Conjoining uncooperative societies facilitates evolution of cooperation

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Social structure affects the emergence and maintenance of cooperation. Here we study the evolutionary dynamics of cooperation in fragmented societies, and show that conjoining segregated cooperation-inhibiting groups, if done properly, rescues the fate of collective cooperation. We highlight the essential role of inter-group ties, that sew the patches of the social network together and facilitate cooperation. We point out several examples of this phenomenon in actual settings. We explore random and non-random graphs, as well as empirical networks. In many cases we find a marked reduction of the critical benefit-to-cost ratio needed for sustaining cooperation. Our finding gives hope that the increasing world-wide connectivity, if managed properly, can promote global cooperation.

A core problem in evolutionary game theory is that of cooperation. Cooperation involves individuals paying a cost to benefit others, and is a ubiquitous feature of the social life [1,2]. The structure of social networks affect pathways of information, exchange, and other interpersonal mechanisms which undergird cooperation [2]. Thus a natural question in the mathematical study of evolutionary dynamics of cooperation is how network structure influences collective cooperative outcomes [5–8,10].

Here we look at the evolution of cooperation from a new perspective. We ask the question of how the interconnection between segregated *groups* can promote cooperation. Similar to individuals forming groups towards collective individually-implausible accomplishments, sometimes groups come together to form larger composite structures. Examples abound throughout history, from trade and intermarriage relations between tribes and communities in antiquity, to the waves of globalization which increasingly connect local entities for economic, cultural, and technological exchange. Another example is project management at different levels in corporations and organizations, which involves the cooperative division of labor between sparsely-interconnected distinctly-specialized units.

We use the framework of evolutionary graph theory [6,7,10] to study settings where groups that are individually undesirable for cooperation can be conjoined to build larger cooperation-promoting structures. We first study the conjoining of cohesive communities (clique-like structurally-homogeneous groups) under different connection schemes. We then focus on extremely-heterogeneous structures. We study stars and their various interconnection schemes, as well as rich clubs, and introduce ensuing topologies that are *super-promoters* of cooperation. Then we focus on bipartite graphs. In addition to these ideal graph families, we consider several random graph models. Finally, we consider empirical social networks and investigate the role of community structure on the evolution of cooperation. The findings are consistent across topologies: sparse interconnections of cooperation-inhibiting graphs leads to composite structures that are better for the evolution of cooperation.

Under the framework of mathematical graph theory, social structure is described by a graph, in which nodes represent individuals and links represent interactions and/or relations. In the simplest setting, individuals are conventionally envisaged with two possible strategies pertaining to a 2×2 context-specific payoff matrix which characterizes their interaction. The outcomes of these interactions ('games') determine the 'fitness' values of the individuals: those who accrue more benefits are endowed with higher fitness, which governs their influence over the peers' choices of strategy. The most stringent form of cooperation is found in the Prisoner's Dilemma (PD) game, in which individuals are either cooperators (paying a cost c and bestowing benefit $b > c$ upon the interaction partner) or defectors (who seek to benefit without paying a cost). The analysis throughout this paper uses the so-called 'donation game' version of PD (as shall be discussed, generalization to arbitrary symmetric 2-player games is straightforward). In this game, mutual cooperation has payoff $b - c$, unilateral cooperation has payoff $-c$ for the cooperator and b for the defector, and mutual defection has payoff 0. The ratio b/c characterizes the trade-off players face. Throughout this paper, without loss of generality, we set $c = 1$. This is simply equivalent to a change of scale in payoffs, and helps brevity of notation. The strategies of the agents change according to death-birth (dB) updating: a random individual is chosen to update; it adopts one of the the neighbors' strategies proportional to payoff. The small 'd' indicates that death is random, while the large 'B' indicates that birth is under selection. The probability that the chosen node copies the strategy of neighbor y is proportional to $1 + \delta\pi_y$, where δ denotes the selection strength and π_y is the average payoff that node y gleans playing with its own neighbors. We consider the limit of weak selection. To see if natural selection favors or hinders collective cooperation, we must calculate the probability that a single cooperator emerging at a random place in the network takes over the population. Natural selection favors cooperation if this fixation probability exceeds that of the fixation probability of a defector. Otherwise, natural selection inhibits cooperation.

Before we proceed, we point out a central feature of network models of cooperation, such as ours. In these models, social influence spreads beyond immediate neighbors. In conventional models of social contagion, such as simple contagion models, which often describe information diffusion, and complex contagion models, which often describe spread of behaviors [11,12], the ego's activation probability depends on the states of the alters. An activated alter exerts the same influence on the ego regardless of the states of the neighbors of that alter. For example, in the simple-contagion model of information diffusion, the ego needs to have heard the news from only one alter to have become informed, and is agnostic to how many neighbors of that alter have heard the news. Or in threshold models of complex contagion, the ego is activated once a certain number or fraction of alters are activated, regardless of the ego's second neighbors. In contrast, due to the strategic nature of cooperative dynamics, in our model, the radius of influence is two [13]. Ego is influenced directly by the strategies of the alters (from whom ego copies its strategy), and also indirectly by those of the neighbors of each alter (who contribute to the payoff of that alter). Our model, with a setting similar to the previous theoretical [5–7,10] and experimental [3,4] studies of human cooperation, thereby adds a strategic element to pure imitation dynamics. Our model shares one similarity with simple contagion processes: having one alter who has adopted each of the strategies makes the ego's adoption probability for that strategy nonzero.

A recently-discovered formulation gives the exact condition under which natural selection favors cooperation on a given network [10]. The solution utilizes the mathematical equivalence of the problem to that of coalescing random walks on the graph, and the solution is in terms of the remeeting times of random walkers initiated at each node. In the Methods section, we provide a brief overview of the framework. For a given network, the framework produces a quantity (which we denote by b^*) that determines the fate of cooperation. For any network, we have $|b^*| > 1$.

If b^* is positive, then b^* is the critical benefit-to-cost ratio. That is, natural selection promotes cooperation on the given network if the benefit-to-cost-ratio is greater than b^*. The closer b^* is to unity, the better the network is for promoting cooperation. Conversely, if b^* is negative, natural selection inhibits cooperation for any benefit-to-cost ratio. In these cases, the network promotes 'spite' instead of cooperation. That is, individuals are willing to pay a cost to reduce the payoff of others. The closer the value of b^* is to -1, the more strongly the network promotes spite. The convention of the literature has hitherto been using b^* to characterize the conduciveness of networks for cooperation [1,4,6,7,10]. In Supplementary Method 1.2., we remark that $1/b^*$ can also be used, we discuss the advantages of each measure, and we find that some of the numerical results are visually better presentable using $1/b^*$ instead of b^*. For consistency with the previous literature, we use b^* to present the results in the main text.

We consider distinct settings in which structures that are known to inhibit cooperation can be connected under various schemes to create larger structures that are conducive to cooperation. In the main text, for brevity, we only provide the simplified version of the results in the large-n limit (that is, the leading term), and present the full expressions in the corresponding Supplementary Methods. We use the terminology of asymptotic analysis throughout. We say that b^* *grows as* an^b, denoted $b^* \sim an^b$, if $\lim_{n\to\infty} b^*/(an^b) = 1$. Equivalently, we call an^b the *leading term* of b^*.

Suppose there is a complete graph (clique) of n nodes. For a clique, selection does not favor cooperation, regardless of b. Namely, the value of b^* that the method gives is negative. This means that cliques promote spite.

In real-world networks, communities can join together to form larger structures that are better for cooperation. Suppose there are two cliques (which for simplicity we consider to be of the same size, and the analytical steps for the general case are the same) and we connect a node from the first one to a node in the second one (Fig. 1a). We call these two nodes ‘gate nodes’, and the rest of the nodes in the two communities ‘commoners’. In organizational settings, for example, these gate nodes are called ‘boundary spanners’. They are essential for intergroup flow of information and ideas, intergroup coordination and collaboration, and organizational effectiveness and novelty [14]. For two communities of size n with the described interconnection, b^* is positive and finite, but it grows as $1 \times n^2$. Thus it is in principle possible that natural selection favors cooperation, but the necessary b^* grows quickly with network size. This might be infeasible for actual settings. Connecting the gate nodes via an intermediary ‘broker’ node (Fig. 1b) reduces the leading term to $(2/5) \times n^2$, which is slightly better, but it still grows quickly with n. Marked reduction of b^* ensues if instead of one broker, there are two brokers on the path between the gate nodes (Fig. 1c). Each group is connected to a third-party trustee node, or representative, and exchange is done via these two nodes. With two broker nodes in the middle, then the leading term of b^* drops to $4n$, thus b^* grows considerably slower with network size. This interconnection scheme offers a substantial improvement and the two communities which individually promote spite can now be conjoined to form a new composite network which supports cooperation with more plausible values of b^*.

Longer chains of intermediary nodes between the two cliques is mathematically possible, but relatively less common in actual settings. The possible exceptions are chain-of-command structures which resemble this topology: a group of decision-makers sit at one end (the first clique) and through a chain of intermediary units, the agenda reaches the bottom-most unit (the second clique) which is in charge of implementation. For chains with more than two intermediary nodes, the analytical results become too lengthy to be presented. But fortunately the employed coalescing random walks framework enables numerical extraction of the leading term. If the chain of intermediaries has length L, with $L \ll n$, then the leading term of b^* drops further to $n \times 4/(L-1)$. The results for intermediate values of L, with the possibility of $L > n$, are presented in Supplementary Method 1.4.

There are also alternative intercommunity connection schemes that offer a marked reduction in b^*. For example, if there is one broker node between the gate nodes, and the broker is connected to $m > 1$ peripheral leaf nodes (Fig. 1d), then the leading term of b^* is given by $n(m+2)(m+5)/[m(m+3)]$, which is linear in n.

In actual settings, often there are more than two communities (local social networks, production units, etc.). Urbanization has led to a proliferation of diverse subcultures and enhanced interaction and diffusion between them as a daily principle of contemporary life [15,16]. In organizational settings, 'network brokers' can bridge existing 'structural holes' and connect multiple segregated sectors and facilitate cooperation among them [17,18]. An simple example of such a setting would be a star of cliques: $m > 2$ communities connected via a highly-central broker node (Fig. 1e). With this m-community structure, with $m > 2$ communities, b^* has the leading term $n \times m/(m-2)$. Linear growth in community size n indicates a substantial improvement over a single community or two communities is attained.

Another interconnection scheme of multiple cohesive communities is the so-called 'caveman graph' from the sociological literature [19] (Fig. 1f). With $L > 2$ cliques, situated on a ring, the leading term of b^* is given by $n \times L/(L-2)$, which is linear in clique size.

Cliques can also be organized hierarchically, such as in modern organizational bureaucracies (Fig. 1g). In this case, too, for large cliques, the leading term of b^* grows linearly with clique size.

A star graph comprises a hub and n leaf nodes connected to the hub. In this strictly-centralized system, natural selection does not promote cooperation regardless of b. Similar to the case of cliques, stars can be connected to promote collective cooperation. If we have two stars, one with n leaf nodes and the other with αn leaf nodes (Fig. 2a), then if we connect the hubs, b^* for large n approaches a constant $(8 + \alpha + 1/\alpha)/4$. The smallest possible b^* for two stars is $5/2$, which pertains to $\alpha = 1$ (identical stars). The independence from network size is a remarkable feature that star structures exhibit.

If we connect the hubs via one intermediary broker node, we get $b^* \sim (10 + \alpha + 1/\alpha)/4$. For two identical stars, this simplifies to $b^* \sim 3$. We can also connect the hubs via a chain of L intermediary brokers, such as in a chain-of-command structure with a decision-making unit at the top and and an implementation unit at the bottom. For $L \geq 1$, the leading term of b^* is given by $(8 + 2L + \alpha + 1/\alpha)/(L+3)$. In all these cases, it is remarkable that for large network size, b^* tends to a constant. This independence from network size evinces the high merit of locally-star-like structures in the promotion of cooperation.

In many actual settings, star-like structures are not directly connected as we envisaged above. Rather, global hubs are connected to local large-scale hubs, which are in turn connected to local peripheral nodes. This leads to a hierarchical organization: the head unit connects to a number of subsidiary units, each of them connect in turn to subordinate units, and so an. To study this interconnection scheme, we consider graphs with megahubs and hubs in a nested manner. We consider only two levels, though the calculation can be in principle extended to more. Out of the n total leaf nodes of a star graph, we take n_g of them and attach n_d nodes to each (Fig. 2b). The total number of nodes will be $1 + n + n_g n_d$, and the number of links is $n + n_g n_d$. The full expressions for b^* are long (see Supplementary Method 1.3), but simplifications can be obtained in some interesting limits. We consider the case where the number of leaf nodes are much larger than the number of hubs. This is the case in many actual settings, to the extent that the marked imbalance between the latter two numbers constitutes the cornerstone of many egalitarian social discourses and movements. If we have $n_g \ll n$, then the leading term of b^* approaches $3/2$. Whether n_d and n are of the same order of magnitude, or if we have$n \ll n_d$, only affects the second leading order terms. This leading behavior of b^* is particularly interesting because the average degree approaches 2 in these cases, and b^* being less than the average degree is a rare property of graphs. Hence we can dub these structures 'super-promoters' of cooperation.

We can readily generalize these results to the fully-hierarchical structure (where $n_g = n$), that is, a star of stars (Fig. 2c). A mega-hub is connected to n hubs which are each connected to n_d leaf nodes. In the limit of $n \ll n_d$, b^* approaches 2, which indicates that this structure is a strong promoter of cooperation.

Hierarchies can also be more ‘flat’, which is getting popular in certain management approaches [20]. The simplest model would be to have the upper layer of nodes connect horizontally instead of hierarchically. We consider the simple case where the hubs of m stars, each with n leaf nodes, are connected on a ring (Fig. 2d). For large n, the leading term of b^* approaches $(3m-1)/(2m-2)$, which is independent of n. This means that for large m, the value of b^* approaches $3/2$. The average degree in this limit approaches 2. Hence, a ring of stars is another super-promoter of cooperation.

A rich-club network is one comprised of a small dense core of connection-rich high-degree nodes and a large sparse periphery. These structures are found across social and technological networks. The notion of ‘oligarchy’ in institutions and organizations is usually linked to structures that can be characterized by such a rich-club feature [21]. Other examples with this feature include the social network of company executives and directors (within-company [22], national inter-company [23], and international inter-company [24]), the collaboration network between academics [25], and the Internet [26].

As a simple example with this characteristic, we consider a clique of n_c nodes (where c denotes ‘core’) and n_p peripheral nodes. Each core node is connected to every other core node and every peripheral node. Each peripheral node is connected to every core node but to none of the other peripheral nodes. In the special case of $n_c = 1$, this becomes a star graph. For a single rich-club network, natural selection does not favor cooperation, regardless of b. Similar to the case of a single clique, single rich-club networks promote spite.

To improve the situation, we connect two rich-club networks by connecting a 'gate' node in the first core to a gate node in the second (Fig. 3a). An actual example of conjoining rich clubs via cores is that director networks of different companies often connect, and they do so predominantly via their cores, rather than the peripheries—creating 'interlocked directorates' [27]. In the simple case of two identical rich-club networks with $n_c \ll n_p$ (small core and large periphery), the leading term of b^* is given by $4n_c - 3/2$, which is a linear function of n_c. That is, the leading behavior in the large-n_p limit only depends on the number of core nodes and is independent of the number of peripheral nodes. In the case of $n_c = 1$, this leading term is $5/2$, which is consistent with our previous findings for star graphs. For $n_c = 2$, the leading term of b^* is 13/2. The results point out a remarkable feature of these structures: when the periphery is large, the fate of the collective outcome is determined solely by the core.

In a bipartite network, nodes can be divided into two distinct groups, where there is no intra-group link. For example, traditional heterosexual marriage networks comprised two disjoint sets; males only connected to females and vice versa. Other examples include buyer/seller [28], and employer/employee [29] bipartite networks.

Here we present the results for the simplest case of a bipartite graph which is analytically tractable: we consider a complete bipartite graph. A complete bipartite network is one which has two groups, and each node is connected to every node in the other group but no node in its own group. Natural selection does not promote cooperation on a complete bipartite graph, regardless of b. If we connect two bipartite networks, however, the situation improves (Fig. 3b). Consider a bipartite graph comprising two groups of nodes with sizes n_x and n_y, respectively. Suppose we connect two identical such bipartite graphs by connecting a type-x node in the first graph in a type-x node in the second. In the special case of $n_x = n_y = n$, b^* grows linearly with n. The leading term of b^* in this case is given by $2n$. Alternatively, if $n_x \ll n_y$, then the leading term of b^* only depends on n_x, and is given by $4n_x - 3/2$. Hence, similar to rich clubs, if a large group of nodes are not interconnected within themselves and are all connected only to another small group of nodes, the collective outcome will be determined by that small group.

Since actual social networks typically have more randomness than the ideal structured considered above, we investigate random networks to check if they have qualitatively similar properties. Our first test (see Supplementary Method 1.9) is to add structural noise to the above-considered topologies and verify that the b^* values are indeed robust against structural deviations. For the next check, we investigate how conjoining cooperation-inhibiting random networks can promote cooperation. We generate 10 random Erdős-Rényi graphs [30], with values of b^* that are undesirable for cooperation: negative (promoting spite) or highly positive (hindering cooperation). Network size is fixed at 40. There are 55 possible network pairs (45 pairs in which the two networks are different and 10 pairs in which they are identical), and there are 1600 ways to conjoin two networks via one gate node in each. We calculate the median value of b^* among all these possible conjoinings for each pair of networks. The lower triangle in Fig. 4a presents the resulting b^* of the conjoined network against the b^* of the first and the second network. The upper triangle presents the results for the same procedure, except the gate nodes are connected via one broker node, instead of being directly connected. It can be seen that in most cases, a substantial improvement is achieved in both conjoining schemes. The most resistant case is the one with $b^* = -50$. Note that networks whose b^* is negative are promoters of spite, and the closer to zero the value of b^* is, the more strongly the structure promotes spite. The results indicate that if the spite-promotion capacity of either group is high, conjoining them would be less helpful collectively. In Supplementary Method 1.7, we present these results using $1/b^*$ instead of b^* to measure the conduciveness to cooperation. In Fig. 4b we illustrate that the conjoining mechanism works also for more than two ER networks. In the example case shown, three of the four ER networks promote spite, and one of them promotes cooperation with $b^* \approx 43$. Creating inter-community links between these four groups with probability 0.01 begets a marked improvement: the overall structure has $b^* \approx 14$, which is considerably better than each of the individual groups for promoting cooperation. A generalization of this procedure gives rise to the stochastic block model, which we investigate in Supplementary Method 1.8.

The same conjoining procedure is applicable to networks with heavy-tailed degree distributions, which emulate actual social networks more realistically than ER networks. Here we use the model proposed by Klemm and Eguiluz [31] to generate scale-free networks with both small-world property and high clustering coefficient, which are both ubiquitous features in social networks. The results are presented in Fig. 4c. Conjoining every pair of networks produces a composite network with positive b^*. In Supplementary Method 1.7, we present results for four additional scale-free models. The results are qualitatively similar, and the improvement in b^* via conjoining ensues consistently.

To study the effect of community structure on the cooperative outcome, we employ the Lancichinetti-Fortunato-Radicchi (LFR) benchmark [32] that are used for comparing community-detection algorithms. The procedure generates networks with community structure in which the degree distribution within each community and the distribution of community sizes are both heavy-tailed. Fig. 4d depicts an example case with 100 nodes divided into three communities. The degree distribution is scale-free with exponent 2. The community sizes are 10, 23, and 67. Only the largest community has a positive b^*, with $b^* \approx 99$. The composite network (with mixing parameter 0.1) has $b^* \approx 35$. In Supplementary Method 1.8, we provide a systematic investigation for LFR networks and show that, consistent with the above findings, when communities are not conducive to cooperation, sparse interconnections tend to generate composite networks better than the individual modules.

We can apply the same mathematical formalism to real-world social network data. We use offline social networks that pertain to friendships, to ascertain that cooperative dynamics would be reasonable. We use two children friendship networks of fourth grade and fifth grade students [33,34] (for the third grade, no community structure is detected because the network is dense and most people are friends with most others, so we did not use it). The second data set is the well-known friendship network of the members of a Karate club [35], and the third data set we use is Coleman's classic highschool friendship network data set [36]. The results are presented in Fig. 4, panels e-h (more detailed results are presented in Supplementary Table 1). We divided the graphs into two communities using the Girvan-Newman method [37]. In cases where using three as the number of communities returned meaningful results, we considered both two and three communities separately. For all networks, the algorithm returned single-node communities for more than three communities, so we did not consider those cases. It can be seen that in all cases, the collective cooperative merit of the network is markedly better than that of the individual communities. This reaffirms the advantageousness of inter-group connection vis-à-vis cooperation.

Each population structure can be quantified according to its intrinsic propensity to promote cooperation (paying a cost to benefit others) or spite (paying a cost to harm others) [10]. Here we report the observation that sparsely conjoining cooperation-inhibiting structures tend to produce cooperation-promoting structures. We have explored this effect when joining together fully connected cliques, star-like structures (which are dominated by a single individual), rich-clubs, and even random graphs. We have found the phenomenon in examples of real social networks that already consist of conjoined sub-structures.

In our findings, conjoining two graphs that are already favorable for cooperation always results in a cooperation-promoting composite structure, though sometimes the composite graph might not promote cooperation as strongly as the two individual graphs did. But we did not find any example in which the composite graph would inhibit cooperation, that is, either with b^* significantly larger than those of the two initial graphs, or with a negative b^*. We investigated random and non-random graph families considered in this paper, and several others.

An extension to our work would be finding better conjoining schemes for cliques. Here we showed that conjoining cliques in the manners described above results in composite networks that are considerably better than individual cliques. These conjoining methods yield b^* values that grow linearly with n. For very large networks, this improvement might still not be enough. A valuable extension would be to find structures that, similar to the case of stars and rich clubs, would produce b^* that reaches a constant for large clique size.

We note that evolutionary graph theory, which we employed in this paper, is a general approach to study the effect of population structure on natural selection. It is not limited to any particular game and not restricted to one shot interactions. The results are generalizable to any matrix game (see Methods). Hence the competing strategies could instantiate repeated interactions and conditional behavior [38]. Extensions of evolutionary graph theory can be used to study direct reciprocity with crosstalk [39], and indirect reciprocity with optional interactions and private information [40]. On the other hand, there are social settings our model is not applicable to. For example, if each individual interacts with only a subset of its neighbors, then exclusion and inclusion become essential elements of network power. This is an important feature in Network Exchange Theory [41]. In this case, broker nodes have leverage over others due to the high exclusion/inclusion asymmetry. Our model does not consider the possibilities of exclusion and inclusion, and each player plays with every neighbor. Thus an interesting extension to the present paper would be to study analytically the aforementioned effects of exclusion/inclusion in a game-theoretical setting to build on the previous experimental work, particularly Network Exchange Theory.

Finally, we highlight that our results are qualitatively consistent with several simulation studies in the literature across different contexts: cooperation is promoted by interdependence between networks in spatial public goods games and the Prisoner's Dilemma on interdependent networks [42–44], even if it is endogenous and inter-population links are only rewarded to high-payoff individuals [45]. The same is true if multiple types of interactions are considered, resulting in a multiplex network [46].

Our findings suggest a recipe for how to build societal structures that effectively promote cooperation, and together with the ensemble of previous results in the literature, they engender hope regarding the increasing interconnection of the contemporary world.

Methods

We follow a recently-discovered framework for unweighted, undirected graphs without self-loops [10]. Let us denote the degree of node x with k_x and its set of neighbors by $\mathcal{N}_x$. Then, we define p_x as the probability that a random walk of length 2 initiated at node x will terminate at node x:

$$p_x \stackrel{\text{def}}{=} \frac{1}{k_x} \sum_{y \in \mathcal{N}_x} \frac{1}{k_y}. \tag{1}$$

We then solve the following system of $\binom{N}{2}$ linear equations for symmetric quantities τ_{xy}, which are the meeting times of two random walkers initiated at nodes x and y:

$$\tau_{xy} = \tau_{yx} = (1 - \delta_{xy}) \left[1 + \frac{1}{2k_x} \sum_{z \in \mathcal{N}_x} \tau_{zy} + \frac{1}{2k_y} \sum_{z \in \mathcal{N}_y} \tau_{zx} \right]. \tag{2}$$

Here, δ_{xy} equals unity if $x = y$ and is zero otherwise. Using these quantities, we define τ_x for each node as the expected remeeting time of two random walkers initiated at node x as follows:

$$\tau_x \stackrel{\text{def}}{=} 1 + \frac{1}{k_x} \sum_{y \in \mathcal{N}_x} \tau_{yx}. \tag{3}$$

The necessary condition for cooperation to be favored by natural selection is that $b(\sum_x p_x \tau_x k_x - 2N\overline{k})$ is greater than $c(\sum_x \tau_x k_x - 2N\overline{k})$. If the coefficient of b in this inequality is nonpositive, cooperation is never favored. If the coefficient is positive, then the critical benefit-to-cost ratio is given by the following relation:

$$b^* = \frac{\sum_x \tau_x k_x - 2N\bar{k}}{\sum_x p_x \tau_x k_x - 2N\bar{k}}. \tag{4}$$

The calculations for specific graphs discussed in the main text can be simplified utilizing their structural symmetry. For example, for a single community (a complete graph), there is only one variable: the remeeting time between any pair of nodes (because τ_{xx} values are zero). For two communities connected directly by a link, there are only four distinct values for τ_{xy}: the remeeting time between two commoners, between a commoner and the gate node of the same community, between a commoner and the gate node of the other community, and between the two gate nodes. This reduces Equation (2) to a system of four equations with four unknowns.

The results are generalizable to arbitrary 2×2 games [47]. For a game with strategies A and B with corresponding payoff matrix R, S, T, P, the condition that natural selection favors strategy A over B in the limit of weak selection is: $(T - S) < (R - P)(b^* + 1)/(b^* - 1)$.

For the KE networks used in Figure. 4c, we used the model of Klemm and Eguiluz [31]. We generated many networks, with the cross-over parameter μ and the number of initial active nodes m both selected randomly in their valid ranges. We selected 6 networks whose b^* differed from the corresponding values used in Fig. 4 by less than 5%.

Data Availability. All the network data sets used in this paper are freely and publicly available in The Colorado Index of Complex Networks (ICON) collection: `https://icon.colorado.edu`

Code Availability. For the LFR benchmark, we used the publicly-available code that the authors of Ref. [32] have provided:

`https://sites.google.com/site/santofortunato/inthepress2`

For the coalescing random walks framework, the code for computing b^* is publicly available in Zenodo at

`http://dx.doi.org/10.5281/zenodo.276933`

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Figure 1 **From spite to cooperation by conjoining cliques.** Cohesive communities (cliques) hinder the flourishing of cooperation. Each clique for itself promotes spiteful behavior. Conjoining cliques to build larger groups facilitates cooperation. This figure illustrates several topologies of conjoining two (a-d) or multiple (e-g) cliques to build composite cooperation-promoting structures. If we connect two cliques, either directly (a) or via an intermediary node (b), then the composite structure is a promoter of cooperation: the critical benefit-to-cost ratio, b^*, grows with the square of the clique size, n^2. This is a steep increase of b^* with network size, thus although cooperation is in principle possible, it might be impractical for actual settings . (c) Having two intermediary nodes leads to further improvement: the critical benefit-to-cost ratio now grows linearly with n. This is a much slower increase of b^* with network science, as compared to the previous case. Thus, this is a more desirable interconnection scheme for actual scenarios. (d) The broker node who bridges two cliques can also be connected to leaf nodes. In this case, too, b^* grows linearly with n. The following conjoining schemes for multiple cliques produce composite structures that promote cooperation with a critical benefit-to-cost ratio, b^*, that grows linearly in n, which is the size of individual cliques. (e) A broker node connects multiple cliques. (f) A ring of cliques which represents the 'caveman graph'. (g) Hierarchical organization of cliques.

Figure 2 **Super-promoters of cooperation.** Star graphs represent extreme core-periphery structures where a central node is connected to many leaf nodes. Although a single star hinders cooperation, connecting stars promotes cooperation. All reported critical benefit-to-cost ratios, b^*, pertain to the limit of large population size. Exact formulas are shown in Supplementary Methods. (a) Two stars, one with n leaf nodes and the other with αn leaf nodes. (b) An imperfect meta-star: a central node has n peripheral nodes, n_g of them are hubs, while n_d of them are leaves. If $n_g \ll n \ll n_d$, then b^* tends to 3/2 and the average degree tends to 2. Thus, the structure is a super-promoter of cooperation, since b^* is less than the average degree. (c) The perfect meta-star is a hierarchical structure with a head node connected to n subsidiary nodes, each of them connected to n_d peripheral nodes. The reported result is for the case $n \ll n_d$, which means most of the population belongs to the bottom layer. (d) A more flat hierarchical structure: there are m head nodes connected on a ring, each with n peripheral nodes. For $m \ll n$, this graph becomes a super-promoter of cooperation, outperforming the strict hierarchy.

Figure 3 Rich clubs and bipartite graphs. (a) Rich-club graphs comprise a dense core and a large, sparse periphery. A single rich club hinders cooperation, but conjoined rich clubs promotes cooperation. For the simple case of two identical rich clubs, with the periphery size, n_p, much larger than the core, n_c, the critical benefit-to-cost ratio b^* grows linearly with n_c. (b) Complete bipartite graphs comprise two distinct groups of nodes, where links exist only between the two groups, but not within each group. Examples are buyer-seller networks or heterosexual marriage networks. A single bipartite graph hinders cooperation, but connecting them promotes cooperation. For the simple case of two identical graphs, each with two groups of the same size, b^* grows linearly with group size n.

Figure 4 Conjoining random graphs and empirical networks. a) Conjoining two Erdős-Rényi random graphs directly (bottom triangle, orange values) and via one broker node (upper triangle, blue values). The critical benefit-to-cost ratio, b^*, of each graph separately (as shown on the x and y axis) is either negative (promoting spite) or highly positive (promoting cooperation but at a very high benefit-to-cost ratio). The graph size is 40. In all cases, connecting two graphs leads to critical benefit-to-cost ratios of order n. Therefore, we find that conjoining cooperation-inhibiting random graphs also promotes cooperation. b) Extension to more than two graphs: four ER graphs with link-formation probabilities 0.8 (top left, promoting spite), 0.7 (top right, promoting spite), 0.45 (bottom right, promoting spite), and 0.35 (bottom left, promoting cooperation, with $b^* \approx 43$). The inter-community link probability is 0.01. The very few inter-community links engender a considerable improvement: the overall structure promotes cooperation $b^* = 14$, which is markedly better than each individual group. c) Conjoining two scale-free networks generated by the model of Klemm and Eguiluz [31]. d) An example network with community structure generated by the LFR benchmark [32]. Community structure is a ubiquitous feature of actual social networks; there are cohesive friendship groups connected by long ties. We use four empirical data sets pertaining to friendship networks (e-h). We employed standard community detection algorithms to partition the data set into communities, and calculated the critical benefit-to-cost ratio for the whole network and for each community. In every case, the whole network is better than individual subnetworks in promoting cooperation.