The evolution of generalized reciprocity on social interaction networks

— Supporting Information —

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Contents

Table S1 – Graph spectra of animal social interaction networks [a)]

Study species	Network of…	Data source	Nodes	Ties	Weighted	f^{*} [b)]	λ_2	λ_3	λ_4	λ_N	μ_2 [c)]	$\bar{T}$ [d)]
Trinidadian guppy (*Poecilia reticulata*)	shoal membership	Croft et al. (2004)	99	1452	yes	0.87	0.14	0.17	0.18	1.43	0.09	2.72
African cichlid [e)] (*Neolamprologus pulcher*)	affiliative interactions	Schürch et al. (2010)	72	370	yes	0.59	0.05	0.08	0.10	1.63	0.20	3.54
			72	345	yes	0.50	0.03	0.04	0.06	1.71	0.25	3.28
			72	473	yes	0.45	0.02	0.03	0.07	1.94	0.24	3.76
House finch (*Carpodacus mexicanus*)	social associations	Oh & Badyaev (2010)	538	22820	no	0.99	0.08	0.10	0.16	1.50	0.03	1.81
			528	13322	no	0.98	0.05	0.11	0.12	1.50	0.05	2.04
			835	28646	no	0.99	0.09	0.11	0.12	1.36	0.04	2.17
Bechstein's bat (*Myotis bechsteinii*)	roosting associations	Kerth et al. (2011)	42	898	yes	0.91	0.65	1.00	1.01	1.06	0.03	0.99
Leaf-roosting bat (*Thyroptera tricolor*)	roosting associations	Chaverri (2010)	55	424	yes	0.48	0.01	0.02	0.08	1.88	0.21	4.29
Yellow bellied marmot (*Marmota flaviventris*)	affiliative interactions	Wey & Blumstein (2010)	35	180	yes	0.58	0.09	0.19	0.24	1.75	0.23	4.07
			45	364	yes	0.47	0.06	0.07	0.15	1.82	0.19	8.13
			40	246	yes	0.56	0.04	0.15	0.17	1.82	0.21	4.74
Galápagos sea lion (*Zalophus wollebaeki*)	social associations	Wolf & Trillmich (2008)	405	14610	yes	0.97	0.07	0.11	0.12	1.50	0.06	3.00

(continued)

Study species	Network of…	Data source	Nodes	Ties	Weighted	f^{*} [b]	λ_2	λ_3	λ_4	λ_N	μ_2 [c]	$\bar{T}$ [d]
Bottlenose dolphin [f] (*Tursiops* spp.)	preferred companionships	Lusseau (2003)	62	318	no	0.72	0.04	0.23	0.25	1.71	0.19	2.54
	school membership	Wiszniewski et al. (2010)	120	8918	yes	0.96	0.29	0.58	0.62	1.16	0.02	1.12
Collared mangabey (*Cercocebus torquatus*)	grooming interactions	Voelkl & Kasper (2009)	35	1188	yes	0.89	0.78	0.87	0.90	1.19	0.04	1.02
Vervet monkey [e] (*Chlorocebus aethiops*)	grooming interactions	Voelkl & Kasper (2009)	31	219	yes	0.80	0.57	0.69	0.74	1.46	0.07	13.4
Hamadryas baboon (*Papio hamadryas*)	grooming interactions	Voelkl & Kasper (2009)	35	178	yes	0.39	0.05	0.09	0.12	1.88	0.28	5.53
Guinea baboon [e] (*Papio papio*)	socio-positive interactions	Voelkl & Kasper (2009)	33	512	yes	0.83	0.41	0.60	0.69	1.45	0.08	6.56

[a] The data set contains 19 networks. Networks with less than 30 nodes were not included, because they are not well suited for individual-based evolutionary simulations. Unless otherwise indicated, data are from free-ranging natural populations.

[b] Critical frequency at $b / c = 5$. Determines in combination with the payoff parameters and the effective population size how strongly the initial spread of reciprocal altruists is opposed by selection.

[c] The second centralized moment of the eigenvalue distribution μ_2 is a measure for the sparseness of the network and corresponds to the probability of direct reciprocation.

[d] The normalized mean access time $\bar{T}$ is defined as the mean number of steps that is needed for the random walk to reach a randomly chosen individual, relative to the expectation in a complete graph. High values of $\bar{T}$ are indicative of community structure, which can shield reciprocal altruists from exploitation by defectors. The mean access time provides a measure for the evolutionary stability of generalized reciprocity.

[e] Lab population, or animals held in captivity.

[f] The two studies on bottlenose dolphins use similar photo-identification surveys to infer preferred companionships/school membership from the presence of individuals in the same school, but different methods were used to translate the raw data into a network of associations.

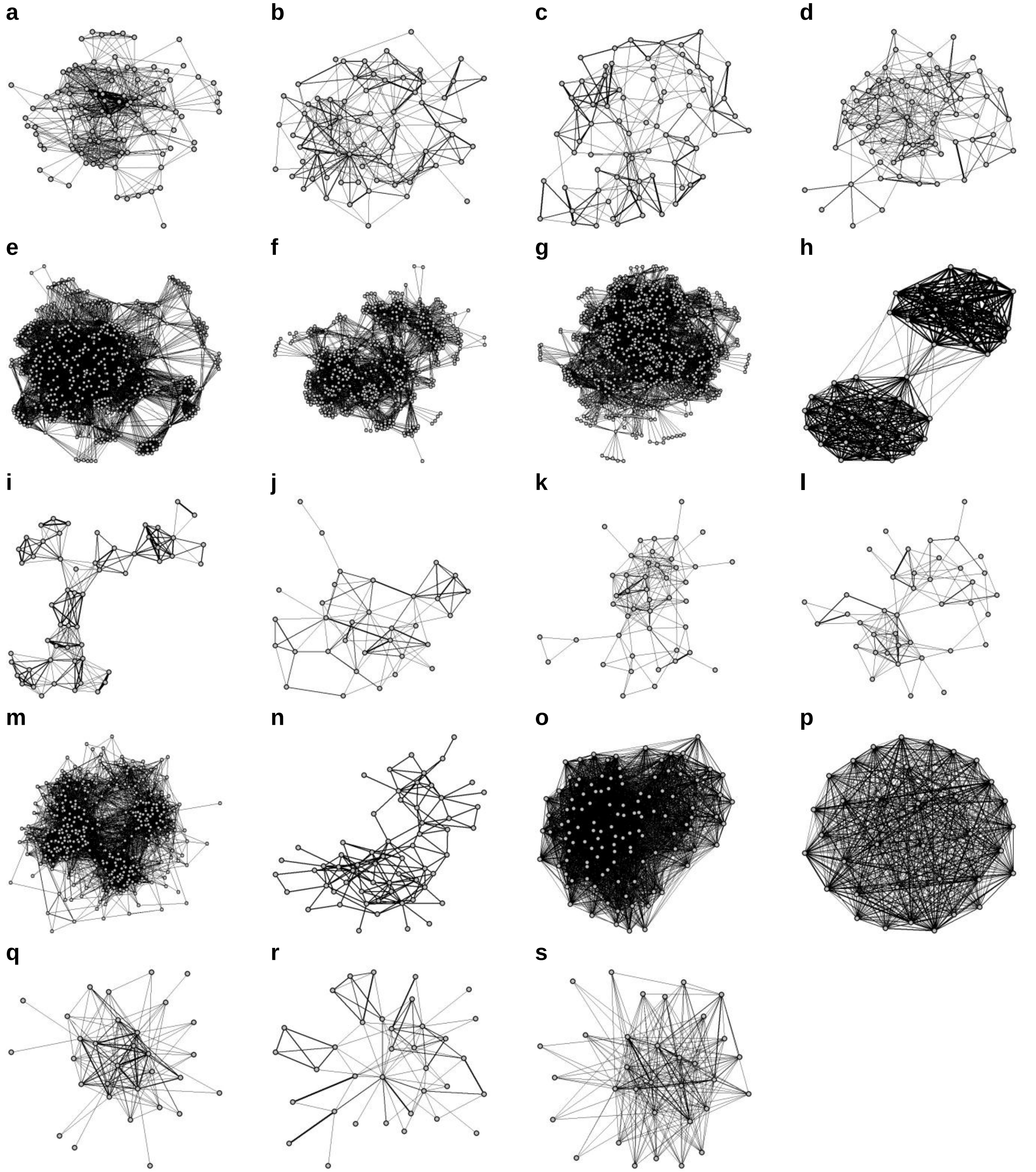

Figure S1 | Visualizations of the interaction networks represented in Figure 5. Networks were drawn using a spring-embedding algorithm (Netdraw 2.087; Borgatti, 2002) and are shown in the same order as represented in Table S1. (a) Trinidadian guppy; (b-d) African cichlid; (e-g) House finch; (h) Bechstein’s bat; (i) Leaf-roosting bat; (j-l) Yellow-bellied marmot; (m) Galapagos sea lion; (n,o) Bottlenose dolphin; (p) Collared mangabey; (q) Vervet monkey; (r) Hamadryas baboon; (s) Guinea baboon. Networks in (b), (d-f), (j), (k) and (o) are not included in Figure 1.

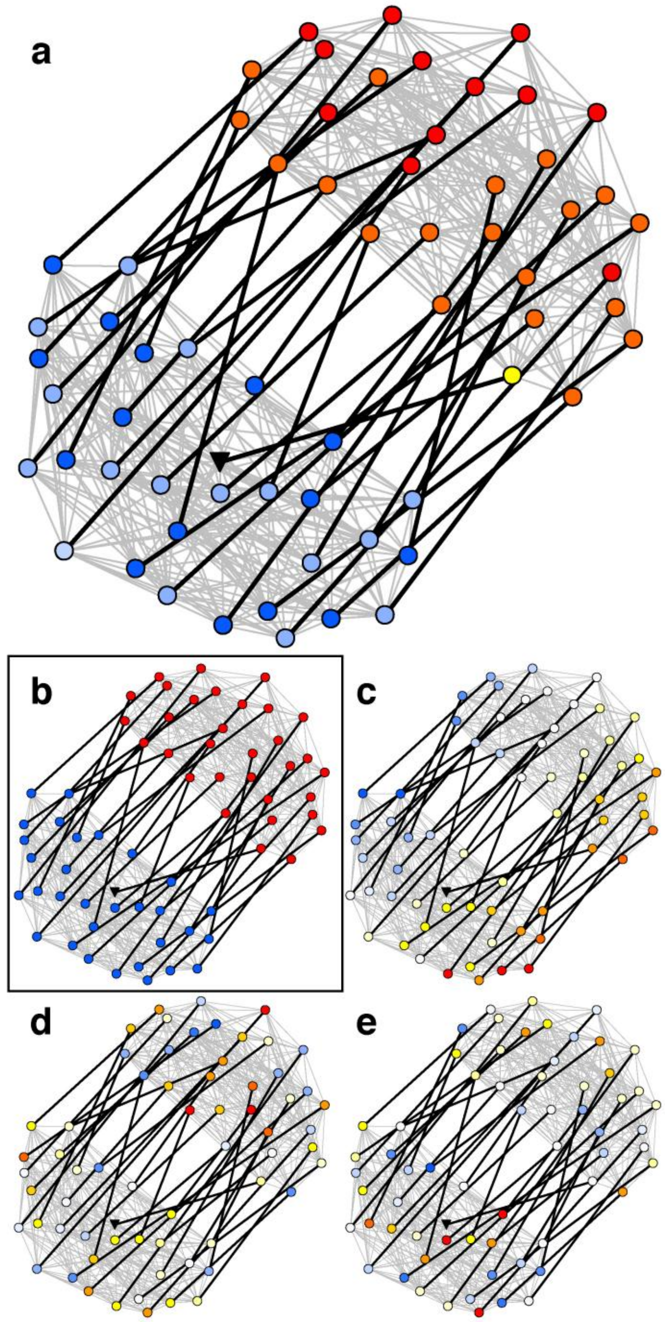

Figure S2 | Hit rates and Laplacian eigenvectors for a network with community structure. Colour version of Figure 4, with (a) the number of times individuals receive help from a single neighbour (cf. Figure 4a), and (b) the eigenvector of the Laplacian that captures the main subdivision of the population into two communities (cf. Figure 4b). The other panels show three additional eigenvectors. (c) Weak structure within the two communities (which is also detected by the algorithm that was used to draw the network) is highlighted by the eigenvector associated with the second smallest non-zero eigenvalue. (d) and (e) show the eigenvectors associated with the second-largest and the largest eigenvalue, respectively.

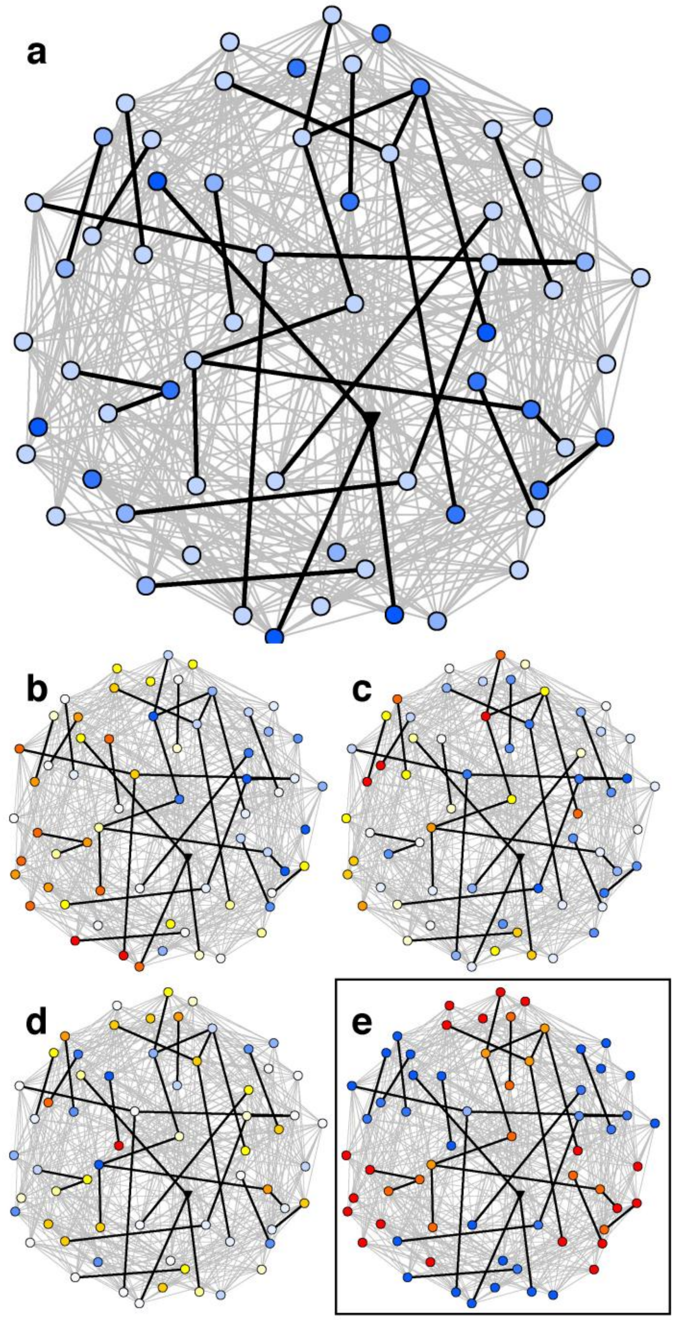

Figure S3 | Hit rates and Laplacian eigenvectors for a network with bipartite structure. Colour version of Figure 4, with (a) the number of times individuals receive help from a single neighbour (cf. Figure 4c), and (e) the eigenvector of the Laplacian that captures the bipartite structure of the population (cf. Figure 4d). The other panels show the eigenvectors associated with the smallest (b), second-smallest (c) and second-largest (d) nonzero eigenvalue of the Laplacian.

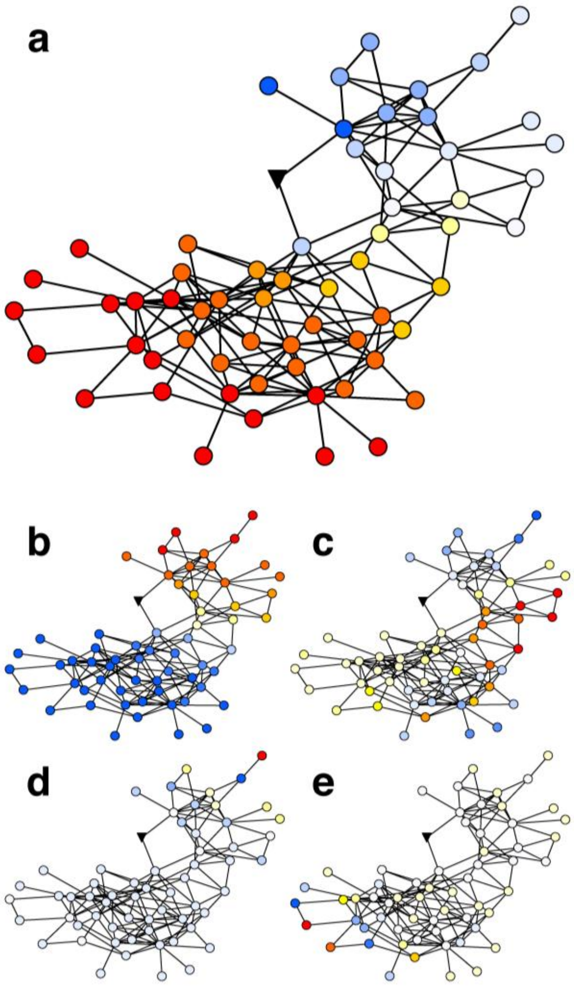

Figure S4 | Modularity in the dolphin network. (a) Simulations of our model on the bottlenose dolphin network (Lusseau 2003) show that a single defector (black triangle) in a population of altruists (circles) can exploit the altruists in its local network, but not those in other parts of the network. Reciprocal altruists are coloured according to the number of times they receive help from a single neighbour; values are mapped to a standard colour temperature scale that ranges from blue (lowest values) to red (highest values). The detrimental effects of the defector are concentrated in its own social environment, such that the defector ultimately undermines its own future prospects of receiving help. (b-e) Each network shows the weight of nodes in an eigenvector of the Laplacian, normalized for node degree. The upper two networks visualize the eigenvectors with the smallest (b) and second smallest (c) nonzero eigenvalues. These highlight communities of densely connected nodes that can also be recognized in panel (a). Mapped onto the lower two networks are the eigenvectors with the highest (e) and second-highest (d) eigenvalues, which highlight local bipartite network structure.

Supporting text | Derivation of the upper and lower bounds on the yield of altruism

Preliminary definitions

The social network is represented by a weighted graph G with N nodes and E edges. The weight of the edge between the nodes i and j is denoted as w_{ij}. The network is undirected (i.e., $w_{ij} = w_{ji}$), it has no self-loops (i.e., $w_{ii} = 0$), and the weights are positive. The degree of a node is defined as the sum of its edge weights, i.e., $d_i = \sum_j w_{ij}$. We assume that the network is connected. This implies that there is a path between each pair of nodes (i, j) and that each node has a degree larger than zero.

Four matrices associated with G will be important in the following analysis. The first one is the adjacency matrix $\mathbf{A}$, a $N \times N$ matrix with elements $\mathbf{A}_{ij} = w_{ij}$ representing the connectivity of the network. The second matrix is the degree matrix $\mathbf{D}$, a $N \times N$ diagonal matrix defined as $\mathbf{D} = \operatorname{diag}(d_1, d_2, \ldots, d_N)$. The third matrix is the normalized incidence matrix $\mathbf{E}$, which is a $N \times E$ matrix with elements

$$\mathbf{E}_{ik} = \begin{cases} \operatorname{sign}(i-j)\sqrt{\dfrac{w_{ij}}{d_i}} & \text{if edge } k \text{ connects node } i \text{ with node } j \\ 0 & \text{otherwise} \end{cases} \tag{S.1}$$

The product $\mathbf{E}\mathbf{E}^{\mathrm{T}}$ gives rise to the fourth matrix, a symmetric $N \times N$ matrix $\mathfrak{L}$ that is known as the normalized Laplacian of the graph (Chung 1997).

The matrices $\mathbf{A}$, $\mathfrak{L}$ and $\mathbf{D}$ are related to each other by

$$\mathbf{D} - \mathbf{A} = \mathbf{D}^{\frac{1}{2}} \mathfrak{L} \, \mathbf{D}^{\frac{1}{2}}, \tag{S.2}$$

and $\mathbf{L} = \mathbf{D} - \mathbf{A}$ is also known as the combinatorial Laplacian or the admittance matrix of the graph (Cvetković et al. 1998).

A random walk of cooperative interactions

We assume that the population at the current generation consists of a mixture of n reciprocal altruists and $N - n$ defectors. An initial spontaneous act of help by player i can trigger a sequence of reciprocated cooperative interactions among the reciprocal altruists. As long as the sequence does not hit a defector, it travels over the network as a random walk. Let $P_{i\to j}(\ell)$ denote the probability that the sequence has reached node j by the time that it has travelled ℓ steps. For $\ell > 0$, the probability $P_{i\to j}(\ell)$ satisfies

$$P_{i\to j}(\ell) = \sum_k p_{k\to j} P_{i\to k}(\ell - 1), \tag{S.3}$$

where

$$p_{k\to j} = c_k \frac{w_{kj}}{d_k} \tag{S.4}$$

denotes the probability that individual k, after having received help, reciprocates to another individual j. In this expression, $c_k = 1$ if individual k is a conditional cooperator and $c_k = 0$ if k is a defector.

An explicit expression for $P_{i\to j}(\ell)$ can be obtained by repeatedly applying the recurrence relation (S.3). The solution takes a simple form in matrix notation

$$P_{i\to j}(\ell) = \mathbf{e}_j^{\mathrm{T}} \left(\mathbf{A}\mathbf{D}^{-1}\mathbf{C}\right)^{\ell} \mathbf{e}_i , \tag{S.5}$$

where $\mathbf{C}$ is a diagonal matrix with elements $\mathbf{C}_{ii} = c_i$ and the $\mathbf{e}_i$ represent the unit base vectors of $\mathbb{R}^N$.

Equation (3) in the main text specifies how the fitness difference between reciprocal altruists and defectors depends on the expected number of return events $\bar{k}$. This quantity can be calculated from the probability distribution $P_{i\to j}(\ell)$: the number of times that the walk returns to conditional cooperator i is given by $k_i = \sum_{\ell\geq 1} P_{i\to i}(\ell)$ and $\bar{k}$ is the average of the k_i over all reciprocal altruists in the network. It is convenient to express the results in terms of the discrete Laplace transform of $P_{i\to j}(\ell)$ (Noh and Rieger 2004), which is defined as $\tilde{P}_{i\to j}(s) = \sum_{\ell=0}^{\infty} \tilde{P}_{i\to j}(\ell) \exp(-\ell s)$. Evaluating the Laplace transform at $s = 0$ gives $\bar{k} = \mathrm{E}\left[\tilde{P}_{i\to i}(0)\right] - 1$.

Relationship with structural properties of the network

Structural network properties, such as the presence of groups of densely connected nodes and the connectivity between such groups, are revealed by the eigenvalue spectrum of the graph. Many useful results are phrased in terms of the eigenvalues of the normalized Laplacian of the network (Chung

1997). We therefore rewrite the solution for $P_{i\to j}(\ell)$ in equation (S.5), using equation (S.2) to replace the adjacency matrix $\mathbf{A}$ by an expression that involves the normalized Laplacian. After some manipulation, we obtain

$$P_{i\to j}(\ell)=\sqrt{\tfrac{d_j}{d_i}}\,\mathbf{e}_j^{\mathrm{T}}\left(\left(\mathbf{I}-\mathfrak{L}\right)\mathbf{C}\right)^{\ell}\mathbf{e}_i\ , \tag{S.6}$$

where $\mathbf{I}$ is the $N\times N$ identity matrix.

Equation (S.6) is an exact result that is conditioned on the stochastic matrix $\mathbf{C}$. This matrix specifies the current distribution of reciprocal altruists over the network. The outcome of evolution over the course of many generations is likely to be only weakly dependent on the exact realization of $\mathbf{C}$ in any particular generation. Therefore, we proceed by studying the properties of the *annealed* random walk, by averaging over realizations of the distribution of altruists over the network.

Given that the random walk starts at a reciprocal altruist ($c_i=1$), the annealed probability that it will have travelled from node i to node j after ℓ steps is given by

$$P_{i\to j}(\ell)=\begin{cases}\mathbf{e}_j^{\mathrm{T}}\,\mathbf{e}_i & \text{if } \ell=0\\ \sqrt{\tfrac{d_j}{d_i}}\,\prod_{k=1}^{\ell}q_k\ \mathbf{e}_j^{\mathrm{T}}\left(\mathbf{I}-\mathfrak{L}\right)^{\ell}\mathbf{e}_i & \text{if } \ell\geq 0\end{cases} \tag{S.7}$$

Here, q_k is the probability that the *k*-th individual in the random walk will provide help, averaged over all possible realizations of the random walk and conditional on the fact that the walk has already travelled $k-1$ steps. It is easy to see that $q_1=1$ (by definition, the random walk is initiated by a reciprocal altruist) and $q_2=(n-1)/(N-1)$; this is the probability that a random neighbour of the individual who initiated help is a reciprocal altruist. Other than that, the sequence q_k depends in a complicated manner on both network structure and the position of individual i, although the latter dependence diminishes for longer random walks. We approximate the sequence q_k by choosing $q_1=1$, $q_2=f$ and $q_k=q_\infty$ for all $k>2$, where $f=n/N$ is the frequency of reciprocal altruists in the current generation, and where q_∞ is the probability that the random walk continues for at least one step after it has reached its stable asymptotic distribution over the network. The probability q_∞ is slightly larger than f, since the individuals that are visited by the random walk are not sampled randomly from the population. Instead, reciprocal altruists are overrepresented among the nodes that are adjacent to the current position of the random walk, since there must be a path connecting reciprocal altruists that leads to the current position (hence, $q_\infty > f$). A similar argument shows that $q_{k+1} \geq q_k$ for $k > 1$, such that the approximation $q_k = q_\infty$ provides an upper bound for the probability $P_{i\to j}\left(\ell\right)$. A lower bound is obtained by taking $q_k = f$ for all $k \geq 2$. In many cases, the upper and lower bounds are close together (see Figure 3a, f and g for exceptions). Moreover, the lower and upper bound predict the limiting behaviour of simulation results for $f \to 0$ and $f \to 1$, respectively (Figure 1). This section continues with a derivation of the upper bound. An expression for the lower bound can be obtained by substituting f for q_∞ in the right-hand side of the main result, equation (S.9).

Since $\mathfrak{L}$ is a symmetric matrix, its eigenvalues λ_k are real. We sort the eigenvalues in the order of increased magnitude, $\lambda_1 \leq \lambda_2 \leq \ldots \leq \lambda_N$, and normalize the corresponding eigenvectors $\mathbf{u}_k$ to unit length. The eigenvectors form an orthonormal basis of $\mathbb{R}^N$, such that the matrix of eigenvectors $\mathbf{U}$ ($\mathbf{u}_k$ is the k-th column of $\mathbf{U}$), can be used to decompose $\mathfrak{L}$ as $\mathbf{U\Lambda U}^\mathrm{T}$. Here, $\mathbf{\Lambda}$ is a diagonal matrix with the eigenvalues of the normalized Laplacian.

After substituting this factorization, we obtain the following expression for the discrete Laplace transform of equation (S.7)

$$\tilde{P}_{i\to j}\left(s\right) = \delta_{ij}\left(1-\tfrac{f}{q_\infty^2}\right) + \left(1-\delta_{ij}\right)\left(1-\tfrac{f}{q_\infty}\right)\tfrac{w_{ij}}{d_i}e^{-s} + \tfrac{f}{q_\infty^2}\sqrt{\tfrac{d_j}{d_i}}\sum_{k=1}^{N}\frac{\mathbf{U}_{ik}\mathbf{U}_{jk}}{1-q_\infty\left(1-\lambda_k\right)e^{-s}}, \tag{S.8}$$

where $\mathbf{U}_{ik}$ is the i-th element of eigenvector $\mathbf{u}_k$. In the final step of the analysis, we substitute $j = i$ and $s = 0$, and use the result to obtain an upper bound for the average number of returns:

$$\bar{k} \leq \tfrac{f}{q_\infty^2}\left[\tfrac{1}{N}\sum_{k=1}^{N}\tfrac{1}{1-q_\infty\left(1-\lambda_k\right)} - 1\right]. \tag{S.9}$$

A lower bound for the number of return events is obtained by substituting $q_\infty = f$, yielding

$$\bar{k} \geq \tfrac{1}{f}\left[\tfrac{1}{N}\sum_{k=1}^{N}\tfrac{1}{1-f\left(1-\lambda_k\right)} - 1\right]. \tag{S.10}$$

The eigenvalues and eigenvectors of the Laplacian reveal information about network community structure. This can be seen most clearly by considering a network that is subdivided into two parts, A and B, with little internal structure (Figures 4, S2 and S3). For such a network, one of the eigenvectors clearly reflects the subdivision of the network. The elements of that eigenvector are approximately

$$\left[\mathbf{v}_{AB}\right]_i \approx \begin{cases} +\tfrac{1}{V_A}\sqrt{d_i}\sqrt{\tfrac{V_A V_B}{V_A+V_B}} & \text{if } i \in A, \\ -\tfrac{1}{V_B}\sqrt{d_i}\sqrt{\tfrac{V_A V_B}{V_A+V_B}} & \text{if } i \in B, \end{cases} \tag{S.11}$$

If λ_{AB} is the eigenvalue associated with $\mathbf{v}_{AB}$, then, by definition, $\lambda_{AB}\left[\mathbf{v}_{AB}\right]_i = \left[\mathfrak{L}\mathbf{v}_{AB}\right]_i$. Working out the matrix multiplication on the right-hand side of this equation yields

$$\lambda_{AB} \approx 1 - \sum_{j\in A}\frac{\mathbf{A}_{ij}}{d_i} + \tfrac{V_A}{V_B}\sum_{j\in B}\frac{\mathbf{A}_{ij}}{d_i}, \tag{S.12}$$

which can be simplified further by multiplying both sides of the equation by d_i and summing over all $i \in A$. The result is

$$\lambda_{AB} \approx V_{A\times B}\left[\tfrac{1}{V_A} + \tfrac{1}{V_B}\right]. \tag{S.13}$$

This approximation is exact for the ideal case that $\mathbf{A}_{ij} = a_{A\times A}$ for all pairs $(i, j) \in A\times A$, $\mathbf{A}_{ij} = a_{B\times B}$ for all $(i, j) \in B\times B$ and $\mathbf{A}_{ij} = \mathbf{A}_{ji} = a_{A\times B}$ for all $(i, j) \in A\times B$, where $a_{A\times A}$, $a_{A\times B}$ and $a_{B\times B}$ are three arbitrary positive constants. The corresponding network exhibits no other structure than the subdivision into parts A and B, and

$$\lambda_{AB} = \tfrac{a_{A\times B}|B|}{a_{A\times A}|A| + a_{A\times B}|B|} + \tfrac{a_{A\times B}|A|}{a_{A\times B}|A| + a_{B\times B}|B|}. \tag{S.14}$$

This limiting case illustrates several general properties of the eigenvalues of the Laplacian: (1) the eigenvalue associated with a given partitioning (A, B) increases with the number of connections between A and B, properly normalized for the size of the groups and the number of connections within groups, (2) the eigenvalue approaches zero if A and B are nearly isolated, and (3) the eigenvalue attains its maximum value if the graph is bipartite and every single edge connects one of the nodes in A with a node in B (i.e., $a_{A\times A} = a_{B\times B} = 0$). In the general case, approximation (S.13) is not very accurate, due to the presence of structure within A and B, the absence of a discrete boundary between A and B, and the discreteness of connections in unweighted networks. It is possible to correct for these factors, but it is more practical to work directly with the eigenvalues of the Laplacian, relying on equation (S.13) only to qualitatively interpret the results.

Approximations for the collective yield

It is useful to examine the collective yield of altruism at low ($f \approx 0$) and high ($f \approx 1$) frequencies of reciprocal altruists, since its behaviour at those frequencies explains differences in the fixation probabilities of mutants. We first consider a neighbourhood of $f = 1$, where the upper bound provides an accurate estimate for the actual number of return events. In the following section we derive that $q_\infty = 1 - (1-f)\bar{T}^{-1}$, where $\bar{T}$ is the normalized mean access time of the random walk (the mean access time is the expected time needed for the random walk to reach a randomly chosen node in the network; Lovász, 1993). Using this result, and in the limit $f \to 1$, we find that $Y = \bar{k} \big/ \left(\bar{k}+1\right)$ is approximated by

$$Y \approx 1 - \frac{(1-f)N}{\bar{T}}. \tag{S.15}$$

To approximate the collective yield in populations that consist mainly of defectors, we first expand the right-hand side of equation (S.10) as a series,

$$\bar{k} \geq \tfrac{1}{f}\left[\tfrac{1}{N}\sum_{k=1}^{N}\sum_{\ell=0}^{\infty} f^{\ell}\left(1-\lambda_k\right)^{\ell} - 1\right] = \sum_{\ell=1}^{\infty} f^{\ell}\left(-1\right)^{\ell+1} \underbrace{\tfrac{1}{N}\sum_{k=1}^{N}\left(\lambda_k - 1\right)^{\ell+1}}_{\mu_{\ell+1}}. \tag{S.16}$$

Realizing that the term indicated by the curly brace represents a centralized moment of the distribution of eigenvalues ($\mathrm{tr}\left[\mathfrak{L}\right] = N$, such that $\mathrm{E}\left[\lambda_k\right] = 1$), this expression corresponds to equation (5) in the main text.

Equation (S.16) relates $\bar{k}$ to the cycle probabilities Z_ℓ, which represent the probabilities that the random walk will return to its point of origin after exactly ℓ steps. This can be seen by calculating Z_ℓ as

$$Z_\ell = \mathrm{E}\left[\left(\mathbf{AD}^{-1}\right)^{\ell}_{ii}\right] = \tfrac{1}{N}\mathrm{tr}\left[\left(\mathbf{AD}^{-1}\right)^{\ell}\right] = \tfrac{1}{N}\sum_{k=1}^{N}\rho_k^{\ell}, \tag{S.17}$$

where the ρ_k are the eigenvalues of the random walk matrix $\mathbf{AD}^{-1}$. If $\mathbf{v}_k$ is an eigenvector of $\mathbf{AD}^{-1}$ with eigenvalue ρ_k, then $\mathbf{D}^{-1/2}\mathbf{v}_k$ is an eigenvector of the Laplacian, i.e.,

$$\mathfrak{L}\,\mathbf{D}^{-1/2}\mathbf{v}_k = \left(\mathbf{I}-\mathbf{D}^{-1/2}\mathbf{A}\,\mathbf{D}^{-1/2}\right)\mathbf{D}^{-1/2}\mathbf{v}_k = \left(1-\rho_k\right)\mathbf{D}^{-1/2}\mathbf{v}_k\,. \tag{S.18}$$

Accordingly, the eigenvalues are related by $\lambda = 1-\rho$, and we find

$$Z_\ell = \tfrac{1}{N}\sum_{k=1}^{N}\left(1-\lambda_k\right)^\ell = \left(-1\right)^\ell \mu_\ell \quad \Rightarrow \quad \bar{k} \ge \sum_{\ell=1}^{\infty} f^{\,\ell} Z_{\ell+1}\,. \tag{S.19}$$

For small values of f, the actual value of $\bar{k}$ approaches the lower bound, and for $f \ll 1$, we can approximate the collective yield by truncating the series expansion in (S.19) at its leading order. This yields

$$Y \approx f\,Z_2 \approx \frac{f}{\bar{d}}\,. \tag{S.20}$$

The second approximation applies only to unweighted networks ($\bar{d}$ is the average degree), and is exact if there is no correlation between the degrees of neighbouring nodes (this assumption is commonly made in approaches that attempt to infer network properties from the degree sequence and appears reasonable in most applications; Baumann and Stiller 2005).

Expected length of the random walk

To estimate the value of q_∞, we calculate the average number of steps τ that the random walk will take before it hits a defector, after it has converged on its stable asymptotic distribution; q_∞ and τ are related by $q_\infty = 1-1/\tau$. The stationary distribution of the random walk over the network is given by

$$P_i^* = \lim_{\ell\to\infty}\frac{P_{j\to i}\left(\ell\right)}{\sum_{k=1}^{N} P_{j\to k}\left(\ell\right)} = \frac{d_i}{V_G}\,, \tag{S.21}$$

where $V_G = \sum_{i\in G} d_i$ denotes the volume of the graph *G*. It can be verified that this solution corresponds to an eigenvector of the random walk matrix $\mathbf{AD}^{-1}$ with eigenvalue 1.

The individual identifiers of the n reciprocal altruists in the population are collected in a set C ($C = \{i \mid c_i = 1\}$) and those of the $N-n$ defectors are collected in a set *D* ($D = \{i \mid c_i = 0\}$). We now define $F_{C\to D}(\ell)$ as the probability that a random walk, started at a node $i\in C$ will reach a defector for the first time after ℓ steps. This probability is identical to a first-passage probability (Noh and Rieger 2004) between two sets of nodes, *C* and *D*, in a population that consists entirely of reciprocal altruists (i.e., in this population, individuals are assigned to one of two groups according to the partitioning of the original population into reciprocal altruists and defectors). Accordingly, $F_{C\to D}(\ell)$ satisfies the relationship

$$P_{C\to D}(\ell)=\sum_{\ell'=0}^{\ell}P_{D\to D}(\ell-\ell')\,F_{C\to D}(\ell'), \tag{S.22}$$

where the coefficients $P_{A\to B}(\ell)=V_A^{-1}\sum_{i\in A,\, j\in B}d_i\,P_{i\to j}(\ell)$ denote the probability of moving from a node in set A to a node in set B in ℓ steps, under the assumption that the starting nodes in A are drawn from the stationary distribution P_i^* of the random walk.

The expected time needed for the random walk to reach one of the nodes in set *D* is given by

$$\tau=\sum_{\ell=0}^{\infty}\ell\,F_{C\to D}(\ell)=-\tilde{F}'_{C\to D}(0). \tag{S.23}$$

The second equality in this expression relates τ to the discrete Laplace transform of $F_{C\to D}$, which is given by $\tilde{F}_{C\to D}(s)=\tilde{P}_{C\to D}(s)/\tilde{P}_{D\to D}(s)$; this result is obtained by applying a Laplace transform on both sides of equation (S.22) and solving the resulting equation (Noh and Rieger 2004). Evaluating the Laplace transform for $\tilde{P}_{i\to j}(s)$ in equation (S.8) for $f=q_\infty=1$ (the first-passage probability is calculated for a population of reciprocal altruists) and expanding $\tilde{F}_{C\to D}(s)$ as a series in *s* before taking the derivative yields,

$$\tau=\tfrac{V_G}{V_D}\sum_{j\in D}\left[\tfrac{1}{V_D}\sum_{i\in D}\left(\mathbf{D}^{\frac{1}{2}}\mathfrak{L}^{+}\mathbf{D}^{\frac{1}{2}}\right)_{ij}-\tfrac{1}{V_C}\sum_{i\in C}\left(\mathbf{D}^{\frac{1}{2}}\mathfrak{L}^{+}\mathbf{D}^{\frac{1}{2}}\right)_{ij}\right], \tag{S.24}$$

where $\mathfrak{L}^{+}=\mathbf{U}\mathbf{\Lambda}^{+}\mathbf{U}^{\mathrm{T}}$ is the Moore-Penrose pseudoinverse of the Laplacian ($\mathbf{\Lambda}^{+}$ is a diagonal matrix with $\mathbf{\Lambda}^{+}_{kk}=\lambda_k^{-1}$ for $k\neq 1$ and $\mathbf{\Lambda}^{+}_{1,1}=0$). Averaging over all possible partitionings (C,D) and assuming that the number of defectors is small, yields,

$$\tau=\tfrac{N\bar{d}}{N-n}\,\tfrac{1}{N-1}\sum_{j}\left[\tfrac{1}{d_j}\,\mathfrak{L}^{+}_{jj}\left(1+2\left(1-\tfrac{1}{N-n}\right)\left(1-\tfrac{\bar{d}}{d_j}\right)\right)\right]. \tag{S.25}$$

Here, we have exploited the fact that the stationary distribution of the random walk spans the null-space of $\mathbf{L}^{+}$, such that elements in each row of the matrix $\mathbf{D}^{\frac{1}{2}}\mathfrak{L}^{+}\mathbf{D}^{\frac{1}{2}}$ sum to zero.

Equation (S.25) simplifies for regular graphs $d_j \approx \bar{d}$, or if the correlation between cluster membership and degree is weak ($E\left[\mathfrak{L}^{+}_{jj} / d_j^2\right] \approx 0$). In that case,

$$\tau \approx \tfrac{N}{N-n}\bar{T}\ , \tag{S.26}$$

where

$$\bar{T} = \frac{1}{N-1}\sum_{k=2}^{N}\left[\frac{1}{\lambda_k}\sum_{i=1}^{N}\tfrac{\bar{d}}{d_i}\mathbf{U}_{ik}^2\right] \tag{S.27}$$

is the normalized mean access time (cf. Lovász, 1993, p. 18). We used approximation (S.26) in all of our numerical calculations. In regular networks, $\bar{T}$ reduces to the inverse of the harmonic mean of the eigenvalues $\lambda_2, \lambda_3, \ldots, \lambda_N$.

Supporting methods | Mean access time in Erdős-Rényi random graphs (methods for Figure 5)

Figure 5 compares the probability of direct reciprocation (μ_2) and the normalized mean access time ($\bar{T}$) between real-world animal interaction networks and (connected) Erdős-Rényi random graphs (Erdős and Rényi 1959). To generate such graphs, we made random connections between pairs randomly drawn with replacement from a set of 400 nodes, and varied the total number of connections to create graphs with varying average degree (each dot in Figure 5 represents values for a single such graph). Only the largest component of the random graph was retained to numerically calculate the eigenvalue spectrum, μ_2 and $\bar{T}$ (the range of values of μ_2 represented in Figure 5 lies below the percolation threshold, i.e., the network contains a giant component to which almost all of the nodes belong).

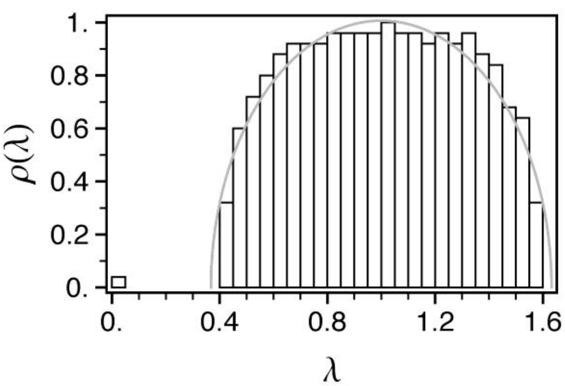

Figure S5 | The semicircle law. The white bars represent a histogram of the eigenvalues of the normalized Laplacian of a large Erdős-Rényi random graph (N = 500; p = 0.02; eigenvalues were calculated numerically). The spectral density converges in the limit of large N to a semi-circular distribution (grey line). This is a special case of Wigner's semicircle law for the distribution of eigenvalues of large random matrices (Wigner 1955, 1958; Equation (S.28)).

The dashed line in Figure 5 was calculated by using the fact that the spectral density of large Erdős-Rényi random graphs converges to a semicircular distribution (Wigner 1955, 1958; Figure S5). That is, if N is the number of nodes in a connected Erdős-Rényi random graph, and p is the probability of finding a tie between a pair of randomly selected nodes, then the probability density distribution of the non-zero eigenvalues of the graph Laplacian approaches

$$\rho(\lambda) = \begin{cases} \frac{1}{\sigma\pi}\sqrt{1-\left(\frac{1-\lambda}{2\sigma}\right)^2} & \text{if } 1-2\sigma < \lambda < 1+2\sigma\,, \\ 0 & \text{otherwise}\,, \end{cases} \tag{S.28}$$

in the limit $N \to \infty$. The width of the semi-circular distribution is given by $\sigma \approx 1/\sqrt{N\,p}$. Given that $0 < \lambda \le 2$, approximation (S.28) applies for $N\,p > 4$.

The correlation between node degree and cluster membership is weak in Erdős-Rényi random graphs, such that, based on equation (S.27), we can calculate the normalized mean access time as

$$\begin{aligned} \bar{T} &\approx \frac{1}{N-1}\sum_{k=2}^{N}\frac{1}{\lambda_k} \times \frac{1}{N}\sum_{i=1}^{N} d_i \times \frac{1}{N}\sum_{i=1}^{N}\frac{1}{d_i} \\ &\approx \int_{1-2\sigma}^{1+2\sigma}\frac{1}{\lambda}\rho(\lambda)\,d\lambda \times \sum_{k=1}^{N} k\,D(k) \times \sum_{k=1}^{N}\frac{1}{k}D(k) \\ &= \frac{2}{1+\sqrt{1-\frac{4}{N\,p}}} \times \frac{N\,p}{1-(1-p)^N} \times \sum_{k=1}^{N}\frac{1}{k}D(k)\,. \end{aligned} \tag{S.29}$$

Here, $D(k)$ is the degree distribution of the network, which, for $k \ge 1$, is given by

$$D(k) = \Pr\left[d_i = k\right] = \frac{\binom{N}{k} p^k (1-p)^{N-k}}{1-(1-p)^N}\,. \tag{S.30}$$

The sum in the last term of expression (S.29) has no simple explicit solution, but it can easily be evaluated numerically. The calculation of μ_2 for Erdős-Rényi random graphs is also straightforward using the semicircle law. We find

$$\mu_2 \approx \int_{1-2\sigma}^{1+2\sigma}(1-\lambda)^2\,\rho(\lambda)\,d\lambda = \frac{1}{Np}\,, \tag{S.31}$$

in agreement with our earlier result that μ_2 is equal to the inverse of the average degree in unweighted networks, if the degrees of neighbouring nodes are uncorrelated (see Equation (S.20)).

Supporting references

(literature not cited in the main text)

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