Evolutionary dynamics of social dilemmas in structured heterogeneous populations

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Real populations have been shown to be heterogeneous, in which some individuals have many more contacts than others. This fact contrasts with the traditional homogeneous setting used in studies of evolutionary game dynamics. We incorporate heterogeneity in the population by studying games on graphs, in which the variability in connectivity ranges from single-scale graphs, for which heterogeneity is small and associated degree distributions exhibit a Gaussian tale, to scale-free graphs, for which heterogeneity is large with degree distributions exhibiting a power-law behavior. We study the evolution of cooperation, modeled in terms of the most popular dilemmas of cooperation. We show that, for all dilemmas, increasing heterogeneity favors the emergence of cooperation, such that long-term cooperative behavior easily resists short-term noncooperative behavior. Moreover, we show how cooperation depends on the intricate ties between individuals in scale-free populations.

complex networks | evolution of cooperation

Cooperation has played a key role throughout evolution (1). Self-replicating cells have cooperated to form multicellular organisms throughout evolutionary history (2, 3). Similarly, we know that animals cooperate in families to raise their offspring and in groups to prey and to reduce the risk of predation (4, 5). Cooperation has been conveniently formulated in the framework of evolutionary game theory, which, when combined with games such as the Prisoner's Dilemma, which is used as a metaphor for studying cooperation between unrelated individuals, enables one to investigate how collective cooperative behavior may survive in a world where individual selfish actions produce better short-term results. Analytical solutions for this problem have been obtained when populations are assumed infinite and their interactions are assumed homogeneous such that all individuals are in equivalent positions. Under such assumptions, noncooperative behavior prevails. Such an unfavorable scenario for cooperation in the Prisoner's Dilemma game, together with the difficulty in ranking the actual payoffs in field and experimental work (6, 7), has lead to the adoption of other games (8, 9), such as the Snowdrift game (also known as Hawk–Dove or Chicken), which is more favorable to cooperation, and the Stag-Hunt game (10), and to numerical studies of cooperation in finite, spatially structured populations (11) in which homogeneity is still retained. Such studies of the role of structured populations have attracted considerable attention, originating from fields ranging from sociology to biology, ecology, economics, mathematics, and physics, to name a few (11–19). More recently, however, compelling evidence has been accumulated that a plethora of biological, social, and technological real-world networks of contacts (NoC) are mostly heterogeneous (20–22). Indeed, analysis of real-world NoC (20) has provided evidence for the following (heterogeneous) types: (*i*) single-scale networks, which are characterized by degree distributions (defined in the *Methods*) that exhibit a fast, typically Gaussian, decaying tail; (*ii*) broad-scale networks, which are characterized by a power-law regime truncated for large connectivities by a fast-decaying tail; and (*iii*) scale-free networks, which are characterized by a distribution that decays as a power-law. In Fig. 1, we show the distribution of connectivities associated with both single-scale and scale-free NoC, on which the results shown in Figs. 2 and 3 were based. To better illustrate the degree of heterogeneity associated with each NoC, we show a double logarithmic plot of the cumulative degree distribution, defined in Fig. 1. Clearly heterogeneity greatly increases as one moves all of the way from single scale to extreme heterogeneous, scale-free NoC. In particular, the broad-scale NoC also identified in ref. 20 exhibit tails that fall off somewhere between the extreme limits depicted in Fig. 1. All of these different levels of heterogeneity stand in sharp contrast with homogeneous NoC.

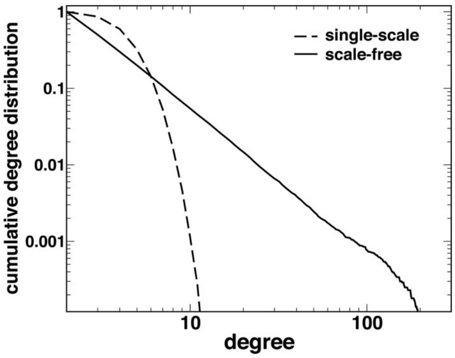

Fig. 1. Heterogeneous NoC. Shown is the cumulative degree distribution, $D(k)$ [defined for a graph with N vertices as $\Sigma_{i=k}^{N-1}(N_i/N)$, where N_i gives the number of vertices with i edges], for two types of NoC for which $N = 10^4$. The first type of NoC are single-scale heterogeneous NoC, depicted with a dashed line, in which most individuals have a similar number of connections, leading to a narrow degree distribution. The Gaussian tail (20) of such a distribution is responsible for the fast decay exhibited by the cumulative degree distribution depicted. The second type of NoC are scale-free NoC, generated according to the Barabási–Albert model and exhibiting a cumulative degree distribution scaling as $D(k) \approx k^{-2}$ (solid line). The tail at the end of the solid line results from the finiteness of the population. For the class of broad-scale networks identified in ref. 20, the cumulative degree distribution will tail-off at degree values intermediate from those associated with the single-scale and scale-free NoC depicted.

What is the impact of moving from a homogeneously structured population, in which everyone has the same amount of interactions, to a heterogeneously structured population, in which some can interact more than others? In particular, what is the impact of more realistic NoC in the evolution of cooperation?

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Abbreviation: NoC, network of contacts.

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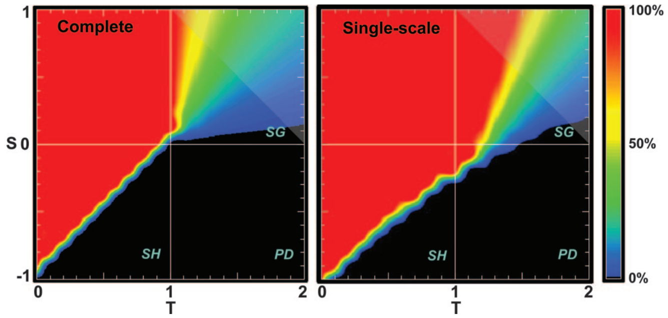

Fig. 2. Evolution of cooperation in different NoC. Results for the fraction of cooperators in the population are plotted as a contour drawn as a function of two parameters: *S*, the disadvantage of a cooperator being defected (when $S < 0$), and *T*, the temptation to defect on a cooperator (when $T > 1$). In the absence of any of these threats ($S \geq 0$ and $T \leq 1$; upper-left quadrant) cooperators trivially dominate. The lower-left quadrant ($S < 0$ and $T \leq 1$) corresponds to the Stag-Hunt domain (SH). The lower triangle in the upper-right quadrant ($S \geq 0$, $T > 1$ and $(T + S) < 2$) corresponds to the Snowdrift game domain (SG). The lower-right quadrant ($S < 0$ and $T > 1$) corresponds to the Prisoner's Dilemma domain (PD). (*Left*) Results obtained in complete NoC that reproduce in finite populations the analytic solutions known for infinite, well mixed populations. These results provide the reference scenario with which the role of population structure will be subsequently assessed. (*Right*) Results obtained for single-scale NoC, characterized by a moderate degree of heterogeneity. Comparison with the results for finite, well mixed populations (*Left*) shows that such small heterogeneity is on the basis of the overall enhancement of cooperation (details provided in main text).

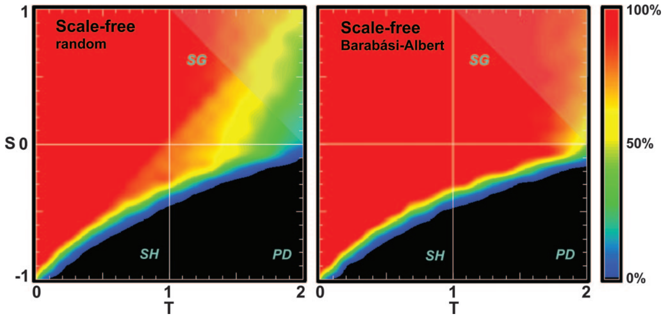

Fig. 3. Evolution of cooperation in scale-free NoC. We use the same notation and scale as Fig. 2. (*Left*) Random scale-free NoC. The interplay between small-world effects and heterogeneity effects leads to a net overall increase of cooperation for all dilemmas. (*Right*) Barabási–Albert scale-free NoC. When highly connected individuals are directly interconnected, cooperators dominate defectors for all values of the temptation to defect $T > 1$, enlarging the range of intensities of $S < 0$ for which they successfully survive defectors, showing how the intricate ties between individuals affect the evolutionary dynamics of cooperators. Abbreviations are the same as those in Fig. 2.

Here we address this problem by examining the emergence of cooperation in terms of the three popular and extensively studied dilemmas of cooperation referred to above. It will be shown that increasing heterogeneity generally favors the emergence of cooperation, irrespective of the dilemma under investigation.

Games and Social Dilemmas

We shall model interactions among individuals in terms of two-person games in which both players can either cooperate or defect when interacting with each other. Mutual cooperation leads to the reward, R (without loss of generality, we make $R = 1$), whereas mutual defection leads to the punishment, P (we make $P = 0$, thereby normalizing the advantage of mutual cooperation over mutual defection to 1 in all games). The other two possibilities occur when one player cooperates and the other defects, for which the associated game payoffs are S (sucker's payoff) and T (temptation) for the cooperator and the defector, respectively. Provided that mutual cooperation is always preferred over mutual defection, the three dilemmas arise naturally (16), depending on the relative ordering of these four payoffs: The Snowdrift game, for which $T > 1 > S > 0$; the Stag-Hunt game, for which $1 > T > 0 > S$; and the Prisoner's Dilemma game, for which $T > 1 > 0 > S$. For all dilemmas, mutual cooperation is also preferred over unilateral cooperation (S) and over an equal probability of unilateral cooperation and defection ($2 > T + S$). Tension becomes apparent when the preferred choices of each player lead to individual actions resulting in mutual defection, despite the fact that mutual cooperation is more beneficial. Indeed, tension will arise when players prefer unilateral defection to mutual cooperation ($T > 1$), when players prefer mutual defection to unilateral cooperation ($S < 0$), or when both situations arise, which is precisely what happens in the Snowdrift game, the Stag-Hunt game and the Prisoner's Dilemma game, respectively. Formally, these dilemmas span a four-dimensional parameter space. By normalizing mutual cooperation to 1 and mutual defection to 0, we are left with two parameters, T and S. We study the behavior of all dilemmas, summarized in Table 1, in the ranges $0 \leq T \leq 2$ and $-1 \leq S \leq 1$, which will be shown to be sufficient to characterize the games under study.

Role of Heterogeneity in the Evolution of Cooperation

Let us consider heterogeneous NoC. Different individuals in the population may engage in different number of rounds per generation because of the number of different ties that each entails. Moreover, the pattern of connectivity may also be different for different individuals: For example, one individual may be connected to few immediate neighbors, whereas another individual may have many connections, some of which may constitute direct links to far-away individuals.

As an illustration, consider two focal individuals, a cooperator with N_1 neighbors, and a defector with N_2 neighbors, and let us imagine that both have the same number of defectors, say N_D. After interacting with all their neighbors, the cooperator accumulates a payoff of $P_C = N_1 + (S - 1)N_D$, whereas the defector ends up with $P_D = (N_2 - N_D)T$. If the NoC were homogeneous, all one needs to do is to make $N_1 = N_2 = z$, the average connectivity of the population, in the previous expressions. This calculation, however, leads to very different outcomes in what concerns the accumulated payoffs in homogeneous and heterogeneous NoC. Indeed, whereas, in homogenous NoC, the answer to whether $P_D > P_C$ relies exclusively on the relative ordering of the payoffs (T, R, P, S); in heterogeneous NoC the

Table 1. Games studied and their parameter range

Game	Abbreviation	Parameters	Tension(s) included in each dilemma
Snowdrift	SG	$T > 1 > S > 0$	Players prefer unilateral defection to mutual cooperation
Stag Hunt	SH	$1 > T > 0 > S$	Players prefer mutual defection to unilateral cooperation
Prisoner's Dilemma	PD	$T > 1 > 0 > S$	Both tensions above are incorporated in this dilemma

For each social dilemma studied, we list the corresponding abbreviation, the parameter range that we consider in this work, and the tension that leads to the dilemma.

answer depends now on the fact that $N_1 \neq N_2$. In other words, the pattern of connectivity also contributes to define the accumulated payoff of each individual, a feature that, being natural, is absent in homogeneous NoC. Indeed, heterogeneity embeds the intuition that different individuals engage in different numbers of interactions with different intensities, which opens a new route to the evolution of cooperation: Cooperators will increase their fitness to the extent they succeed in maximizing their amount of cooperative interactions per generation. However, defectors may also increase their fitness by exploiting more cooperators per generation. Results presented as supporting information, which is published on the PNAS web site, show that cooperators are able to profit from heterogeneity to outperform defectors.

Results and Discussion

Well Mixed Populations. Before addressing heterogeneous, structured populations (results for homogeneous structured populations are provided in the supporting information), we examine the effect of the dynamics on the finite population analog to the infinite well mixed limit, which is well known from the standard analytical treatment (23): a complete, fully connected graph. Evolution is implemented via the stochastic dynamics described in *Methods*. As usual in evolutionary biology, the fitness of each individual is associated with the accumulated payoff at the end of a life cycle. The results are shown in Fig. 2 *Left*, in which the Stag-Hunt, Snowdrift, and Prisoner's Dilemma games span the three domains that fill the lower-left, upper-right, and lower-right squares of the contour plot, respectively. Note further that in the Snowdrift domain, only the lower triangle of the domain strictly satisfies the requirement $2 > T + S$.

The results obtained here for a well mixed population of $N = 10^4$ individuals retain all of the features familiar from the analytical results for infinite well mixed populations: the (*i*) dramatic fate of cooperators in the Prisoner's Dilemma domain, (*ii*) a similar fate for cooperators in the Stag-Hunt domain when the disadvantage of being defected exceeds the temptation to defect, and (*iii*) the coexistence of cooperators and defectors in the Snowdrift domain when only the temptation to defect undermines mutual cooperation.

Heterogeneous Populations. Let us examine now the evolutionary dynamics in structured heterogeneous populations. We start with the single-scale type of populations identified in ref. 20, in which heterogeneity is small (Fig. 1), exhibiting a Gaussian tail for the degree distribution. Finite populations exhibiting such features were generated by using the configuration model (24), which leads to random graphs compatible with a given degree distribution (additional details are provided in *Methods*). The corresponding results are shown in Fig. 2 *Right*. Taking the results for well mixed populations as a reference, it is clear that cooperation is enhanced for all dilemmas. Specifically, cooperators now resist invasion by defectors in the Prisoner's Dilemma domain. Moreover, only for larger intensities of the temptation to defect will cooperators be outweighed by defectors in the Snowdrift domain. Finally, for the Stag-Hunt domain, cooperators are now able to resist defectors even when the disadvantage of being defected exceeds the temptation to defect.

The net results shown in Fig. 2 *Right* and Fig. 3 hide a detailed interplay of two mechanisms related to the small-world and heterogeneous nature of the underlying scale-free NoC: the occurrence of many long-range connections (so-called shortcuts) in these graphs precludes the formation of compact clusters of cooperators, thereby facilitating invasion by defectors when $S < 0$. However, the increase in heterogeneity of the NoC opens a new route for cooperation to emerge, because, now, different individuals interact different number of times per generation, which enables cooperators to outperform defectors. In other words, whereas the increased difficulty in aggregating clusters of cooperators would partially hamper cooperation (see the supporting information), heterogeneity counteracts this effect with a net increase of cooperation. Indeed, the results discussed below for scale-free NoC show how cooperation is sensitive to the overall degree of heterogeneity of the underlying NoC, leading to an increase of cooperation as one evolves from homogeneous populations (Fig. 2 *Left*) to extreme heterogeneous populations (Fig. 3).

The effects of heterogeneity become indeed more prominent when we consider scale-free NoC.[¶] The results for the evolution of cooperation in populations exhibiting a scale-free degree distribution such that all connections between individuals are purely random are shown in Fig. 3 *Left*. Notice that, despite the abundance of scale-free behavior identified in real NoC, the detailed cartographic representation of the ties between individuals remains to a large extent unknown (25). In this sense, random scale-free populations, generated in the way described in *Methods* provide a general bias-free scenario. The results in Fig. 3 *Left* provide further evidence of the determinant role played by such heterogeneous population structures on the evolution of cooperation for all dilemmas. Maintaining Fig. 2 *Left* as a reference, we observe that, over all, scale-free NoC efficiently neutralize the detrimental role of the temptation to defect (when $T > 1$) in the evolution of cooperation, whereas the disadvantage of being defected (when $S < 0$) remains a strong deterrent of cooperation. Indeed, in the Snowdrift domain, cooperators dominate for all values of $T > 1$. In the Stag-Hunt domain, cooperators now survive even when $S < T - 1$. For the Prisoner's Dilemma domain, the region of coexistence between cooperators and defectors is clearly broadened. Moreover, the small slope of the borderline between cooperators and defectors provides further evidence that the disadvantage of being defected ($S < 0$) constitutes the major threat to cooperation.

The sustainability of cooperation, however, is not affected solely by the overall heterogeneity of the NoC associated with a given degree distribution. In fact, cooperation is particularly susceptible to the detailed and intricate ties between individuals in a population. Indeed, if we do not randomize the pattern of connectivity between individuals such that the NoC exhibit the correlations arising naturally in the Barabási and Albert (21) model, a different result emerges for the evolution of cooperation, as shown in Fig. 3 *Right*. Under the presence of such correlations, the temptation to defect no longer poses any threat to cooperation, defectors being wiped out from populations in the entire Snowdrift domain. In the Stag-Hunt domain, cooperators now wipe out defectors, where, before (Fig. 3 *Left*), they managed to coexist. In the Prisoner's Dilemma domain, cooperators also get a strong foothold up to larger intensities of $|S|$.

As is well known, the Barabási and Albert (21) model exhibits so-called age correlations in which the older vertices not only acquire the highest connectivity but also become naturally interconnected with each other. These correlations result from the combined mechanisms of growth and preferential attachment, which lie at the heart of the model (21). As a result, the formation of compact clusters of cooperators, which was inhibited by the occurrence of many shortcuts in random scale-free NoC, will be partly regained in such NoC, mostly for the few individuals that exhibit high connectivity. Of course, such a

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[¶] In ref. 20, a third class of NoC was identified and described as ''broad-scale.'' The associated degree distribution of broad-scale NoC exhibits a region of scale-free behavior truncated by a fast-decaying tail for large values of the connectivity, which leads naturally to intermediate levels of heterogeneity as compared with those discussed in this work. In view of the results obtained here, one expects to obtain levels of cooperation intermediate from those associated with single-scale and scale-free graphs. Our results (data not shown) for uncorrelated broad-scale NoC entirely corroborate this picture.

clustering of cooperators will occur only to the extent that cooperators are able to occupy such highly connected sites, which indeed happens. The results shown in Fig. 3 have the additional feature that the degree distributions of the NoC used in studying the evolution of cooperation actually coincide, the difference between the two NoC residing solely in the detailed pattern of ties between individuals. Finally, we would like to point out that all our results remain unchanged both for larger (we have checked up to $N = 10^5$) and smaller population sizes, down to values of $N \approx 10^2$ individuals. For such small population sizes, stochastic effects resulting from both the graph generation procedures and the evolutionary dynamics preclude a clear-cut result for the evolution of cooperation.

Conclusions

The present results demonstrate that, in more realistic, heterogeneous populations, the sustainability of cooperation is simpler to achieve than in homogeneous populations, a result that is valid irrespective of the dilemma adopted as a metaphor of cooperation. The results shown in Fig. 2 *Right* show that heterogeneity constitutes a powerful mechanism for the emergence of cooperation, because, even for mildly heterogeneous populations, heterogeneity leads to sizeable effects in the evolution of cooperation. The results also show that the disadvantage of being defected ($S < 0$) constitutes a stronger deterrent of cooperation than the temptation to defect ($T > 1$), a feature found before for the Prisoner's Dilemma in the context of homogeneous, infinite populations (26).

The overall enhancement of cooperation obtained on single-scale and scale-free graphs may be understood as resulting from the interplay of two mechanisms: (*i*) the existence of many long-range connections in random and small-world NoC, which precludes the formation of compact clusters of cooperators (this effect acts to inhibit cooperation when $S < 0$) and (*ii*) the heterogeneity exhibited by these NoC, which opens a new route for cooperation to emerge and contributes to enhance cooperation (which increases with heterogeneity), counteracting the previous effect. The net result is that cooperation is enhanced, as shown in Figs. 2 *Right* and 3.

Finally, the sustainability of cooperation depends also on the intricate ties between individuals, even for the same class of graphs, features not accounted for by mean-field or pair approximations.

In this context, it is noteworthy that the present model assumes a given population structure that remains immutable throughout evolution. A more realistic model, however, should take into account that individuals have the capacity to establish new links as well as to severe others throughout evolution, leading to an adaptive coevolution of strategy and structure. It remains an open problem the extent to which such a possibility will naturally lead to the scale-free populations studied here.

Methods

Homogeneous and Heterogeneous Graphs. In the language of graph theory, well mixed populations of size N are represented by complete graphs, which correspond to a regular, homogeneous graph with average connectivity $z = N - 1$, because all vertices share the same number of connections and are topologically equivalent. Indeed, all homogeneous graphs exhibit the same single-peak shape for the degree distribution $d(k)$, defined for a graph with N vertices as $d(k) = N_k/N$, where N_k gives the number of vertices with k edges. In Fig. 1, we show the cumulative degree distribution associated with the heterogeneous types of NoC explicitly considered in this work [the cumulative degree distribution $D(k)$ is defined in Fig. 1]. Real-world NoC are clearly heterogeneous, corresponding to populations in which different individuals exhibit distinct patterns of connectivity, portraying the coexistence of local connections (spatial structure) with nonlocal connections (or shortcuts) and often exhibiting regions with a power-law dependence of their degree distributions (20–22). When heterogeneity is moderate, such that the connectivities of most individuals do not deviate significantly from the average connectivity value, the pattern of connectivity has been classified as "single-scale," as in ref. 20, where it was found that such NoC typically exhibit a Gaussian tail. Those NoC exhibit cumulative degree distributions such as that illustrated in Fig. 1 with a dashed line. The results in Fig. 2 *Right* correspond to populations modeled in terms of such NoC, making use of the configuration model (24), which provides a maximally random graph compatible with such a degree distribution.[‖] Scale-free graphs, in contrast, constitute examples of strongly heterogeneous NoC. The Barabási–Albert model (21) provides the best known model leading to overall scale-free degree distributions, $d(k) \approx k^{-\gamma}$, with $\gamma = 3$, and cumulative degree distributions scaling as $\approx k^{-(\gamma - 1)}$, as shown in Fig. 1 with a solid line. The scale-free features of the Barabási–Albert model result from the combined effect of the two processes of growth[**] and preferential attachment,[††] the latter corresponding to the well known "rich get richer" effect in economics (27), which is also known as the Matthew effect in sociology (28). After t time steps, this algorithm produces a graph with $n = t + m_0$ vertices and mt edges. Because vertices appear at different moments in graph-generation time, so-called age correlations (21) arise. Such age-correlated NoC with $n = 10^4$ vertices and average connectivity $z = 4$ are on the basis of the results shown in Fig. 3 *Right*.

The role of heterogeneity in evolution may be singled out by removing any correlations (including age correlations) in a graph, which is easily accomplished by randomly and repeatedly exchanging the ends of pairs of edges of the original graph (29), a procedure that washes out correlations without changing the degree distribution (29) of the graphs. The results shown in Fig. 3 *Left* were obtained on Barabási–Albert scale-free NoC subsequently randomized in this way.

Evolutionary Games on Graphs. For $R = 1, P = 0, 0 \leq T \leq 2$ and $-1 \leq S \leq 1$, evolution is carried out by implementing the finite population analog of replicator dynamics (18, 30), to which simulation results converge in the limit of infinite, complete graphs (well mixed populations). These dynamics are obtained by defining the following transition probabilities: In each life cycle (one generation), all pairs of directly connected individuals x and y engage in a single round of the game, their accumulated payoff being stored as P_x and P_y, respectively. At the end of the generation, all strategies are updated simultaneously (synchronous updating). When a site x is updated, a neighbor y is drawn at random among all k_x neighbors; then, only if $P_y > P_x$ the strategy of chosen neighbor y replaces that of x with probability given by $(P_y - P_x)/[k_> D_>]$, where $k_> = \max(k_x, k_y)$ and $D_> = \max(T,1) - \min(S,0)$. This denominator ensures a proper normalization of the transition probability.[‡‡] The results obtained

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[‖] To generate a graph with the configuration model, one assigns to each vertex a number of "stubs" that constitute the tips of edges-to-be. The number of stubs must, of course, conform with the given degree distribution. Subsequently, one chooses, at random, pairs of stubs and joins them together, in this way generating the edges of the corresponding graph.

[**] Starting with a small number (m_0) of vertices, at every time step we add a new vertex with $m \leq m_0$ edges that link the new vertex to m different vertices already present in the system.

[††] When choosing the vertices to which the new vertex connects, we assume that the probability, p_i, that a new vertex will be connected to vertex i depends on the degree k_i of vertex i: $p_i = k_i/\Sigma k_i$.

[‡‡] It is noteworthy that the present stochastic dynamics relies entirely on local information pertaining to each pair of individuals involved. Furthermore, the update rule is invariant under translation and rescaling of the payoff matrix, the dynamics converging to the well known replicator dynamics in the limit of complete, infinite graphs. Such an update rule typically models cultural evolution, in which individuals tend to imitate the strategies of those performing better.

are robust and therefore insensitive to replacement of the previous expression by a transition probability function $W(P_y - P_x)$, being zero when $P_y \leq P_x$ and increasing monotonously to 1 when $P_y > P_x$. We have also confirmed that replacing synchronous updating by asynchronous updating does not bring any qualitative modifications to the results presented here.

Simulations. Simulations were carried out on graphs with $N = 10^4$ vertices and average connectivity $z = 4$ (except in Fig. 2 *Left*, where $z = N - 1$). Equilibrium frequencies of cooperators and defectors were obtained for each value of T and S by averaging over 1,000 generations after a transient time of 10,000 generations (we confirmed that averaging over larger periods or using different transient times did not change the results). Furthermore, final data results from averaging over 100 simulations, corresponding to 10 runs for each of 10 different realizations of a given type of NoC specified by the appropriate parameters (N and z). All simulations start with an equal percentage of strategies (cooperators and defectors) randomly distributed among the elements of the population. In this way, all vertices are initially populated with a strategy, and no initial advantage is given to cooperators or to defectors. Finally, even when graphs are generated stochastically, as is the case for the Barabási–Albert NoC, the evolution of cooperation is studied in full-grown graphs; that is, the topology of the graph remains frozen throughout evolution.

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