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LETTERS

Social diversity promotes the emergence of cooperation in public goods games

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Humans often cooperate in public goods games[1–3] and situations ranging from family issues to global warming[4,5]. However, evolutionary game theory predicts[4,6] that the temptation to forgo the public good mostly wins over collective cooperative action, and this is often also seen in economic experiments[7]. Here we show how social diversity provides an escape from this apparent paradox. Up to now, individuals have been treated as equivalent in all respects[4,8], in sharp contrast with real-life situations, where diversity is ubiquitous. We introduce social diversity by means of heterogeneous graphs and show that cooperation is promoted by the diversity associated with the number and size of the public goods game in which each individual participates and with the individual contribution to each such game. When social ties follow a scale-free distribution[9], cooperation is enhanced whenever all individuals are expected to contribute a fixed amount irrespective of the plethora of public goods games in which they engage. Our results may help to explain the emergence of cooperation in the absence of mechanisms based on individual reputation and punishment[10–12]. Combining social diversity with reputation and punishment will provide instrumental clues on the self-organization of social communities and their economical implications.

The *N*-person prisoner's dilemma constitutes the most used metaphor to study public goods games (PGGs): cooperators (C) contribute an amount *c* ('cost') to the public good; defectors (D) do not contribute. The total contribution is multiplied by an enhancement factor *r* and the result is equally distributed between all *N* members of the group. Hence, Ds get the same benefit of the Cs at no cost. Collective action to shelter, protect and nourish, which abounds in the animal world, provides examples of PGGs, because the cooperation of group members is required. Ultimately, the success (and survival)[5] of the human species relies on the capacity of humans for large-scale cooperation. In the absence of enforcement mechanisms[7,13,14], conventional evolutionary game theory predicts that the temptation to defect leads individuals to forgo the public good[4] in the *N*-person prisoner's dilemma. Whenever interactions are not repeated, and reward and punishment[4,8,13] can be ruled out, several mechanisms were explored that promote cooperation. Individuals were either constrained to interact only with their neighbours on spatial lattices[4,8,15], or given the freedom to opt out of participating[4,15], leading to a coexistence of cooperators and defectors, even on spatial lattices.

Here we investigate what happens in the absence of reputation and punishment and when participation is compulsory. Unlike previous studies involving PGGs[4,8,15], individuals now interact along the social ties defined by a heterogeneous graph[16–18]. This reflects the fact that individuals have different roles in social communities. Empirical studies show that social graphs have a marked degree of heterogeneity combined with small-world effects[19–21], as illustrated in Fig. 1b. Hence we introduce diversity in the study of cooperation under PGGs in the context of evolutionary graph theory[22], and in the presence of spatial and network reciprocity[18,23,24].

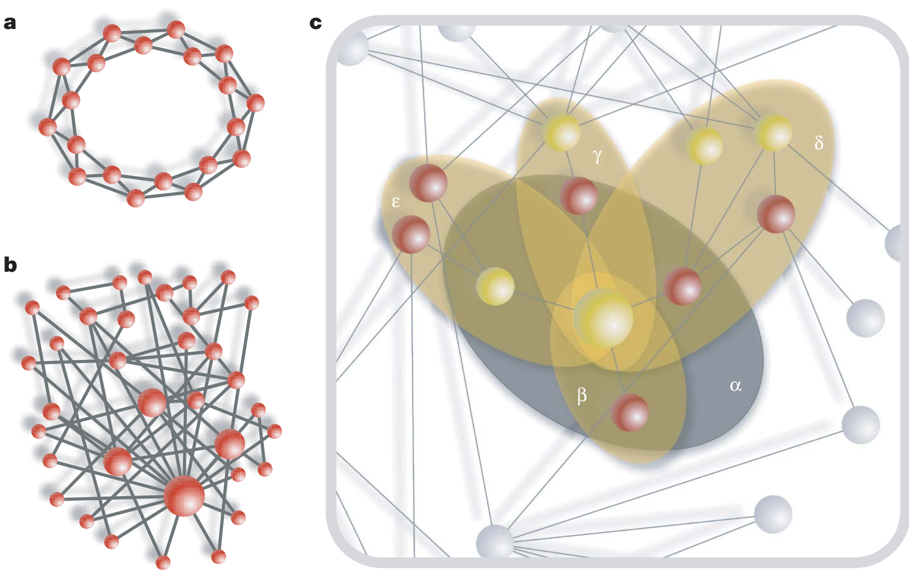

Figure 1 | Population structure and local neighbourhoods. **a**, Regular graphs studied so far, which mimic spatially extended systems. **b**, Scale-free graphs[9] in which small-world effects coexist with a large heterogeneity in neighbourhood size. **c**, The focal individual (largest sphere) belongs to different groups (neighbourhoods) of different sizes in a heterogeneous graph. Given his/her connectivity $k = 4$, we identify five neighbourhoods, each centred on one of the members of the focal individual's group, such that individual fitness derives from the payoff accumulated in all five neighbourhoods (α, β, γ, δ and ε).

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Figure 1c shows how diversity is introduced, in which we enumerate the different PGGs in which the focal individual (large sphere) engages. Each PGG is associated with a fixed neighbourhood defined by the social graph; given the focal individual's connectivity $k = 4$, he/she participates in five PGGs; that centred in his/her neighbourhood α (group size of 5) plus those associated with the neighbourhoods centred on his/her neighbours: β (2), γ (3), δ (5) and ε (4). Hence graph heterogeneity leads individuals to engage in different numbers of PGGs with different group sizes. Furthermore, there is no reason for every C to contribute the same amount to each game in which he/she participates (see below).

Figure 2a shows results for the evolution of cooperation corresponding to the conventional situation in which every C pays a fixed cost c in every game that he/she plays. We plot the fraction of cooperators in the population that survive evolution as a function of the renormalized PGG enhancement factor $\eta = r/(z+1)$, where z is the average connectivity of the population graph (see Methods). In infinite, well-mixed populations, a sharp transition from defection to cooperation takes place at $\eta = 1$. Comparison between the results obtained on regular graphs (Fig. 1a) with those on strongly heterogeneous graphs (scale-free; Fig. 1b) reveal the sizable impact of heterogeneity on the evolution of cooperation. For regular graphs (in which, from the perspective of a population structure, every individual is equivalent to any other) cooperators become predominant (their fraction exceeds 50%) at $\eta \approx 0.7$: network reciprocity[18,23,24] leads to an enhancement of cooperation also under PGGs[4,8,15]. This number decreases to $\eta \approx 0.6$ on scale-free graphs, in which individual participation now reflects both a diversity in the size of each individual's PGGs and in the different number of PGGs in which each individual participates.

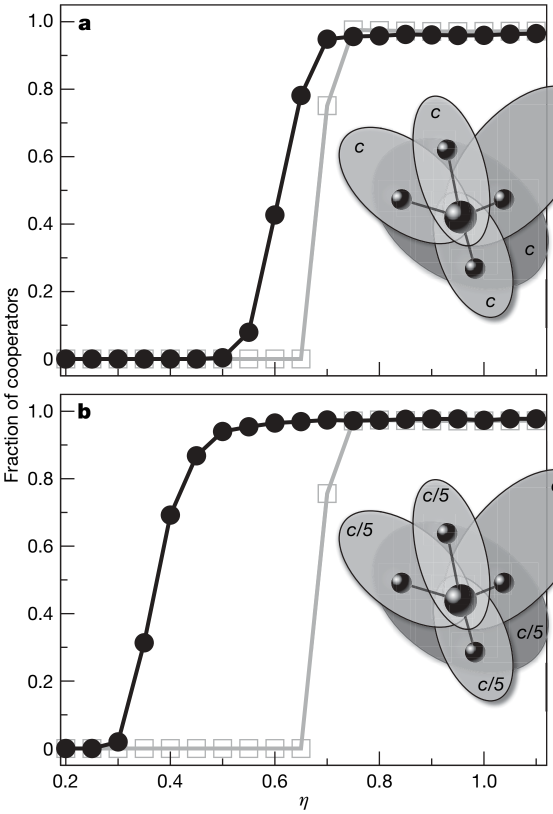

Figure 2 | Evolution of cooperation in networked PGGs. Black lines and filled circles show results for scale-free graphs; grey lines and open squares show results for regular graphs. In all cases $z = 4$. **a**, Fixed cost per game. Cs pay a cost $c = 1$ for each PGG in which they participate: diversity in number of PGGs and size of each PGG associated with scale-free graphs merits a significant enhancement of cooperation. **b**, Fixed cost per individual. Each C contributes a total cost c equally shared between all $k + 1$ PGGs in which he/she engages. This change of model leads to an impressive boost of cooperation.

The contribution of each C in Fig. 2a has been proportional to $k + 1$, where k is the number of neighbours (vertex degree). This may be unrealistic, because individuals have limited resources and social rules often accommodate a more egalitarian overall contribution from individuals[25]. In the extreme opposite limit, all Cs contribute the same overall cost, equally shared between all games in which each individual participates. In this limit, still another new type of diversity is introduced—that of individual contributions to each game. Real-world situations will naturally fall somewhere between these limits, as individuals learn[26] to cooperate (or defect) in better ways. In general, however, one expects diversity of contributions from individuals. Depending on the problem at stake, any contribution may be necessary and even welcome, however small. Below we show that, whenever all contributions are interpreted as acts of cooperation, cooperation blooms.

Figure 2b shows the results including this additional diversity in which Cs contribute $c/(k+1)$ for each game, k being their degree in the social graph. This new model leads to an impressive boost of cooperation. In all cases, cooperation now dominates for values of η below 0.4.

What is the origin of such a boost of cooperation? Because each C now contributes $c/(k+1)$ to each game, diversity resulting from heterogeneous graphs determines a richer spectrum of individual fitness. In a single PGG, the fitness difference between a C and a D is no longer constant and proportional to c, as on homogeneous graphs, but now depends on the social context of the individual. As shown in detail in Supplementary Information, the highly connected nodes (hubs) are those that turn most quickly into cooperation. This is because, under this contribution model, the relative fitness of a single cooperator increases with its connectivity, as illustrated in Fig. 3 (derivation details are given in Supplementary Information). Consequently, heterogeneity confers a natural advantage on hubs. In practice, Cs survive extinction for values of η about 0.25. Because $z = 4$, $\eta = 0.25$ implies that $r = 1.25$, much lower than the size $N = 3$ of the smallest group in the entire population. Note that, in those games for which $\eta_k \equiv r/(k+1) > 1$ (the smaller groups), the social dilemma might become relaxed, because in this case it is better to play C than D. As Fig. 2b shows, cooperation prevails despite $\eta_k < 1$ in every PGG played. In fact, the impact of diversity is preserved even when the social dilemma is transformed such that defection is always preferred, irrespective of η.

It still remains to explain how a D sitting on a large hub can be taken over by a C. As shown in the Supplementary Information, Ds are victims of their own success—successful Ds breed Ds in their neighbourhood, inducing a negative feedback mechanism that reduces their fitness[27]. Consequently, they become vulnerable to nearby cooperators. Once invaded by a C, a hub will remain C, as by placing Cs on nearby sites, successful Cs increase their fitness. The role of Cs is therefore crucial and twofold: they efficiently disseminate the cooperator strategy across social networks, whereas they get a stronghold on hubs by minimizing the potential loss from exploitation by free-riding Ds. It is noteworthy that the results shown in Fig. 2b, in which selection is strong, are robust with respect to the detailed evolutionary dynamics (pairwise comparison[28], birth–death[18], death–birth[18]), to the updating strategy (synchronous, asynchronous), and even to errors (mutations cannot destroy C-dominance).

What about the defectors? They have a minor role as social parasites when they survive on such graphs. Figure 2b shows that some residual Ds continue to exploit Cs. In the Supplementary Information we provide a detailed analysis showing how the evolutionary dynamics inexorably leads cooperators to invade the hubs quickly, whereas defectors are able to survive only on loosely connected nodes, with low fitness and exploiting cooperators of low fitness.

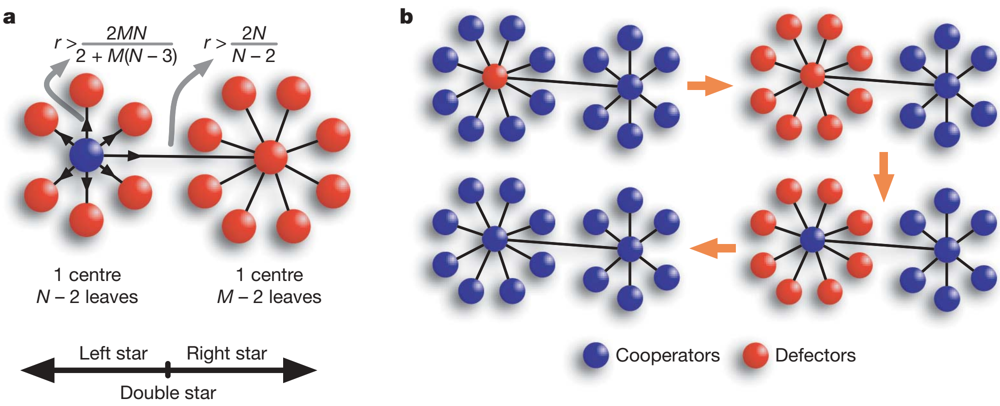

Figure 3 | Dynamics on the double star. a, When a single C (blue) occupies the centre of the left star, the critical r above which his/her fitness exceeds that of any of the leaves decreases whenever the size (number of leaves) of the left star increases or the size of the right star decreases. Taking over the D (red) on the right centre does not depend on his/her connectivity. **b,** When a D occupies a high-fitness location, the fact that he/she places other Ds in his/her neighbourhood leads to his/her own demise (see Supplementary Information for details).

In a more economical perspective, our results also portray different evolutionary outcomes even in communities in which all individuals cooperate. Now we consider populations of 100% cooperators and look at their 'wealth' (fitness) distribution according to different underlying models. We consider homogeneous (regular) and heterogeneous (scale-free) graphs. In Fig. 4 we plot the fraction of the population that holds a given fraction of the total wealth.

The differences are striking. On regular graphs an egalitarian wealth distribution is obtained, irrespective of the contribution model. On scale-free graphs wealth distributions follow a power law. However, for a fixed cost per individual, the population has significantly fewer poor and more rich (note the logarithmic scale in Fig. 4). Given that the emergence of cooperation is easiest in this case, the results provide an impressive account of the role of diversity and its implications in both the emergence of cooperation and the resulting wealth distribution.

In this study any contribution has been identified with cooperation. In communities under the influence of social norms, individual contributions will be easily classified as acts of cooperation (or not). In this context, our results suggest the possibility that successful communities are those in which the act of giving is more important than the amount given. This may be of particular relevance whenever the survival of the community is at stake, in which case any help is necessary[14,25]. Most probably, in such cases selection is strong, as considered here.

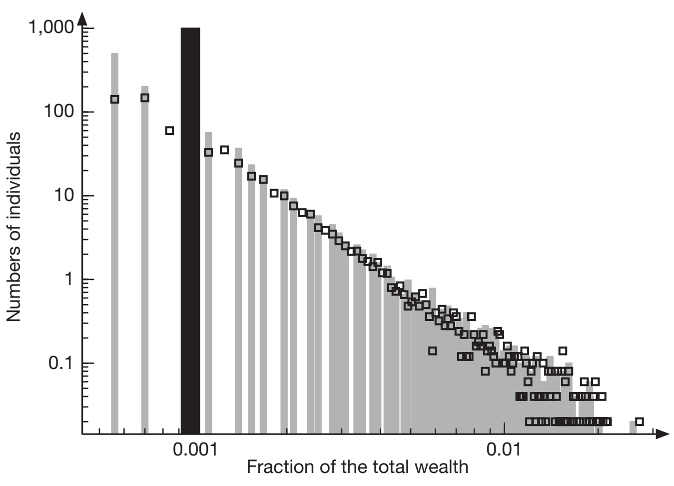

Figure 4 | Wealth distribution. On scale-free graphs, the wealth (fitness) distribution follows a power law, both when each individual invests a fixed cost per game (thin grey bars) or when he/she spends an overall fixed cost (open squares). The latter case leads to communities with fewer 'poor' and more 'rich'. These behaviours contrast with the egalitarian wealth distribution characteristic of homogeneous graphs (thick black bar).

METHODS SUMMARY

According to Fig. 1c, each individual and his/her k neighbours statically define a group (of size $k+1$). The fitness of individual i is associated with the accumulated payoff resulting from all PGGs in which he/she participates. Strategy evolution is implemented by using the finite population analogue of the replicator dynamics: at each time step each individual will adopt the strategy of a randomly chosen neighbour (if more fit) with a probability proportional to the fitness difference[16,29]. Consequently, the results become independent of the specific value used for the cost of cooperation c (we set c to 1). The results shown were obtained for communities of 10^3 individuals starting with 50% of cooperators randomly distributed on the population graph. The equilibrium fraction of cooperators results from averaging over 2,000 generations after a transient period of 10^5 generations. This procedure was repeated 100 times for 10 different realizations of each class of graph. Finally, the distributions depicted in Fig. 4 were obtained by averaging the fitness distributions over 50 scale-free graphs with average connectivity $z = 4$ and populations of 10^3 individuals, all cooperators.

Full Methods and any associated references are available in the online version of the paper at www.nature.com/nature.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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METHODS

Population structure. Population structure is represented by a graph; individuals occupy the vertices of the graph, and social interactions proceed along the edges. Figure 1 depicts the two topologies considered in this study. Figure 1a represents one-dimensional lattices, namely communities in which all individuals (nodes) are topologically equivalent, similar to those previously investigated. In Fig. 1b we provide a diagram of more realistic social structures, portraying populations in which different individuals have a distinct number of connections. Such strongly heterogeneous populations were obtained by means of the Barabási–Albert scale-free model based on growth and preferential attachment[9]. As is well known, realistic social structures fall somewhere between regular and scale-free graphs[19]. The blue circles in Fig. 2 were obtained on scale-free populations with 10^3 individuals generated in this way, with average connectivity $z = 4$. This implies that the smallest group in this population has three individuals[9]. In all simulations, the networks remain unchanged throughout evolution and each individual adopts a pure strategy: cooperator (C) or defector (D).

Public goods games. Every individual participates in all possible PGGs, accumulating the benefits and costs resulting from each of them. The accumulated value of the payoffs resulting from all possible PGGs contributes to individual fitness (neighbourhoods α, β, γ, δ and ε in Fig. 1c). In each PGG, the income of individual x will depend on the size of the group $k_x + 1$ (defined by the size of the neighbourhood centred on individual x; see Fig. 1), on the number n_C of Cs in his/her neighbourhood and on the multiplication factor r applied to the group investment. The incomes of a defector and a cooperator in one group are given by $P_D = crn_C/(k_x + 1)$ and $P_C = P_D - c$, respectively, in the case where all cooperators contribute the same cost c per game, such that the contribution of an individual is proportional to his/her number of social ties. In the opposite limit, we considered the case in which C individuals with k_x neighbours contribute a cost $c/(k_x + 1)$ per game, such that the individual contribution of each C equals c independently of the number of social ties. Hence, the payoff of an individual y with a strategy s_y (1 if C, 0 if D) associated with the PGGs centred in a individual x is given by

$$P_{y,x} = \frac{r}{k_x+1}\sum_{i=0}^{k_x}\frac{c}{k_i+1}s_i - \frac{c}{k_y+1}s_y$$

where $i = 0$ stands for x, s_i is the strategy of the neighbour i of x, and k_i is his/her degree.

Evolution. The network structure of the population defines not only the game interactions but also the structure through which strategy evolution proceeds. For non-repeated two-player games, this has been shown to constitute the most favourable model for cooperation[30]. After engaging in all games, the accumulated payoff is mapped onto individual fitness. After each game round, all strategies are updated synchronously by following the finite population analogue of the replicator dynamics[16,29]. When a site x with a payoff P_x is selected for update, a neighbour y (with a payoff P_y) is drawn at random between all k_x neighbours. If $P_x > P_y$, no update occurs. If $P_x < P_y$, x will adopt y's strategy with a probability given by $(P_y - P_x)/M$. M ensures the proper normalization and is given by the maximum possible difference between the payoffs of x and y. The results are robust with respect to changes both in the detailed form of the normalization factor or if we adopt an asynchronous update instead of the synchronous one.

Simulations. The results were obtained for communities with $N = 10^3$ individuals and an average connectivity of $z = 4$. Each equilibrium fraction of cooperators was obtained by averaging more than 2,000 generations after a transient period of 10^5 generations. We started with 50% of Cs randomly placed on the graph. Each data point depicted in Fig. 2 corresponds to an average over 1,000 simulations; that is, 100 runs for 10 different realizations of the same class of graph. Finally, the distributions depicted in Fig. 4 were obtained by averaging the fitness distributions over 50 scale-free graphs with $z = 4$ and populations of 10^3 individuals, all cooperators.

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