

The evolution of generalized reciprocity in social interaction networks



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ABSTRACT

Generalized reciprocity has been proposed as a mechanism for enabling continued cooperation between unrelated individuals. It can be described by the simple rule “help somebody if you received help from someone”, and as it does not require individual recognition, complex cognition or extended memory capacities, it has the potential to explain cooperation in a large number of organisms. In a panmictic population this mechanism is vulnerable to defection by individuals who readily accept help but do not help themselves. Here, I investigate to what extent the limitation of social interactions to a social neighborhood can lead to conditions that favor generalized reciprocity in the absence of population structuring. It can be shown that cooperation is likely to evolve if one assumes certain sparse interaction graphs, if strategies are discrete, and if spontaneous helping and reciprocating are independently inherited.

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1. Introduction

Animal cooperation between unrelated individuals has puzzled biologists for a long time as its existence seems to contravene the basic notion of evolutionary biology that natural selection favors genes that promote only their own well-being. It has been suggested that cooperation between unrelated individuals can be established by direct reciprocity, where individuals take turns in helping each other (Trivers, 1971; Axelrod and Hamilton, 1981). Reciprocation is a reactive strategy where individuals condition their behavior on the previous behavior of their interaction partner. The decision to cooperate is based on the expected outcome of future interactions, which is inferred from past experience (Rutte and Taborsky, 2007). Alexander (1987) proposed that large-scale human cooperation could be sustained by a network of indirect reciprocation, where individual A helps individual B, while B is not reciprocating by helping A but individual C instead, etc. –until, at one point, this chain of reciprocation returns to individual A. Under the headings “up-stream tit-for-tat” this idea was formalized by Boyd and Richerson (1989) who could show that reciprocation can evolve if reciprocators are sufficiently common. Introducing the term “up-stream indirect reciprocity”, Nowak and Roch (2007) showed that this kind of indirect reciprocity is unlikely to evolve

unless it is coupled with some mechanism that ensures assortment of reciprocating individuals, as it is the case in spatial or network models with local reproduction or reputation-based reciprocity.

However, more recently it was suggested that, even in the absence of phenotype assortment, generalized reciprocity alone can enable cooperation if individuals of a population do not interact randomly but only with a small subset of the population (Pfeiffer et al., 2005; Rankin and Taborsky, 2009; van Doorn and Taborsky, 2012). In a recent study van Doorn and Taborsky (2012) presented a simple model for generalized reciprocity, where individuals occupy vertices on a sparse graph and interact with neighboring individuals. The authors assumed two fixed strategies, which they dubbed ‘altruists’ and ‘defectors’. Altruists spontaneously help other individuals and, upon receiving help, also help someone for exactly one time, while defectors never help others. They could show that in this case, the average payoffs for individuals of both strategy types are frequency dependent: if the proportion of altruists exceeds a certain threshold value, then altruists will receive higher payoffs and gain higher fitness, while below this threshold defectors will gain higher payoffs. The threshold value depends not only on the cost–benefit ratio of helping, but also on the structure of the interaction graph, as structuring can ensure that reciprocators are on average more often receivers of help than defecting non-reciprocators. Yet, this model makes one stringent assumption which limits its scope and applicability substantially. By assuming that only individuals who reciprocate acts of helping are those who can also spontaneously initiate help, this model implicitly assumes perfect genetic linkage

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for two different underlying behaviors. This assumptions seem unwarranted for behavioral phenotypes of biological systems. In the following I will, therefore, provide a generalizations of this model by presenting a discrete model that does not assume genetic linkage between strategies.

2. Population model with two phenotypes

2.1. Population

I assume a finite panmictic population of individuals who settle into a social structure with well-defined neighbor relations. Neighboring individuals can engage in repeated social interactions which affect their fitness (Nunney, 1985). The social neighborhood structure can be represented as a simple undirected graph, where vertices correspond to individuals and edges link potential interaction partners (Lieberman et al., 2005; Taylor et al., 2007). Individuals do not change their position on the graph during their life-time, though the population is panmictic as newly born individuals are placed on the graph randomly, independent of the position of their parents. The social interaction of interest is helping, which is defined broadly as a dyadic interaction where one individual performs a behavior at cost c in terms of lifetime fitness, which brings along some benefit b for the other individual, where the benefit is always larger than the cost.

2.2. Strategies

I envisage two discrete and fixed actions for helping: an individual can either spontaneously help another individual in its direct neighborhood (phenotype A), or it cannot (phenotype D). Upon receiving help, an individual of type A will reciprocate by helping one randomly selected individual from its neighborhood for exactly one time. Individuals of type D never reciprocate upon receiving help. A single individual adheres to the same actions for spontaneous and conditional helping over its whole lifetime. Note that strategies A and D are equivalent to the strategies “altruist” and “defector” in the model presented by van Doorn and Taborsky (2012). For better comparability I keep the same notation (A and D), though I do not refer to the strategy A as “altruist”, because the strategy does not comply with the original meaning of the term. It is assumed that spontaneous initiation of helping is a rare event. Once, it happens that an A type individual spontaneously helps a randomly chosen individual of its neighborhood, this can lead to a “chain reaction” of conditional reciprocation, which terminates as soon as help is directed towards a non-reciprocating D -type individual (Fig. 1). The time from spontaneous initiation to the termination of the chain of reciprocation is called one round. As initiation is considered to be rare, no further initiation events can occur within one round. At the end of the round, payoffs arising from all helping interactions are evaluated and added to the individuals’ payoff-values.

2.3. Results for the cycle

The cycle is a simple, symmetric graph where each vertex has exactly two neighbors. In a population of size N where the two strategy phenotypes A and D occur at frequencies a/N and d/N respectively, we can evaluate the expected payoff for a single individual of each strategy type. Assuming that all individuals make their decisions independently, the likelihood that within a given time period an individual will spontaneously help is dependent on the proportion of A individuals in the population. Once, an A individual has spontaneously helped someone and, thereby, initiated a random walk of reciprocal help, the random

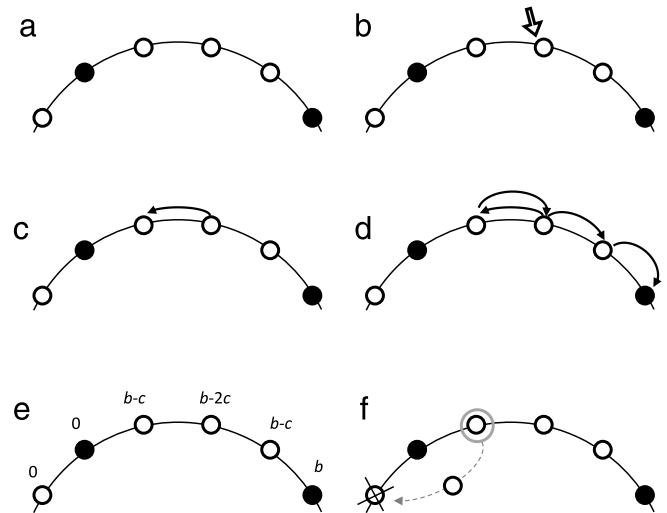


Fig. 1. Scheme of one round of the game. Reciprocating individuals (open circles) and non-reciprocating individuals (filled circles) are randomly placed on a cycle graph (a). One individual is randomly chosen as initiator (b). The initiator randomly chooses one neighbor and helps it for one time (c). If the recipient of help is a reciprocator, it will itself randomly chose one of its neighbors and help this neighbor for one time. This process is repeated until help is directed towards a non-reciprocator (d). Payoffs of all individuals are evaluated and added to their fitness value (e). One individual is randomly selected for reproduction, proportional to its fitness, and the offspring replaces a randomly chosen individual in the population (f).

walk will stop no sooner as it hits a D -type individual. Hence, the expected length of such a random walk will depend on the proportion of D individuals in the population. Each time help is given to a D -type individual, this individual receives a benefit of b at no cost. As all D -individuals are equally likely to be on the receiving end of help, the expected payoff for any D -type individual is, therefore, indirect proportional to the number of D -individuals in the population and dependent on the proportion of spontaneous initiators (A -type individuals):

$$\Pi_D = \frac{a}{N} \frac{1}{d} b = \frac{1}{N} \frac{ab}{d}. \quad (1)$$

Spontaneous helping by an A -type individual is associated with a cost of $-c$ for A . Thereafter, every time an A -type receives help it will reciprocate, earning a net benefit of $b - c$. Consequently, evaluating the expected payoff for an A -type individual requires considering the expected length of the chain of conditional reciprocation. For the cycle the chain of reciprocal helping can be modeled as a symmetric random walk in one dimension on a segment of the cycle consisting only of A -type individuals and enclosed on both sides by D -type individuals. For a symmetric random walk in one dimension with boundaries 0 and $j+1$ starting at u the expected length of the walk is given by $u(j+1-u)$, where j is the length of the segment (i.e. the number of A -type individuals aligned next to each other). It can be shown that for a segment on the circle consisting of j A -type individuals the expected length of the random walk started by a randomly chosen A individual is given by

$$\frac{(j+1)(j+2)}{6} - 1. \quad (2)$$

If we denote with φ_j the probability of hitting a segment of j A -type individuals by randomly selecting an A -type individual, we get the expected payoff for an A -type individual as

$$\Pi_A = \frac{1}{a} \frac{a}{N} \left(-c + \sum_{j=1}^a \left(\frac{(j+1)(j+2)}{6} - 1 \right) \varphi_j (b - c) \right). \quad (3)$$

We can get φ_j by evaluating α_j , the number of different ways we can get a chain of length j by placing a A -type individuals on a cycle of size N , and finding the proportion of A -type individuals which are part of chains of length j . Noting that $\alpha_j = N \binom{N-2-j}{a-j}$, we find that

$$\varphi_j = \frac{\alpha_j j}{\sum_{i=1}^a \alpha_i i} = \frac{\binom{N-2-j}{a-j} N - a}{\binom{N-2}{a-1} N - 1} j. \quad (4)$$

Substituting for φ_j in Eq. (3) and simplifying allows giving the expected payoff for A in closed form as

$$\Pi_A = \frac{1}{N} \left(-c + \frac{(a-1)(2N+2-a)}{(N+1-a)(N+2-a)} (b-c) \right). \quad (5)$$

Considering the deterministic dynamics of a large population, we can follow the discrete replicator dynamics as used by van Doorn and Taborsky (2012), i.e.,

$$\Delta x = x(1-x) \frac{\Pi_A - \Pi_D}{\bar{W}}, \quad (6)$$

where $\bar{W} = 1 + x\Pi_A + (1-x)\Pi_D$. If we rescale the time by multiplying the right hand side by N and then take the limit $N \rightarrow \infty$ of the resulting expression we obtain the fitness gradient

$$\delta W = \frac{-c + bx}{(1-x)^2}, \quad (7)$$

which shows that $x = 0$ and $x = 1$ are both stable, and there is an unstable equilibrium at $x^* = c/b$ dividing the basins of attraction of the two pure equilibria.

2.4. Results for the star graph

The cycle is the regular graph, where the effects of spatial structure on evolutionary dynamics are strongest. It is, therefore, of interest to compare the results for the cycle with the ones for other graphs. The star graph can be considered as a simple model for an asymmetric graph. As there are two different types of vertices – a central vertex connected to all other vertex, and the leaves which are just connected to the central vertex – we consider the two possible scenarios where the central vertex is either of type A or D , separately. These scenarios will occur with frequencies a/N , and d/N , respectively. I denote with j_a the expected length of a random walk given that an A type individual occupying the central vertex initiated the walk. This length is determined by the number of non-reciprocating D -type vertices in the leaves: each time the central A individual is reciprocating, it will direct its help towards a non-reciprocator with a likelihood of $d/(N-1)$, which will then terminate the walk. The expected length j_a is therefore given as

$$j_a = \frac{2N-2}{d} - 1. \quad (8)$$

If the center is occupied by an A individual, but the chain is started by an A individual at one of the leaves, then walk would first go from the respective leave to the center and from there on it would behave exactly like a random walk initiated by an A individual in the center. The expected length of such a walk would consequently be $j_a + 1$. Denoting the expected payoff of an individual of strategy X , given that an individual of strategy Y is in the center and helping was started by an individual of strategy Z in the center (*) or on a leaf (') as $\Pi_{X|Y,Z^*}$ or $\Pi_{X|Y,Z'}$, respectively, the conditional payoffs

are given as follows:

$$\Pi_{A|A,A^*} = \frac{a}{N} \frac{1}{a} (j_a - 1)(b - c) - c,$$

$$\Pi_{A|A,A'} = \frac{a}{N} \frac{1}{a} j_a (b - c) - c,$$

$$\Pi_{A|D,A'} = \frac{a}{N} \frac{1}{a} - c, \quad (9)$$

giving

$$\Pi_A = \frac{1}{N} \Pi_{A|A,A^*} + \frac{a-1}{N} \Pi_{A|A,A'} + \frac{d}{N} \Pi_{A|D,A'}, \quad (10)$$

with a closed form of

$$\Pi_A = \frac{1}{N} \left(\frac{2a^2 - 2a + ad - d}{Nd} (b - c) - c \right). \quad (11)$$

As Π_D for a D -type individual is the same as in the cycle given in Eq. (1), we get

$$\delta W = \frac{x^2(c-b) + c}{x-1}, \quad (12)$$

from which we can see that for $b < 2c$ the selection gradient is always going towards D while for $b > 2c$ there is an unstable equilibrium point,

$$x^* = \sqrt{\frac{c}{b-c}}. \quad (13)$$

Comparing Eq. (13) with the equilibrium point for the cycle, it can be seen that for $b > 2cx_{star}^* > x_{cycle}^*$. Thus, the basin of attraction for A is always larger for the cycle than for the star graph. For more complicated graphs analytical solutions become difficult to obtain but approximate solutions can be given using simulation studies as it was done in e.g. van Doorn and Taborsky (2012).

3. Population model with four phenotypes

3.1. Population

The same assumptions about the population are made as for the A - D model (detailed in 2.1).

3.2. Strategies

In the previous model I assumed, following van Doorn and Taborsky (2012), only two phenotypes: individuals which do spontaneously help and reciprocate whenever they receive help (A) and individuals which do neither (D). Here, I will investigate what happens if one considers spontaneous initiation of help and conditional reciprocation as independent traits. That is, I envisage two discrete and fixed actions for spontaneous helping: an individual can either spontaneously help another individual in its direct neighborhood, or it does not. Independently of this, I define two discrete and fixed actions for conditional helping. Upon receiving help, an individual will either reciprocate by randomly helping one individual from its neighborhood for exactly one time, or it will not. A single individual adheres to the same actions for spontaneous and conditional helping over its whole lifetime. As a result, there are four possible phenotypes (strategies): individuals who spontaneously initiate help and reciprocate (A), individuals who do not spontaneously initiate but who do reciprocate (L), individuals who spontaneously initiate but who do not reciprocate (S), and individuals who do neither initiate nor reciprocate (D).

3.3. Results for the cycle

In a population of size N where the strategy phenotypes A , L , S , D occur at frequencies a/N , l/N , s/N and d/N respectively, the expected payoff for a single individual of strategy $X \in A, L, S, D$ occurring at frequency x/N is given by

$$\Pi_X = \frac{1}{x} \left(\frac{s}{N} \Pi_{X|S} + \frac{a}{N} \Pi_{X|A} \right), \quad (14)$$

where $\Pi_{X|S}$ is the expected payoff for all X individuals given that a random walk was initiated by an S type and $\Pi_{X|A}$ is the expected payoff for all X given that a random walk was initiated by an A type. As payoffs depend on which type initiated the random walk I will consider the conditional payoffs separately.

If a random walk is initiated by an S individual, this induces a cost of $-c$ for the subpopulation of all S type individuals. The initiating individual will give its help directly to another S type with a probability of $(s-1)/(N-1)$. If this is case the random walk terminates immediately and the gain for the population of S individuals is b . If the random walk is terminated by a D type, the benefit for S is zero. With a probability of $(a+l)/(N-1)$ the initiator will direct its help towards a conditional reciprocator (A or L). In this case the expected gain for S will be b if the random walk of conditional reciprocation returns to the initiating S -type individual and $(s-1)/(s+d-1)$ times b otherwise. The probability that the random walk returns to the initiating S -individual depends on the length j of the segment of reciprocators neighboring the initiator and is given by $1/(j+1)$. With a probability of $1-1/(j+1)$ the random walk does not return to the initiating S -individual but reaches the other boundary of the segment of reciprocators. To get the expected payoff for S we have to consider the probability $\tilde{\varphi}_j$ for an S -type individual being placed next to an uninterrupted chain of conditional reciprocators of length j . The expected payoff for S given that the walk was initiated by an S -type individual is therefore given by

$$\begin{aligned} \Pi_{S|S} = \frac{a+l}{N-1} \sum_{j=1}^{a+l} \left(1 - \frac{1}{j+1} + \frac{1}{j+1} \frac{s-1}{s+d-1} \right) \tilde{\varphi}_j b \\ + \frac{s-1}{N-1} b - c. \end{aligned} \quad (15)$$

If a random walk is initiated by an A type, then the likelihood that it will be terminated by an S type is determined by the relative frequency of S types in the sub-population of non-reciprocators. Hence, the expected payoff for S is given by

$$\Pi_{S|A} = \frac{s}{s+d} b. \quad (16)$$

D -type individuals never initiate nor reciprocate, thus as soon as a D -type is the recipient of help, the random walk stops. The probability with which that happens is the complement to the probability of a termination by S . The conditional payoff for D given that the random walk was started by S is therefore given by

$$\Pi_{D|S} = \frac{a+l}{N-1} \sum_{j=1}^{a+l} 1 - \frac{1}{j+1} \frac{d}{s+d-1} \tilde{\varphi}_j b + \frac{d}{N-1} b. \quad (17)$$

Likewise, the payoff for D given that the random walk was started by A is

$$\Pi_{D|A} = \frac{d}{s+d} b. \quad (18)$$

The expected combined payoff for A and L individuals, aligned in a segment of length j , is $j(b-c)$. From this combined payoff A -types will acquire $a/(a+l)$, while $l/(a+l)$ will fall to L -type individuals.

The expected payoff for A given that the random walk was started by S is therefore

$$\Pi_{A|S} = \frac{a+l}{N-1} \sum_{j=1}^{a+l} j \tilde{\varphi}_j \frac{a}{a+l} (b-c). \quad (19)$$

For the case that the random walk was started by an A -type individual we have to find the probability with which a randomly chosen A -type individual is member of a segment of reciprocators of length j . We should consider only those segments of reciprocators, which contain at least one A individual. Furthermore, it has now to be acknowledged that the expected number of visits differs for the different positions within a segment of reciprocators. It can be shown that the expected number of re-visits of the initiator (A -type) by the random walk is $(j-1)/3$, while the expected number of visits of all other reciprocators in that segment is $(j^2+j-2)/6$. On average all of the re-visits of the initiator and $(a-1)/(a-1+l)$ of the remaining visits will fall on A individuals. The expected payoff for A given that the random walk was initiated by A is therefore given by

$$\Pi_{A|A} = \sum_{j=1}^{a+l} \left(\frac{j-1}{3} + \frac{j^2+j-2}{6} \frac{a-1}{a-1+l} \right) \hat{\varphi}_j (b-c) - c. \quad (20)$$

The expected payoffs for L can be evaluated likewise with the only difference that one has to take the proportion of L , and that L -types never pay costs for initiating. The expected conditional payoffs for L are therefore

$$\Pi_{L|S} = \frac{a+l}{N-1} \sum_{j=1}^{a+l} j \tilde{\varphi}_j \frac{l}{a+l} (b-c), \quad (21)$$

and

$$\Pi_{L|A} = \sum_{j=1}^{a+l} \frac{j^2+j-2}{6} \frac{l}{a-1+l} \hat{\varphi}_j (b-c). \quad (22)$$

What remains to be done is finding expressions for $\hat{\varphi}$ and $\tilde{\varphi}$. It can be shown that the likelihood $\tilde{\varphi}_j$ of an S -type individual neighboring a segment of reciprocators of length j is given by

$$\tilde{\varphi}_j = \frac{\binom{N-2-j}{a-j}}{\binom{N-2}{a-1}}. \quad (23)$$

As $\tilde{\varphi}$ defines the probability distribution in $\{1, 2, \dots, a+l\}$ with the first two moments given by

$$\sum_{j=1}^{a+l} \tilde{\varphi}_j j = \frac{N-1}{N-(a+l)}, \quad (24)$$

and

$$\sum_{j=1}^{a+l} \tilde{\varphi}_j j^2 = \frac{(N-1)(N-1+a+l)}{(N-(a+l))(N+1-(a+l))}, \quad (25)$$

we can substitute $\sum \tilde{\varphi}_j j$ in Eqs. (19) and (21) by Eq. (24) leading to

$$\Pi_{A|S} = \frac{a(b-c)}{N-(a+l)} \quad (26)$$

and

$$\Pi_{L|S} = \frac{l(b-c)}{N-(a+l)}. \quad (27)$$

How to evaluate the likelihood $\hat{\varphi}_j$ that a randomly picked A -type individual is part of a segment of reciprocators of length j , bordered by a non-reciprocator on each side, is detailed in the [Appendix](#).

Table 1
Expected frequencies for small-world graphs.

Graph	k	r	A	L	S	D
Small	4	0.002	26.8 (3.7)	25.2 (3.3)	19.5 (3.3)	28.5 (3.4)
World	4	0.02	22.8 (3.0)	25.1 (3.1)	21.7 (3.0)	30.4 (3.5)
	8	0.002	17.0 (2.1)	26.5 (2.8)	23.2 (2.5)	33.3 (3.0)
	8	0.02	18.5 (2.5)	25.6 (3.0)	28.4 (3.0)	27.5 (3.1)
Random	8		14.7 (1.9)	25.1 (2.7)	30.5 (3.6)	29.7 (3.4)
Random	5.1		16.5 (2.8)	22.0 (3.3)	30.1 (3.4)	31.4 (2.9)
Dolphin	5.1		20.1 (2.7)	28.6 (3.2)	22.7 (2.5)	28.6 (3.7)

Expected frequencies for the four strategy phenotypes A, L, S, D for graphs with $N = 62$, average degree k , re-wiring probability for small world graphs r , $b/c = 10/3$, and $\sigma = 0.05$.

$$M = \begin{pmatrix} 1 - \rho_{la} - \rho_{sa} - \rho_{da} & \rho_{al} & \rho_{as} & \rho_{ad} \\ \rho_{la} & 1 - \rho_{al} - \rho_{sl} - \rho_{dl} & \rho_{ls} & \rho_{ld} \\ \rho_{sa} & \rho_{sl} & 1 - \rho_{as} - \rho_{ls} - \rho_{ds} & \rho_{sd} \\ \rho_{da} & \rho_{dl} & \rho_{ds} & 1 - \rho_{ad} - \rho_{ld} - \rho_{sd} \end{pmatrix}. \quad (36)$$

Box 1.

However, it can be noted that for the case $l = 0$ (there are no L -type individuals in the population), $\hat{\varphi}_j$ is equivalent to φ_j .

In order to characterize the evolutionary dynamics of a finite population we can consider the limit of rare mutations with the mutation rate $\mu \ll 1/N^2$ (Fudenberg et al., 2006; Hauert et al., 2008). In this case the population consists usually of a single phenotype and any mutation will either disappear or reach fixation, leading to a new monotypic population, before a new mutation arises. This restricts the evolutionary dynamics to the edges of the simplex \mathcal{S}_4 where only two strategy types are present at any time. For this case we can derive the stationary distribution, giving the probability of finding the population in any of the four monotypic states consisting of either only A, L, S or D -type individuals. The payoffs for types D and A along the A - D edge are given by Eqs. (1) and (5), respectively. For the A - S edge $\Pi_{S|A} = b$ and $\Pi_{S|S} = b - c$, which gives after substitution in Eq. (10) an expected payoff for an S -type individual of

$$\Pi_S = \frac{ab + s(b - c)}{Ns}. \quad (28)$$

The conditional payoffs for strategy A are given in Eqs. (20) and (26). Substituting φ_i in Eq. (20) and noting that $l = 0$ (and, hence $\hat{\varphi}_j = \varphi_j$) and $N = a + s$, the expected payoff for an A -type individual simplifies to

$$\Pi_A = \frac{1}{N} \left(b - 2c + \frac{(a - 1)(a + 2s + 2)(b - c)}{(a + s - 1)(s + 1)(s + 2)} \right). \quad (29)$$

For the edge $A - L$ we have to note that, once an initiator started a chain of reciprocation, this will theoretically go on forever as the population consists entirely of reciprocators. Both, A and L individuals receive a net benefit of $b - c$, each time the random walk passes through them. Strategy A has a small disadvantage due to the cost for the initial help, though this advantage vanishes in the limit with the consequence, that there is no selection gradient along the $A - L$ edge. Likewise there are no selection forces along the $L - D$ edge, as there are no initiators in this population and the payoff for all members is zero. For the $L - S$ edge we find that individuals of both strategy types obtain the same payoff $\Pi_L = \Pi_S = (b - c)/N$, which again means that there is no selection gradient along this edge and population changes are due to random drift, alone. Finally, for the $S - D$ edge the costs of initiating help are exclusively carried by the S -type individuals and, as there is no reciprocation, the benefits from spontaneous help is reaped-off proportionally by S and D ,

yielding

$$\Pi_S = \frac{1}{N} \left(\frac{(s - 1)b}{s + d - 1} - c \right) \quad (30)$$

and

$$\Pi_D = \frac{sb}{N(s + d - 1)}. \quad (31)$$

These payoffs determine together with the selection strength σ the transition probabilities that a number of individuals m_i of type i increases by one, T_{ij}^+ , or decreases by one T_{ij}^- (Hauert et al., 2007, 2008):

$$T_{ij}^+ = \frac{m_i(1 - \sigma + \sigma \Pi_{ij})}{N(1 - \sigma) + \sigma(m_i \Pi_{ij} + (N - m_i) \Pi_{ji})} \frac{N - m_i}{N}, \quad (32)$$

$$T_{ij}^- = \frac{(N - m_i)(1 - \sigma + \sigma \Pi_{ji})}{N(1 - \sigma) + \sigma(m_i \Pi_{ij} + (N - m_i) \Pi_{ji})} \frac{m_i}{N}. \quad (33)$$

For all those edges with no selection gradient (i.e. all edges connected to L) the increase and decrease of the proportion of i -type individuals is governed by random drift only and given by

$$T_{ij}^+ = T_{ij}^- = \frac{x_i(N - x_i)}{N^2}. \quad (34)$$

These transition probabilities define a master equation, describing the time-evolution of the system. From this master equation, one can derive the fixation probability ρ_{ij} of a single mutant of type i in a population of j -type individuals, which is given by

$$\rho_{ij} = \frac{1}{1 + \sum_{k=1}^{N-1} \prod_{m_i=1}^k \frac{T_{ij}^-}{T_{ij}^+}}. \quad (35)$$

As we are considering the case of rare mutations and as mutations for spontaneous and conditional helping are assumed to be independent, combined mutations, where both properties change simultaneously occur only with a rate of $\mu \ll 1/N^4$ and are, effectively, so rare that they can be safely excluded from further consideration. The fixation probabilities along the edges $A - S$ and $L - D$ are therefore set to zero: $\rho_{AS} = \rho_{SA} = \rho_{LD} = \rho_{DL} = 0$. The fixation probabilities allow calculating the transition probabilities of a Markov process between the monotypic states of the population. The transition matrix of this process is given by: (see the equation in Box 1).

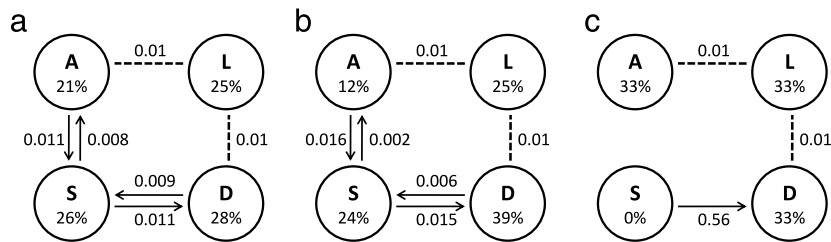


Fig. 2. Stationary probability distributions (in percent) and transition probabilities for the four phenotypes (A, L, S, D) for a population with low mutation rate ($\mu = 1/(2N^2)$), population size $N = 100$ and a benefit/cost ratio of 10/3. Evolution is modeled as a Moran process with selection strength $\sigma = 0.072$ (a) and $\sigma = 0.24$ (b, c). The interaction graph is a cycle (a, b) or a star graph (c). The transition probability $\rho(X \rightarrow Y)$ denotes the probability that a single mutant of type X in a population of type Y reaches fixation.

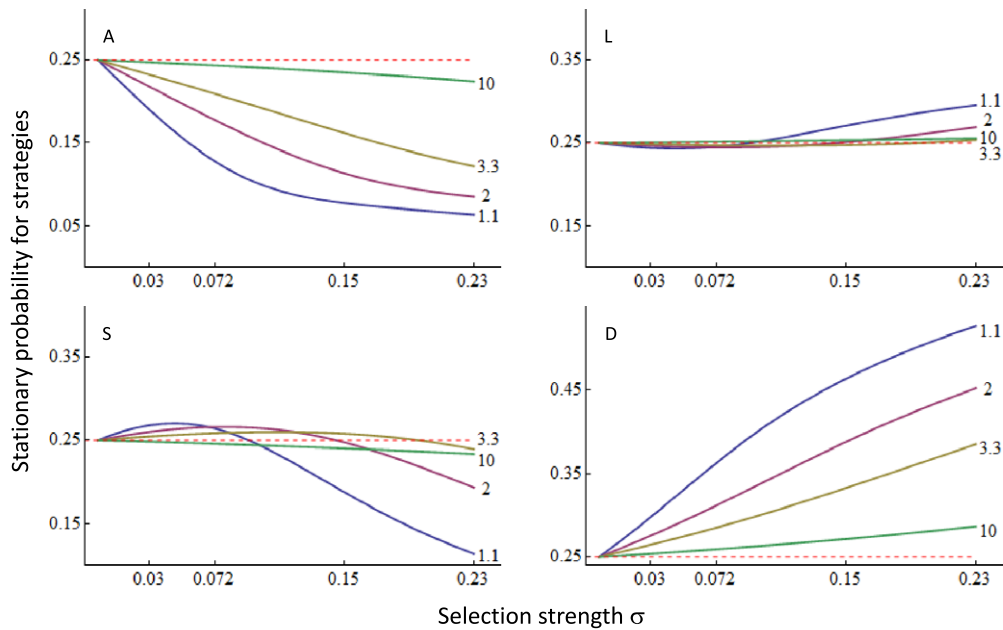


Fig. 3. Stationary probability distributions for the four phenotypes A, L, S, and D for four different benefit/cost ratios (10/9, 1/2, 10/3, and 10) and selection strength σ ranging from 2×10^3 to 0.23. The dashed line gives the expected value if transitions were due to random drift, only.

The stationary distribution of this process can be obtained from the normalized right eigenvector of the largest eigenvalue and gives the probabilities of finding the population in one of the four monotypic states (Hauert et al., 2007). This allows us calculating the stationary probability distribution and transition probabilities for given population size and selection strength analytically. It can be seen that for weak selection (Fig. 2a) all four phenotypes are almost equally likely to occur (for a selection strength of zero all four phenotypes would occur with $p = 0.25$), while for a higher selection strength the likelihood to find the population in state D increases, while A becomes a less likely phenotype. This effect is robust with respect to changes in selection strength and population size, though, it is weaker for larger benefit/cost ratios (Fig. 3).

In the case that mutations are more frequent, transitions along the $A - S$ and $L - D$ edges cannot be ignored and, furthermore, it cannot be assumed that fixation (or extinction) of a mutant is reached before a new mutation arises. As a consequence, it is possible that the population consists of more than two types at a time and an analysis should not be restricted to the edges of the simplex but comprise the full simplex \mathcal{S}_4 . For this case numerical solutions can be found for any proportion of A, L, S and D-type individuals using Eqs. (14)–(22), respectively.

3.4. Results for the star graph

As for the two-phenotype model we can evaluate expected payoffs for the four-phenotype model for the star graph (see

Appendix C). It can be seen (Fig. 2c) that populations of S-type individuals get easily invaded by D-type mutants while the transition probabilities from A and D towards S are very low. As the transition between A and L and L and D is governed by random drift alone, the system will be in either of the three states A, L, or D for one third of the time, irrespective of the other parameters.

3.5. Four-phenotype models for other graphs

The cycle is a rather extreme graph: it is the regular, non-trivial graph with the lowest density¹ and the highest characteristic path length,² and consequently the largest effective population size (Broom and Voelkl, 2012). Strategies that profit from localized interactions will often perform best on the cycle (e.g. Grafen, 2007) and this is supposedly also the case with generalized reciprocity. Yet, while the cycle is useful for providing a proof of principle it tells us little about how likely this scenario is in natural situations. I have therefore added results from numeric simulations for more realistic small-world networks and a graph based on a real-world example from bottlenose dolphins (Lusseau and Newman, 2004). The motivation for including the dolphin network was to facilitate comparison with another study (van Doorn and Taborsky,

¹ The density of a graph is the ratio of existing edges to possible edges.

² The characteristic path length of a graph is the average shortest path from every vertex to any other vertex.

2012), where simulations were run on the same network. For these simulations I assumed a haploid birth–death process, weak selection (where the fitness of an individual is given by $1 - \sigma + \sigma \times$ payoff, with $\sigma = 0.05$), population sizes of $N = 62$, a mutation rate of $1/(2N^2)$, and a benefit–cost ratio of 10/3. The simulation was run over $2, 19 \times 10^6$ rounds with one random walk started by one spontaneous initiation of a randomly selected individual and reproduction of a single individual at the end of the round. For each population the simulation was run 64 times; the first 365,000 rounds of each run were regarded as burn-in phase and discarded prior to analysis. While the average frequencies for the four strategies differ between graphs (Table 1), the overall picture is for all presented simulations similar: the non-cooperative strategy D is observed for less than one third of the time, while for the remaining time the population consists of individuals who either spontaneously help, reciprocate received help or do both.

4. Discussion

Cooperative helping can evolve by means of natural selection when helpers are more likely to direct their help towards other individuals carrying the same gene for helping behavior (Hamilton, 1964). Three mechanisms which can achieve this have been studied extensively (Wilson and Dugatkin, 1997; Fletcher and Doebeli, 2009; Godfrey-Smith and Kerr, 2009). The first one is spatial assortment due to limited dispersal (e.g. Hamilton, 1964; Eshel, 1977; Kelly, 1992; Nowak and May, 1992; Wilson et al., 1992; van Baalen and Rand, 1998; Santos and Pacheco, 2005; Ohtsuki and Nowak, 2007; Débarre et al., 2014), which enables the evolution of cooperation based on kin selection (e.g. Queller, 1994; Mitteldorf and Wilson, 2000; West et al., 2006, 2007). If individuals are engaged in repeated interactions, then direct (Trivers, 1971) or indirect reciprocity (Nowak and Sigmund, 1998, 2005; Hauert et al., 2007) can lead to continued cooperation. Yet, in addition to being vulnerable to defection, these mechanisms are cognitively demanding as they require individual recognition and memory for book-keeping of past interactions (Stevens and Hauser, 2004). Indirect reciprocity requires furthermore reputation building based on observations of third-party interactions (Nowak and Sigmund, 1998; Leimar and Hammerstein, 2001; Nowak and Sigmund, 2005; Fu et al., 2008). More recently, generalized reciprocity has been proposed as a further mechanism to establish reciprocal helping. In a well-mixed population where individuals randomly interact with each other helping cannot evolve (Lehmann and Keller, 2006; Fletcher and Doebeli, 2009; Godfrey-Smith and Kerr, 2009; Rankin and Taborsky, 2009), though if the population is sufficiently structured in the sense that any individual is interacting only with a small well-defined subset of the population – its neighborhood –, then generalized reciprocators can prosper. The reason why this can work is that the average length of a chain of reciprocation – and, with it, the net payoff for reciprocators – increases disproportionately to the number of conditional reciprocators aligned next to each other (see Eqs. (23) and (24) and Pena et al., 2011). Studying a population arranged on a cycle allows proving this assertion. Randomly placing individuals on a cycle will lead to a certain variation in the local abundance of reciprocators. This weak random assortment can be sufficient to produce long chains of reciprocation at some places on the cycle and, hence, to raise the average payoff of reciprocators to a level where it exceeds the average payoff of non-reciprocators. As a consequence, generalized reciprocity can evolve, even in the absence of any active assortment mechanisms, with the help of neutral drift alone if interaction networks are sufficiently structured and spontaneous and conditional helping are independent and discrete encoded traits.

In an earlier study van Doorn and Taborsky (2012) suggested a model with only two phenotypic strategies (“altruists” and “defectors”), implicitly assuming complete genetic linkage between reciprocation and initiation of helping acts. This has the effect that the selection gradient was frequency dependent, and that evolution of reciprocation from a non-cooperative population would require an initial drift against a selection gradient. For the regular cycle and the non-regular star graph proofs were provided that this must always be the case. The extended model with four phenotypic strategies brings in more biological realism, as it seems neither plausible that two rather diverse behavioral mechanisms – spontaneous initiation and conditional reciprocation – should be governed by the same gene, nor warranted to demand that genes coding for these mechanisms must be perfectly linked.

The cycle is a highly arbitrary structure, which has no close resemblance with any natural population of interacting individuals. Thus, in order to see whether similar effects can be found in differently structured interaction networks, I added the results of evolutionary simulations on other graphs – including a graph based on a real-world animal social network. While long-term expected frequencies were not the same, the overall theme – that cooperative strategies dominated – was found in all cases. Yet, while adding more plausible interaction structures adds some biological realism, the discrete model is still arbitrary in the sense that it assumes that (a) the costs and benefits for help are constant and irrespectively of the number or temporal distance of interactions (b) reciprocation is absolutely faithful and error-free, (c) individuals pursue only one strategy throughout their entire lives and always respond in the same way and (d) strategies are encoded by single genes. Extending the model by incorporating those points might be a worthwhile endeavor, but is beyond the scope of this study.

Here, I modeled reciprocity of individuals of a panmictic population which engage in repeated interactions during their lifetime. In this respect this study differs from several other studies which investigated the effect of population structure or viscosity on cooperation (Lieberman et al., 2005; Taylor et al., 2007). For example, in their model of generalized reciprocity Rankin and Taborsky (2009) explicitly excluded the possibility of repeated interactions by demanding that ‘no two individuals interact together more than once in a lifetime’. Such a model might be useful for e.g. modeling one-shot interactions between mating partners in semelparous species with a single reproductive cycle, but it cannot be applied to many other cases of cooperation like support in foraging tasks in rats (Rutte and Taborsky, 2007), or cooperation in economic games in humans (Fowler and Christakis, 2010). Yet, it were especially the latter cases where generalized reciprocity had been put forward as a potential explanation.

Most mammalian and bird species and also several fish species have highly structured populations, where individuals repeatedly interact with the same conspecifics. Such a strong assortment is sometimes due to spatial proximity, but sometimes also due to group formation processes. In all those cases repeated interaction might be the norm if the behavior in question is of a kind that allows for repeated expression. Thus, I argue that for many instances of cooperation in nature, including food sharing (Wilkinson, 1984; Kasper et al., 2008), support in agonistic interactions (Loretto et al., 2012), alarm calls (Marler, 1967), allogrooming (Hart and Hart, 1992; Fruteau et al., 2009), or brood care in iteroparous species (Lazarus and Inglis, 1986), it is appropriate and necessary to assume repeated interactions. Having a truly panmictic population might be an unrealistic assumption, yet it helps to discern effects of generalized reciprocity from effects of kin selection due to limited dispersal. The fact that kin selection can foster the evolution of cooperative behavior is well understood (e.g. Lehmann et al., 2007) and not of further interest, here.

In this model help is reciprocated until it is given to a D or S type. As a consequence, the frequency of helping is frequency

dependent – the more reciprocators are around, the more help is given. Such an assumption seems to be warranted for some social interactions; however in other cases, where opportunities for helping are determined by the environment, this will not be the case. The final point where this model deviates from previous ones is that it assumes two independent genetic loci for spontaneous initiation of helping and reciprocation. In order to reciprocate an individual needs the ability to recognize and memorize that it had received help from another individual. This requires certain perceptive abilities which, clearly, differ from the abilities required for spontaneously helping someone. Independent loci for helping and reciprocation should, therefore, be the default assumption, though whether linkage between these loci can evolve secondarily, remains an open question worth exploring.

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Appendix A. Expected length of the random walk

In order to get the expected number of visits of the initiator and the remaining reciprocators given that the random walk was initiated by an A -type individual, we can consider the random walk as a Markov process with two absorbing states and j transient states. How to determine the length of such a random walk is detailed in e.g. Grinstead and Snell (1997, p. 417). If we rearrange the transition matrix so that the transient states come first we will get

$$\mathcal{P} = \begin{pmatrix} \mathcal{Q}_{j,j} & \mathcal{R}_{j,2} \\ \mathcal{O}_{2,j} & \mathcal{I}_{2,2} \end{pmatrix}. \quad (37)$$

The fundamental matrix \mathcal{N} for \mathcal{P} is then given by

$$\mathcal{N} = (\mathcal{I}_{j,j} - \mathcal{Q}_{j,j})^{-1} \quad (38)$$

and $\text{tr}(\mathcal{N})/j - 1$ gives the expected number of re-visits of the initiator. For a simple, symmetric random walk with $p = q = 1/2$ and two absorbing boundaries we get a closed form for the trace of \mathcal{N} as

$$\text{tr}(\mathcal{N}) = \frac{j(j+2)}{3}. \quad (39)$$

This gives an expected number of re-visits of the initiator of

$$E[\text{visit initiator}] = \frac{\text{tr}(\mathcal{N})}{j} - 1 = \frac{j-1}{3}. \quad (40)$$

As the expected length of the random walk until absorption at a boundary is given by

$$E[\text{visit}] = \frac{1}{j} \sum_{u=1}^j u(j+1-u), \quad (41)$$

which has a closed form of $(j+1)(j+2)/6$, the expected number of visits of the remaining reciprocators is

$$E[\text{visit other reciprocators}] = \frac{(j+1)(j+2)}{6} - 1 - \frac{j-1}{3} = \frac{j^2 + j - 2}{6}. \quad (42)$$

Appendix B. Expected value for $\hat{\phi}$

If the population contains both A and L -type individuals, the likelihood that a randomly selected A -type individual is part of an uninterrupted chain of reciprocators of length j is given by:

$$\hat{\phi}_j = \frac{\hat{\alpha}_j \gamma_j \eta_j}{\sum_{i=1}^{a+l} \alpha_i \gamma_i \eta_i}, \quad (43)$$

where $\hat{\alpha}_j$ is the total number of chains of reciprocators of length j for all permutations of $a+l$ reciprocators on a cycle of size N , which is given by

$$\hat{\alpha}_j = N \binom{N-2-j}{a+l-j}, \quad (44)$$

γ_j is the ratio of all chains of length j , which can be built out of a A -type and l L -type individuals, that contain at least one A ,

$$\gamma_j = \frac{\binom{a+l}{j} - \binom{l}{j}}{\binom{a+l}{j}}, \quad (45)$$

and η_j is the expected number of A s in those chains, given by

$$\eta_j = 1 + (j-1) \frac{a-1}{a-1+l}. \quad (46)$$

Appendix C. Supplementary data

Supplementary material related to this article can be found online at <http://dx.doi.org/10.1016/j.tpb.2015.06.005>.

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