Scale-Free Networks Provide a Unifying Framework for the Emergence of Cooperation

F. C. Santos[1] and J. M. Pacheco[2,1]

[1]*GADGET, Apartado 1329, 1009-001 Lisboa, Portugal*
[2]*Centro de Física Teórica e Computacional and Departamento de Física da Faculdade de Ciências,*
P-1649-003 Lisboa Codex, Portugal

We study the evolution of cooperation in the framework of evolutionary game theory, adopting the prisoner's dilemma and snowdrift game as metaphors of cooperation between unrelated individuals. In sharp contrast with previous results we find that, whenever individuals interact following networks of contacts generated via growth and preferential attachment, leading to strong correlations between individuals, cooperation becomes the dominating trait throughout the entire range of parameters of *both* games, as such providing a unifying framework for the emergence of cooperation. Such emergence is shown to be inhibited whenever the correlations between individuals are decreased or removed. These results are shown to apply from very large population sizes down to small communities with nearly 100 individuals.

Cooperation plays a key role in the evolution of species, from cellular organisms to vertebrates. Yet, understanding the emergence of cooperation in the context of Darwinian evolution remains a challenge to date, met by scientists from many different fields of natural and social sciences [1], who often resort to Evolutionary Game Theory [2,3] as a common mathematical framework, and games such as the prisoner's dilemma (PD) and the snowdrift game (SG) as metaphors for studying cooperation between unrelated individuals [3]. In the PD, two players simultaneously decide whether to cooperate or defect. They both receive R upon mutual cooperation and P upon mutual defection. A defector exploiting a cooperator gets an amount T and the exploited cooperator receives S, such that $T > R > P > S$. As a result, in a single round of the PD it is best to defect regardless of the opponent's decision which, in turn, makes cooperators unable to resist invasion by defectors, whenever evolution under replicator dynamics [3] takes place in well-mixed populations. Such an unfavorable scenario for cooperators in the PD, together with the difficulty in ranking the actual payoffs in field and experimental work [4,5] has stimulated (i) the study of cooperation in more realistic situations [6], departing from the well-mixed population regime and also (ii) the adoption of other games [7,8], such as the SG, which are more favorable to cooperation. Indeed, in the SG the order of P and S is exchanged, such that $T > R > S > P$. Thus, at variance with the PD, the best action depends now on the opponent: to defect if the other cooperates, but to cooperate if the other defects. As a result, evolution under replicator dynamics [3] carried out in well-mixed populations leads to an equilibrium frequency for cooperators given by $1 - r$, with $0 \le r \le 1$ being the cost-to-benefit ratio of mutual cooperation (defined below).

Departure from the well-mixed population scenario has been pioneered by Nowak and May [6] who included spatial structure in the PD, such that individuals are constrained to play only with their immediate neighbors. Under such constraints, cooperators are now able to resist invasion by defectors. One decade later, laboratory experiments [9] have confirmed that topological constraints indeed affect in a sizeable way the evolution of cooperation. However, recent studies [10] carried out using the SG have shown that, contrary to PD, cooperation is inhibited whenever evolution in the SG takes place in a spatially-structured population, a result which renders the role of spatial structure as game specific and not necessarily beneficial in promoting cooperative behavior.

Graph theory provides a natural and very convenient framework to describe the population structure on which the evolution of cooperation is studied. Indeed, placing the elements (of a given population) on the vertices of a graph, whose edges define the network of contacts (NOCs) between those elements, one trivially concludes that both well-mixed populations and spatially-structured populations are represented by regular graphs, exhibiting a degree distribution [11] $d(k)$ which is sharply peaked at a single value of the connectivity k, since *all* vertices have the same connectivity. In particular, well-mixed populations are associated with complete (fully-connected, regular) graphs. As is well known [11], regular graphs constitute rather unrealistic representations of real-world NOCs, in which one expects local connections (spatial structure) to coexist with long-range connections (or shortcuts), features recently identified as characteristic of a plethora [11–13] of natural, social, and technological NOCs. In particular, a characteristic fingerprint [11–13] of many real-world NOCs is associated with a scale-free (SF), power law dependence of the degree distribution, $d(k) \sim k^{-\gamma}$, with the exponent γ typically satisfying $2 \le \gamma \le 3$ [11]. Furthermore, interactions in real-world NOCs are heterogeneous, in the sense that different individuals have different numbers of average neighbors whom they interact with, a feature which is present in SF NOCs.

In this Letter the impact of such NOCs in the evolution of cooperation is investigated. It will be shown that, contrary to previous results, cooperation becomes the dominating trait on both the PD and the SG, for all values of the relevant parameters of both games, whenever the NOCs correspond to scale-free graphs generated via the mechanisms of *growth* and *preferential attachment*. These results, which subsist in larger populations, being robust down to community sizes of the order of 100 individuals, are also shown to be characteristic of these types of SF NOCs, which provide a unifying framework for the emergence of cooperation, irrespective of whether the game in which individuals engage is the PD or the SG.

Following common practice [6,10], we start by rescaling the games such that each depends on a single parameter. For the PD, we make $T = b > 1$, $R = 1$, and $P = S = 0$, where b represents the advantage of defectors over cooperators [6], being typically constrained to the interval $1 < b \leq 2$. For the SG, we make $T = \beta > 1$, $R = \beta - 1/2$, $S = \beta - 1$, and $P = 0$, such that the cost-to-benefit ratio of mutual cooperation can be written as $r = 1/(2\beta - 1)$, with $0 \leq r \leq 1$.

Evolution is carried out implementing the finite population analogue of replicator dynamics [3,10] (to which simulation results converge in the limit of well-mixed populations) by means of the following transition probabilities: In each generation, all pairs of individuals x and y, directly connected, engage in a single round of a given game, their accumulated payoffs being stored as P_x and P_y, respectively. Whenever a site x is updated, a neighbor y is drawn at random among all k_x neighbors; whenever $P_y > P_x$ the chosen neighbor takes over site x with probability given by $(P_y - P_x)/(Dk_>)$, where $k_>$ is the largest between k_x and k_y and $D = T - S$ for the PD and $D = T - P$ for the SG. Simulations were carried out for a population of $N = 10^4$ individuals occupying the vertices of a regular ring graph with periodic boundary conditions. Initially, an equal percentage of strategies (*cooperators* or *defectors*) was randomly distributed among the elements of the population. Equilibrium frequencies of cooperators and defectors were obtained by averaging over 1000 generations after a transient time of 10 000 generations [14]. The evolution of the frequency of cooperators as a function of b for the PD and r for the SG has been computed. To this end, each data point results from an average over 100 simulations for the same type of NOCs specified by the appropriate parameters (the population size N and the average connectivity z). Even when graphs are generated via growth and preferential attachment (see below), the evolution of cooperation is studied in full grown graphs, that is, the number of vertices and edges is conserved throughout evolution.

The top panels of Fig. 1 show the results of simulations carried out for both the PD and the SG on regular ring graphs for different values of the average connectivity z,
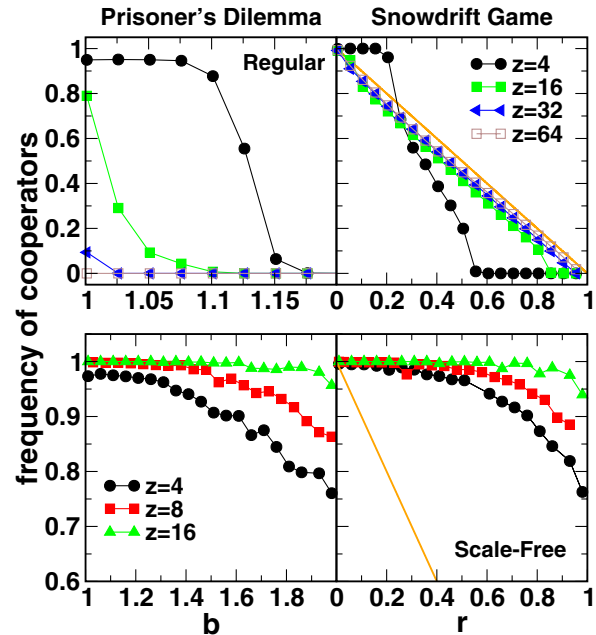

FIG. 1 (color online). Frequency of cooperators on different NOCs. Results shown as functions of the advantage of defectors b for the PD (left panels) and the cost-to-benefit ratio r for the SG (right panels). Results for regular NOCs and different values of z are shown on upper panels and for SF NOCs and different values of z on lower panels. Cooperation is dramatically enhanced on SF NOCs for both games, dominating over the entire ranges of b and r.

and confirm results obtained previously [6,10]. Deviations from the well-mixed population limits (the zero baseline for the PD and the solid diagonal line $1 - r$ for the SG) are more pronounced the smaller the value of z, the well-mixed limit being recovered for sufficiently large values of z [15]. The lower panels of Fig. 1 show the corresponding results for SF NOCs, constructed according to the following growth and preferential attachment rules, associated with the Barabasi and Albert model (BAM) [12]: Starting from a small number (m_0) of vertices, at every time step one adds a new vertex with $m \leq m_0$ edges that link the new vertex to m different vertices already present in the system (*growth*). When choosing the vertices to which the new vertex connects, one assumes that the probability p_i that a new vertex will be connected to vertex i depends on the degree k_i of vertex i: $p_i = k_i/\Sigma k_i$ (*preferential attachment*). After t time steps this algorithm produces a graph with $N = t + m_0$ vertices and mt edges, in which older vertices in the graph generation process are those which naturally tend to exhibit larger values of the connectivity, being also interconnected with each other, leading to the appearance of so-called "age-correlations" [11,13].

The simulations on these NOCs were carried out along the same lines of those associated with regular graphs, the SF NOCs being generated for $m = m_0 \geq 2$ [$z = \langle d(k) \rangle = 2m$] and the same number $N = 10^4$ of vertices. In sharp

contrast with previous results [6,10], we now obtain the unprecedented result that *cooperation dominates for both games over the entire range of their respective parameters*. Not only does cooperation dominate on both games, but also the qualitative behavior of cooperation is very similar, for the SG as a function of r and for the PD as a function of b. In both cases, the higher the value of the parameter, the more unfavorable cooperation becomes. Yet, only for large values of both parameters does the equilibrium frequency of cooperators fall below 80%, a result which renders cooperative behavior as a very competitive trait throughout evolution [16].

Figure 2 shows how cooperation evolves, whenever the population size is reduced to values more akin to small communities. It shows results for communities with $N = 512$ (upper panels) and $N = 128$ (lower panels), where one clearly observes the same qualitative behavior as a function of the game parameters, for *both* games, a feature which is most remarkable if one takes into account that for such smaller community sizes, one cannot attribute a SF behavior to the associated degree distribution. Yet, age correlations between vertices of the graph, which result from the dynamical rules of growth and preferential attachment, are still built-in and dictate the same dominance of cooperation

already obtained in larger populations. Figure 2 shows also that for small community sizes, the results evidence larger oscillations, which increase for even smaller values of N, a feature which is naturally related to the fact that, for $N \approx 100$ or less, the averages over many realizations of graphs of a given type do not converge to a well defined value. Indeed, the probabilistic rules of construction of the graphs allow the possibility (for small values of N) of stochastic extinction of cooperators or defectors for particular realizations of a given type of NOCs, as such precluding a clear cut result for the evolution of cooperation. This feature is a size effect which disappears for larger N. In the following we provide insight into how the combined rules of growth and preferential attachment influence the evolution of cooperation in both games. To this end, we consider two other types of NOCs, related to the BAM used so far, and which can be seen as different limiting cases of this model. A comparison of the different results obtained is shown in Fig. 3, in which we kept $z = 4$ and $N = 10^4$: Solid circles show the results obtained with the BAM whereas with solid squares we show results obtained with the configuration model [18], which provides a maximally random graph consistent with a predetermined degree distribution, for which we took those produced with the BAM. In this way, we remove any type of correlations between vertices
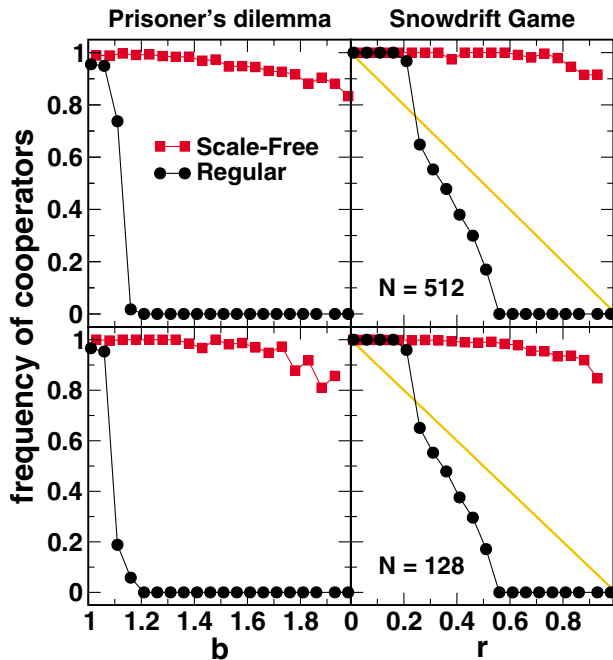

FIG. 2 (color online). Evolution of cooperation on small communities. Simulations were carried out for $N = 512$ (upper panels) and $N = 128$ (lower panels). Left (Right) panel: Results for the PD (SG). Comparison between these results and those of Fig. 1 show that the qualitative features of the evolution of cooperation are maintained. For $N = 128$ the oscillations at high values of b in the PD game indicate that, for such unfavorable regimes for cooperators, the small population size leads to an increasing sensitivity of the results on the particulars of each realization of a NOCs.
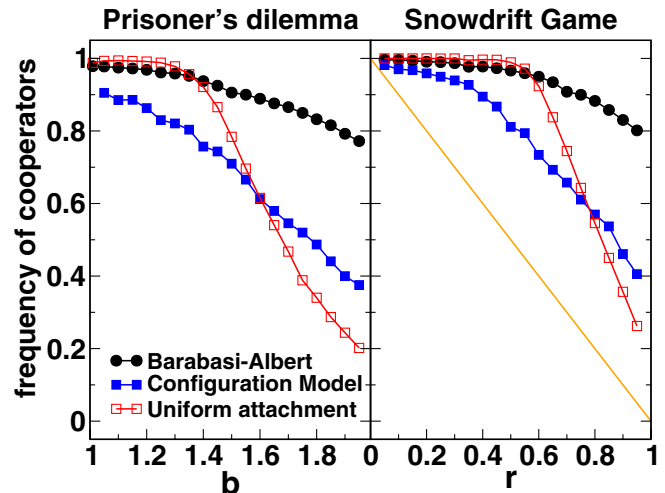

FIG. 3 (color online). Evolution of cooperation in NOCs with different levels of correlations. Simulations were carried out for $N = 10^4$ individuals in NOCs associated with graphs of different types (details provided in main text). In all cases, we fixed $z = 4$. Left (Right) panel: Results for the PD (SG) as a function of b (r). Results for NOCs generated with the BAM are shown with solid circles. Results for NOCs exhibiting the *same* degree distribution as the BAM, but maximally uncorrelated according to the configuration model are shown with solid squares. Finally, results for NOCs resulting from modifying the rules of graph construction, replacing the preferential attachment rule by the uniform attachment rule are shown with open squares. Results show that whenever age correlations are suppressed, cooperation is inhibited and no longer dominates for large values of b and r.

(individuals) for a given degree distribution $d(k)$. On the other hand, age correlations may be reduced by replacing preferential attachment with uniform attachment in the BAM, as proposed originally in Ref. [19]—shown in Fig. 3 with open squares—with an associated degree distribution exhibiting an exponential tail. Comparison between the results obtained with the BAM and the configuration model, with identical degree distributions, shows that cooperation is significantly inhibited as one suppresses the age-correlations due to growth and preferential attachment, such that cooperation no longer dominates for large values of the parameters in both games. In spite of this, cooperation is still greatly enhanced when compared to the results obtained on regular NOCs, a feature which is mostly due to the heterogeneous nature of the NOCs, which acts to promote cooperation [17,20]. Suppressing preferential attachment, as shown with open squares in Fig. 3, strongly inhibits cooperation for large values of b and r, in spite of the marginal enhancement obtained for small values of the parameters, in comparison with the BAM. Clearly, the fact that as a result of growth and preferential attachment, the vertices with highest connectivity (so-called hubs) become directly interconnected contributes to the observed dominance of cooperation for all values of the parameters [21]. By their own nature, cooperators will tend to occupy the hubs and, since hubs are directly connected, even if a defector occasionally takes over one hub, the probability that it gets reoccupied by a cooperator becomes essentially one. Overall, the present results support the conclusion that growth and preferential attachment ensure the prevalence of cooperation in both games. It is worth pointing out, however, that preferential attachment may be also achieved via alternative, local rules of attachment [11], which may prove more realistic in describing communities of simple organisms, to which the games adopted here are best applicable. Naturally, on NOCs generated using such rules, cooperation dominates [17]. To sum up, scale-free networks of contacts lead to unprecedented values for the equilibrium frequencies of cooperators, such that cooperation becomes not only competitive but often the predominant trait throughout evolution. Graphs generated via growth and preferential attachment provide sufficient conditions for cooperation to dominate, irrespective of whether individuals engage in the prisoner's dilemma or the snowdrift games, features which subsist down to small community sizes. These results may help us understand why cooperation is so widespread and evolutionary competitive in nature. The combination of evolutionary game theory and graph theory provides the flexibility for carrying out realistic simulations in heterogeneous populations, features

which may find applicability well beyond the context studied here.

[1] *Genetic and Cultural Evolution of Cooperation*, edited by Peter Hammerstein (MIT, Cambridge, MA, 2003).
[2] J. Maynard Smith, *Evolution and the Theory of Games* (Cambridge University Press, Cambridge, England, 1982).
[3] H. Gintis, *Game Theory Evolving* (Princeton University, Princeton, NJ, 2000).
[4] H. Milinsky, J. H. Lüthi, R. Eggler, and G. A. Parker, Proc. R. Soc. B **264**, 831 (1997).
[5] P. E. Turner and L. Chao, Nature (London) **398**, 441 (1999).
[6] M. A. Nowak and R. M. May, Nature (London) **359**, 826 (1992).
[7] R. Heinsohn and C. Parker, Science **269**, 1260 (1995).
[8] T. Clutton-Brock, Science **296**, 69 (2002).
[9] B. Kerr, M. A. Riley, M. W. Feldman, and B. J. M. Bohannan, Nature (London) **418**, 171 (2002).
[10] C. Hauert and M. Doebeli, Nature (London) **428**, 643 (2004).
[11] S. N. Dorogotsev and J. F. F. Mendes, *Evolution of Networks: From Biological Nets to the Internet and WWW* (Oxford University, Oxford, 2003).
[12] A.-L. Barabási and R. Albert, Science **286**, 509 (1999).
[13] R. Albert and A.-L. Barabási, Rev. Mod. Phys. **74**, 47 (2002).
[14] We confirmed that averaging over larger periods or using different transient times did not change the results.
[15] For the SG, the well-mixed population limit is recovered only when $z \approx N - 1$, whereas for the PD Fig. 1 shows that the well-mixed limit is already reached at $z = 64$ for a population of size $N = 10^4$.
[16] Contrary to regular NOCs, on SF NOCs, for small z, cooperation increases with z. Nonetheless we have checked that, for larger values of z, the well-mixed limit is recovered. The transition to the well-mixed limit is size dependent [17] and takes place in the PD at smaller values of z than in the SG.
[17] F. C. Santos and J. M. Pacheco, Proc. R. Soc. B (to be published).
[18] M. Molloy and B. Reed, Random Struct. Algorithms **6**, 161 (1995).
[19] A.-L. Barabási, R. Albert, and H. Jeong, Physica A (Amsterdam) **272**, 173 (1999).
[20] J. M. Pacheco and F. C. Santos, in *Science of Complex Networks: From Biology to the Internet to the WWW*, edited by J. F. F. Mendes, AIP Conf. Proc. No. 776 (AIP, New York, 2005).
[21] If, starting from BAM NOCs, we remove by hand the direct links between hubs, cooperation is also inhibited, in accord with the results shown in Fig. 3.