Emergence of Cooperation in Heterogeneous Structured Populations

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Abstract

Real-world networks of contacts have been shown to be heterogeneous concerning their patterns of interactions. This feature contrasts with the traditional homogeneous ansatz made when studying the evolution of cooperation employing well-known social-dilemmas in the framework of evolutionary game theory, in which cooperation may be undermined by Fear and Greed. Here we show that an entirely new picture emerges whenever the pattern of interaction in populations exhibits scale-free behaviour, such that long-term collective-beneficial behaviour easily resists short-term, self-regarding, individual behaviour. We show that Fear is more detrimental to cooperation than Greed, which ceases to be a threat in strongly heterogeneous populations. Furthermore, we show how the introduction of age correlations between individuals helps promoting cooperative behaviour. The picture emerging from our study shows that in a world in where cooperation is determined by a balance between greed and fear, cooperation constitutes a viable trait to the extent that the threat posed by fear is minor.

Introduction

Cooperation has played a key role throughout evolution (Sigmund, 1993), being present at all biological scales, from simple organisms, which have cooperated to produce more complex organisms during evolutionary history (Smith and Szathmàry, 1995; Michod, 1999), all the way up to vertebrates (Hammerstein, 2003). However, and in spite of its relevance and abundance, cooperation remains an evolutionary conundrum (Hammerstein, 2003). The problem has been conveniently formulated in the framework of evolutionary game theory which, when combined with games such as the Prisoner's Dilemma (**PD**), used as a metaphor for studying cooperation between unrelated individuals, enables one to investigate how collective cooperative behaviour may survive in a world where individual selfish actions produce better short-term results. Analytical solutions for this problem have been obtained whenever populations are assumed infinite and their interactions homogeneous. Under these assumptions, cooperation is not an evolutionary competitive trait, which is at odds with empirical observation. Such an unfavourable scenario for cooperation in the **PD**, as well as the wish to contemplate other possible cooperative scenarios has led to the adoption of other games (Heinsohn and Parker, 1995; Clutton-Brock, 2002), such as the Snowdrift-Game (**SG**) (also known as Hawk-Dove or Chicken, more favourable to cooperation) or the Stag-Hunt game (**SH**) (a coordination-type game favouring cooperation) as well as numerical simulations in finite, often spatially extended, populations (Nowak and May, 1992) (Figure 1-a), which nonetheless retain a homogeneous pattern of connectivity.

Recently, however, compelling evidence has been accumulated that a plethora of natural, social and technological real-world networks of contacts (**NoC**) between individuals are heterogeneous, different individuals engaging in different patterns of interactions, exhibiting scale-free behaviour in the most extreme case (Amaral et al., 2000; Albert and Barabási, 2002; Dorogotsev and Mendes, 2003; Vespignani and Pastor-Satorras, 2004) (Figure 1-b). Here we examine how cooperation evolves whenever individuals interact following heterogeneous, scale-free **NoC**, engaging in single rounds of a social dilemma characterized by given intensities of greed and fear. Because no analytic solutions exist for this problem, agent-based simulations (Macy and Flach, 2002; Riolo et al., 2001) provide a viable alternative to study the evolution of cooperation in these more realistic population structures, a framework we shall adopt here, with details provided below. We shall conveniently map a given population onto a graph, in which individuals (agents) occupy the vertices and their patterns of interactions are defined by the edges linking the vertices (Pacheco and Santos, 2005; Santos and Pacheco, 2005).

It is noteworthy that biologically and sociologically (Bonabeau et al., 1999) inspired models have been on the basis of several studies of the emergence of cooperation, both in the framework of artificial intelligence (Kraus, 1997) and Artificial Life research (Akiyama and Kunihiko, 1995). Nonetheless, the inherent complexity of the problem leads to artificial individual agents which, instead of embodying an intrinsically adaptive structure, often exhibit a pre-defined (and complex) set of rules which are used to establish cooperation. Here we undertake a different approach, in which

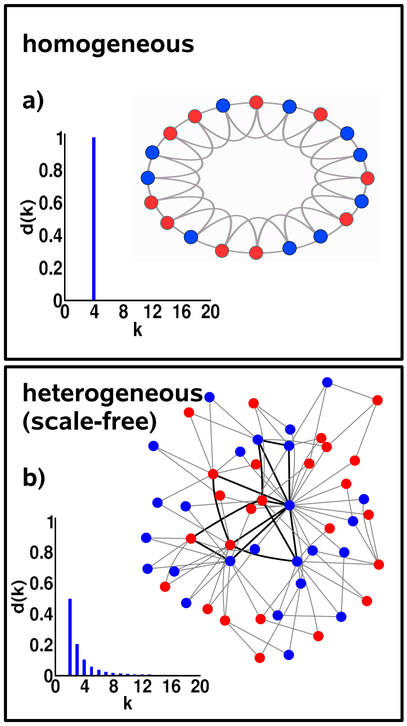

Figure 1: Heterogeneous versus Homogeneous **NoC**. a) Scale-free graph, built following the Barabási-Albert model. The thick black edges illustrate the direct ties which link the most connected individuals. b) Homogeneous regular graph, in which every individual is equivalent to any other, exhibiting a degree distribution characterized by a single peak. The limit $z = N - 1$ leads to a complete graph. Histograms : Degree distributions, computed for each type of graph and $N = 10^4$. In both cases the average connectivity z is 4. The colouring of vertices illustrates one possible realization at the start of a simulation, in which 50

individual agents are devoid of any complexity, capable only of adopting a (binary) strategy. However, the individual strategy is allowed to evolve and, therefore, to adapt to the context in which such a simple agent is immersed which, as will be shown, may lead to surprisingly cooperative scenarios, whenever the adaptive co-evolution of these strategies takes place in populations with a structure exhibiting context preservation.

This article is structured as follows. First, we discuss how the different social dilemmas are defined wherein the emergence of cooperation will be investigated. The next section describes how the simulations were constructed focussing on the graph generation mechanism, the stochastic evolutionary dynamics adopted and the parameter settings. Finally the results for all dilemmas in the well-mixed and scale-free scenarios are described and compared in a discussion section.

Defining the Space of Social Dilemmas.

At the most elementary level, social dilemmas can be formalized in terms of symmetric two-person games based on two choices - to cooperate (C) or to defect (D). These two choices lead to four possible outcomes: CC, CD, DC and DD. With each outcome, a particular payoff is associated: R (reward) and P (punishment) are the payoffs for mutual cooperation (CC) and defection (DD), respectively, whereas S (sucker) and T (temptation) are the payoffs associated with cooperation by one player and defection by the other, respectively. Several social dilemmas (Macy and Flach, 2002) arise naturally, depending on the relative ordering of these four payoffs, obeying the following constraints:

i) $R > P$: players prefer mutual cooperation (CC) over mutual defection (DD).

ii) $R > S$: players prefer mutual cooperation over unilateral cooperation (CD).

iii) $T > R$: players prefer unilateral defection (DC) to mutual cooperation or $P > S$: players prefer mutual defection to unilateral cooperation (CD).

Dilemmas will exhibit different degrees of tension between individual and collective interests, based on the above relations. Given that $R > P$, tension becomes apparent when the preferred choices of each player lead to individual actions resulting in mutual defection, in spite of the fact that mutual cooperation is more beneficial. The extent to which such individual actions occur may be adjusted introducing different intensities of *greed* (the temptation to cheat, whenever $T > R$), of *fear* (of being cheated, whenever $P > S$) or both, leading to three well-known social-dilemma games:

- The Snowdrift game **SG** game, for which $T > R > S > P$, where tension is due to greed but not fear,
- the game of Stag Hunt (**SH**), for which $R > T > P > S$, where tension results from fear but not greed, and
- the **PD** game, in which both fear and greed are present, that is, $T > R > P > S$.

Formally, these dilemmas span a four-dimensional parameter space. We simplify the problem by normalizing the advantage of mutual cooperation over mutual defection, in all games, to the same base value, making $R = 1$ and $P = 0$. With this choice for R and P, we are left with two parameters, T and S. Depending on their values, these parameters may add (or not) different intensities of greed, fear or both to each game.

We study the behaviour of all dilemmas 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, fear being present whenever $S < 0$ while greed is present whenever $T > 1$

Modelling Evolutionary Dynamics in Structured Populations.

Games on 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 $z = N - 1$, since all vertices share the same number of connections. Indeed, all homogeneous graphs exhibit the same 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 (Figure 1), reflecting the topological equivalence of all vertices.

Real-world **NoC**, on the other and, are clearly heterogeneous, corresponding to populations in which different individuals exhibit distinct patterns of connectivity, portraying the coexistence of local connections (spatial structure) with non-local connections (or shortcuts) and often exhibiting a power-law dependence of their degree distributions (Amaral et al., 2000; Albert and Barabási, 2002; Dorogotsev and Mendes, 2003). The Barabási-Albert (Barabási and Albert, 1999) model provides the best-known model leading to distributions $d(k) \sim k^{-\gamma}$, with $\gamma = 3$ (Figure 1-b). The construction of a scale-free graph using the Barabási-Albert model involves two processes:

1. Growth: Starting with a small number (m_0) of vertices, at every time step we add a new vertex with $m = m_0$ edges that link the new vertex to m different vertices already present in the system;

2. Preferential attachment: 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: $p_i = k_i / \sum k_i$.

Preferential attachment corresponds to the well-known *rich get richer effect* in economics (Simon, 1955), also known as the *Matthew effect* in sociology (Merton, 1968). 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 (Albert and Barabási, 2002; Dorogotsev and Mendes, 2003) arise. In order to single out the role of heterogeneity in evolution, we may remove any correlations (including age-correlations) by subsequently exchanging, randomly and repeatedly, the ends of pairs of edges of the original graph (Maslov and Sneppen, 2002), a procedure which washes out correlations without changing the scale-free degree-distribution (Maslov and Sneppen, 2002).

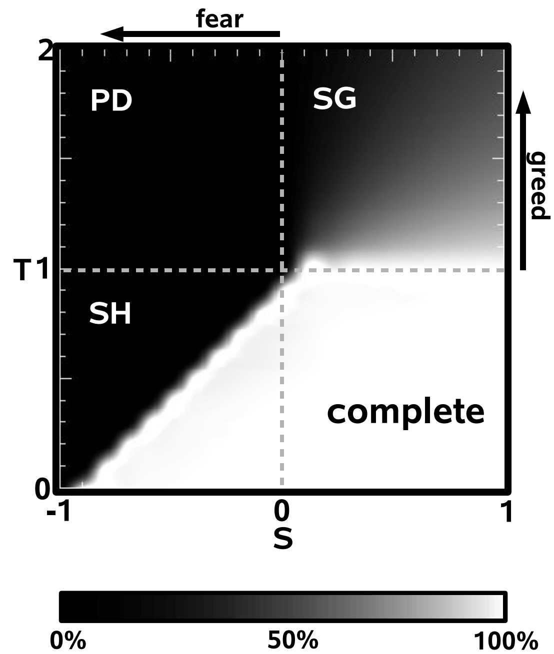

Figure 2: Evolution of cooperation in well-mixed NoC. Results for the fraction of cooperators in the population is plotted as a contour, drawn as a function of the intensity of greed and fear which characterizes a given dilemma. In the absence of greed and fear (lower right square) cooperators trivially dominate. Fear without greed leads to the SH game (lower left square), greed without fear leads to the SG (upper right square), and when both fear and greed are present we obtain the PD game (upper left square). Results were obtained in complete **NoC**, the finite population analog of infinite well-mixed populations. These results provide the reference scenario with which the role of population structure will be assessed (see Figure 3).

Stochastic Evolutionary Dynamics

For $R = 1$, $P = 0$, $0 \leq T \leq 2$ and $-1 \leq S \leq 1$, evolution is carried out implementing the finite population analogue of replicator dynamics (Gintis, 2002; Hauert and Doebeli, 2004), to which simulation results converge in the limit of homogeneous, well-mixed populations. This corresponds to define the following transition probabilities: In each generation, all pairs of individuals x and y, directly connected, engage in a single round of the game, their accumulated payoff being stored as P_x and P_y, respectively. Whenever a site x is updated, a neighbour y is drawn at random among all k_x neighbours; then, only if $P_y > P_x$ the chosen neighbour takes over site x with probability given by

$$\frac{(P_y - P_x)}{[k_> D_>]}, \qquad (1)$$

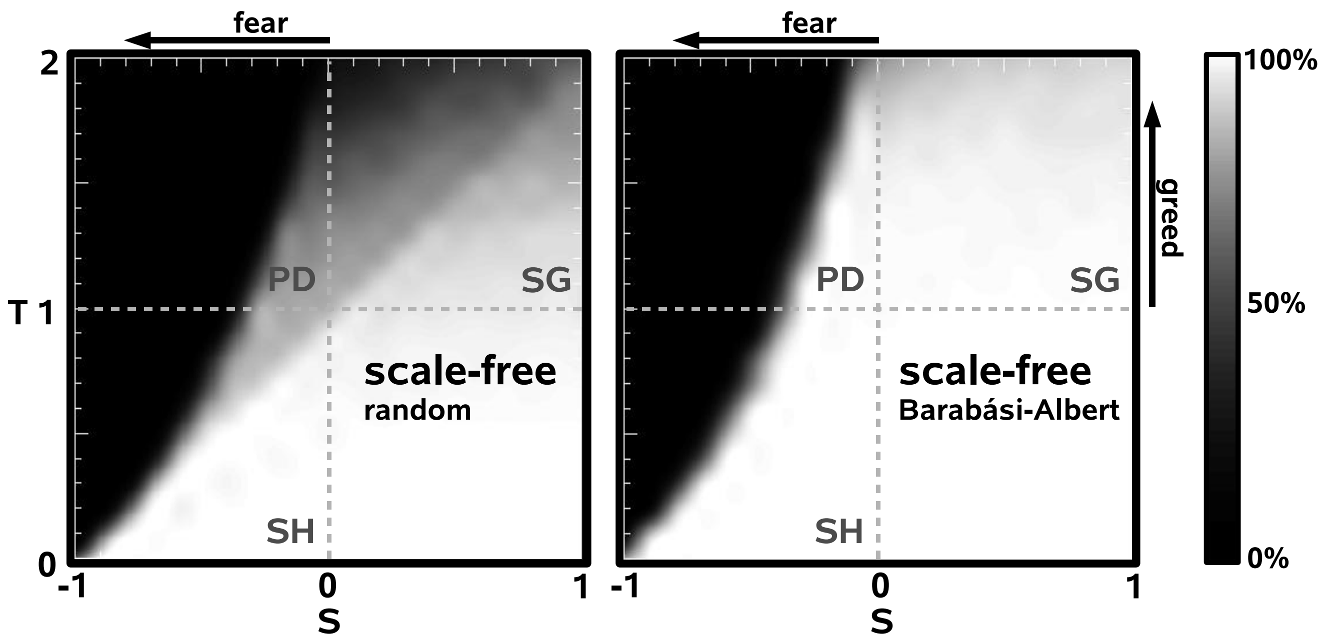

Figure 3: Evolution of cooperation in scale-free **NoC**. We use the same notation and scale as Figure 2. Left: Random scale-free **NoC**. The interplay between small-world effects and heterogeneity effects, discussed in the main text, leads to a net overall increase of cooperation for all dilemmas. Right: Barabási-Albert scale-free **NoC**. Whenever age-correlations are retained, highly-connected individuals become naturally inter-connected and cooperators dominate defectors for all intensities of greed, enlarging the range of intensities for which they successfully survive defectors under the action of fear.

where $k_{>} = max(k_x, k_y)$ and $D_{>} = max(T,R,S,P) - min(T,R,S,P)$.

Simulation Settings

Simulations were carried out on graphs with $N = 10^3$ vertices and average connectivity z=4 (except in connection with Figure 2, where where $z = N - 1$). Equilibrium frequencies of cooperators and defectors were obtained, for each value of T and S, by averaging over 1000 generations after a transient time of 10000 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 realizations of the same 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. Moreover, even when graphs are generated stochastically, the evolution of cooperation is studied in full grown graphs, that is, the number of vertices and edges is conserved throughout evolution.

Results and Discussion

Figure 2 shows the results of our simulations for all social dilemmas as a contour plot. The underlying **NoC** correspond to complete, fully connected graphs, which provide the finite population analogue to the infinite, well-mixed limit well-known from the standard analytical treatment (Weibull, 1997). In particular, the results confirm the

i) dramatic fate of cooperators under the simultaneous threat of greed and fear (**PD**);

ii) a similar fate for cooperators in the absence of greed (**SH**) whenever fear exceeds the advantage of mutual cooperation over temptation to defect.

iii) the coexistence of cooperators and defectors in the absence of fear, such that cooperators increasingly dominate the lower the intensity of greed (**SG**).

Replacing the well-mixed ansatz for the population by a heterogeneous population exhibiting a scale-free degree distribution such that all connections between individuals are purely random (see previous sections), leads to the results shown in Figure 3-a.

The results in Figure 3-a evidence the determinant role played by population structure on the evolution of cooperation for all dilemmas.

Using Figure 2 as reference we observe that, overall, scale-free **NoC** efficiently neutralize the detrimental role of greed in the evolution of cooperation, whereas fear remains a strong deterrent of cooperation. Indeed, under greed alone (**SG**) cooperators dominate for all values of greed. Under fear alone (**SH**) cooperation becomes now more likely for small intensities of fear. For the **PD** the domain of coexistence between cooperators and defectors is clearly broadened. Moreover, the small slope of the borderline between cooperators and defectors provides further evidence that fear constitutes the major threat to cooperation.

The net results shown in Figure 3-a hide in fact 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 scale-free graphs precludes the formation of compact clusters of cooperators, thereby facilitating invasion by defectors. However, the increase in heterogeneity of the **NoC** opens a new route for cooperation to emerge, since now different individuals interact different number of times per generation, which enables cooperators to outperform defectors. In other words, while on one hand the increased difficulty in aggregating clusters of cooperators would partially hamper cooperation, heterogeneity, on the other hand, counteracts this effect, with a net increase of cooperation (Santos et al., 2005).

The scale-free **NoC** of Barabási and Albert (Barabási and Albert, 1999) help us demonstrate how one may go beyond the scale-free properties of given **NoC** with the purpose of increasing cooperation. 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 model, a different result emerges for the evolution of cooperation, as shown in Figure 3-b). As is well-known, this model exhibits so-called age-correlations, in which the older vertices not only become the ones acquiring highest connectivity, but also they become naturally interconnected with each other. In other words, 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 which exhibit high connectivity. Of course, such a clustering of cooperators will only occur to the extent that cooperators are able to occupy such highly connected sites, which indeed happens.

The results in Figure 3-b) show that now greed poses no threat to cooperation, defectors being wiped out from populations under greed alone (**SG**). Under fear alone (**SH**), cooperators now wipe out defectors where before (Figure 3-a) they managed to coexist. Under the joint threat of greed and fear (**PD**), cooperators also get a strong foot-hold up to larger intensities of fear.

The present results show that inclusion of realistic population structure in evolutionary game theory restores cooperation as a competitive evolutionary trait, being more competitive the more heterogeneous the pattern of interactions of a given population.

Furthermore, re-formulating three well-known dilemmas in terms of the relative intensities of greed and fear allows a unified analysis of all dilemmas, showing the relative importance of greed and fear as deterrents of cooperation. Finally, by understanding the mechanisms which ensure the sustainability of cooperation, it is possible to conceive specific interaction patterns with the purpose of promoting cooperation. At any rate, fear is a much stronger deterrent of cooperation than greed, a feature which is well-supported by empirical evidence on many biological species, including humans.

Acknowledgements

FcS acknowledges the support of $COMP^2SYS$, a Marie Curie Early Stage Training Site, funded by the EC through the HRM activity. JmP acknowledges financial support from FCT, Portugal.

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