

THE EVOLUTION OF GENERALIZED RECIPROCITY ON SOCIAL INTERACTION NETWORKS

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Generalized reciprocity (help anyone, if helped by someone) is a minimal strategy capable of supporting cooperation between unrelated individuals. Its simplicity makes it an attractive model to explain the evolution of reciprocal altruism in animals that lack the information or cognitive skills needed for other types of reciprocity. Yet, generalized reciprocity is anonymous and thus defenseless against exploitation by defectors. Recognizing that animals hardly ever interact randomly, we investigate whether social network structure can mitigate this vulnerability. Our results show that heterogeneous interaction patterns strongly support the evolution of generalized reciprocity. The future probability of being rewarded for an altruistic act is inversely proportional to the average connectivity of the social network when cooperators are rare. Accordingly, sparse networks are conducive to the invasion of reciprocal altruism. Moreover, the evolutionary stability of cooperation is enhanced by a modular network structure. Communities of reciprocal altruists are protected against exploitation, because modularity increases the mean access time, that is, the average number of steps that it takes for a random walk on the network to reach a defector. Sparseness and community structure are characteristic properties of vertebrate social interaction patterns, as illustrated by network data from natural populations ranging from fish to primates.

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The occurrence of cooperation between unrelated individuals is an evolutionary riddle, because bearing fitness costs for the sole benefit of nonkin others appears maladaptive at first sight (West et al. 2007; Clutton-Brock 2009). Theoretical models (Doebeli and Hauert 2005; Lehmann and Keller 2006) provide proof-of-principle that seemingly altruistic behavior can nevertheless evolve and persist if it is based on reciprocity (Trivers 1971; Axelrod and Hamilton 1981; Nowak and Sigmund 1998; Pfeiffer et al. 2005; Nowak 2006). If others reciprocate, it is beneficial to cooperate, because the costly act of providing help increases the probability of receiving assistance in the future, whereas defection is likely to be punished by the withdrawal of future help.

To what extent reciprocity can explain the behavior and sociality of biological organisms is subject to debate (Hammerstein 2003; Clutton-Brock 2009). One concern is that the assumptions of theoretical models differ in important ways from the observed structure of real interactions. For example, animals are usually not restricted to interact repeatedly with the same partner, nor do social interactions occur at random (Croft et al. 2008; Whitehead 2008). Moreover, individuals often have strategic options that are not captured by traditional models of reciprocal altruism (Hauert et al. 2002; Connor 2010). Several authors have therefore emphasized alternative processes that may have contributed to the evolution of cooperation (e.g., pseudo-reciprocity, by-product

mutualism, and biological markets; Connor 1995; Leimar and Hammerstein 2010). Others have explored the consequences of population structure on the evolution of reciprocal cooperation (Ohtsuki et al. 2006; Santos et al. 2006; Taylor et al. 2007; Rankin and Taborsky 2009). Dissatisfaction with models of reciprocity has also grown because the strategies proposed in theoretical models are unlikely to be realized by evolution in real organisms (Clutton-Brock 2009). Specifically, direct and indirect reciprocity require memory of the identity and past behavior of social partners, which has been shown to constrain cooperation in animals (Stevens et al. 2005), including even humans (Milinski and Wedekind 1998).

Here, we explore several of these issues by investigating the evolution of generalized reciprocity, a cognitively simple conditional cooperation mechanism, in populations with a realistic interaction structure. Generalized reciprocity, also known as upstream tit-for-tat (Boyd and Richerson 1989), upstream indirect reciprocity (Nowak and Roch 2007), or pay-it-forward reciprocity (Fowler and Christakis 2010), works by the simple rule “help anyone, if helped by someone” and has been demonstrated in humans and other animals (Greiner and Levati 2005; Bartlett and DeSteno 2006; Rutte and Taborsky 2007, 2008; Stanca 2009). In comparison to other types of reciprocity, generalized reciprocity requires minimal cognitive abilities and very little information retention and retrieval. Individuals decide to cooperate or not just dependent on whether they have been helped or not, irrespective of who has helped and who is there to be helped. In other words, there is contingency between received help and cooperation, but not between the identities of donors and receivers. The simplicity of generalized reciprocity comes at a cost in terms of an increased vulnerability to exploitation. Because the strategy is anonymous, it is impossible to single out and punish defectors. Nevertheless, generalized reciprocity has been shown to be evolutionarily stable if individuals interact repeatedly in groups consisting of a few individuals (Pfeiffer et al. 2005), in viscous populations (Rankin and Taborsky 2009), or when evolving in combination with group leaving strategies (Hamilton and Taborsky 2005), more complex forms of reciprocity (Nowak and Roch 2007) or state-dependent updating rules (Barta et al. 2011). However, it is unclear whether interaction patterns found in real organisms would be able to support cooperation based on generalized reciprocity.

Social interactions among animals are structured according to obvious factors such as sex, age, and kinship (Berman 1982; Ruckstuhl 2007; Wiszniewski et al. 2010), as well as less-apparent characteristics such as familiarity, personality, and sociability (McPherson et al. 2001; Manno 2008; Pike et al. 2008; Croft et al. 2009; Pinter-Wollman et al. 2009; Schürch et al. 2010). As a result, individuals differ in the quality and quantity of their interactions with others, contributing to a heterogeneous network of social interactions within a population (Croft et al. 2008;

Wey et al. 2008; Sih et al. 2009). Such social networks have been studied for a long time in humans (Newman 2003, and references therein). More recently, they have been scrutinized also in animal species ranging from eusocial insects (Naug 2008) to fish (Croft et al. 2004), birds (Oh and Badyaev 2010), and mammals (Chaverri 2010; Wey and Blumstein 2010; Kerth et al. 2011), including cetaceans (Lusseau and Newman 2004; Wiszniewski et al. 2010), primates (Voelkl and Kasper 2009), and farm animals (Gygax et al. 2010). Some social network studies have been performed in relatively large populations (e.g., Wolf and Trillmich 2008; Oh and Badyaev 2010), providing opportunities to confront evolutionary models of cooperative behavior with observed patterns of social organization in animals.

Network structure can influence the evolution of generalized reciprocity by two mechanisms that act on different time scales. The first mechanism is network reciprocity (Nowak 2006), which can in principle be explained by inclusive fitness arguments (Taylor et al. 2007). It occurs when dispersal is limited and offspring settle in the network neighborhood of their parents, such that individuals are on average more likely to interact with kin (Wolf and Trillmich 2008; Wolf et al. 2011). Such population structure favors the evolution of cooperation in general (Ohtsuki et al. 2006; Taylor et al. 2007; but see West et al. 2002), be it by direct (Ohtsuki and Nowak 2007) or generalized reciprocity (Iwagami and Masuda 2010). The second mechanism, which will be the focus of this article, is directly related to the pattern of social interactions and the way in which it controls the flow of information in animal populations (Krause et al. 2007; Croft et al. 2008). It is particularly relevant to the evolution of generalized reciprocity, which, unlike direct reciprocity, can cause cooperative behavior to spread through a social network like an information transfer process. That is, if reciprocity is generalized, an initial act of cooperation triggers a sequence of cooperative acts that cascades in the social network from one anonymous partner to the next (Nowak and Roch 2007; see Fowler and Christakis 2010 for an experimental demonstration of this effect in humans). Individuals who participate in a sequence of generalized reciprocation can expect to receive future help in return for providing assistance to an anonymous partner, if the same sequence on average visits an individual more than once. The probability of this happening is expected intuitively to depend on structural properties of the social interaction network, such as sparseness, clustering, and modularity. For example, groups of cooperators are partially shielded from exploitation by defectors in populations that are subdivided into smaller communities (Hamilton and Taborsky 2005; Pfeiffer et al. 2005). By extension, one would therefore predict modular networks to provide a more favorable context for the evolution of generalized reciprocity than randomly connected ones. The aim of this article is to make these qualitative arguments more precise, and to investigate which particular network properties are critical

to the evolution of cooperation based on generalized reciprocity. To this end we will develop a simple model of anonymous reciprocal cooperation and study its dynamics on various networks, using individual simulations and analytical techniques. The insights from these systematic investigations are then applied to a dataset of empirical networks collected from the literature, to see to what extent realistic interaction patterns are conducive to the evolution of generalized reciprocity.

The Model

We consider a group of N individuals that exhibit pairwise interactions with their immediate neighbors on a social interaction network. The cooperative interactions occurring on the network are based on generalized reciprocity. When individuals receive help, they may reciprocate to a random individual among their neighbors in the network. We consider two simple discrete strategies. Individuals are either reciprocal altruists or defectors. Reciprocal altruists always reciprocate when they receive help; defectors never reciprocate. Providing assistance is costly for the actor and beneficial for the receiver of the helpful act. The corresponding fitness cost and benefit are measured by the parameters c and b , respectively, with $0 \leq c \ll 1$ and $0 \leq b \ll 1$, implying that selection is weak. [Correction made here after initial online publication.]

To keep track of the state of the population, we define f_t as the frequency of reciprocal altruists at generation t . The expected change in f_t from one generation to the next is proportional to the relative fitness difference between altruists and defectors, that is,

$$\Delta f_t = f_t (1 - f_t) \frac{\pi_A - \pi_D}{\bar{W}}, \tag{1}$$

where $\bar{W} = 1 + f_t \pi_A + (1 - f_t) \pi_D$ is the mean fitness, and π_A and π_D denote the expected payoffs of altruists and defectors, respectively (Hofbauer and Sigmund 1998).

PAYOFFS AND FITNESS GRADIENT

A spontaneous act of altruism initiates a sequence of reciprocated interactions that will jump from one reciprocal altruist to the next until it eventually hits a defector. This sequence travels over the network as a random walk (Nowak and Roch 2007), due to the fact that generalized reciprocation is anonymous. The random walk may return one or several times to an arbitrary reciprocal altruist i that it has already visited, before it eventually terminates. Let k_i denote the number of such return events. As indicated by the subscript, k_i depends on the position of individual i in the network. At each return event, the payoff of the focal individual increases by b and then decreases by c as help is reciprocated to a random neighbor. If individual i initiated cooperation, then its payoff has changed by an amount $k_i b - (k_i + 1) c$ by the time

the random walk ends. If cooperation was initiated by another individual, then individual i gains $(k_i + 1)(b - c)$ payoff units over the total length of the random walk. The expected payoff accumulated by reciprocal altruists is therefore given by

$$\pi_A = E[(n + n'_i)(b - c)(k_i + 1) - n b], \tag{2}$$

where n is the expected number of times that the focal individual initiates cooperation, and n'_i denotes the expected number of times that individual i is hit for the first time by a sequence of altruistic interactions that originated elsewhere on the network. Without loss of generality, we choose $n = 1$ in the analytical treatment of the model. As elsewhere in this manuscript, the expectation in equation (2) is taken over all positions in the network.

If we conservatively assume that only reciprocal altruists initiate cooperation, then the expected payoff of defectors is given by $\pi_D = b \bar{n}'$, where $\bar{n}' = E[n'_i] = f_i / (1 - f_i)$. This follows because every sequence that is initiated by a reciprocal altruist must eventually terminate at a defector. Combining this result with equation (2) and assuming $E[n'_i k_i] \approx \bar{n}' \bar{k}$ produces an approximate expression for the fitness gradient, ∂W ,

$$\partial W = \frac{\pi_A - \pi_D}{\bar{W}} \approx \frac{b \bar{k} - c (\bar{k} + 1)}{1 - f_t + f_t (b - c) (\bar{k} + 1)}. \tag{3}$$

Since n'_i and k_i both increase with the degree (i.e., the number of neighbors) of individual i , the approximation $E[n'_i k_i] \approx \bar{n}' \bar{k}$ amounts to assuming that the coefficient of variation of the network's degree distribution is small.

INDIVIDUAL-BASED SIMULATIONS

Throughout this article, analytical results, based on equations (1)–(3) and the derivations in the online supporting information, are complemented with the results of individual-based computer simulations. The simulations keep track of a population of individuals with a constant size N , corresponding to the number of nodes in the social interaction network. Generations are discrete and nonoverlapping. At the start of each generation, each individual is randomly assigned a node in the network, which it then occupies for its entire life (global offspring dispersal prevents kin selection from operating in our model). We simulate a large number of $n \times N$ random walks to estimate the payoff of each individual (individual i has payoff $\pi_i = 0$ at the start of its life).

Each random walk is initiated by selecting a random individual. If that individual is a defector then the random walk stops immediately. Otherwise, the random walk jumps to a random neighboring node until it arrives at a defector. When the random walk jumps from node i to node j , the payoff of individual i is decreased by c/n and the payoff of individual j is increased by b/n (this scaling of the payoffs makes the simulations directly comparable to the analytical results, where we took $n = 1$ for simplicity). When all random walks have terminated, individuals

produce offspring. The individuals who reproduce are sampled with replacement from the population with probabilities proportional to their relative fitness values $w_i = (1 + \pi_i)/\bar{W}$. Reproduction is assumed to be clonal. The life cycle is completed when the offspring undergo mutation and replace the parental generation. Mutations occur with probability μ and induce an individual to switch strategy.

Results

GENERAL PROPERTIES OF THE MODEL

Solving $\partial W > 0$ from equation (3) shows that selection favors reciprocal altruism if

$$c < b \frac{\bar{k}}{\bar{k} + 1}. \quad (4)$$

Given that $\bar{k} \geq 0$, this condition cannot be satisfied if $c > b$, implying that generalized reciprocity cannot evolve if the costs of a helpful act to the actor outweigh its benefits to the receiver. More interesting outcomes occur when $b > c$, and we will focus on this parameter regime from here onwards.

The fraction $\bar{k}/(\bar{k} + 1)$ that appears in condition (4) measures the expected future yield to reciprocal altruists of help that is currently being provided. As this quantity applies to the population of reciprocal altruists as a whole, we will refer to it as the collective yield (denoted as Y). We also define the individual yield for a specific node i in the network as $y_i = k_i/(k_i + 1)$. Note that, in general, $Y \neq E[y_i]$, although our simulations indicate that the approximation $Y \approx E[y_i]$ is reasonably accurate in most cases.

The collective and individual yields depend strongly on the frequency of conditional altruists in the population. Clearly, if an individual is the only conditional altruist in the population, then its individual yield is minimal; the other individuals do not reciprocate, and $y_i = Y = 0$. Conversely, if the entire population consists of reciprocal altruists, then the individual and collective yields attain their maximal value $y_i = Y = 1$. In this case, help is transmitted indefinitely such that, in a finite population, an individual who initiated or reciprocated help is bound to reap the benefits of that act at some time in the future. Between these two extremes, the collective yield increases monotonically with the frequency of reciprocal altruists (see the analytical results in the online supporting information), which leads to the prediction that there is a unique intermediate frequency f^* at which reciprocal altruists and defectors have equal fitness.

The initial spread of reciprocal altruists in a population of defectors is opposed by selection as long as the frequency of reciprocal altruists is below the critical frequency ($\partial W < 0$ if

$f_i < f^*$). However, it is conceivable that mutation, drift, or migration (temporarily) cause the frequency of reciprocal altruists to increase beyond f^* , in which case, selection can promote the further spread of reciprocal altruists ($\partial W > 0$ if $f_i > f^*$). Whether this is likely depends on the magnitudes of b and c relative to the effective population size (i.e., on the importance of drift relative to that of selection) and on the functional dependence of Y on f_i , which determines the value of f^* for a given ratio of b and c . Figure 1A shows an example that was calculated for a published network of preferred companionships in a small isolated population of bottlenose dolphins (*Tursiops* spp.) (Lusseau 2003). This example network (depicted in the upper left corner of Fig. 1A) contains 62 nodes and 159 edges. Large differences in the individual yield of altruism exist between nodes in the network (stepped gray lines indicate the distribution of individual yields), but the collective yield falls accurately within the range that is predicted by the analytical results (dashed lines; see the online supporting information and the section Analytical Results below). Variation in the individual yields is explained by differences in the positions of individuals in the network (e.g., yields are positively associated with degree and various measures of node centrality; data not shown). The critical frequencies indicated for this network (dotted lines) are for $b/c = 10$ (lower line; $f^* = 0.44$), $b/c = 5$ (middle line; $f^* = 0.71$), and $b/c = 2.5$ (upper line; $f^* = 0.92$). Results for other animal social interaction networks collected from the literature (Fig. 1B–L; see Table S1 for references to the original data sources) show a similar correspondence between analytically predicted upper and lower bounds for the collective yield and individual-based simulations, while demonstrating considerable variation in the shapes of the curves and the critical frequencies across species with different types of social interaction patterns.

Individual-based simulations of the model illustrate that reciprocal altruists can spread on the dolphin network under the influence of mutation, drift, and selection. Figure 2A shows how the frequency of the reciprocal altruists changes during a run with $b = 0.025$, $c = 0.005$, and $\mu = 1 \cdot 10^{-4}$. Evolution is mutation-limited for this combination of parameters: the population is fixed for either defectors or reciprocal altruists during most of the time and we occasionally observe rapid transitions between the two states. The waiting time to a transition from a population of defectors to one that consists entirely of reciprocal altruists is shorter than the time to a transition in the reverse direction. Longer simulations show that the difference is more than three-fold (Fig. 2B), indicating that a population of altruists is relatively stable against invasion by defectors (more so than a population of defectors against invasion by altruists, even though the critical frequency is as high as 0.71). The long-term average frequency of reciprocal altruists reaches 0.75 under these particular

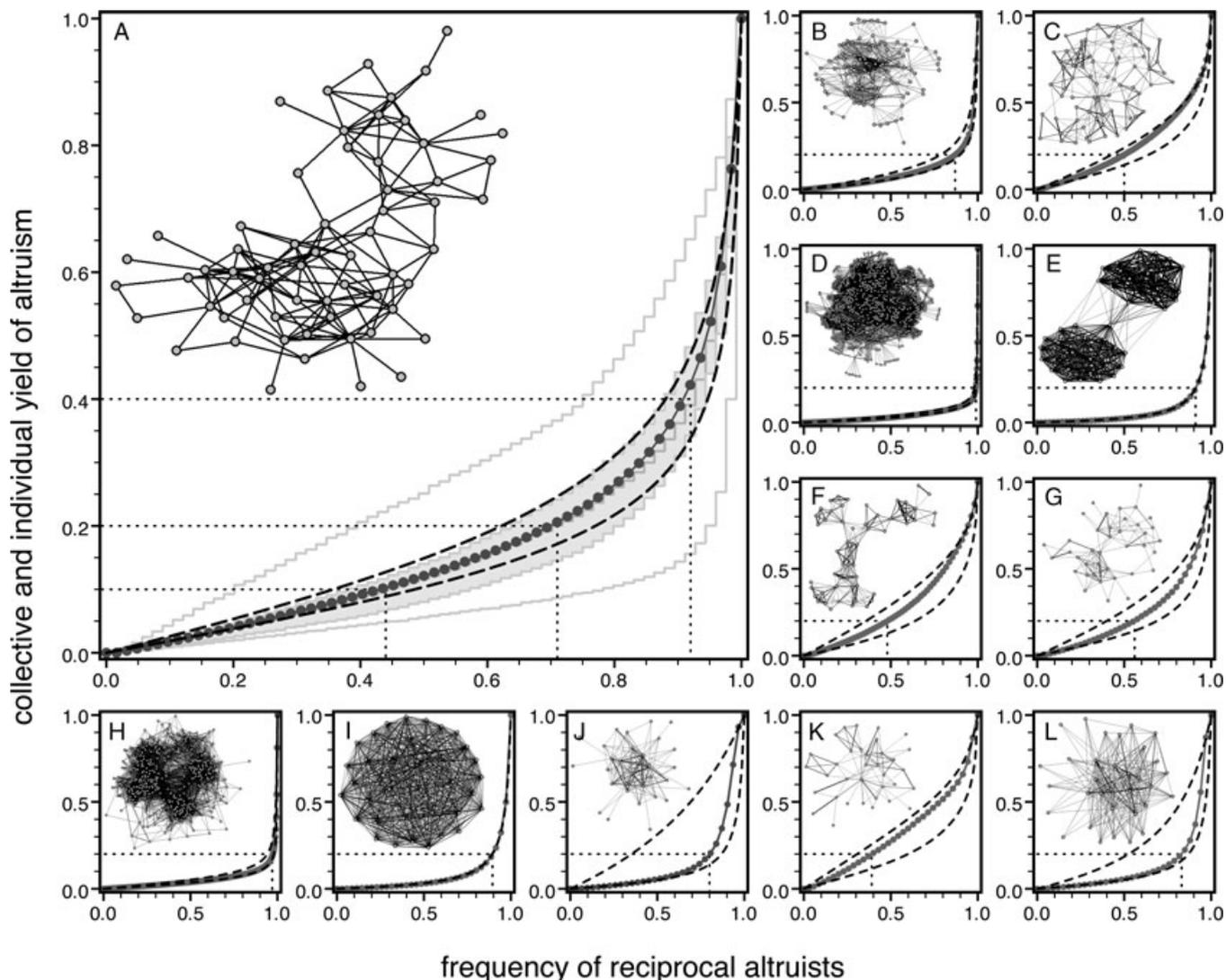


Figure 1. Collective and individual yield of altruism in various animal social interaction networks. (A) The yield of altruism $y_i = k_i/[1 + k_i]$ for individual nodes in a bottlenose dolphin network was estimated at discrete values of the frequency of reciprocal altruists ($f = 0, \frac{1}{62}, \frac{2}{62}, \dots, \frac{61}{62}, 1$). Each estimate was based on 62,000 replicate individual-based simulations to obtain an expectation over the distribution of reciprocal altruists over the network. Gray stepped lines indicate the distribution of individual yields at each frequency (shown are minimum, maximum, and median, and the 1st and 3rd quartiles with the interquartile range shaded in light-gray). The median of the individual yields nearly coincides with the collective yield (dark-gray line with filled circles), which converges at high and low frequencies of reciprocal altruists, respectively, to the upper and lower bounds predicted by our analytical results (dashed lines). Critical frequencies for the spread of reciprocal altruism under selection are indicated by dotted lines for different ratios of the payoff parameters b and c ($b/c = 2.5$, $b/c = 5$, and $b/c = 10$). The other panels show simulation results, analytical upper and lower bounds for the collective yield, and the critical frequency at $b/c = 5$, for a selection of networks from our dataset (see Table S1). (B) Trinidadian guppy, (C) African cichlid, (D) House finch, (E) Bechstein's bat, (F) Leaf-roosting bat, (G) Yellow-bellied marmot, (H) Galapagos sea lion, (I) Collared mangabey, (J) Vervet monkey, (K) Hamadryas baboon, (L) Guinea baboon. All networks in this study were drawn using a spring-embedding algorithm implemented in Netdraw 2.087 (Borgatti 2002).

parameter conditions. The difference in the stability of populations fixed for either defectors or reciprocal altruists is explained by the fact that selection against cooperation in populations with a majority of defectors is much weaker than selection favoring cooperation in populations with a majority of conditional altruists (Fig. 2C). Generalized reciprocity is a conditional strategy that

induces cooperation only in the presence of other cooperators. The per-capita cooperation rate is therefore inherently higher in populations nearly fixed for reciprocal altruism (Peña et al. 2011), generating large selection differentials that are far harder to overcome by drift than the selection differentials in populations that consist mainly of defectors. This asymmetry would even be more

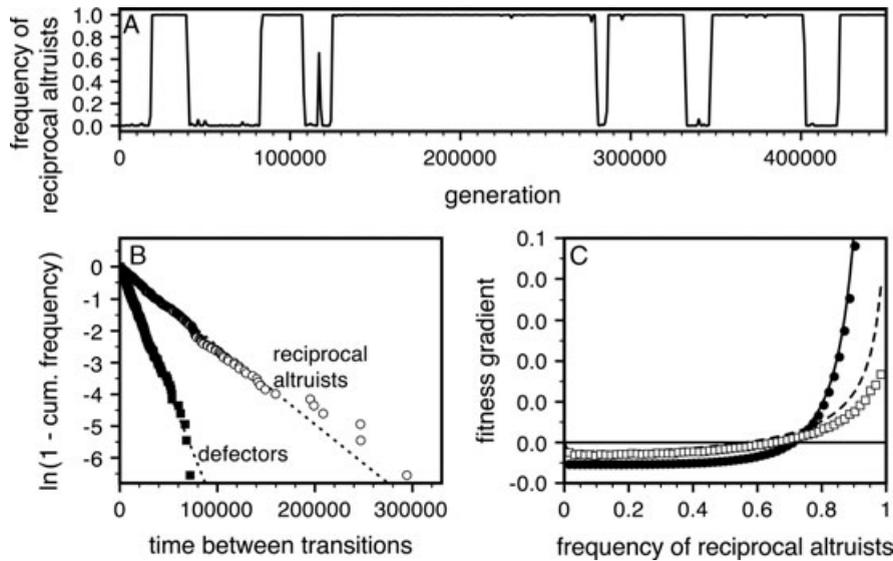


Figure 2. Evolution of generalized reciprocity in individual-based simulations. (A) Trajectory of the frequency of reciprocal altruists during an individual-based simulation on the dolphin network with $b = 0.025$, $c = 0.005$, and $\mu = 1 \cdot 10^{-4}$. The population is nearly fixed for either defectors or reciprocal altruists for most of the time, showing occasional rapid transitions between the two states. (B) The time between transitions follows an exponential distribution (plotted on log-linear axes, the data fall along a straight line), but transitions from a population of defectors to a population of reciprocal altruists (solid squares) tend to occur sooner than transitions in the reverse direction (open circles). Based on the slopes of the least-squares best linear fits to the data (dotted lines), the transition rates are estimated at, respectively, $8.77 \cdot 10^{-5}$ and $2.68 \cdot 10^{-5}$ per generation. (C) The difference in transition rates is explained by the high number of cooperative interactions at high frequencies of reciprocal altruists, which has a proportional effect on the absolute magnitude of the relative payoff difference between reciprocal altruists and defectors (∂W as defined in the text; solid circles: simulation results; solid line: analytical prediction). The long-term fitness gradient estimated from the fixation probabilities (open squares: simulation; dashed line: analytical prediction based on a Wright–Fisher model) show the same effect, indicating that selection is stronger (relative to drift) in populations of altruists than in populations of defectors.

pronounced if also defectors would occasionally spontaneously initiate cooperation, for example, as a result of errors in decision making.

DEPENDENCE ON THE STRUCTURE OF THE SOCIAL NETWORK

To further investigate the connection between network structure and the collective yield of altruism, we artificially constructed networks with varying structural properties. A comparison between the results of simulations on these networks indicates that sparsely connected, small communities offer an optimal substrate for the evolution of generalized reciprocity. Figure 3 illustrates the effects of three key structural network properties: average connectivity, modularity, and the pattern of connections between communities. A comparison of the critical frequencies (i.e., the frequency f^* that must be reached before selection can support the spread of generalized reciprocity; eq.4) between different networks provides a simple heuristic to predict differences in the likelihood of invasion of reciprocal altruism. The example networks shown in Figure 3 all have 128 nodes and are regular, meaning that nodes within a network have identical degree. The networks differ in the total number of links (Fig. 3A–C), the amount of clustering

(Fig. 3D–F) and the distribution of links over different levels of social organization (Fig. 3G–I).

Average degree has a strong effect on the evolution of reciprocal altruism. Figure 3A–C illustrates this for regular networks with degrees 2, 4, and 8, respectively (the only connected regular network with degree 2 is a cycle). The collective yield of altruism increases linearly with the frequency of reciprocal altruists in populations that predominantly consist of defectors (see the section Analytical Results below). For unweighted networks, the slope of this linear relationship is given by the inverse of the average degree. Accordingly, the critical frequency for the spread of reciprocal altruists becomes prohibitively large if individuals interact with many other individuals within their population. In highly connected networks, a random walk of altruistic interactions can typically reach any arbitrary individual in the population within a small number of steps. As a consequence, the random walk quickly diffuses away from the social neighborhood of the individual who initiated help, reducing the probability that help is reciprocated and undermining the incentives for altruistic behavior (Fletcher and Doebeli 2009).

The dominant effect of network sparseness is mitigated by community structure. The networks in Figure 3D–F were created

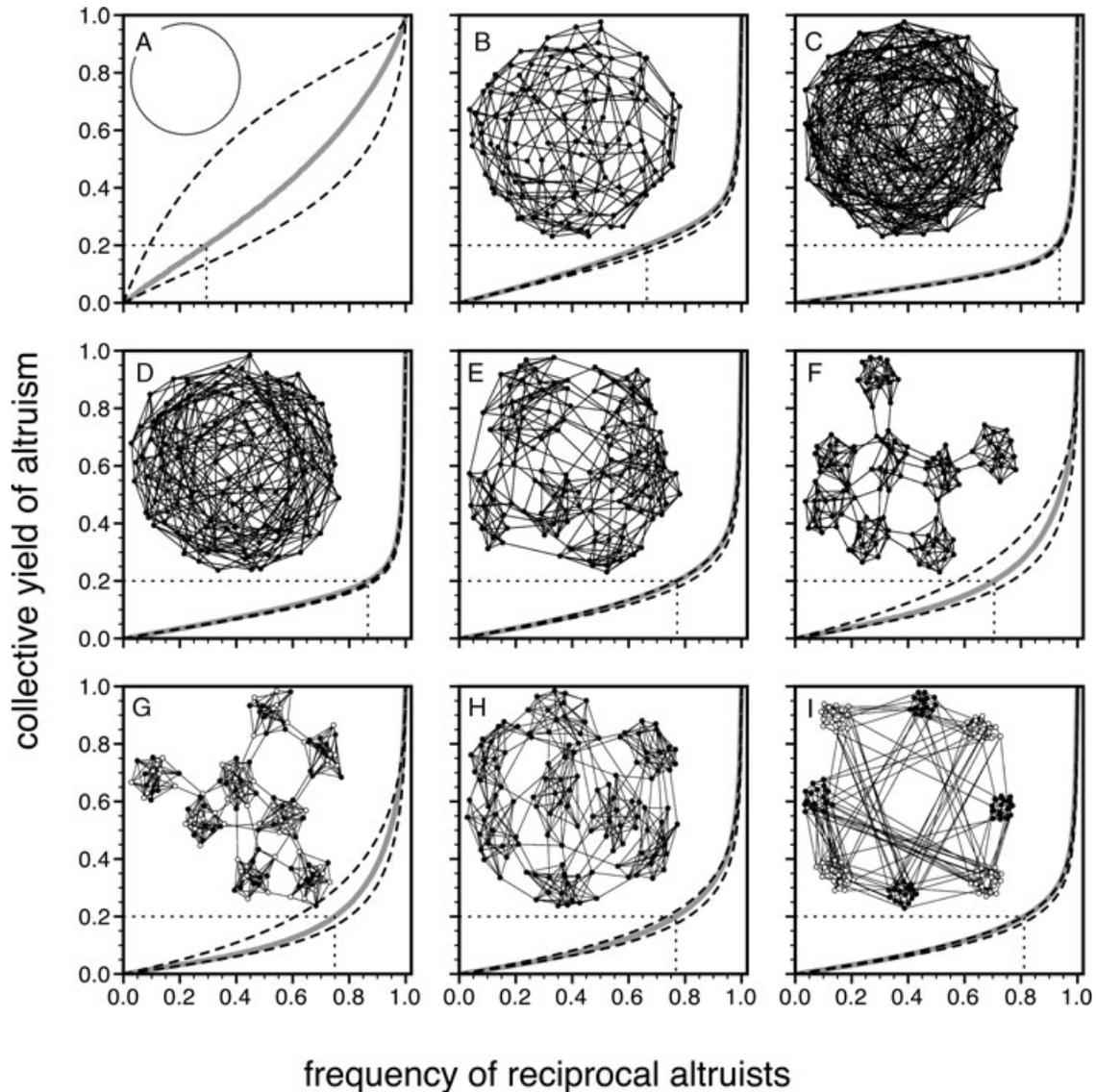


Figure 3. Dependence of the collective yield of altruism on network structure. Each panel shows individual-based simulation estimates of the collective yield (gray curves) as a function of the frequency of reciprocal altruists, with the corresponding upper and lower bounds (dashed lines) predicted by the analytical results. Dotted lines indicate critical frequencies for $b/c = 5$. (A–C) Regular networks with degrees 2, 4, and 8, respectively. (D–F) Regular networks with degree 6 and no, little, or strong clustering. (G–I) Regular networks with degree 7 that differ in the distribution of links across levels of social organization (see text for details; white and black node coloring highlights bipartite structure at low (G) or a high (I) level of organization).

by randomly replacing links within densely connected elementary clusters of 16 individuals with links between these clusters, without changing the degree of the nodes involved in the rewiring step (all nodes have degree 6 in the networks of Figure 3D–F). We varied the number of rewiring steps to create an unclustered network (Fig. 3D), in which connections between individuals were randomized, as well as weakly and strongly modular networks (Fig. 3E,F). Modularity facilitates the evolution of generalized reciprocity (the critical frequency f^* is lowest in panel F), but its positive effects on the collective yield appear primarily in populations that consist mainly of reciprocal altruists. This is because

community structure increases the frequency of random walks that visit (at least) two other reciprocal altruists before returning to the individual who initiated cooperation. The probability that such a random walk occurs is of the order of f_i^2 (i.e., the probability that two adjacent neighbors are reciprocal altruists), which bounds the effect of modularity on the collective yield. The biological implication is that community structure does little to promote the invasion of reciprocal altruists in a population of defectors, but can greatly support the stability of a population of altruists against invasion by defectors. This effect is illustrated in Figure 4A,B for an idealized network that consists of

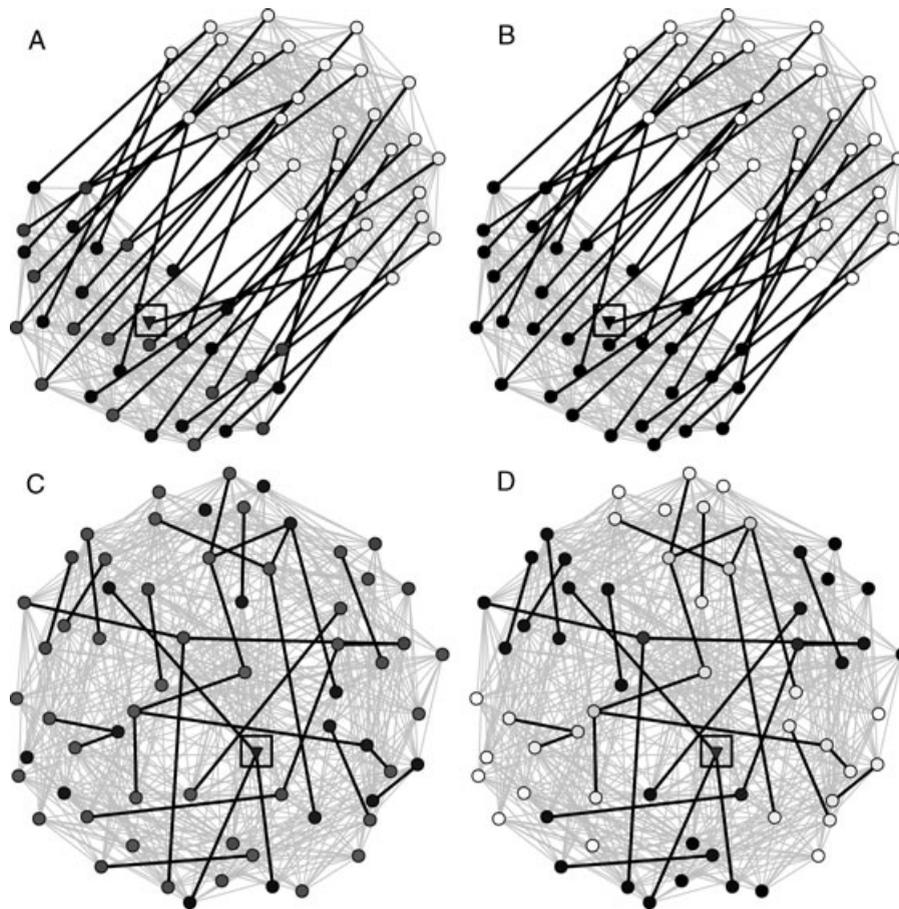


Figure 4. Modularity shelters altruists against exploitation by defectors. The network in (A) is subdivided in two dense communities with sparse connections between them. A single defector (triangle in box) in a population of altruists (circles) can exploit the altruists in its own community, but not those in other parts of the network. Nodes are colored according to the number of times individuals receive help from a single neighbor (lighter shades of gray correspond to higher values and indicate a higher payoff). (B) The two-community structure of the network is captured by the eigenvector of the Laplacian that is associated with the smallest nonzero eigenvalue λ_2 (nodes are colored according to the elements of this eigenvector). Equation (8) accurately predicts the Laplacian eigenvalue associated with the partitioning. With $V_A = V_B = 512$ and $V_{A \times B} = 32$, the value of λ_{AB} calculated from equation (8) matches exactly with the numerically calculated value, $\lambda_2 = 0.125$. The network in (C) is almost a bipartite graph, that is, the nodes can be subdivided in two groups with sparse connections within each group but many links between the two parts. A single defector is able to exploit the entire population of reciprocal altruists, strongly reducing the average payoff (panels [A] and [C] use identical gray scales). (D) The structure of the network is accurately reflected by the Laplacian eigenvector with the highest eigenvalue ($\lambda_{64} = 1.888$). Equation (8) (with $V_A = V_B = 512$ and $V_{A \times B} = 480$) predicts $\lambda_{AB} = 1.875$. The networks shown in this figure are unweighted; different line styles used for the ties are for illustrative purposes, to highlight the sparse connections between groups in (A) and (B), and within groups in (C) and (D). Figures S2 and S3 in the supporting material show color versions of this figure with additional eigenvectors of the Laplacian.

two communities. The distribution of payoffs over the network shows that community structure shields reciprocal altruists from exploitation by defectors that occur elsewhere in the network (Fig. 4A). Likewise, community structure concentrates the deleterious effects of defectors in their own social environment, such that they ultimately undermine their own future prospects of receiving help.

Connections between communities may exist at different levels of social organization, and also this has consequences for the collective yield of altruism (Fig. 3G–I). Panel H shows a network

with random connections within and between clusters of 16 individuals; each individual has five links with other individuals. In panel G, the network within each cluster is bipartite, with twice as many connections as in panel H, but there are only half as many connections between the clusters. A random walk on the network of Figure 3G can therefore quickly reach all the individuals within a cluster, but will jump between clusters with a low probability. The reverse is true for the network in panel I, which has twice as many connections between clusters as the one in panel H, a bipartite structure of connections between clusters,

and half the number of connections within clusters, creating two subcommunities of eight individuals within each group of 16. A random walk on this network is relatively slow to reach all other individuals within the group, but once it has left the cluster, it is likely to visit several other distant parts of the network before returning to its point of origin. A comparison across panels G–I in Figure 3 shows that the absence of connections at high levels of social organization has a stronger positive effect on the yield of altruism than the existence of subcommunities within groups. Long-distance links that connect individuals across several levels of social organization dramatically increase the number of individuals that have an opportunity to exploit an act of altruism. Such links, which are responsible for the “small-world” phenomenon observed in various types of networks (Watts and Strogatz 1998), tend to reduce the yield of altruism and improve the chances of defectors.

ANALYTICAL RESULTS

The derivation in the supporting information shows formally how social network structure affects the costs and benefits of generalized reciprocity. Here, we present only the main results of the analysis. Our analytical results are phrased in terms of the eigenvalues of the normalized Laplacian matrix, a commonly used matrix representation of networks that combines information about the degree of nodes and their connections with other nodes (Chung 1997). The Laplacian figures prominently in the theory of random walks on networks (Lovász 1993) and is important in methods to detect clusters in networks based on spectral graph partitioning algorithms (Pothen et al. 1990). The eigenvalue spectrum of the Laplacian contains information about the connectivity of the network, community structure, the average path length, and other network properties (Chung 1997). The same eigenvalues can also be related to the collective yield of altruism. For instance, the average number of return events at low frequencies of reciprocal altruists is given by

$$\bar{k} = \sum_{\ell=1}^{\infty} (-1)^{\ell+1} f^{\ell} \mu_{\ell+1}, \tag{5}$$

where μ_{ℓ} is the ℓ th centralized moment of the distribution of eigenvalues. These moments have a straightforward interpretation: it can be shown that $(-1)^{\ell} \mu_{\ell}$ is equal to the average probability that a random walk will return to its point of origin after exactly ℓ steps. For example, μ_2 is the probability that an individual reciprocates to the individual from whom it received help one step earlier (hence, we will refer to μ_2 as the probability of direct reciprocation). This leads to a simple linear approximation,

$$Y \approx f \mu_2 \tag{6}$$

for the collective yield at small f . The expansion can be continued with higher order terms; the second-order term introduces a

dependency on μ_3 , which is related to the clustering coefficient of the network. In unweighted networks, μ_2 simplifies to the inverse of the average degree \bar{d} , if the degrees of neighboring nodes are uncorrelated.

An alternative representation of equation (5),

$$\bar{k} = \frac{1}{N} \sum_{k=1}^N \frac{1 - \lambda_k}{1 - f(1 - \lambda_k)}, \tag{7}$$

directly relates \bar{k} and the (ordered) eigenvalues of the Laplacian, $\lambda_1 \leq \lambda_2 \leq \dots \leq \lambda_N$. Several general properties of the spectrum of the Laplacian help to interpret this result. The smallest eigenvalue, λ_1 , is equal to zero. This causes \bar{k} to diverge as $f \rightarrow 1$, in agreement with the fact that help is transmitted indefinitely in a population of reciprocal altruists. For connected networks, the other eigenvalues λ_k ($k = 2 \dots N$) are strictly positive and not larger than 2. The eigenvectors associated with these eigenvalues can be interpreted as mutually independent partitionings that each divide the network into two nonoverlapping sets of nodes. For example, the nodes in the two-community network of Figure 4 have either a large positive or a large negative weight in the second eigenvector (Fig. 4B), depending on whether the node occurs in the upper-right or the lower-left cluster in the network.

To develop an intuitive interpretation for equation (7), it is useful to consider a network that is subdivided into two parts, A and B , with little internal structure (as in Fig. 4). In this idealized case, the eigenvalue associated with the partitioning (A, B) is given by

$$\lambda_{AB} = V_{A \times B} \left[\frac{1}{V_A} + \frac{1}{V_B} \right], \tag{8}$$

where V_A and V_B denote the total number of connections to nodes in A and B , respectively, and $V_{A \times B}$ measures the total number of links between A and B . Equation (8) reduces to $\lambda_{AB} = 1$ if $V_{A \times B}$ is equal to its random expectation (i.e., $V_{A \times B} = \frac{V_A V_B}{V_A + V_B}$). In that case, the partitioning has no effect on the expected number of return events, as its contribution to the sum in equation (7) vanishes. The partitioning has a positive effect on \bar{k} if its eigenvalue is less than 1. This requires $V_{A \times B} < \frac{V_A V_B}{V_A + V_B}$, meaning that the partitioning (A, B) must separate two densely connected groups of nodes with only sparse connections between these groups (Fig. 4A,B). The opposite effect can occur as well: the network exhibits features of a bipartite graph if connections between A and B are relatively more frequent than connections within A or B (i.e., $V_{A \times B} > \frac{V_A V_B}{V_A + V_B}$; Fig. 4C,D). The eigenvalue associated with the partitioning is then bounded by $1 < \lambda_{AB} \leq 2$, resulting in a negative contribution to the expected number of return events. Unlike community structure, which helps to contain the detrimental effects of defectors (Fig. 4A), bipartite structure allows defectors to exploit cooperators all over the network, thus acting against the

evolution of generalized reciprocity by effectively equalizing payoff differences between network parts with and without defectors (Fig. 4C).

Social interaction networks observed in animal populations are different from the idealized example networks of Figure 4 in several respects. First, most realistic networks combine features of modularity and bipartiteness, having a spectrum with some eigenvalues $0 < \lambda_k < 1$ and others $1 < \lambda_k \leq 2$ (in fact, the mean of the eigenvalues is always equal to 1). However, bipartite structure is typically highly localized in networks that show evidence of modularity. In the dolphin network, for example, the distribution of payoffs is almost fully determined by the eigenvectors associated with the smallest and the second smallest nonzero eigenvalue, which highlight the main structure of the dolphin population (Fig. S4A–C). The eigenvectors associated with the largest and second largest eigenvalue, by contrast, are concentrated on a few adjacent nodes on a small bipartite subgraph of the network (Fig. S4D,E). Second, the eigenvalues λ_k of realistic networks are only partially determined by the total number of links within and between communities. For instance, based on equation (8), we predict $\lambda_2 \approx 0.09$ for the dolphin network, whereas the actual smallest nonzero eigenvalue of the Laplacian is $\lambda_2 \approx 0.04$. This difference can be fully accounted for by taking into consideration that network partitionings are often fuzzy, and some nodes may be some distance away from the cluster boundary (Fig. S4). To accommodate these quantitative refinements, we work directly with the complete eigenvalue spectrum of the Laplacian to measure how sparsely communities are connected with one another and to predict the effects of network structure on the expected number of return events.

At high values of f , we can improve the accuracy of equation (7) by taking into account that reciprocal altruists are (slightly) overrepresented among the neighbors of a reciprocating individual (see the derivation for the analytical upper bound in the online supporting information). This is because, most of the time, an individual that provides help has previously been helped by a reciprocal altruist in its network neighborhood. With this correction, the collective yield at small frequencies of defectors can be approximated as

$$Y \approx 1 - \frac{(1-f)N}{\bar{T}}, \quad (9)$$

where \bar{T} is the normalized mean access time (i.e., the average number of steps needed for the random walk to reach a randomly chosen individual relative to the expectation in a fully connected network; Lovász 1993). As equation (9) applies in the vicinity of $f = 1$, this approximation relates the evolutionary stability of a population of reciprocal altruists against invasion by defectors to a specific measure of the characteristic distance between nodes. Network modularity increases the

mean access time, consistent with our conclusion that community structure supports the evolutionary stability of generalized reciprocity.

EVALUATION OF EMPIRICAL NETWORK PROPERTIES

We used the analytical approximations for the collective yield at low and high frequencies of reciprocal altruists to quantify the variation illustrated in Figure 1 in terms of (1) how strongly realistic interaction networks support the invasion of generalized reciprocity, and (2) how well they protect communities of reciprocal altruists against exploitation by defectors. Following equations (6) and (9), we therefore calculated the probability of direct reciprocation, μ_2 , and the mean access time, \bar{T} , for each network in our dataset of animal social interaction networks (Table S1, Fig. S1). These indicators are interpreted, respectively, as measures for the likelihood of invasion and the evolutionary stability of generalized reciprocity.

Observed interaction networks in animal societies differ widely in their average connectivity, but almost invariably, the mean access time is much higher than one would expect for randomly connected networks with a similar connectivity (Fig. 5). This implies that, depending on network connectivity, effective population size and the ratio between the costs and benefits of cooperation, it may be more or less likely for reciprocal altruists to spread in a population of defectors but, in almost all cases, it will be relatively difficult for defectors to invade when cooperation has established itself. The high mean access time of real-world interaction networks is often caused by the presence of more or less clearly recognizable subcommunities (e.g., Fig. 1A–C, F–H), but in some cases it is due to a starlike group structure, where a few individuals form a densely connected core to which other peripheral individuals are connected (Fig. 1J,L). Exceptions to the rule that the structure of animal social interaction networks supports the evolution of generalized reciprocity are provided by the three datapoints in the lower left corner of Figure 5. Two of these, a network of grooming interactions in the collared mangabey (Voelkl and Kasper 2009; Fig. 1I) and a second association network in bottlenose dolphins (Wiszniewski et al. 2010; Fig. S1B), are similar to a large, well-mixed group (corresponding to the point [0,0] in Fig. 5), as one would expect. They have a very high connectivity and show only weak signs of modularity. The other exception is provided by a roosting network in a colony of Bechstein's bats (Kerth et al. 2011). This network also features a high connectivity but, surprisingly, exhibits a very clear community structure (Fig. 1E). In this case, the single individual connecting the two communities has the highest number of connections of all individuals, which eliminates the barriers that would normally prevent random walks of reciprocated cooperative interactions to jump from one part of the network to the other.

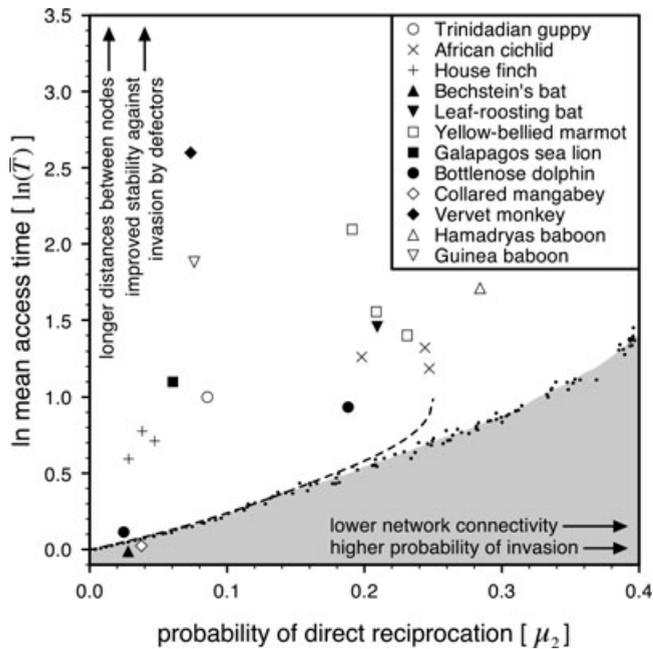


Figure 5. Connectivity and mean access time in real-world animal social networks. When reciprocal altruists are rare, the chance of being rewarded for providing help is proportional to the probability of direct reciprocity μ_2 (eq. 6). Accordingly, μ_2 quantifies the effect of network structure on the probability of invasion of generalized reciprocity. The mean access time \bar{T} determines the success of defectors in a population of reciprocal altruists (eq. 9). This quantity provides a measure of the extent to which network structure supports the persistence of cooperation. Values of μ_2 and \bar{T} were calculated for a set of 19 vertebrate social interaction networks collected from the literature (not all of these are represented in Figure 1; see Table S1 and Figure S1 for literature references, additional spectral properties, and visualizations of the networks). For most networks, the mean access time is higher than one would expect for a random network with a similar connectivity (small dots indicate reference values of μ_2 and $\ln \bar{T}$ for large Erdős–Rényi random graphs with varying mean degrees; the dashed line shows the analytical prediction for such graphs at high connectivity; see the methods in the online supporting information).

Discussion

Our analysis shows that generalized reciprocity can evolve in populations with varying types of interaction networks, provided that cooperation increases the mean fitness of the interacting individuals ($b > c$). The initial invasion of generalized reciprocity in a population of defectors is opposed by selection, at least, if reciprocal altruists are more likely than defectors to spontaneously initiate cooperation. However, if this is not the case or if individuals only rarely provide help spontaneously, it is conceivable that mutation or gene flow, in combination with genetic drift, can cause the frequency of reciprocal altruists to rise above a critical level

beyond which selection can favor the further spread of cooperation. Because generalized reciprocity is a conditional strategy, the expression of cooperative acts by reciprocal altruists is dependent on the presence of other cooperators. As a result, the observed rate of cooperative interactions increases sharply as generalized reciprocity nears fixation. This effect generates strong selection against defectors in populations that mainly consist of reciprocal altruists (Fig. 2C), effectively stabilizing such populations against the invasion of defectors (Fig. 2B).

The structural properties of the social network have a strong effect on both the initial spread of generalized reciprocity and its evolutionary stability. At low frequencies of reciprocal altruists, the yield of altruism is equal to the probability of direct reciprocity. Accordingly, the invasion of generalized reciprocity is facilitated in sparse networks where individuals interact frequently with a small number of social partners. This result is reminiscent of group size effects on the evolution of generalized reciprocity in well-mixed small social groups (Pfeiffer et al. 2005) and consistent with simulations comparing different cooperation strategies in heterogeneous contact networks (Iwagami and Masuda 2010). Low average network degree might also be viewed as an indicator of population viscosity, which has been shown to have significant effects on the occurrence and persistence of generalized reciprocity (Rankin and Taborsky 2009).

The yield of altruism is closely related to the mean access time (i.e., the mean number of steps needed for a random walk on the network to reach a randomly chosen individual) in populations that contain few defectors. Given that the mean access time is higher in networks that consist of sparsely interconnected communities, network modularity strongly supports the evolutionary stability of generalized reciprocity. Modularity is an important feature of many networks (Girvan and Newman 2002), including most of the animal social networks that we have analyzed. Group structure helps to contain the detrimental effects of defectors in their own social neighborhood, partially protecting reciprocal altruists elsewhere in the network from being exploited. A similar mechanism has been found to operate in a model where the decisions to cooperate and to disperse can evolve jointly (Hamilton and Taborsky 2005). In this case, groups of more and less-cooperative individuals arise, which introduces scope for between-group selection to act against defectors.

Our model provides an example of a mechanism by which conditional behavior can create differences between the interaction environments of cooperators and defectors. A reciprocal altruist induces other reciprocal altruists in its social environment to provide help, whereas a defector does not have such an effect. This difference results in positive assortment between altruists and the helping behaviors of others with whom they interact, satisfying a fundamental necessary condition for the evolution of altruism (Fletcher and Doebeli 2009). From this perspective, the

collective yield of altruism can be interpreted as a measure of the extent to which cooperators are capable of modifying their own interaction environment, highlighting network structure as a factor that quantitatively determines the degree of assortment between an individual's genotype and the amount of help it receives from others.

In this study, we have treated the social network as an externally imposed feature of the population that has arisen independently of the context of cooperation. This applies, for example, when attributes of the environment induce individuals to assort, either passively (e.g., by wind or water movement) or actively (e.g., in response to differences in food abundance, light, or temperature). Alternatively, heterogeneous networks may be structured by individual characteristics such as size, sex, age, condition, personality, and other properties that may not be obviously related to cooperative tendencies (Berman 1982; McPherson et al. 2001; Ruckstuhl 2007; Pike et al. 2008; Pinter-Wollman et al. 2009; Schürch et al. 2010). In other cases, however, animal social networks may have been directly shaped by the cooperative interactions that take place among their members. For instance, individual differences in cooperativeness may underlie behavioral assortment (Croft et al. 2009), or individuals may actively shape their personal social network to maximize the net benefit of cooperation (Hauert et al. 2002; Santos et al. 2006; Cao et al. 2011). Cooperative behaviors are frequent in the social species that have been subject to social network analysis, and it is not clear whether the observed properties of animal social networks are affected by this bias. One way to disentangle the interplay between the evolution of cooperation and the structure of social networks is to study theoretical models that allow cooperative behavior to coevolve with decision rule that govern the maintenance and establishment of network ties (Santos et al. 2006; Cao et al. 2011). Such models can clarify whether adaptive networking strategies lead to networks that are conducive to the evolution of cooperation. However, a major challenge for this approach is that the space of potential networking strategies is enormous, and it is not obvious which part of this strategy space might be accessible to animals with cognitive constraints and limited abilities to predict or observe the fitness consequences of the various options to build, maintain, or break social ties. Empirical studies on the development of social networks in animals are therefore essential to motivate minimal mechanistic models of strategic network formation, but, presently, such studies are scarce.

Another aspect that can be considered once more detailed social network data become available is that interaction structures are often dynamic. We expect that temporal variability would matter for the quantitative predictions of our model, if changes in network structure occur on a timescale comparable to the mean access time. In practice, there is a trade-off between the ability to resolve details of an individual's network neighborhood and

the temporal resolution of the inferred social structure. Animal social networks are thus often reconstructed from observations of individual interactions collected over an extended period of time (Croft et al. 2008). As a consequence, relevant temporal variability may have been averaged out in some of the empirical networks that we have analyzed, particularly those that are based on long-term association data (e.g., Lusseau 2003; Wiszniewski et al. 2010; Kerth et al. 2011). If this is indeed the case, interpreting these networks as snapshots of the social structure at a certain moment in time will have caused us to overestimate the number of potential interaction partners available to an individual at a given point in time, and underestimate the extent to which the population is subdivided into smaller communities. We note, however, that correcting for these biases would only reinforce the pattern shown in Figure 5.

Relatedness has an important effect on interaction patterns in many social species (Wolf and Trillmich 2008; Wey and Blumenstein 2010; Wiszniewski et al. 2010; Wolf et al. 2011). We have deliberately ignored kin structure in our study, to evaluate the impact of network properties on the propagation of generalized reciprocity separate from kin selection effects mediated by network reciprocity (Nowak 2006; Ohtsuki et al. 2006; Ohtsuki and Nowak 2007; Taylor et al. 2007). A recent simulation study (Iwagami and Masuda 2010) demonstrates that network reciprocity can support the evolution of generalized reciprocity in heterogeneous, scale-free networks. Scale-free networks (Barabási and Albert 1999) contain a small number of highly connected nodes (hubs) that offer the possibility to reach otherwise distant parts of the network in a small number of steps. As this so-called "small-world" property (Watts and Strogatz 1998) dramatically reduces the mean access time (Pandit and Amritkar 2001), our analysis predicts that scale-free social networks are not conducive to the evolution of generalized reciprocity (see also Fig. 3G–I). Nevertheless, if offspring disperse locally on the network, reciprocal altruists can persist and spread in scale-free networks if they manage to occupy some of the hubs and their surrounding nodes (Iwagami and Masuda 2010). The interaction between kin selection and network effects on the patterns of social information flow (central to this article) deserves further attention. Nevertheless, it is likely that the establishment of clusters of cooperators will also support the evolution of generalized reciprocity in networks with community structure like the ones we see in animal societies. There are thus several reasons to expect that the evolution of cooperation in animals is easier than theoretical models of idealized, well-mixed populations appear to suggest.

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Supporting Information

The following supporting information is available for this article:

Table S1. Graph spectra of animal social interaction networks.

Figure S1. Visualizations of the interaction networks represented in Figure 5.

Figure S2. Hit rates and Laplacian eigenvectors for a network with community structure.

Figure S3. Hit rates and Laplacian eigenvectors for a network with bipartite structure.

Figure S4. Modularity in the dolphin network.

Supporting Text. Derivation of the upper and lower bounds on the yield of altruism.

Supporting Information may be found in the online version of this article.

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