

Emergence of communities and diversity in social networks

Xiao Han^a, Shinan Cao^b, Zhesi Shen^a, Boyu Zhang^{c,1}, Wen-Xu Wang^{a,d,1}, Ross Cressman^e, and H. Eugene Stanley^{f,1}

^aSchool of Systems Science, Beijing Normal University, Beijing 100875, People's Republic of China; ^bSchool of Finance, University of International Business and Economics, Beijing 100029, People's Republic of China; ^cLaboratory of Mathematics and Complex Systems, Ministry of Education, School of Mathematical Sciences, Beijing Normal University, Beijing 100875, People's Republic of China; ^dBusiness School, University of Shanghai for Science and Technology, Shanghai 200093, China; ^eDepartment of Mathematics, Wilfrid Laurier University, Waterloo, ON N2L 3C5, Canada; and ^fCenter for Polymer Studies and Department of Physics, Boston University, Boston, MA 02215

Contributed by H. Eugene Stanley, December 27, 2016 (sent for review March 14, 2016; reviewed by Alex Arenas and David G. Rand)

Communities are common in complex networks and play a significant role in the functioning of social, biological, economic, and technological systems. Despite widespread interest in detecting community structures in complex networks and exploring the effect of communities on collective dynamics, a deep understanding of the emergence and prevalence of communities in social networks is still lacking. Addressing this fundamental problem is of paramount importance in understanding, predicting, and controlling a variety of collective behaviors in society. An elusive question is how communities with common internal properties arise in social networks with great individual diversity. Here, we answer this question using the ultimatum game, which has been a paradigm for characterizing altruism and fairness. We experimentally show that stable local communities with different internal agreements emerge spontaneously and induce social diversity into networks, which is in sharp contrast to populations with random interactions. Diverse communities and social norms come from the interaction between responders with inherent heterogeneous demands and rational proposers via local connections, where the former eventually become the community leaders. This result indicates that networks are significant in the emergence and stabilization of communities and social diversity. Our experimental results also provide valuable information about strategies for developing network models and theories of evolutionary games and social dynamics.

communities | fairness | social diversity | networks | ultimatum game

Communities are ubiquitous in nature and society (1, 2). Nodes that share common properties often self-organize to form a community. Internet users with common interests, for example, establish online communities and frequently communicate (3). In human society, social communities with distinctive social norms form spontaneously (4). In protein–protein interaction networks, related proteins group together to execute specific functions within a cell (5).

How social communities emerge is one of the fundamental problems in social science. Game theory and models have offered powerful tools for exploring collective behaviors in animal and human society and our evolutionary origins (6–10). Recent theoretical studies found that network structure is significant in the emergence of mutually reinforcing communities among altruistic subjects in social games, such as the prisoner's dilemma (PD) game, the public goods game (PGG), and the ultimatum game (UG) (11–20). Although some experiments found that cooperation is stabilized in dynamical networks (21–24), stable communities have been rarely observed in laboratory experiments on a variety of static networks (25–32). As a result, how communities emerge in social network systems associated with evolutionary games continues to be an unanswered question.

Social game experiments demonstrate that there is inherent diversity among individuals in cultural and social attitudes toward cooperation, fairness, and punishment (33–37). However, communities with diverse individuals but common internal prop-

erties are ubiquitous in society, prompting us to wonder how diverse individuals are able to form communities. Our goal is to answer this question by experimentally exploring the emergence of communities in social networks associated with the UG. This game has been a paradigm for exploring fairness, altruism, and punishment behaviors that challenge the classical game theory assumption that people act in a fully rational and selfish manner (34–38). Thus, exploring social game dynamics allows us to offer a more natural and general interpretation of the self-organization of communities in social networks. In the UG, two players—a proposer and a responder—together decide how to divide a sum of money. The proposer makes an offer that the responder can either accept or reject. Rejection causes both players to get nothing. In a one-shot anonymous interaction if both players are rational and self-interested, the proposer will offer the minimum amount and the responder will accept it to close the deal. However, much experimental evidence has pointed to a different outcome: Responders tend to disregard maximizing their own gains and reject unfair offers (34–36, 38, 39). Although much effort has been devoted to explaining how fairness emerges and the conditions under which fairness becomes a factor (38, 40–46), a comprehensive understanding of the evolution of fairness in social networks via experiments is still lacking.

We conduct laboratory experiments on both homogeneous and heterogeneous networks and find that stable communities

Significance

Understanding how communities emerge is a fundamental problem in social and economic systems. Here, we experimentally explore the emergence of communities in social networks, using the ultimatum game as a paradigm for capturing individual interactions. We find the emergence of diverse communities in static networks is the result of the local interaction between responders with inherent heterogeneity and rational proposers in which the former act as community leaders. In contrast, communities do not arise in populations with random interactions, suggesting that a static structure stabilizes local communities and social diversity. Our experimental findings deepen our understanding of self-organized communities and of the establishment of social norms associated with game dynamics in social networks.

Author contributions: S.C., B.Z., W.-X.W., R.C., and H.E.S. designed research; X.H., S.C., Z.S., B.Z., W.-X.W., and H.E.S. performed research; S.C. and R.C. contributed new reagents/analytic tools; X.H., Z.S., B.Z., W.-X.W., and H.E.S. analyzed data; and X.H., B.Z., W.-X.W., R.C., and H.E.S. wrote the paper.

Reviewers: A.A., Universitat Rovira i Virgili; and D.G.R., Yale University.

The authors declare no conflict of interest.

Freely available online through the PNAS open access option.

¹To whom correspondence may be addressed. Email: zhangby@bnu.edu.cn, wenzuxu@bnu.edu.cn, or hes@bu.edu.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1608164114/-DCSupplemental.

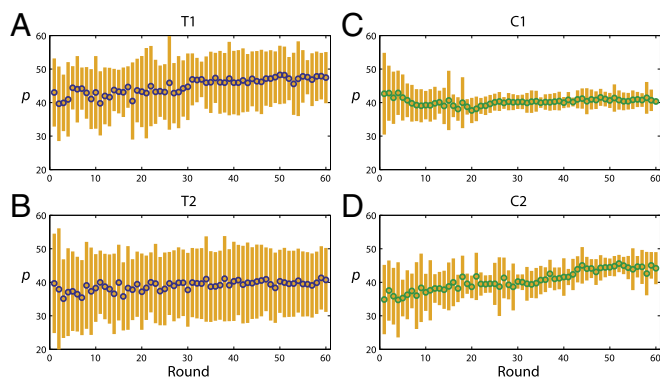


Fig. 1. Evolution of proposals in the treatment and control groups. (A–D) The proposers’ offers p from round 1 to round 60 in the two treatment groups, T1 (A) and T2 (B), and the two control groups, C1 (C) and C2 (D), respectively. The mean value and the SD of p in each of the 60 rounds are denoted by circles and column bars, respectively. The average value of p in T1 is slightly higher than in the other groups, and the SD of p in T1 and T2 is much larger than that in C1 and C2. The results demonstrate that whether a structured network is regular or random has little effect on the average fairness of proposers, whereas the diversity in proposers, reflected by the SD, is remarkably promoted by network structure, in contrast to the two control groups with random interactions.

with different internal agreements emerge, which leads to social diversity in both types of networks. In contrast, in populations where interactions among players are randomly shuffled after each round, communities and social diversity do not emerge. To explain this phenomenon, we examine individual behaviors and find that proposers tend to be rational and use the (myopic) best-response strategy (43, 47), and responders tend to be irrational and punish unfair acts (34–36, 38, 39). Social norms are established in networks through the local interaction between irrational responders with inherent heterogeneous demands and rational proposers, where responders are the leaders followed by their neighboring proposers. Our work explains how diverse communities and social norms self-organize and provides evidence that network structure is essential to the emergence of communities. Our experiments also make possible the development of network models of altruism, fairness, and cooperation in networked populations.

Results

We conduct four groups of experiments with two treatment groups (T1 and T2) and two control groups (C1 and C2) (*Materials and Methods*). In T1 and T2 there is a static network structure among the players, a regular bipartite network for T1, and a random bipartite network for T2. In C1 and C2 the interactions among the players constantly change. Each subject plays a single unchanging role, either proposer or responder. We focus on the evolution of a proposer’s offer p and a responder’s minimum acceptance level q , which measures the degree of fair and unfair behaviors. Our main findings include (i) the diversity of p characterized by a much larger SD in T1 and T2 than in C1 and C2; (ii) the formation of local proposer communities in T1 and T2, seen in the spatiotemporal patterns of proposers; and (iii) the best-response strategy followed by proposers and the leader effect of irrational responders, i.e., they jointly establish social norms. Observation iii explains observations i and ii.

Diversity of Proposers. We first explore the evolution of p and q . Fig. 1 and *SI Appendix, Fig. S1* show the mean values \bar{p} and \bar{q} of p and q and their SDs in each round for T1, T2, C1, and C2. We find that \bar{p} in T1 is slightly higher than in the other groups. In T1, \bar{p} slowly increases from approximately 40 to 45. In all of the other

groups \bar{p} is approximately 40 within 60 rounds. Similar phenomena are observed in \bar{q} ; i.e., \bar{q} of T1 is slightly higher than in the other groups and \bar{q} of all groups is maintained at approximately 30. Table 1 shows the mean values \bar{p} and \bar{q} over 60 rounds. These findings in the experimental UG with limited neighbors are consistent with many one-pair experimental UGs in which on average $p = 40$ and $q = 30$ (34–36, 38, 39). These results indicate that network structure has little effect on the average behaviors of proposers and responders in a population.

On the other hand, the SD of p differs sharply between the treatment groups and the control groups. The SD of p in T1 and T2 is much larger than that in C1 and C2 (Fig. 1 and Table 1), indicating that network structures, whether regular or random, enable a strong proposer diversity that is lacking in populations with random interactions. In contrast, there are big SDs in q in both the treatment and control groups and there is little difference between them (details in Table 1 and *SI Appendix, Fig. S1*). In addition, both the mean value and the SD of q are constant in the experiments, which implies that the average behavior of responders changes little during the experiments. Although population structure plays a prominent role in the UG—reflected in the difference in the SD of p in the two classes—it does not affect the behavior of responders. Thus, we expect that network structure has a subtle effect on the UG and that this subtle effect will account for why proposer diversity emerges.

Emergence of Proposer Communities. To discover how network structure affects proposer diversity, we study the spatiotemporal patterns of the proposers. Surprisingly, Fig. 2 shows that in T1 and T2 proposers form local communities, which are shown in different colors (values of p). A community is a group of subjects with similar behavior and internal agreement. Proposer communities have similar values of p . After communities emerge, and especially in the final 10 rounds, their boundaries are clear and relatively invariant, indicating that they are approximately stable and rarely change. Each community is composed of adjacent proposers who make similar high or low offers and in Fig. 2 exhibit the same community color. Adjacent communities exhibit different colors, indicating that offers differ among communities. In C1 and C2, however, there are no clear communities and eventually a single homogeneous community of proposers with similar values of p (similar color) emerges. A snapshot in round 60 in T1 is shown in Fig. 3A. Four local communities are composed of adjacent proposers in the regular network (Fig. 3A). Analogous to T1, there are four local communities in the random network (Fig. 3B). Although in the random network there is no naturally occurring spatial order of nodes, we find a spatial order of nodes by using a simulated annealing algorithm to maximize the sum of shared neighbors between any two adjacent nodes (details in *SI Appendix, Supplementary Note 1*). The existence of local communities with different internal features accounts for the proposer diversity in structured populations.

Table 1. The mean value and SD of strategies in experiments

Group	Mean(p)	SD(p)	Mean(q)	SD(q)
T1	44.89	5.90	36.43	12.72
C1	40.27	1.64	31.66	7.61
T2	38.93	8.27	32.81	9.93
C2	40.74	2.25	31.53	7.87

Mean(p) and SD(p) represent the mean value and the SD of offers of all proposers, in which a proposer’s offer is taken as the average of his/her offers p over 60 rounds, respectively. Similarly, mean(q) and SD(q) represent the mean value and the SD of minimum acceptance levels of all responders, respectively, in which a responder’s minimum acceptance level is taken as the average of his/her minimum acceptance levels q over 60 rounds. T1, C1, T2, and C2 have the same meanings as those in Fig. 1.

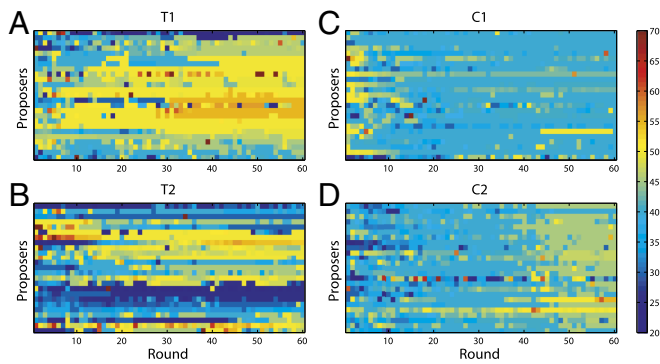


Fig. 2. Spatiotemporal patterns of proposers. (A and B) Spatiotemporal patterns of the proposers' offers p in the two treatment groups T1 and T2. (C and D) Spatiotemporal patterns of the proposers' offers p in the two control groups C1 and C2. The ordinate represents the spatial orders of proposers. Two proposers with most common neighbors will be adjacent to each other. The color bar represents the value of p . In A and B, neighboring proposers gradually form some local communities that can be distinguished by different colors (different values of p). The communities are stable as reflected by the presence of relatively clear and invariant boundaries among the communities after a number of rounds (e.g., 30 rounds in A). Each community is composed of some neighboring proposers who offer similar p as represented by a similar color. By contrast, in C and D, there are no local communities and a single homogeneous community of proposers with similar values of p as represented by a similar color arises. The local communities with different internal agreements in T1 and T2 account for the diversity in proposers. By contrast, in C1 and C2, the absence of local communities and the homogeneity of proposers account for the relatively small SD of proposals.

Note that although the formation of stable local communities has been predicted by a number of evolutionary game models, it has seldom been observed in experiments using both the UG and other social dilemma games, such as the PD and the PGG. Our work provides experimental evidence that local agreements in the form of communities are spontaneously achieved, which indicates that network structure plays a significant role in evolutionary games. It is worth noting that because the behavior of neighbors (i.e., values of p or q) in previous rounds returns in a descending order, the feedback information cannot be related to specific neighbors, precluding participants from using the reputations of their neighbors to make decisions (SI Appendix, Fig. S2). Thus, the network effect plays a deterministic role in the formation of proposer communities. Our findings provide evidence for network-induced communities and insight into the evolution of fairness and altruism in structured populations with limited social ties.

Behaviors of Proposers and Responders. To discover how diverse communities emerge, we explore the spatiotemporal diagram of responder behavior. Unlike the behavior of proposers, there is no obvious difference in the behavior of responders between the treatment and the control groups (SI Appendix, Fig. S3). There are no local responder communities, and adjacent responders exhibit inhomogeneity that increases the SD of q in all groups. The irrational behavior of responders reflected in the spatiotemporal diagram is consistent with the high SD of q (SI Appendix, Fig. S3). All of these results indicate that network structure has little influence on the decision-making process of responders. Unlike responders, most proposers are rational and make offers based on the (myopic) best-response strategy, as predicted by theoretical models (43, 47). Proposers tend to maximize their profits by using information about their neighbors' behaviors in the previous round. As the game progresses, over half of the proposers give a best response to their neighbors according to the

definition of best response in the literature (43, 47) (details in SI Appendix, Fig. S4 and Supplementary Note 2).

Knowing how subjects make decisions is the key to understanding how proposer communities emerge. Proposer communities emerge from local interactions between the inherent diverse behaviors of responders (SI Appendix, Table S1) and the best-response behaviors of proposers. Within communities, proposers share a large fraction of neighbor responders. Because proposer behavior obeys the best-response strategy, they use their knowledge of the previous behavior of their common responders and offer similar amounts of money. These best-response behaviors induce the emergence of a local community. On the other hand, the inherent diverse behaviors of responders result in different communities with different internal agreements. In particular, when responders insist on high acceptance levels, they force their proposer neighbors to increase their offers, which leads to stable communities (Fig. 3C). Thus, local interactions are essential in the formation of local communities. This interpretation is supported by the absence of local communities in control groups with random interactions.

To examine whether some differences between the responders in the treatment group and those in the control groups may be responsible for the communities, we apply a shuffle technique in all of the experiments to test the effect of responder differences (28, 30). Specifically, we exchange the behavior sequences of the responders in the treatment groups with the behavior sequences of their counterparts in the control groups. This reshuffling does

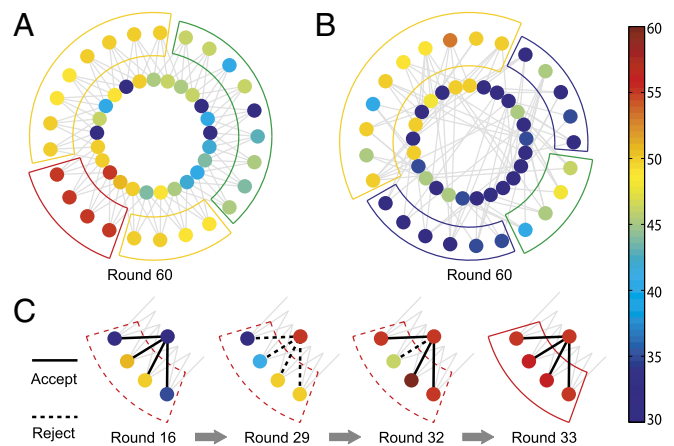


Fig. 3. Local communities of proposers. (A and B) A snapshot of the proposers' offers p and the responders' q in round 60 for (A) T1 with a regular network and for (B) T2 with a random network. The subjects are arranged in two rings, where the outside ring represents proposers and the inside ring represents responders. The color bar represents the value of p and q . Communities are highlighted by colored boxes. The arrangement of proposers is the same as in Fig. 2 (two subjects with most common neighbors are adjacent to each other) but with periodic boundary conditions. The regular network offers a natural sequential order but there is no such order for the random network. We assign the spatial order of the nodes in random networks by using a simulated annealing algorithm. The order is exclusively based on the topology rather than the acts of subjects. (C) The evolution of a fairly stable community in T1. The snapshots of the community in four rounds are shown. The responder can be regarded as a "leader" of this community and is followed by the four neighboring proposers. In round 16, the responder's minimum acceptance level q was relatively low and all neighboring proposal p s were accepted. In round 29, the responder's q was increased and all neighboring p s were rejected. Because the proposers are relatively rational, they gradually increased their p s to make deals with the responder. In round 32, three proposers made deals by enhancing their p s, and a proposer's p is higher than the responder's q . In round 33, all of the proposers made deals with the responder and their p s were equal to or slightly higher than the responder's q .

not change a player's dependence on his or her own previous actions because the order of the actions over 60 rounds is not altered. We then calculate the best-response offers in each group and find that the SD of p in the shuffle games with network structures is still higher than that in the shuffle games with random interactions, suggesting that the differences between the responders in the treatment and control groups do not account for the emergence of the communities (SI Appendix, Table S2). Thus, local interactions play an essential role in the emergence and maintenance of local communities.

Simulations on Complex Networks. Recent interest in evolutionary games in scale-free networks prompts us to explore the UG on scale-free networks (11–13, 15, 18, 20, 30). In general, a scale-free network must be of a certain size to exhibit its typical structural feature, that is, the presence of hubs with a large number of neighbors (48). However, an experimental UG on a large network is limited by our ability to conduct large-scale experiments. To overcome this, we simulate the UG on scale-free networks. Specifically, because proposers use the best-response strategy in treatment and control groups, we assume that proposers in scale-free networks exhibit a similar behavior (31). In contrast, it is difficult to use simple mechanisms to capture the irrational behavior of responders. This problem can be solved by focusing on responder behavior in the experiments and discovering that behaviors are quite similar in the different experiments. We build a database of all responder behavior sequences obtained in the four experiments, randomly pick sequences from the database, and assign them to responders in the scale-free network. Table 2 shows that for different network sizes and average degrees, the SD of p in scale-free networks is always much higher than that in populations with random interactions, but that there is no obvious difference in the mean value of p . The spatiotemporal pattern of proposers in scale-free networks also exhibits the formation of local communities (SI Appendix, Fig. S5). These results agree with our experimental findings in regular and random networks.

To test whether our findings depend on the specific ratio between proposers and responders, we carry out additional simulations for networks with different proposer–responder ratios. Two types of bipartite networks are considered. In the first type all proposers and responders have the same degrees, respectively, and in the second type the degrees of proposers and responders can differ. Similar to the simulations in scale-free networks, we randomly choose responder behaviors from the database that includes all responder behavior sequences and assume that proposers follow the best-response strategy. As

shown in SI Appendix, Table S3, for four different proposer–responder ratios, the SD of p in structured populations is much higher than in populations with random interactions. Thus, our results are robust against changes in the ratio between proposers and responders.

Discussion

Our experimental results, shuffle tests, and simulations demonstrate that stable communities with different internal agreements emerge in both regular and complex networks governed by the UG. Thus, the social diversity among proposers emerges and persists. In contrast, in populations with random interactions the proposers remain homogeneous and no communities are established. The diverse communities emerge from the local interactions between irrational responders with inherent heterogeneous demands and rational proposers. In general, proposers with common neighbor responders who act as leaders constitute a community with internal agreement. The different findings between the treatment and control groups indicate that networks are significant in the emergence of social norms, communities, and social diversity. Thus, our work explains how communities with common internal properties and social norms can emerge in a social network in which individuals are diverse. Note that our findings also suggest that even when all proposers have the same intelligent strategy (i.e., best response) and all subjects in the social network have equal status, diverse communities can arise. This result may explain why different social norms can be established even in homogeneous environments (4, 49, 50).

Our results also indicate that local interactions in network structures are only a necessary and not a sufficient condition for the formation of local communities. The self-organization of communities also requires an inherent diversity among individuals. In our UG experiments, local agreements are achieved because a majority of proposers are rational. Some of the irrational responders who insist on high acceptance levels become “leaders” who are followed by their neighboring proposers. This leader effect has been observed in other evolutionary games. For example, previous studies report that cooperating leaders play an important role in increasing a group's average contribution in PGGs (51, 52). However, how the cooperative communities are established in social dilemma games in social networks remains an open question.

Our work also raises other questions about the emergence of communities and their effects on evolutionary dynamics. First, how does inherent diversity among individuals arise? One possible answer is provided in a recently proposed model by Bear and Rand (53) in which intuitive rejection and deliberative acceptance have evolutionary advantages (53). Thus, heterogeneity at an individual level in our experiments might stem from different deliberation costs in which responders with a higher deliberation cost tend to make decisions based on intuition. Thus, they may have higher acceptance level q for closing a deal with their neighboring proposers. Second, how does cultural difference affect the experimental findings of communities and social diversity? Although additional experiments are needed to fully address this question, previous experiments provide hints that anticipate the effect of cultural difference. Specifically, there is no significant difference between responder behavior in our experiments and that in previous experiments of UG conducted in different countries (34). Thus, qualitatively similar results may be obtained if the experiments are conducted in other countries. Third, most theoretical models for networked UG assume that a subject can act as both a proposer and a responder (18–20). Thus we may ask how the two identities of subjects influence each other and affect the formation of local communities predicted by theoretical models. Taken together, further effort is needed to offer a better understanding of the emergence of communities in social networks.

Table 2. The mean value and SD of proposers' offers in scale-free networks

N	$\langle k \rangle$	Structured/unstructured	
		Mean(p)	SD(p)
100	4	41.30/41.30	5.36/2.14
	6	42.81/42.89	4.26/1.54
	8	43.60/43.52	3.46/1.17
500	4	41.10/41.11	5.71/2.16
	6	42.73/42.71	4.58/1.55
	8	43.60/43.58	3.81/1.18
1,000	4	40.95/40.92	5.78/2.17
	6	42.69/42.70	4.66/1.54
	8	43.61/43.60	3.89/1.19

N represents the network size and $\langle k \rangle$ represents the average nodal degree. Structured and unstructured correspond to virtual experiments with static scale-free networks and constantly changing networks with the same node degrees as their counterparts with fixed structures. Other notations have the same meaning as that in Table 1. The results are calculated by using from round 2 to round 60 and implementing 1,000 independent realizations.

Materials and Methods

This research was approved by School of Systems Science, Beijing Normal University on the use of human subjects, and informed consent was obtained from subjects before participation. We recruit 50 participants in each of four groups. Half of them are randomly assigned proposers and half are randomly assigned responders, and assigned player roles do not change during the experiment. Each participant in the treatment groups is assigned a location within a static network and designated either a proposer or a responder. In the treatment groups the UG is structured and participants must play the UG with their immediate neighbors (two subjects are neighbors if they are directly connected). All of the proposers' neighbors are responders and vice versa. To be consistent with theoretical models, in each round all subjects must use one decision behavior as they interact with their neighbors; that is, a proposer must make the same offer p ($0 \leq p \leq 100$) to all of his or her neighboring responders, and a responder must indicate the same minimum acceptance level q ($0 \leq q \leq 100$) to all of his or her neighboring proposers (18–20). For T1 we construct a regular bipartite network in which each node has four neighbors. For T2 we build a random bipartite network in which the number of neighbors ranges from two to six (with an average degree of four).

We compare the results from the treatment groups with the results from the two control groups (populations with random interactions), C1 and C2, to explore the network effect on fairness and altruism. Specifically, to make an unbiased comparison between the treatment and control groups, in C1 and C2 we use a randomly rewired bipartite network with the same node

degrees as in the treatment groups. In the rewired network the neighbors of each node are chosen randomly from the other type of nodes in each round, but the number of each node's neighbors is unchanged.

Each group of experiments includes 60–70 rounds. To prevent any final-round effect, we do not tell the participants the number of rounds they will play. In each round, information gathered in the previous round is given to each player, including the player's own behavior and payoff and the behavior of the player's neighbors. The payoff of a player in each round is the sum of the benefits gained from interacting with all of the neighbors of the player normalized by the number of neighbors. To simplify their decision-making processes, we rank neighbor behaviors in a descending order such that players can easily evaluate their behaviors (SI Appendix, Fig. S2). For a further explanation of the experimental design, see SI Appendix, Supplementary Notes 3–5.

ACKNOWLEDGMENTS. We thank Zengru Di, A. Sánchez, T. Sasaki, J. Honda, A. Traulsen, and F. Fu for valuable discussion and suggestions. This work was supported by the National Nature Science Foundation of China under Grants 61573064, 71631002, 71401037, and 11301032; the Fundamental Research Funds for the Central Universities and Beijing Nova Programme; and the Natural Sciences and Engineering Research Council of Canada (Individual Discovery Grant). The Boston University work was supported by NSF Grants PHY-1505000, CMMI-1125290, and CHE-1213217, and by Defense Threat Reduction Agency Grant HDTRA1-14-1-0017, and Department of Energy Contract DE-AC07-05ld14517.

- Jackson MO (2010) *Social and Economic Networks* (Princeton Univ Press, Princeton).
- Barabási A-L (2014) *Linked: How Everything is Connected to Everything Else and What It Means for Business, Science, and Everyday Life* (Basic Books, New York).
- Dourisboure Y, Geraci F, Pellegrini M (2007) Extraction and classification of dense communities in the web. *Proceedings of the 16th International Conference on World Wide Web* (ACM, New York), pp 461–470.
- Ostrom E (2009) *Understanding Institutional Diversity* (Princeton Univ Press, Princeton).
- Rives AW, Galitski T (2003) Modular organization of cellular networks. *Proc Natl Acad Sci USA* 100(3):1128–1133.
- Axelrod RM (2006) *The Evolution of Cooperation* (Basic Books, New York).
- Von Neumann J, Morgenstern O (2007) *Theory of Games and Economic Behavior* (60th Anniversary Commemorative Edition) (Princeton Univ Press, Princeton).
- Sigmund K (2010) *The Calculus of Selfishness* (Princeton Univ Press, Princeton).
- Skyrms B (2010) *Signals: Evolution, Learning, and Information* (Oxford Univ Press, New York).
- Nishi A, Shirado H, Rand DG, Christakis NA (2015) Inequality and visibility of wealth in experimental social networks. *Nature* 526:426–429.
- Santos FC, Pacheco JM, Lenaerts T (2006) Evolutionary dynamics of social dilemmas in structured heterogeneous populations. *Proc Natl Acad Sci USA* 103(9):3490–3494.
- Szabó G, Fath G (2007) Evolutionary games on graphs. *Phys Rep* 446(4-6):97–216.
- Santos FC, Santos MD, Pacheco JM (2008) Social diversity promotes the emergence of cooperation in public goods games. *Nature* 454(7201):213–216.
- Roca CP, Cuesta JA, Sánchez A (2009) Evolutionary game theory: Temporal and spatial effects beyond replicator dynamics. *Phys Life Rev* 6(4):208–249.
- Kun Á, Diekmann U (2013) Resource heterogeneity can facilitate cooperation. *Nat Commun* 4:2453.
- Perc M, Gómez-Gardeñes J, Szolnoki A, Floría LM, Moreno Y (2013) Evolutionary dynamics of group interactions on structured populations: A review. *J R Soc Interface* 10(80):20120997.
- Matamalas JT, Poncela-Casasnovas J, Gómez S, Arenas A (2015) Strategical incoherence regulates cooperation in social dilemmas on multiplex networks. *Sci Rep* 5: 9519.
- Sinatra R, et al. (2009) The ultimatum game in complex networks. *J Stat Mech Theory Exp* 2009(09):P09012.
- Szolnoki A, Perc M, Szabó G (2012) Defense mechanisms of empathetic players in the spatial ultimatum game. *Phys Rev Lett* 109(7):078701.
- Iranzo J, Floría LM, Moreno Y, Sánchez A (2012) Empathy emerges spontaneously in the ultimatum game: Small groups and networks. *PLoS One* 7(9):e43781.
- Fehl K, van der Post DJ, Semmann D (2011) Co-evolution of behaviour and social network structure promotes human cooperation. *Ecol Lett* 14(6):546–551.
- Rand DG, Arbesman S, Christakis NA (2011) Dynamic social networks promote cooperation in experiments with humans. *Proc Natl Acad Sci USA* 108(48):19193–19198.
- Wang J, Suri S, Watts DJ (2012) Cooperation and assortativity with dynamic partner updating. *Proc Natl Acad Sci USA* 109(36):14363–14368.
- Shirado H, Fu F, Fowler JH, Christakis NA (2013) Quality versus quantity of social ties in experimental cooperative networks. *Nat Commun* 4:2814.
- Cassar A (2007) Coordination and cooperation in local, random and small world networks: Experimental evidence. *Games Econ Behav* 58(2):209–230.
- Kirchkamp O, Nagel R (2007) Naive learning and cooperation in network experiments. *Games Econ Behav* 58(2):269–292.
- Traulsen A, Semmann D, Sommerfeld RD, Krambeck H-J, Milinski M (2010) Human strategy updating in evolutionary games. *Proc Natl Acad Sci USA* 107(7):2962–2966.
- Grujić J, Fosco C, Araujo L, Cuesta JA, Sánchez A (2010) Social experiments in the mesoscale: Humans playing a spatial prisoner's dilemma. *PLoS One* 5(11):e13749.
- Suri S, Watts DJ (2011) Cooperation and contagion in web-based, networked public goods experiments. *PLoS One* 6(3):e16836.
- Gracia-Lázaro C, et al. (2012) Heterogeneous networks do not promote cooperation when humans play a Prisoner's Dilemma. *Proc Natl Acad Sci USA* 109(32):12922–12926.
- Grujić J, Röhl T, Semmann D, Milinski M, Traulsen A (2012) Consistent strategy updating in spatial and non-spatial behavioral experiments does not promote cooperation in social networks. *PLoS One* 7(11):e47718.
- Rand DG, Nowak MA, Fowler JH, Christakis NA (2014) Static network structure can stabilize human cooperation. *Proc Natl Acad Sci USA* 111:17093–17098.
- Wu J-J, et al. (2009) Costly punishment does not always increase cooperation. *Proc Natl Acad Sci USA* 106(41):17448–17451.
- Oosterbeek H, Sloof R, van de Kuilen G (2004) Cultural differences in ultimatum game experiments: Evidence from a meta-analysis. *Exp Econ* 7(2):171–188.
- Henrich J, et al. (2006) Costly punishment across human societies. *Science* 312(5781):1767–1770.
- Henrich J, et al. (2010) Markets, religion, community size, and the evolution of fairness and punishment. *Science* 327(5972):1480–1484.
- Peysakhovich A, Nowak MA, Rand DG (2014) Humans display a 'cooperative phenotype' that is domain general and temporally stable. *Nat Commun* 5:4939.
- Rand DG, Tarnita CE, Ohtsuki H, Nowak MA (2013) Evolution of fairness in the one-shot anonymous Ultimatum Game. *Proc Natl Acad Sci USA* 110(7):2581–2586.
- Cooper DJ, Dutcher EG (2011) The dynamics of responder behavior in ultimatum games: A meta-study. *Exp Econ* 14(4):519–546.
- Fehr E, Schmidt KM (1999) A theory of fairness, competition, and cooperation. *Q J Econ* 114(3):817–868.
- Bolton GE, Ockenfels A (2000) ERC: A theory of equity, reciprocity, and competition. *Am Econ Rev* 90(1):166–193.
- Sanfey AG, Rilling JK, Aronson JA, Nystrom LE, Cohen JD (2003) The neural basis of economic decision-making in the Ultimatum Game. *Science* 300(5626):1755–1758.
- Brenner T, Vriend NJ (2006) On the behavior of proposers in ultimatum games. *J Econ Behav Organ* 61(4):617–631.
- Dawes CT, Fowler JH, Johnson T, McElreath R, Smirnov O (2007) Egalitarian motives in humans. *Nature* 446(7137):794–796.
- Wallace B, Cesarini D, Lichtenstein P, Johannesson M (2007) Heritability of ultimatum game responder behavior. *Proc Natl Acad Sci USA* 104(40):15631–15634.
- Yamagishi T, et al. (2012) Rejection of unfair offers in the ultimatum game is no evidence of strong reciprocity. *Proc Natl Acad Sci USA* 109(50):20364–20368.
- Ellison G (1993) Learning, local interaction, and coordination. *Econometrica* 61:1047–1071.
- Barabási A-L, Albert R (1999) Emergence of scaling in random networks. *Science* 286(5439):509–512.
- Young HP (2001) *Individual Strategy and Social Structure: An Evolutionary Theory of Institutions* (Princeton Univ Press, Princeton).
- Peysakhovich A, Rand DG (2015) Habits of virtue: Creating norms of cooperation and defection in the laboratory. *Manage Sci* 62(3):631–647.
- Gächter S, Nosenzo D, Renner E, Sefton M (2012) Who makes a good leader? Cooperativeness, optimism, and leading-by-example. *Econ Inquiry* 50(4):953–967.
- Wu J-J, Li C, Zhang B-Y, Cressman R, Tao Y (2014) The role of institutional incentives and the exemplar in promoting cooperation. *Sci Rep* 4:6421.
- Bear A, Rand DG (2016) Intuition, deliberation, and the evolution of cooperation. *Proc Natl Acad Sci USA* 113(4):936–941.