value of the number of interactions that must be exceeded by R in Fig. 2 in the paper was derived by numerically solving this equation given that the other parameters were fixed. The threshold value for T was calculated in the same manner given that $W(T) = W_0 + \sum_{x=0}^{n-1} p(x) \cdot V(T|m = x+1)$ where $V(T|m = x+1)$ is $(x+1)B/n-1$ when $x < n-1$ and $((x+1)B/n-1)/(1-w)$ when $x = n-1$.

Second, we investigated a situation in which the proportion p of an invading strategy takes any value other than zero. Fig. 1b and 1d in the paper show the results of this analysis.

Appendix C. When an unconditional cooperator (C) exists

When the three strategies R, C and D coexist in a group, the contribution made by any R player in round i is

$$z_i = v^{i-1} + s \cdot \sum_{j=1}^{i-1} v^{j-1} = v^{i-1} + s(1 - v^{i-1})/(1-r)$$

where $v = (m-1)/(n-1)$, $s = k/(n-1)$, and m and k are the number of R and C players in the group, respectively. Thus, the average payoff to R in a group of m R and k C is

$$V(R|m,k) = \sum_{i=1}^{\infty} w^{i-1} \cdot B \cdot z_i \cdot m/n + \sum_{i=1}^{\infty} w^{i-1} \cdot B \cdot k/n - \sum_{i=1}^{\infty} w^{i-1} \cdot z_i.$$

Likewise, the average payoffs to C and D in the same group are

$$V(C|m,k) = \sum_{i=1}^{\infty} w^{i-1} \cdot B \cdot z_i \cdot m/n + \sum_{i=1}^{\infty} w^{i-1} \cdot B \cdot k/n - \sum_{i=1}^{\infty} w^{i-1},$$

and

$$V(D|m,k) = \sum_{i=1}^{\infty} w^{i-1} \cdot B \cdot z_i \cdot m/n + \sum_{i=1}^{\infty} w^{i-1} \cdot B \cdot k/n,$$

respectively. Hence, the average payoffs to R, C, and D in a population are

$$W(R) = W_0 + \sum_{x=0}^{n-1} \sum_{y=0}^{n-1-x} p(x,y) \cdot V(R|m = x+1, k = y),$$

$$W(C) = W_0 + \sum_{x=0}^{n-1} \sum_{y=0}^{n-1-x} p(x,y) \cdot V(C|m = x, k = y+1),$$

and

$$W(D) = W_0 + \sum_{x=0}^{n-1} \sum_{y=0}^{n-1-x} p(x,y) \cdot V(D|m = x, k = y),$$

where $p(x,y)$ is the probability of finding x R and $y = n-1-x$ C in a group given that the proportion of R and C in a population is p_m and p_k, respectively. In general, the probability that a focal player

of a strategy s_1 will find himself in a group of j s_1 players, k s_2 players and $n-x-1$ s_3 players is $p(j,k) = (j,k,n-1)!(r+(1-r)p_1)^j \{(1-r)p_2\}^k \{(1-r)(1-p_1-p_2)\}^{n-1-j-k}$ given that the proportion of s_1 and s_2 in a population are p_1 and p_2 and that the degree of assortative interaction is r.

When reciprocity is discrete (T_{n-1}), the average payoffs to T_{n-1}, C and D in a group of x T_{n-1} and y C are

$$V(T_{n-1}|m,k) = \sum_{i=1}^{\infty} w^{i-1} \left\{ \frac{B \cdot (m+k)}{n} - 1 \right\}, \quad \text{when } n = m+k,$$

$$V(T_{n-1}|m,k) = \frac{B \cdot (m+k)}{n} - 1 + \sum_{i=2}^{\infty} w^{i-1} \frac{B \cdot k}{n}, \quad \text{when } n > m+k,$$

$$V(C|m,k) = \sum_{i=1}^{\infty} w^{i-1} \left\{ \frac{B \cdot (m+k)}{n} - 1 \right\}, \quad \text{when } n = m+k,$$

$$V(C|m,k) = \frac{B \cdot (m+k)}{n} - 1 + \sum_{i=2}^{\infty} w^{i-1} \left(\frac{B \cdot k}{n} - 1 \right), \quad \text{when } n > m+k,$$

and

$$V(D|m,k) = \frac{B \cdot (m+k)}{n} + \sum_{i=2}^{\infty} w^{i-1} \frac{B \cdot k}{n},$$

respectively. The average payoffs to the three strategies in a population are derived in the same manner as when reciprocity is continuous.

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