Conditional cooperation can hinder network reciprocity

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Social networks are ubiquitous in our internet-dominated culture, and the new virtual social networks have a lot in common with traditional social networks (e.g., friends and colleagues). In all cases, it is important who interacts with whom. Lately, there has been much theoretical and empirical work on how the behavior of individuals can be influenced by their social ties and how ties are distributed within a network. Theoretical findings of the effects of such population structures on cooperative behavior in humans have been inconsistent (1–4), and empirical tests have lacked—from a theoretical point of view—sufficient system sizes. Gracia-Lázaro et al. (5) have now conducted an impressively large-scaled experiment of 1,229 humans simultaneously playing a prisoner's dilemma in two different network environments. Specifically, they test whether homogenous or heterogeneous networks—both static environments—influence cooperative behavior (Fig. 1).

Human networks are an essential feature of social behavior (6). In addition, in many other social species, interactions between individual behavior and population-level structure have been identified as important ecological factors (7, 8). In general, the network structure poses a significant ecological factor for the evolution of cooperative behavior. The model of Nowak and May (9)—in which individuals interacted in a prisoner's dilemma on a spatial grid—inspired a great amount of work in this field, especially on humans. One mechanism that has been put forward to explain how the structure of static networks can support the evolution of cooperation under various conditions is network reciprocity (9–11), with some exceptions (e.g., ref. 12). Here, the population structure (e.g., spatial lattices) promotes cooperative behavior by enabling cooperative individuals to assort into clusters. Clusters "protect" cooperative individuals from exploitation through defective individuals by reducing opportunities to interact with them (refs. 9, 13, and 14; see also ref. 15). Homogenous networks are generally not found in nature; instead, natural social networks are usually heterogeneous networks (8, 16). In particular for the latter, theoretical models show positive effects on cooperation levels (17–21). Congruent with this theoretical work, evolutionary simulations based on social networks of nonhuman primates show that, for example, these natural networks have the appropriate static structure to potentially support cooperation (8). By using social network analysis, we can now investigate not only the effects on the evolution of cooperative behavior, but also the existing social network properties and their effects on the individual's behavior (22).

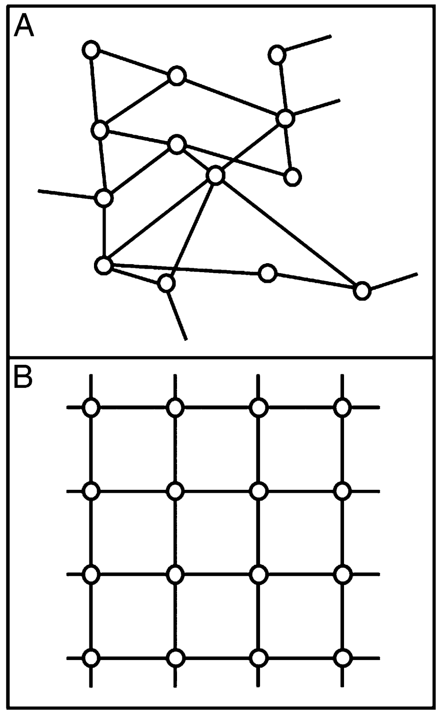

Fig. 1. Visualization of network types. In heterogeneous networks, individuals (i.e., nodes) differ in number of social connections (i.e., ties). In the experiment of Gracia-Lázaro et al. (5), the 604 nodes each had between 2 and 16 ties, whereas, in *A*, the 13 nodes have between 2 and 5 ties. In contrast, in homogenous networks, all nodes have the same number of ties, as in *B*, in which each node has 4 ties (example square lattice size is 4 × 4, experimental square lattice size of Gracia-Lázaro et al. (5) 25 × 25). Lines (*A* and *B*) represent the ties connecting the nodes, each represented by a circle.

However, in relation to the more extensive theoretical work, it is somewhat surprising that, so far, experiments with humans cannot show that static network structure promotes cooperation. Spatial lattices and other network topologies caused cooperation to decrease over time (2, 4) or could not convincingly reveal differences in levels of cooperation between network structures (2, 4, 23, 24). Empirically, only dynamic networks have been shown to have cooperation enhancing properties (e.g., refs. 1 and 3).

Potential reasons for the lack of experimental proof are (*i*) the large gap between the experimental group sizes and the theoretical population sizes. Effects of population structure on cooperative behavior are usually shown in very large populations, which often include thousands of individuals (i.e., nodes) and social connections (i.e., ties). In contrast, empirical studies generally are constrained to group sizes in the lower two-digit numbers. Therefore, from a theoretical point of view, the existing experiments until now lack size to be true tests for the model predictions. Furthermore, (*ii*) many models use an imitation rule as an update mechanism for the agents. However, the existing experiments show that humans playing a prisoner's dilemma using only one strategy for all neighbors do not seem to imitate their best neighbor (2, 4).

Gracia-Lázaro et al. (5) base their empirical predictions on a previously published model (25). Instead of using imitation as the update rule, they implement a model that uses behavioral update rules derived from a previous empirical study (2). Their results with this previously published model (25) challenge the existing predictions of cooperation enhancing effects of homogenous and heterogeneous network environments, and actually predict that neither structure enhances overall cooperation levels. To test the new predictions, Garcia-Lazaro et al. (5) performed an experiment with 604 and 629 humans playing a prisoner's dilemma in a homogenous or heterogeneous network setting, respectively. Here, the experimental network size is considered large enough that model-like cooperative clusters can form and thereby favor cooperation (26, 27). The participants played a repeated weak prisoner's dilemma with their neighbors (i.e., 4 neighbors in the homogeneous network and between 2 and 16 neighbors in the heterogeneous network). Without knowledge of the duration of the game, the participants had to make only one decision for all neighbors, i.e., whether to cooperate or to defect. Therefore, the situation

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becomes similar to a repeated public goods game. Public goods games pose a social dilemma because one cannot directly reciprocate defective behavior without also defecting toward cooperative partners. In public good experiments, humans usually start highly cooperatively, but, in the absence of cooperation-enhancing mechanisms such as punishment (28) or reputation (29), their cooperation decreases over time.

Gracia-Lázaro et al. (5) present a very convincing, large-scale experimental study that shows that static population structure is not affecting cooperation in public goods-like social dilemmas. According to network reciprocity, the formation of clusters should help sustain cooperation in this dilemma situation and increase cooperation on the global level. However, the potential effects of the underlying structure are precluded in the experiment because the participants behaved as conditional cooperators. The participants reacted in both networks—homogeneous and heterogeneous—to the level of cooperation in the neighborhood. The resulting cooperation levels are the same for both network types, and are comparable to those in smaller network sizes and unstructured populations. This study (5) bridges, to a large extent, the gap between theoretical models sizes and experimental group sizes.

Static population structure is not affecting cooperation in public goods-like social dilemmas.

Cutting-edge computer technology has provided us with better simulation tools and enables us to analyze network structures in completely new dimensions. With their study, Gracia-Lázaro et al. (5) show strikingly that this is true not only for theoretical work, but also for experimental work that can now be conducted in new and innovative ways. The resulting large networks sizes are a very important contribution for testing the existing theoretical predictions, and their results have high potential to impact future work in this field.

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