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ASSORTMENT AND THE EVOLUTION OF GENERALIZED RECIPROCITY

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Reciprocity is often invoked to explain cooperation. Reciprocity is cognitively demanding and both direct and indirect reciprocity require that individuals store information about the propensity of their partners to cooperate. By contrast, generalized reciprocity, wherein individuals help on the condition that they received help previously, only relies on whether an individual received help in a previous encounter. Such anonymous information makes generalized reciprocity hard to evolve in a well-mixed population, as the strategy will lose out to pure defectors. Here we analyze a model for the evolution of generalized reciprocity, incorporating assortment of encounters, to investigate the conditions under which it will evolve. We show that, in a well-mixed population, generalized reciprocity cannot evolve. However, incorporating assortment of encounters can favor the evolution of generalized reciprocity in which both indiscriminate cooperation and defection are both unstable. We show that generalized reciprocity can evolve under both the prisoner's dilemma and the snowdrift game.

KEY WORDS: Cooperation, direct reciprocity, population viscosity, relatedness, spatial structure.

Reciprocity has long been invoked as a mechanism to explain the evolution of cooperation between unrelated individuals (Trivers 1971). Direct reciprocity, in the form of tit-for-tat, can lead to the evolution of cooperative behaviors when individuals return one favor with another (Axelrod and Hamilton 1981). Reciprocity can also come in the form of indirect reciprocity (Nowak and Sigmund 1998b, 2005), in which individuals cooperate with other individuals that they have previously seen engaging in cooperation with others (Nowak and Sigmund 2005). Both direct and particularly indirect reciprocity require highly advanced cognitive abilities (Milinski and Wedekind 1998; Dugatkin 2002; Stevens et al. 2005), in which individuals must recognize a cooperating individual, and use this information to act accordingly. As such, it has been argued that direct and indirect reciprocity will be limited to animals with more advanced cognitive powers (Pfeiffer et al. 2005; Stevens et al. 2005).

By contrast, generalized reciprocity (Hamilton and Taborsky 2005; Pfeiffer et al. 2005; Rutte and Taborsky 2007), in which an individual cooperates if it has experienced cooperation, only relies on information from the previous interaction, regardless of the identity of the partner, and therefore hardly requires sophisticated cognitive abilities. Also known as "upstream indirect reciprocity" (Nowak and Roch 2007), generalized reciprocity is much less likely to evolve in a well-mixed population than other forms of reciprocity that involve the use of more complicated information (such as reputation, in the case of indirect reciprocity). This has been illustrated by previous models, which suggested that generalized reciprocity could only evolve either in small groups (Pfeiffer et al. 2005), in combination with group leaving strategies (Hamilton and Taborsky 2005), or on a one-dimensional lattice in connection with direct reciprocity (Nowak and Roch 2007).

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Reciprocity can evolve by increasing the probability that a helpful behavior will be returned at some point in the future. As such, it is obvious that generalized reciprocity will not incur any feedback as a result of the behavior in a large, well-mixed population. However, Pfeiffer et al. (2005) showed that generalized reciprocity could only evolve in small groups. It has also been shown that simple one-dimensional spatial structure, with interactions only occurring between two neighboring individuals, could allow generalized reciprocity to invade (Nowak and Roch 2007). In their model, Nowak and Roch (2007) described a situation in which a focal individual would return an act of help to a neighbor to the left or right with a probability of $\frac{1}{2}$, respectively. This situation meant that a cooperating individual would have an act of helping reciprocated with a 50% probability.

In well-mixed populations, the relatedness between interacting individuals approaches zero (West et al. 2002), whereas when there is some form of nonrandom assortment, relatedness between interacting individuals becomes positive. Spatial structure and relatedness between interacting individuals have both been shown to promote the evolution of cooperation, as well as forms of reciprocity, by increasing interactions between genetically similar individuals (Queller 1985; Axelrod et al. 2004; Santos et al. 2006). If interactions between individuals are local and competition is global, cooperative strategies can invade (West et al. 2001; Griffin et al. 2004; Pfeiffer et al. 2005). Assortment is likely to favor the evolution of generalized reciprocators. Generalized reciprocators who have experienced cooperation in the past will reciprocate by indiscriminately cooperating with the next individual they meet. When there is assortment between similar strategies, it is more likely than random that ones partner will be another generalized reciprocator, rather than an indiscriminate defector.

Here we investigate whether assortment between strategies can favor the evolution of generalized reciprocity. Our model examines two classic payoff-matrices, the prisoner's dilemma and the snowdrift game (Doebeli and Hauert 2005). We incorporate the degree of assortment between strategies into our model. This allows us to look at a continuum of different degrees of assortment, ranging from a completely mixed population to full assortment between strategies. We analyze the model to investigate the conditions under which generalized reciprocity will invade, and be immune to the invasion of, unconditional cooperators and defectors.

Model and Results

GAME STRUCTURE AND PAYOFFS

We start with an infinite population composed of individuals with three strategies: pure cooperators (which always invest in cooperation), pure defectors (which never invest in cooperation), and generalized reciprocators (which either help if they have been helped in the previous round, or do not help if they did not receive help in the previous round). We denote the frequency of cooperators as x, defectors as y, and generalized reciprocators as z. Generalized reciprocators cooperate on the condition that they have received cooperation in their last encounter, and will defect (not cooperate) conditionally on experiencing defection in their previous encounter. Thus, at any given time, a generalized reciprocator can be either in a cooperative (helping) or a defecting (nonhelping) state. We use a simple method from Eshel and Cavalli-Sforza (1982) to incorporate assortment among strategies into our model. This degree of assortment is given by the parameter v and, when positive, can be described as the probability of a given individual to interact with one's own strategy. As such, the probability K that a given strategy interacts with it's own type (of frequency k) can be described as $K = v + k(1 - v)$, and the probability, K', that a strategy interacts with a given other strategy (of frequency k') is $K' = k'(1 - v)$. Interactions are random when $v = 0$. When $v > 0$, an individual interacts with its own type more often than it would if interactions were random, and when $v < 0$ an individual is more likely to interact with strategies different to it's own than it would if interactions were completely random. Here we only consider the (most plausible) case where $v \geq 0$. It should be noted that our way of calculating assortment is the same as the regression definition of relatedness (Hamilton 1970; Grafen 1985; Frank 1998).

We assume that, in each round, every player interacts with another, random player. As such, generalized reciprocators in our model represent a distinctive strategy from direct reciprocators, as they do not interact subsequently with the same individuals, and cooperation is based purely on the actor's prior experience, and not on one's experience with, or the reputation of, one's partner. We denote the frequency of reciprocators in the population that are in a helping state (i.e., they have experienced cooperation in the previous round) in round n as $z_C(n)$, and the frequency of reciprocators in the population that are in a state of defection (i.e., they experienced defection in the previous round) in round n as $z_D(n)$ (where $z_C(n) + z_D(n) = z$). In the first round, generalized reciprocators will cooperate with a probability a (and therefore defect with a probability $1-a$). The frequency of reciprocators in the population that are in a cooperating state in round n is (see Appendix 1):

$$z_C(n) = \frac{z(x - (x - a(1 - z))(v + z(1 - v))^n)}{1 - z}, \qquad (1)$$

and the frequency of reciprocators in the population which are in a defecting state in round n is $z_D(n) = z - z_C(n)$. In this analysis, we consider a to be a fixed parameter that does not evolve. We assume an infinite population size and track only the frequency of the three respective strategies in the population.

From the above frequencies, we can calculate the payoff for each strategy. We assume that, in each round, individuals behave as both an actor (and may potentially give help by cooperating, depending on which strategy they play) and as a recipient. As we assume a large population size, no two individuals interact together more than once in their lifetime. Thus, each partner is a stranger. Following a similar approach to Nowak & Sigmund (1998a,b), we assume that each generation lasts for a certain number of rounds, and that, after each round, the game will continue to another round with a probability w (Axelrod and Hamilton 1981). The expected number of rounds in a game is given as $1/(1-w)$. The total payoff for strategy i is $P_{i,total} = \sum_{n=0}^{\infty} w^n P_i(n)$. Full details of how the total payoffs to each strategy are derived are given in Appendix 2. As the proportion of generalized reciprocators in a cooperative or defective state changes after each round, the separation between evolutionary and behavioral time-scales depends on w. We have, however, checked the results of our model for the case where the number generalized reciprocators in a cooperative or defective state has reached the equilibrium proportion $\hat{z}_C \equiv z_C(\infty)$ and $\hat{z}_D(\infty) \equiv z_D(\infty)$, respectively. This assumes that the behavioral state of generalized reciprocators (i.e., whether they are in a cooperative or defective state) equilibrates very quickly, relative to the evolutionary dynamics. Under this assumption, we were able to derive exactly identical results to the model with a random number of rounds, supporting the robustness of our approach (see Appendix 3 for details).

The dynamics of strategy i with frequency $q_i(t)$, at time t, changes according to the replicator equation $q_i(t+1) = \frac{q_i(t)P_{i,total}}{\bar{P}_{total}}$, where $\bar{P}_{total}$ is the average payoff in the population, and is equal to $\bar{P}_{total} = q_x(t)P_{x,total} + q_y(t)P_{y,total} + q_z(t)P_{z,total}$. Examples of these dynamics are given in Figure 1. We wish to find the conditions under which generalized reciprocity is an evolutionary stable strategy (ESS), and immune to invasion from other strategies. This occurs if generalized reciprocators are both an ESS with respect to pure cooperators (i.e., $P_{z,total} > P_{x,total}$ when $z = 1$ $y = 0$, $x \to 0$ and $P_{z,total} > P_{x,total}$ when $x = 1$, $y = 0$, $z \to 0$) and an ESS with respect to pure defectors (i.e., when $P_{z,total} > P_{y,total}$ when $x = 0$, $y = 1$, $z \to 0$ and $P_{z,total} > P_{y,total}$ when $z = 0$, $x = 0$, $y \to 0$). Full details of how we calculate the ESS are given in Appendix 2.

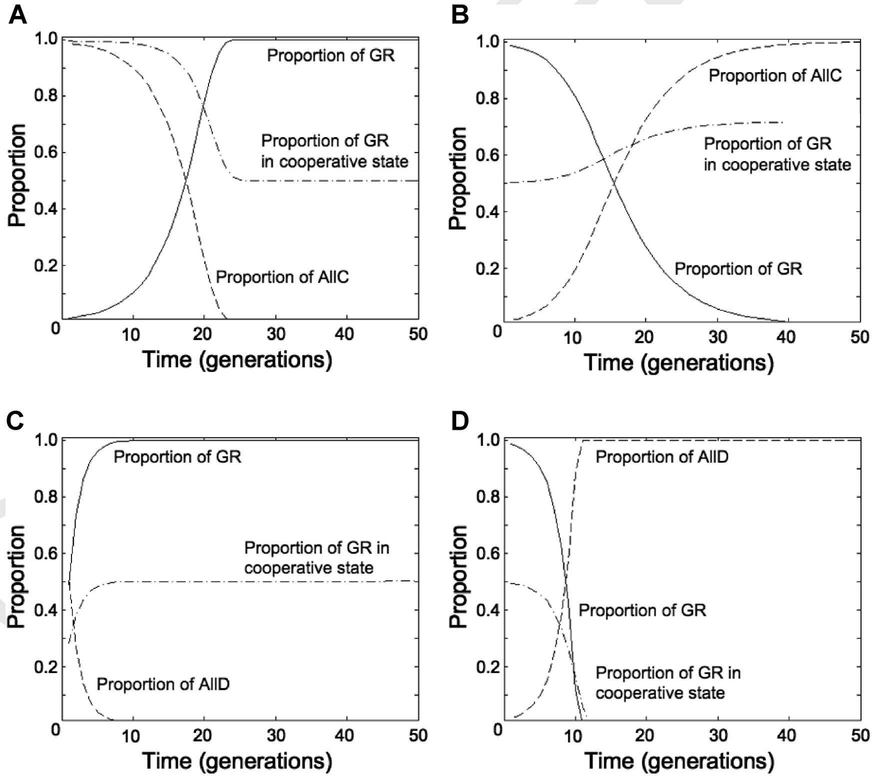

Figure 1. **Replicator dynamics of invasion of generalized reciprocity under a prisoner's dilemma payoff matrix ($R = b - c + d$, $T = b$, $S = -c$, $P = 0$). (A) Invasion of generalized reciprocators (GR) into a population of unconditional cooperators (AllC) where $v = 0.1$; (B) invasion of AllC into a population of GR when $v = 0.75$; (C) invasion of GR into a population of unconditional defectors (AllD) when $v = 0.75$; (D) invasion of AllD into a population of GR when $v = 0.25$. The proportion of generalized reciprocators at the end of each generation (i.e., which is at round $n = 1/(1-w)$, on average), which are in a state of cooperation, is given by the dotted-dashed line. Other parameters are $b = 2$, $c = 1$, $d = -0.1$, $a = 0.5$, and $w = 0.5$. Starting values for the simulation were (A) $x = 0.99$, $y = 0$, $z = 0.01$; (B) $x = 0.01$, $y = 0$, $z = 0.99$; (C) $x = 0$, $y = 0.99$, $z = 0.01$; and (D) $x = 0$, $y = 0.01$, $z = 0.99$.**

Table 1. Invasion criteria for generalized reciprocity (GR) with respect to pure defectors (AllD) and pure cooperators (AllC) for two payoff matrices.

	Prisoner's dilemma matrix (T=b, S=$-c$, P=0, R=$b-c+d$)	Snowdrift matrix (T=b, S=$b-c$, P=0, R=$b-c/2$)
GR can invade population of AllD	$\frac{c-bv}{1-vw}-\frac{adv}{1-v^2w}<0$	$\frac{2(b-c+bv)}{1-vw}-\frac{av(2b-c)}{1-v^2w}>0$
GR are immune to invasion from AllD	$bv>c-da$	$2b(1-a+v)-c(2-a)>0$
GR can invade population of AllC	$c+v^2\,w(ad+v\,(b+d)-c)-d>0$	$\frac{c(2-a-v)}{2(1-a)}>b$
GR are immune to invasion from AllC	$c-d(a+v)>bv$	$\frac{c(1-av-v^2(2-v-a)w)}{2(1-a)v(1-vw)}>b$
GR ESS and immune to invasion overall	$c-da<bv<c-d(a+v)$	$\frac{c(2-a)}{2(1-a+v)}<b<\frac{c(2-a-v)}{2(1-a)}$

ASSORTMENT IS NEEDED FOR BOTH EVOLUTIONARY AND CONVERGENT STABILITY

From these invasion criteria (see Appendix 2, equations A5–A8), we can investigate whether generalized reciprocity will be an ESS when there is no assortment among strategies and the population is completely mixed. In this case, $v = 0$ and all strategies will interact equally. Generalized reciprocators will be able to invade, and be immune to invasion from pure defectors (derived from equations A5–A6 in Appendix 2) if $S > P$, and either $T < R$ or both $T \geq R$ and $a < \frac{P-S}{P-S+R-T}$. On the other hand, generalized reciprocators will be able to invade, and be immune to invasion from, pure cooperators (derived from equations A7–A8 in Appendix 2) if $T > R$ and either $P \geq S$ or both $S > P$ and $a > \frac{P-S}{P-S+R-T}$. Therefore, it is not possible that generalized reciprocity can be evolutionarily stable against *both* pure defectors and pure cooperator if there is no assortment (i.e., when $v = 0$). This means that, under any payoff structure, generalized reciprocity cannot invade, and remain stable, in a completely mixed population.

SPECIFIC PAYOFF MATRICES

We now can investigate the evolution of generalized reciprocity under specific payoff matrices. Full equations, for both a prisoner's dilemma payoff matrix ($T = b$, $S = -c$, $P = 0$, and $R = b - c + d$, which satisfies the conditions where $T > R > P > S$) and a snowdrift payoff matrix ($T = b$, $S = b - c$, $P = 0$, and $R = b - c/2$, which satisfies the conditions $T > R > P > S$) are given in Table 1. Here b represents the benefits conferred upon a social partner by cooperating, and c is the cost of cooperating. The parameter d, in the prisoner's dilemma, determines whether the payoff matrix is additive when $d = 0$ or nonadditive when $d \neq 0$ (Fletcher and Zwick 2006). If $d > 0$, we have a positive synergy of mutual action (such as in which the benefits of mutual cooperation are more than acting on one's own: Queller 1985) and if $d < 0$ we have a negative synergy of mutual action (such as diminishing returns from mutual cooperation).

If $d = 0$ or $d > 0$, there is no condition under which generalized reciprocity is evolutionarily stable with respect to both pure cooperation and pure defection under a prisoner's dilemma payoff matrix. When there is negative synergy in mutual cooperation (i.e., $d < 0$), generalized reciprocity is an ESS (i.e., it is immune to invasion) and cannot be invaded, against both pure cooperators and defectors if

$$c - da < bv < c - d(a + v).$$

This means that $v > 0$, $0 < a < 1$, and $d < 0$ are all required for generalized reciprocity to both invade a population of pure cooperators or defectors and be immune to invasion from pure cooperators or defectors. If $a = 1$, then generalized reciprocators cooperate on the first round, and behave the same when invading a population of cooperators, or when being invaded by a population of cooperators. Similarly, if $a = 0$, then generalized reciprocators will behave identically to defectors when invading a population of defectors. Thus, if $a = 1$ or $a = 0$, then generalized reciprocity will be identical to, and hence neutrally stable with respect to, pure cooperators or pure defectors, respectively. Figure 2 plots the conditions for generalized reciprocity to be an ESS for either weak negative synergy ($d = -0.25$, Fig. 2A) or stronger negative synergy ($d = -1$, Fig. 2B).

Generalized reciprocity will be a be an ESS, and be immune to invasion from either pure defectors of pure cooperators, under a snowdrift payoff if

$$\frac{c(2-a)}{2(1-a+v)} < b < \frac{c(2-a-v)}{2(1-a)},$$

which, as for the prisoner's dilemma, requires that $v > 0$ and $0 < a < 1$. The criteria for generalized reciprocity to be evolutionarily stable under a snowdrift game are shown in Figure 3. From these inequalities we can see that, when a (the probability of cooperating in the first round) is low ($a = 0.2$, Fig. 3A), the conditions for

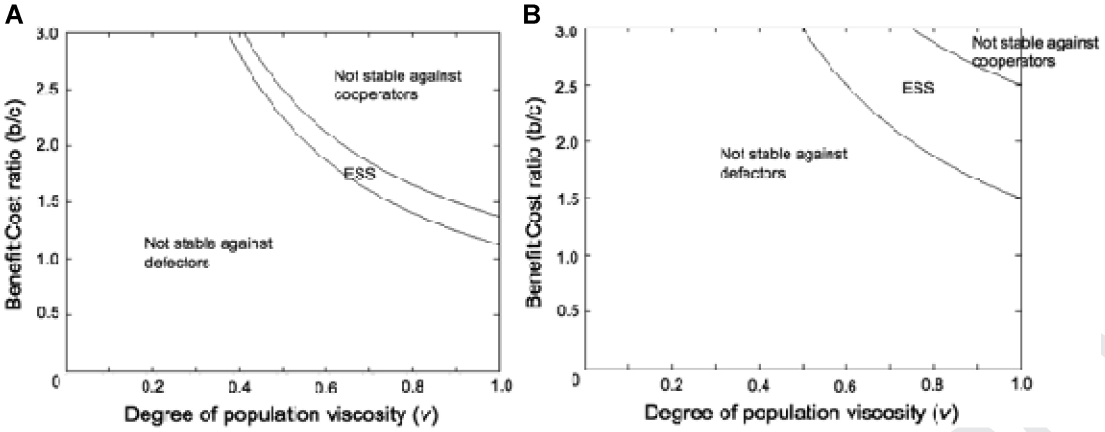

Figure 2. Contour plot showing the regions where generalized reciprocators are evolutionarily stable, and when they can be invaded by pure cooperators or pure defectors, under a prisoner's dilemma payoff matrix ($R = b - c + d$, $T = b$, $S = -c$, $P = 0$). Parameters used are $c = 1$ and $a = 0.5$. In (A) $d = -0.25$ and (B) $d = -1$.

generalized reciprocity to be an ESS are more stringent than when a is high ($a = 0.8$, Fig. 3B). In other words, cooperating in the first round gives generalized reciprocators a larger benefit over both unconditional cooperators and defectors.

Discussion

Our results confirm that generalized reciprocity cannot evolve in the absence of population assortment (Figs. 2 and 3, when $v = 0$). This is because, in a well-mixed population, generalized reciprocity will indiscriminately confer benefits on strangers who will not necessarily return an act of cooperation. When we include some degree of assortment, we find that generalized reciprocity can invade and can be immune to invasion from pure defectors (Fig. 1).

Our results show that it is possible for generalized reciprocity to be a true ESS in both a snowdrift (Fig. 3) and prisoners dilemma (Figs. 1 and 2) game. The fact that generalized reciprocity can evolve under both payoff matrices is significant, as comparisons have been made between them in terms of the level of cooperation (Kümmerli et al. 2007). Under a prisoner's dilemma matrix, however, generalized reciprocity is only evolutionarily stable if there is negative synergy in the prisoner's dilemma matrix (i.e., when $d < 0$). In this case, generalized reciprocity can be an ESS as long as there is, importantly, a critical degree of assortment between strategies (see Fig. 2). In the absence of negative synergy (i.e., $d \geq 0$), generalized reciprocity is not a true ESS as the conditions under which it will invade a population of defectors simultaneously make it susceptible to invasion by pure cooperators, and vice versa. Negative synergy comes about in a prisoner's dilemma

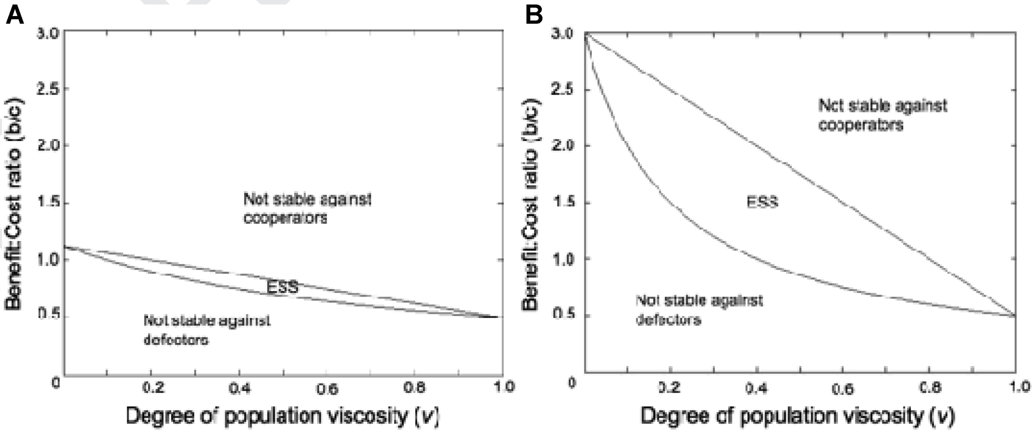

Figure 3. Contour plot showing the regions where generalized reciprocators are evolutionarily stable, and when they can be invaded by pure cooperators or pure defectors, under a snowdrift payoff matrix ($R = b - c/2$, $T = b$, $S = b - c$, $P = 0$). Parameters used are $c = 1$. In (A) $a = 0.2$ and (B) $a = 0.8$.

when the overall gain from mutual cooperation is less than the overall investment of both partners (i.e., there are diminishing returns from mutual cooperation). For example, collaborating on a scientific paper with a co-author (as opposed to working as the sole author) reduces the workload significantly, but there is a baseline level of investment by both partners in terms of discussions and proofreading. In the case of scientific collaboration, there is a clear reward from collaborating compared to sole authorship, but negative synergy arises because collaborating does not necessarily correspond to halving the time on a co-authored paper compared to writing the whole thing alone. In their classic work on direct reciprocity, Axelrod and Hamilton (1981) assumed negative synergy in their prisoner's dilemma matrix (where $R = 3$, $T = 5$, $S = 0$, and $P = 1$, which corresponds to each individual has a base-line fitness of 1 and the payoffs being $b = 4$, $c = 1$, and $d = -1$: Axelrod and Hamilton 1981; Axelrod 1984; Fletcher and Zwick 2006). Diminishing returns in payoffs from cooperation are widespread in nature, as shown for instance in group vigilance (Roberts 1996) or group size effects on group productivity in social insects and cooperatively breeding vertebrates (Michener 1964; Stacey and Koenig 1990; Balshine et al. 2001; Foster 2004).

The benefits of generalized reciprocity come from receiving a benefit as a result of a feedback from the cost paid by investing in cooperation. This comes from interacting with one's own strategy with a higher probability than would occur if interactions were completely random. Such assortment can come about in various ways. The most obvious is population viscosity and spatial structure in which strategies are more likely to be assorted with one another (Hamilton 1971; Nowak and May 1992; Le Galliard et al. 2003; Taylor et al. 2007; Lion and van Baalen 2008). In this case, assortment will depend on the demography of the species (which in turn will be affected by the average outcome of social interactions, through the affect on births, deaths, and dispersal). For example, limited dispersal increases the chance that related individuals are aggregated, and hence that they interact with each other. However, limited dispersal also increases competition between relatives, and so the benefit of viscosity can cancel out (Taylor 1992). Although there has been some debate as to the effect of population viscosity on the evolution of cooperative behaviors, if competition is global, but interactions are more local (as is the case when $v > 0$ in our model), then cooperative behaviors such as reciprocity will be favored (West et al. 2002). Although spatial structure is ubiquitous in nature, global competition is not always the norm, and competition between relatives can be common (West et al. 2001, 2002). Local interactions, in combination with global competition, can come about if helping occurs before dispersal, meaning that strategies will initially be assorted (and will often share common descent; Hamilton 1964), but the level of assortment will later be reduced due to mixing through dispersal (West et al. 2002). Assortment in our model can come about through simple assortment between nonrelatives, although kin structure is likely to be a common cause of this assortment. In fact, our parameter for nonrandom assortment v is equivalent to relatedness r (Hamilton 1964), and as we assume that our strategies have a genetic basis, any form of positive assortment will result in a positive value of r. The level of assortment may vary between strategies—for example, cooperators may be less likely to disperse than noncooperators and this would result in different levels of assortment between strategies. However, as long as generalized reciprocators were more assorted than other strategies, we expect them to gain an advantage by directing cooperation towards other reciprocators.

Another way in which assortment between reciprocators can arise is by discriminately favoring reciprocators over other individuals (e.g., Bernhard et al. 2006). This can occur through green-beard mechanisms (Hamilton 1964; Dawkins 1976; Keller and Ross 1998; Jansen and van Baalen 2006), in which the reciprocating strategy is marked in some way, making it recognizable to other reciprocators. Such recognition results in individuals with the green beard being associated with one another, and thus facilitates assortment (Jansen and van Baalen 2006). However, such systems have been shown to be rather unstable, and susceptible to individuals displaying "recognition traits" without cooperating (Gardner and West 2007; Rousset and Roze 2007).

Previous models of generalized reciprocity have all incorporated some form of assortment between strategies. For example, Pfeiffer et al. (2005) showed that generalized reciprocity was only evolutionarily stable in small groups. Interacting in small groups increases the probability that two individuals will interact more than once, and the probability that two generalized reciprocators will meet again, when rare, will therefore be higher. This will then increase the benefit to generalized reciprocators. In a model incorporating contingent movement (i.e., cooperative individuals can leave a group if they experience defection), Hamilton and Taborsky (2005) found that generalized reciprocators that defected or left a group after experiencing defection were favored. If cooperative individuals leave a group to join a new group as a consequence of defection, groups composed of mostly generalized reciprocators will eventually form as a result. This would create assortment between strategies, and thus, as the current model suggests, increase the feedback gained from cooperating (Sachs et al. 2004). Nowak and Roch (2007) modeled generalized reciprocity on a one-dimensional lattice in which individuals were constrained to only interact with their two closest neighbors, creating very strong assortment between reciprocators and increasing the chance that a helpful act would be reciprocated. An additional constraint of their model was that it did not allow for acts of defection to be passed on and reciprocated, so only cooperative acts could be passed on and reciprocated. In contrast to this, in our model generalized reciprocity is capable of passing on both cooperative and noncooperative acts to social partners. Our model builds on these results by showing that in the absence of any assortment between strategies, regardless of the payoff structure, it is impossible for generalized reciprocity to evolve because it is prone to invasion by either indiscriminate cooperators or defectors. We have explicitly shown that when there is some assortment between strategies, generalized reciprocity can evolve, which has only been implied by results obtained under more specific conditions in previous models (Hamilton and Taborsky 2005; Pfeiffer et al. 2005; Nowak and Roch 2007).

Arbitrary cues can also be used to stabilize cooperation (e.g., Hammond and Axelrod 2006), and could work with generalized reciprocity. However, we wish to emphasize that the importance of generalized reciprocity will be greatest under limited information. It has recently been shown that generalized reciprocity can be maintained if it exists in a population containing direct reciprocators, which play "tit-for-tat" (Nowak and Roch 2007). However, this model (Nowak and Roch 2007) ignores the potentially large cognitive costs of memory involved in direct reciprocity (Milinski and Wedekind 1998; Stevens et al. 2005). These costs arise because direct reciprocators must not only remember the outcome of a larger number of previous encounters, but also remember which individuals those encounters were with. Although direct reciprocity will invariably be a more favored strategy due to the ability to remember and reciprocate a cooperative act to the original donor (Rutte and Taborsky 2008), costs involved in memory and recognition may be strong enough to hinder the evolution of direct reciprocity (F. Eggimann, unpubl. MSc. thesis). If costly information prevents the evolution of cognitively complex strategies, such as direct or indirect reciprocity, the only way that generalized reciprocators will be able to gain a benefit from reciprocating (and therefore evolve) is through disproportionately interacting with other generalized reciprocators. As our model shows, this can come about through assortment.

According to the "hierarchical information hypothesis" (Rutte and Taborsky 2008), generalized reciprocity should apply when no specific information about the propensity for cooperation is available for a social partner. This limitation may have different origins, among them being a lack of previous individual experience and a constraint in cognitive abilities or memory. Under complete spatial assortment, generalized reciprocity will become indistinguishable from direct reciprocity: in groups of two individuals, for instance, generalized reciprocity will behave the same way as tit-for-tat (Pfeiffer et al. 2005). As generalized reciprocity requires less information than direct reciprocity, it may be more common, as it will be applicable to a greater variety of situations and a wider range of organisms. This maybe especially important due to the fact that memory and individual learning mechanisms may be associated with fitness costs (Mery and Kawecki 2002; Rouder et al. 2008).

Generalized reciprocity has been repeatedly shown in studies involving humans (Berkowitz and Daniels 1964; Isen 1987), in which it is often referred to as gratitude (e.g., Bartlett and DeSteno 2006). Generalized reciprocity has often been neglected in empirical studies (Rutte and Taborsky 2007, 2008). Studies that set out to test for direct reciprocity between individuals usually fail to test for generalized reciprocity. However, generalized reciprocity has been found to work in Norway Rats (Rutte and Taborsky 2007) and we think it is safe to assume that it may be much more common than previously thought (Trivers 1971), and therefore requires future experimental scrutiny. Given that little information from previous social encounters and only very limited cognitive ability are a needed for generalized reciprocity to work, our results suggest that it could be a common phenomenon. As such, generalized reciprocity is reminiscent of winner and loser effects, which are also based on anonymous information from previous encounters and are extremely widespread in animals (Hsu et al. 2006; Rutte et al. 2006).

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Appendix 1

DERIVATION OF STATE OF GENERALIZED RECIPROCATORS $z_C(n)$

We first calculate the frequency of reciprocators in each round that are in a cooperating state ($z_C(n)$) and the frequency of those that are in a defecting state ($z_D(n)$). If an individual reciprocator has experienced cooperation in the previous round, it will become a cooperator in the current round, whereas if it has experienced defection in the previous round it will become a defector in the current round. The probability that a reciprocator begins the game by cooperating in the first round is given by a. Thus, the frequencies of cooperating reciprocators and defecting reciprocators in the first round are $z_C(0) = za$ and $z_D(0) = z\,(1 - a)$, respectively. We can now look at the proportion of reciprocators that will either be in a state of cooperation or defection in the nth round. We now introduce v, the degree of assortment between strategies.

The probability that a given individual will interact with it's own strategy is $v + k(1 - v)$ (where k is the frequency of its own strategy) and the probability that it will interact with a given other strategy is $k'(1 - v)$ (where k' is the frequency of the strategy in question). The proportion of reciprocators that cooperate in round $n + 1$ is:

$$\begin{aligned} z_C(n+1) = {} & z_C(n)z_C(n)(v + z(1-v))/z \\ & + z_C(n)z_D(n)(v + z(1-v))/z \\ & + z_C(n)x(1-v) + z_D(n)x(1-v) \qquad \text{(A1)} \end{aligned}$$

This equation deals with the overall proportion of generalized reciprocators that are in a state of cooperation in the population, and so we divide the first two terms on the right-hand side by z, as $z_C(n) + z_D(n) = z$. The proportion of reciprocators that defect in round $n + 1$ is $z_D(n + 1) = z - z_C(n + 1)$.

By expanding and simplifying equation A1 (and, as $x + y + z = 1$, we can write $y = 1 - x - z$), we obtain:

$$z_C(n+1) = z_C(n) + z(1-v)(x - a(1-z))(v + z(1-v))^{n-1},$$

which we can then re-write as:

$$z_C(n) = az + \sum_{N=1}^{n} (1-v)(x - a(1-z))(v + z(1-v))^{N-1}. \qquad \text{(A2)}$$

The second term on the right-hand side can be written as

$$\sum_{N=1}^{n} (1-v)(x - a(1-z))(v + z(1-v))^{N-1} = \frac{z(x - a(1-z))(1 - (v + z(1-v))^n)}{1-z}.$$

Substituting this into equation (A2) gives us

$$z_C(n) = az + \frac{z(x - a(1-z))(1 - (v + z(1-v))^n)}{1-z},$$

which simplifies to

$$z_C(n) = \frac{z(x - (x - a(1-z))(v + z(1-v))^n)}{1-z}. \qquad \text{(A3)}$$

Appendix 2

DERIVATION OF INVASION CRITERIA

We can now calculate the payoff of the respective strategies in round n (see text for exact details of payoff structure). We then obtain the following payoffs for round n:

$$\begin{aligned} P_x(n) = {} & Sy(1-v) + R(v + x(1-v)) + Rz_C(n)(1-v) \\ & + Sz_D(n)(1-v) \qquad \text{(A4a)} \end{aligned}$$

$$\begin{aligned} P_y(n) = {} & Tx(1-v) + Tz_C(n)(1-v) \\ & + Py(1-v) + Pz_D(n)(1-v) \qquad \text{(A4b)} \end{aligned}$$

$$\begin{aligned} P_z(n) = {} & \frac{z_C(n)}{z}(Rx(1-v) + Sy(1-v) + Rz_C(n)(v + z(1-v))/z \\ & + Sz_D(n)(v + z(1-v))/z) \\ & + \frac{z_D(n)}{z}(Py(1-v) + Tx(1-v) \\ & + Tz_C(n)(v + z(1-v))/z + Pz_D(n)(v + z(1-v))/z) \qquad \text{(A4c)} \end{aligned}$$

where R is the payoff for mutual cooperation ("reward"), P is the payoff for mutual defection ("punishment"), T is the payoff for defecting against a cooperator ("temptation") and S is the payoff for cooperation when the other individual defects (the "sucker's payoff"). $z_C(n)/z$ and $z_D(n)/z$ are the probabilities of a given generalized reciprocator being in a cooperative or defective state, respectively.

From the above equations we can now calculate the total payoff to strategy i as:

$$P_{i,total} = \sum_{n=0}^{\infty} w^n P_i(n),$$

where w is the probability of reaching another round. We now wish to investigate the conditions under which generalized reciprocity is evolutionarily stable with respect to both unconditional defectors (which never cooperate) and unconditional cooperators (which always cooperate). Generalized reciprocity will be immune to invasion from unconditional cooperators if $P_{z,total} > P_{x,total}$ (when $z = 1$, $y = 0$, and $x \to 0$) and will be immune to invasion from unconditional defectors if $P_{z,total} > P_{x,total}$ (when $z = 1$, $x = 0$, and $y \to 0$). We then analyze the model for when generalized reciprocity can invade a population of pure defectors (i.e., when $P_{z,total} > P_{y,total}$ and $x = 0$, $y = 1$, and $z \to 0$), and pure cooperators (i.e., when $P_{z,total} > P_{x,total}$ and $y = 0$, $x = 1$, and $z \to 0$). If all of these four conditions are fulfilled then we can say that generalized reciprocity will evolve and be evolutionarily stable.

The conditions for generalized reciprocity to invade a population of pure defectors is:

$$a\left(\frac{av(P + R - S - T)}{1 - v^2 w} - \frac{P(1+v) - S - vT}{1 - vw}\right) > 0 \qquad \text{(A5)}$$

and will be immune to invasion from pure defectors if:

$$a\frac{(P(a - v - 1) + S + a(R - S - T) + vT)}{1 - w} > 0 \qquad \text{(A6)}$$

Generalized reciprocity will be able to invade a population of pure cooperators if:

$$(1-a)\frac{(T - R + v(-T + a(S+T-R) + v((a+v)(R-S)+S-aT)w + P(a-1)(vw-1)))}{(1-vw)(1-v^2w)} > 0 \qquad \text{(A7)}$$

And will be immune to invasion by pure cooperators if:

$$(1-a)\frac{(P(a-1)+(a+v)(R-S)+S-aT)}{1-w} < 0 \qquad \text{(A8)}$$

Appendix 3

SEPARATION OF TIME-SCALES

The separation of time scales between the behavioral dynamics (in terms of the proportion of generalized reciprocators that are in a cooperative or defective state) and evolutionary dynamics depend on w, the probability of rounds continuing: the larger w, the greater the separation between behavioral dynamics and evolutionary dynamics. This is because, as w increases, the proportion of generalized reciprocators in the population that are in a cooperative state will start to equilibrate. We now look at the case in which the proportion of cooperating and defecting reciprocators is at equilibrium, and therefore in which there is a full separation of behavioral and evolutionary time-scales. From equation (A3), we can look at the case after an infinitely long number of rounds, such that $n \rightarrow \infty$. In the case in which we only have generalized reciprocators in the population (i.e., $z = 1$), the equilibrium proportion of generalized reciprocators in a cooperative state is simply $\hat{z}_D = a$ and $\hat{z}_D = 1 - a$. We can then substitute $z_C(\infty) = \hat{z}_C = a$ and $z_D(\infty) = \hat{z}_D = 1 - a$ into the payoffs for the three strategies, given by equation A4. The criteria for generalized reciprocity to be immune to invasion from unconditional cooperators (i.e., when $z = 1$, $y = 0$, $x \rightarrow 0$) is:

$$(1-a)(P - S - a(P + R - S - T) + v(S - R)) > 0$$

and the condition for generalized reciprocity to be immune to invasion from unconditional cooperators (i.e., when $z = 1$, $x = 0$, $y \rightarrow 0$) is:

$$a(S + a(R - S - T) - P(1 - a + v) + Tv) > 0$$

Applying the prisoner's dilemma payoff matrix ($R = b - c + d$, $T = b$, $S = -c$, $P = 0$) to these criteria, we recover the same condition as the original model:

$$c - ad < vb < c - d(a + v)$$

and the same applies to the snowdrift payoff matrix ($R = b - c/2$, $T = b$, $S = b - c$, $P = 0$), in which we obtain:

$$\frac{c(2-a)}{2(1-a+v)} < b < \frac{c(2-a-v)}{2(1-a)}.$$

This demonstrates that the structuring of time-scales does not influence the conditions under which generalized reciprocity is an ESS.

Queries

Q1 Author: Please provide the city location of publisher for Reference "Axelrod (1984)."

Q2 Author: If "Nowak and May (1992)" is not a one-page article please supply the first and last pages for this article.