Natural selection of cooperation and degree hierarchy in heterogeneous populations

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A B S T R A C T

One of the current theoretical challenges to the explanatory powers of Evolutionary Theory is the understanding of the observed evolutionary survival of cooperative behavior when selfish actions provide higher fitness (reproductive success). In unstructured populations natural selection drives cooperation to extinction. However, when individuals are allowed to interact only with their neighbors, specified by a graph of social contacts, cooperation-promoting mechanisms (known as lattice reciprocity) offer to cooperation the opportunity of evolutionary survival. Recent numerical works on the evolution of Prisoner's Dilemma in complex network settings have revealed that graph heterogeneity dramatically enhances the lattice reciprocity. Here we show that in highly heterogeneous populations, under the graph analog of replicator dynamics, the fixation of a strategy in the whole population is in general an impossible event, for there is an asymptotic partition of the population in three subsets, two in which fixation of cooperation or defection has been reached and a third one which experiences cycles of invasion by the competing strategies. We show how the dynamical partition correlates with connectivity classes and characterize the temporal fluctuations of the fluctuating set, unveiling the mechanisms stabilizing cooperation in macroscopic scale-free structures.

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1. Introduction

The Prisoner's Dilemma (PD) models situations where cooperation is expensive (Hamilton, 1964; Axelrod and Hamilton, 1981; Nowak and Sigmund, 2005; Nowak, 2006; Hofbauer and Sigmund, 1998, 2003). In this two-players game, each individual adopts (independently and simultaneously) one of the two available strategies, cooperation (C) or defection (D); both receive R under mutual cooperation and P under mutual defection, while a cooperator receives S when confronted to a defector, which in turn receives T, where $T > R > P > S$. Under these conditions, defection is unbeatable[1] and reaches fixation in a well-mixed population of replicators. However, if individuals only interact with their neighbors as dictated by the underlying network of (social) contacts, several studies (Nowak and May, 1992; Killingback and Doebeli, 1996; Santos and Pacheco, 2005; Lieberman et al., 2005; Abramson and Kuperman, 2001; Gómez-Gardeñes et al., 2007; Poncela et al., 2007; Ohtsuki et al., 2006; Eguíluz et al., 2005; Santos et al., 2006; Szabó and Fáth, 2007; Szolnoki

et al., 2008; Vukov et al., 2008) have reported the asymptotic survival of cooperation for $T \geqslant R$, on different types of networks. Notably, cooperation even dominates over defection in scale-free (SF) networks where the distribution density of local degree (or connectivity) follows a power law (Santos and Pacheco, 2005; Gómez-Gardeñes et al., 2007; Poncela et al., 2007). In these latter structures, micro-motives and asymptotic macro-behavior are much more complexly related and its degree heterogeneity offers the opportunity of positive feedback evolutionary mechanisms allowing cooperation to defeat defection, even not being a best reply to itself (Nash).

In well-mixed populations, there is a transition at $P = S$ between fixation of defection in the PD ($P > S$) and strategies' coexistence in the Hawks and Doves (HD) game ($P < S$). However, in SF networks, it has been recently shown (Gómez-Gardeñes et al., 2007) that there is a wide region of $P > S$ where fixation of the unbeatable strategy is generically an impossible event, under the updating rule considered here (see below). In this region, there is an asymptotic partition of the network into three sub-populations ($\mathscr{C}, \mathscr{D}, \mathscr{F}$). In $\mathscr{C}$ (and $\mathscr{D}$), cooperative (and resp. defective) strategy reaches fixation, while in $\mathscr{F}$ no fixation is possible and cycles of node invasions follow indefinitely. In this way, the macroscopic average index of cooperation $\langle c \rangle$ has the form

$$\langle c \rangle = \rho_c + \rho_f \langle T_c \rangle, \tag{1}$$

[1] Strict best response to itself and strict better response to others than themselves (Nowak, 2006).

where (ρ_c, ρ_d, ρ_f) is the measure of the partition's sets, and $\langle T_c \rangle$ is the average proportion of time spent by the fluctuating subpopulation $\mathscr{F}$ as cooperators.

In this paper, we go one step forward in the characterization of the dynamical organization of cooperation. Capitalizing on a model network, we analytically argue that the type of partition previously reported (Gómez-Gardeñes et al., 2007) also arises generically in a much wider class of heterogeneous networks. Scale-free networks are then further scrutinized to show the continuous variation of the average level of cooperation and the three kinds of strategists in a two parameter space covering the PD game. Next, we show how the densities of the subpopulations $\mathscr{C}$ and $\mathscr{F}$ are correlated with the structural division of the network into degree classes, so unveiling the role of degree heterogeneity in the evolutionary cooperation enhancement. Additionally, the random variables describing fluctuations of strategies in $\mathscr{F}$ are also analyzed numerically.
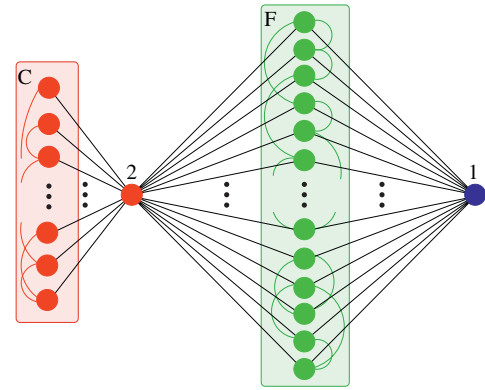
In what follows the payoffs are scaled to the reward for mutual cooperation, $R = 1$, and punishment for mutual defection is set to $P = 0$, so there are two free parameters $T = b > 1$, and $S = \varepsilon$. The PD corresponds to values of $\varepsilon \leqslant 0$. The players occupy the vertices of a fixed graph (i.e. connections between players do not coevolve with strategies) where agents are represented by nodes, and a link between nodes indicates that they interact (play). We implement the finite population analogue of replicator dynamics (Santos and Pacheco, 2005; Gómez-Gardeñes et al., 2007) with synchronous update.[2] In this setting, a player i adopts the strategy of a randomly chosen neighbor j with probability $\Pi_{i \to j} = \beta(P_j - P_i)$, being P_i and P_j the payoffs accumulated after playing with all their neighbors once. If k_i (k_j) is the number of neighbors (connectivity or degree) of agent i (j), and Δ is the maximal possible payoff difference ($\Delta = \max\{b, b - \varepsilon\}$), $\beta = (\max\{k_i, k_j\}\Delta)^{-1}$ is related to the characteristic inverse time scale. This updating rule has the theoretical advantage of leading rigorously, in the well-mixed population limit, to the celebrated replicator equation (Gintis, 2000). Note that (irrational) imitation of a neighbor with a lower payoff is forbidden, a feature which is at the root of the existence of the $(\mathscr{C}, \mathscr{D}, \mathscr{F})$ partition.

In an equilibrium configuration the probability of change in one time step is null. For generic irrational values of b and ε, only all-C (fixation of cooperation) and all-D (fixation of defection) are equilibria. However, in networks, the asymptotic state of evolutionary dynamics is often not an equilibrium configuration under the above rules (Gómez-Gardeñes et al., 2007). To see that this generically holds for a wide class of heterogeneous networks, we first consider a model network where we prove the existence of the asymptotic partition $(\mathscr{C}, \mathscr{D}, \mathscr{F})$, for a macroscopically large set of initial conditions. The bipolar model network mimics a local environment of a heterogeneous graph, with simplifications that allow analytical insights. It is perhaps the minimal (though general enough) network model where the partition can be rigorously proved, so illustrating the dynamical organization of cooperation in heterogeneous graphs.

2. A bipolar model network

Let us consider the graph schematized in Fig. 1, composed of the following:

(a) A component $\mathscr{F}$ of n_F nodes with arbitrary connections among them.

Fig. 1. *Bipolar model network.* Nodes 1 and 2 are connected to all nodes in $\mathscr{F}$. Node 2 is also linked to all nodes in $\mathscr{C}$. Connections inside $\mathscr{F}$ and $\mathscr{C}$ are arbitrary. The colors represent a set of 2^{n_F} different initial configurations. Blue means defector, red stands for cooperator and green means arbitrary strategy.

(b) A node, say node 1, which is connected to all the nodes in $\mathscr{F}$ and has no other links.
(c) A component $\mathscr{C}$ of n_C nodes with arbitrary connections among them.
(d) A node, say node 2, which is connected to all the nodes in $\mathscr{F}$ and $\mathscr{C}$, but not to node 1.

Consider the set of initial conditions defined by: (i) node 1 is a defector, (ii) node 2 is a cooperator, and (iii) all nodes in component $\mathscr{C}$ are cooperators. Note that this choice allows 2^{n_F} different initial configurations. We now prove that, provided some sufficient conditions (see below), this is an invariant set for the evolutionary dynamics.

The payoff of a cooperator node i in $\mathscr{F}$ is $P_i^c = k_i^c + 1 + \varepsilon(k_i - k_i^c + 1)$, where k_i is the number of its neighbors in $\mathscr{F}$ and $k_i^c \leqslant k_i$ is the number of those that are cooperators. The payoff of node 1 is then $P_1 \geqslant (k_i^c + 1)b$. For the PD game, where $\varepsilon < 0$, the inequality $P_1 > P_i^c$ always holds, so that node 1 will always be a defector.

The payoff of a defector node i in $\mathscr{F}$ is $P_i^d = (k_i^c + 1)b$, where k_i^c is the number of its cooperator neighbors in $\mathscr{F}$, while the payoff of node 2 is $P_2 = n_C + n_F \varepsilon + n_F^c(1 - \varepsilon)$, where $n_F^c \leqslant n_F$ is the number of cooperators in $\mathscr{F}$. Thus, a sufficient condition for $P_2 > P_i^d$ is $n_C > \mathrm{Int}(b(k_F + 1) - n_F \varepsilon)$, where k_F ($< n_F$) is the maximal degree in component $\mathscr{F}$, i.e. the maximal number of links that a node in $\mathscr{F}$ shares within $\mathscr{F}$. With this proviso, node 2 will always be a cooperator, which in turn implies that all the nodes in the component $\mathscr{C}$ will remain always cooperators.

This argument proves that provided the sufficient condition

$$n_C > \mathrm{Int}(b(k_F + 1) - \varepsilon n_F), \tag{2}$$

holds, the set of initial conditions defined by (i)–(iii) is an invariant set: any stochastic trajectory starting in the set remains there. Moreover, as no equilibrium configuration is included in this set, one concludes that no trajectory from this set evolves to an equilibrium configuration. While nodes in $\mathscr{C}$ and node 2 are permanent cooperators, and node 1 is a permanent defector, nodes in $\mathscr{F}$ are forced to fluctuate: at every time, a defector in $\mathscr{F}$ has a positive probability to be invaded by the cooperation strategy, and a cooperator in $\mathscr{F}$ has a positive probability of being invaded by the defection strategy. In other words, every configuration in the set of initial conditions is reachable (in one time step) from any other, thus it is almost sure that it will be reached (ergodicity).

Along any stochastic trajectory starting from the set of initial conditions the network is partitioned into three subsets, a set of

pure cooperator nodes, a set of pure defector nodes and a set of fluctuating individuals. The fluctuations inside the subpopulation $\mathscr{F}$ reflect the competition for invasion among two non-neighboring hubs with fixed opposite strategies in their common neighborhood, a local situation that occurs in heterogeneous networks. It is also a schematic model for the competition for influence of two powerful superstructural institutions like "mass media", political parties, or lobbies on a target population.

Let us now obtain some exact results for the simplest choice of topology of connections inside the fluctuating set, namely $k_F = 0$. In this case each node in $\mathscr{F}$ is only connected to nodes 1 and 2. Note that the sufficient condition for fixation of cooperation at node 2 is, $n_C > b - \varepsilon n_F$. Denoting by $c(t)$ the instantaneous fraction of cooperators in $\mathscr{F}$, the payoffs of nodes 1 and 2 are

$$P_1 = bcn_F, \quad P_2 = n_C + cn_F + \varepsilon(1 - c)n_F,$$

and the payoffs of a cooperator node and a defector node in $\mathscr{F}$ are, respectively,

$$P_c = 1 + \varepsilon, \quad P_d = b.$$

Then one finds for the (one time-step) probability Π_{CD} of invasion of a cooperator node in $\mathscr{F}$

$$\Pi_{CD} = \frac{cb - (1 + \varepsilon)/n_F}{2\Delta}, \tag{3}$$

and using the notation $A = \varepsilon + (n_C - b)/n_F$ and $B = 1 + n_C/n_F$

$$\Pi_{DC} = \frac{A + c(1 - \varepsilon)}{2\Delta B}, \tag{4}$$

for the probability of invasion of a defector node in $\mathscr{F}$. Note that $A > 0$ due to the non-invadability of node 2. At time $t + 1$, the expected fraction of cooperators is

$$c(t + 1) = c(t)(1 - \Pi_{CD}) + (1 - c(t))\Pi_{DC},$$

provided $n_F \gg 1$, the fraction of cooperators c in $\mathscr{F}$, evolves according to the differential equation

$$\dot{c} = (1 - c)\Pi_{DC} - c\Pi_{CD},$$

which after insertion of Eqs. (3) and (4) becomes

$$\dot{c} = f(c) \equiv A_0 + A_1 c + A_2 c^2, \tag{5}$$

where the coefficients are

$$A_0 = \frac{A}{2\Delta B},$$
$$A_1 = \frac{1 - \varepsilon - A + B(1 + \varepsilon)/n_F}{2\Delta B},$$
$$A_2 = -\frac{1 - \varepsilon + bB}{2\Delta B}. \tag{6}$$

One can easily check ($A_0 > 0$ and $A_2 < 0$) that there is always one positive root c^* of $f(c)$, which is the asymptotic value for any initial condition $0 \leqslant c(0) \leqslant 1$ of Eq. (5). Thus, cooperation is never driven to extinction even for large values of the temptation to defect b.

Back to the general case, i.e. arbitrary structure of connections in $\mathscr{F}$, it should be emphasized that the sufficient condition (Eq. (2) above) does not impose bounds on the network's average connectivity $\langle k \rangle$, that can take on arbitrarily large values independent of the game parameters. This result differs from the bound on $\langle k \rangle$ reported in Ohtsuki et al. (2006) and Nowak (2006) for different stochastic updating rules in the weak selection limit.

3. The partition $(\mathscr{C}, \mathscr{D}, \mathscr{F})$ in SF networks

Scale-free networks (Newman, 2003; Boccaletti et al., 2006) are constructed here following the Barabási and Albert (1999) (BA) model. For this purpose, one starts from a fully connected set

of m_0 nodes and at each time step a new node is added and linked to m nodes. These m nodes are chosen following the preferential attachment rule, namely, the probability that node i receives a new link is proportional to its degree, $k_i/\sum_j k_j$. Avoiding multiple connections and iterating the preferential attachment rule $N - m_0$ times a network of N nodes and mean degree $\langle k \rangle = 2m$ is constructed. The degree distribution of the resulting network is a power law, $P(k) \propto k^{-\gamma}$, with exponent $\gamma = 3$. It is worth recalling that scale-free networks constructed with the BA method do not show degree–degree correlations between neighboring nodes. In this way, the probability that a node of degree k is connected to another one with degree k' is independent of k, $P(k'|k) = k'P(k')/\langle k \rangle$. The networks used in our simulations have typically $N = 4 \times 10^3$ nodes and $\langle k \rangle = 4$.

We start the simulations from a network where agents have the same probability of adopting either of the two available strategies: cooperation or defection. Evolutionary dynamics is then iterated over a fixed transient of 5×10^3 generations. After this transient we check whether or not the system has reached a stationary state as given by the fraction, $c(t)$, of individuals that are cooperators. We consider that the population is in equilibrium when, taken over a time window of 10^3 additional generations, the slope of $c(t)$ is smaller than 10^{-2}. Once the dynamical equilibrium is reached the system is further evolved over 10^4 additional generations, and we identify the agents that act as pure cooperators (defectors), i.e. those individuals that always co-operate (defect). The dynamical patterns of the rest of the agents (fluctuating nodes) are also stored during these 10^4 generations to characterize the fluctuations (cycles of invasion). All the results are averaged over at least 10^3 different realizations of scale-free networks and initial conditions.

Fig. 2 shows the numerical estimates of the partition measure (ρ_c, ρ_d, ρ_f) as well as the average index of cooperation $\langle c \rangle$ (i.e. the overall fraction of time spent by all the nodes as cooperators averaged over stochastic trajectories on all realizations) for BA networks in the range of parameter values $1 < b < 2.3$ and $-0.25 < \varepsilon$. These results convincingly show the generic existence (as well as its sizeable importance) of the asymptotic partition $(\mathscr{C}, \mathscr{D}, \mathscr{F})$ for the replicator dynamics (imitation of a neighbor of a higher payoff proportional to payoff differences) of the PD game on SF graphs. In fact, though limited to a smaller range of parameter values, the partition is generic for general graphs, as our own results in random Erdös-Renyi graphs corroborate (Gómez-Gardeñes et al., 2007; Poncela et al., 2007). Thus the question is how degree heterogeneity influences the partition so enhancing the positive feedback mechanisms of network reciprocity.

3.1. Strategy-degree correlations

To investigate in detail the role that degree heterogeneity plays in the replicator dynamics in SF networks, we have measured the proportions $\rho_\alpha^{(k)}$ ($\alpha = c, d, f$) of each type of individuals inside the class of nodes with degree k, for all values of k. Note that $\rho_c^{(k)} + \rho_f^{(k)} + \rho_d^{(k)} = 1$ for each k, and denoting the degree distribution density by $P(k)$ ($\propto k^{-\gamma}$ for a SF network), one has that $\rho_\alpha = \sum_k P(k)\rho_\alpha^{(k)}$ for each α. For definiteness we consider hereafter in this section a value of $\varepsilon = 0$, i.e., the so-called (Szabó and Fáth, 2007) weak PD, at the borderline separating PD and HD. One should not expect, however, qualitative differences when moving from it, as suggested by results in Fig. 2.

In Fig. 3 we show $\rho_c^{(k)}$ (left panel) and $\rho_f^{(k)}$ (right panel) versus $\log k$ and the temptation to defect b for BA networks. The figure shows four clearly differentiated ranges of b values. The first one, $1 < b < 1.7$, corresponds to the regime where pure cooperation
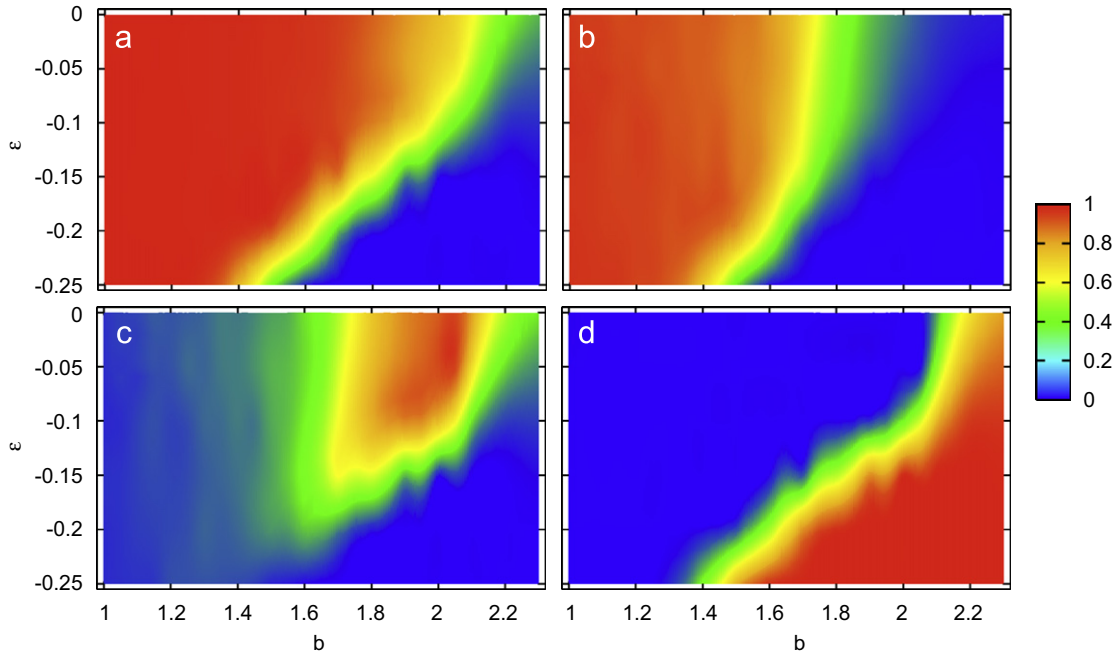
Fig. 2. *Strategists' asymptotic partition in BA networks.* The panels represent in color-code: (a) the average level of cooperation ⟨c⟩, and (b), (c) and (d) the densities ρ_c, ρ_f and ρ_d, respectively, as a function of game parameters b and ε. The substrate network is a Barabási–Albert scale-free graph made up of $N = 4 \times 10^3$ nodes and $\langle k \rangle = 4$.
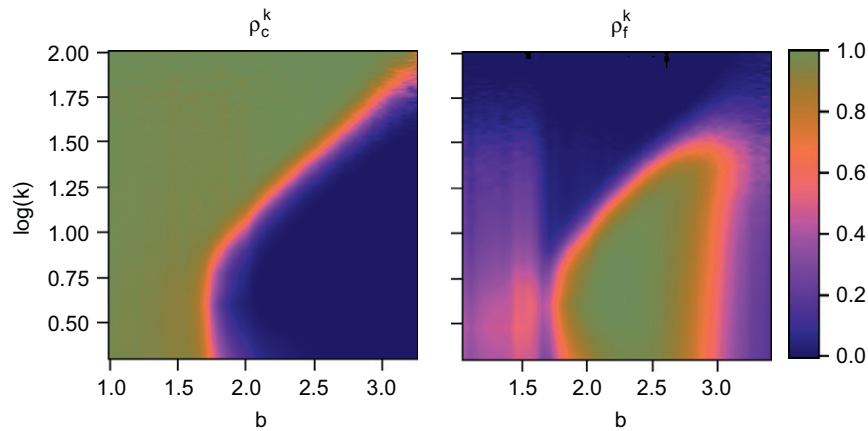

Fig. 3. *Strategists proportion by degree classes.* Color-coded densities of pure cooperators ρ_c^k and fluctuating individuals ρ_f^k by degree classes k, as a function of b, for BA networks and $\varepsilon = 0$. Note that $\rho_d^k = 1 - \rho_c^k + \rho_f^k$. More details are given in the main text.

dominates the asymptotic behavior (i.e. $0.9 \leqslant \rho_c < 1$); in this range only a small number of fluctuating individuals occupy some nodes with low and intermediate degree k. In the second range, $1.7 < b < 2$, the fluctuating set fully invades the classes with low values of k ($\leqslant 11$), corresponding to the decrease of ρ_c down to 10%. In the third range, the fluctuating set invades progressively higher k-classes as b increases, with pure cooperators still predominating in even higher k-classes. At around $b \simeq 2.9$, only nodes with the highest degree (hubs) remain as pure cooperators. For larger values of b, the growth of $\rho_d^{(k)}$ at the expense of the fluctuating individuals is, on the contrary, fairly insensitive to the degree value, as inferred in the right part of the right panel of Fig. 3.

The preferential fixation of cooperation at nodes with high degree k when cooperation is very expensive can be understood by the following plausible argument: A necessary (though non-sufficient) condition for a node i to be a pure cooperator is that (at a given time t) the number k_i^c of instantaneous cooperators in

its neighborhood (i.e. the payoff of i in the current round) must be greater than the current payoff of any instantaneous defector neighbor j, that is, $k_i^c > b k_j^c$. This condition is clearly favored when the cooperator node i belongs to a high k class and its fluctuating neighbors j belong to lower k classes.[3] Furthermore, the imitation of a successful (high payoff) cooperator by its neighbors reinforces its future success (Santos and Pacheco, 2006), then favoring the fixation of cooperation in highly connected nodes. On the contrary, the imitation of a successful defector undermines its future success, so that defection cannot take long-term advantage from degree heterogeneity.

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[3] Note that the argument is consistent provided that the heterogeneous network either has not degree–degree correlations (so that the neighbors of a node of degree k have no preferential degrees) or the network is assortative (i.e. neighbors of high degree nodes have preferentially also high degrees). We remind that degree–degree correlations are absent in the (undirected) BA network.
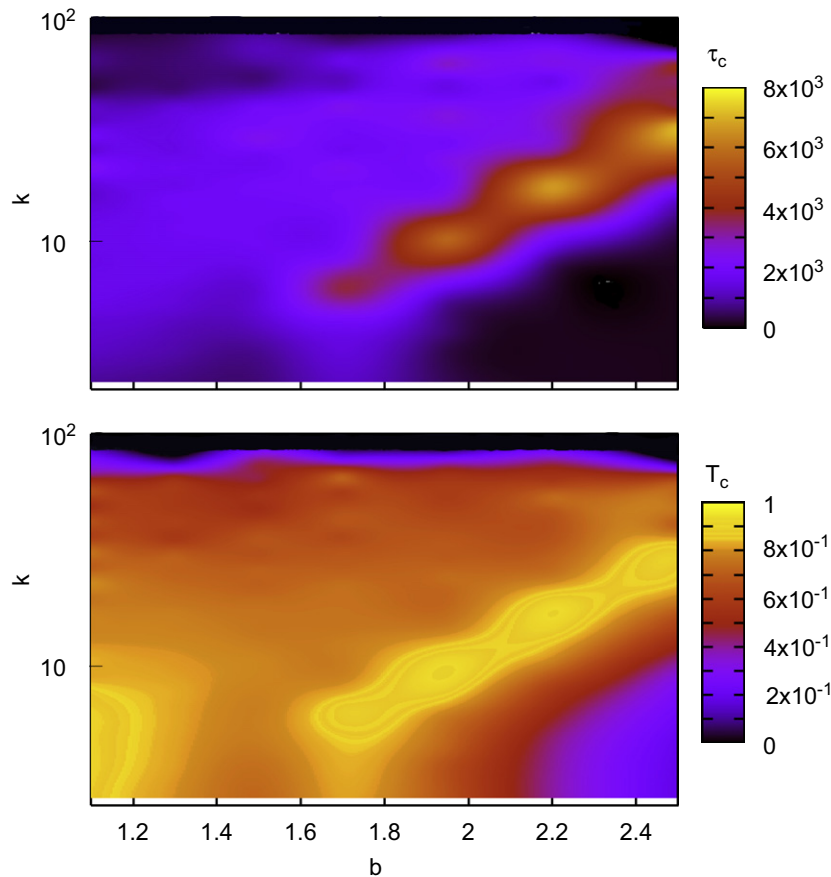
Fig. 4. *Hierarchy of cooperation times in the fluctuating set.* Permanence times, τ_c, of the cooperation strategy of a fluctuating node (top) and the fraction of time, T_c it cooperates (bottom) as a function of the node's degree k and the game parameter b for $\varepsilon = 0$. See main text for details.

In the left panel of Fig. 3, for $b > 2$, one observes that at fixed value of b, $\rho_c^{(k)}$ varies rather quickly from 0 to 1 in a small interval of values of k centered around some b-dependent value $k^*(b)$, so that the nodes with degree $k > k^*(b)$ are mostly pure cooperators and those with degree $k < k^*(b)$ are mostly fluctuating (see right panel, $2 < b < 2.9$). In the absence of degree–degree correlations the degree distribution density in the neighborhood of a given node is independent of the node degree, and thus the proportion of cooperators in the neighborhood of a given node is that of the whole network. This implies that the necessary condition for a pure cooperator i, stated in the previous paragraph, becomes $k_i > b k_j$, where j is the fluctuating neighbor of i with highest degree, say $k_j \simeq k^*$. Now, a small increase Δb makes those pure cooperators i fulfilling $(b + \Delta b)k^* > k_i > bk^*$ to become fluctuating, so that $\Delta k^* \simeq k^* \Delta b$. With these provisos one concludes that $k^*(b)$ grows exponentially with b, $k^*(b) \propto \exp(b)$. The linear shape of the bright-color line in the $(b, \log k)$ plane at the left panel of Fig. 3, for $b > 2$, nicely confirms this prediction, so supporting the validity of the heuristic argument.

3.2. Fluctuations

We have noted that the fluctuating subpopulation in the bipolar model is such that any fluctuating individual has a positive probability of changing strategy in one time step, so that the dynamics is ergodic in the set of all configurations compatible with the partition. This is not necessarily the case in a general heterogeneous network, being perfectly possible that a fluctuating node at a given time has a null one-time-step probability of

invasion, but a positive n-time-steps probability for some $n > 1$; thus, ergodicity in the set of configurations compatible with the partition is neither ensured nor discarded.

In SF graphs each fluctuating individual is wired to (and then invadable by) a different number of fluctuating individuals, and (eventually) pure strategists, so that one should expect that the fraction of time T_c it spends as cooperator differs widely from node to node. The lower panel of Fig. 4 shows the average fraction of time $T_c^{(k)}$ a fluctuating node of degree k spends cooperating. The average of these quantities $\sum_k P(k) T_c^{(k)}$ in the subpopulation $\mathscr{F}$, defines the parameter $\langle T_c \rangle$ that appears in Eq. (1), i.e. the average individual contribution of fluctuating nodes to the macroscopic index of cooperation $\langle c \rangle$. To avoid misunderstandings concerning the relative importance of the contribution of connectivity classes to $\langle c \rangle$, it is important to bear in mind both, the power-law shape of $P(k)$ and the left panel of Fig. 3, showing the fraction $\rho_f^{(k)}$ of fluctuating nodes inside the class of degree k.

In the extent that T_c is a proportion of time, it does not provide information on the time scales of the invasion cycles that fluctuating nodes experience. The random variable τ_c (cooperation permanence time) is defined as the time spent as cooperator by a fluctuating node in each cycle. For the bipolar network, when $k_F = 0$, the one time step invasion probabilities, Π_{CD} and Π_{DC} (Eqs. (3) and (4)) become time independent in the asymptotic regime. Then one can compute the probability that the cooperation strategy remains for a time $\tau_c \geqslant 1$ at a fluctuating node, simply as $P(\tau_c) = \Pi_{CD}(1 - \Pi_{CD})^{\tau_c - 1}$. In a similar way, the distribution density $P(\tau_d)$ of defection permanence times is obtained as $P(\tau_d) = \Pi_{DC}(1 - \Pi_{DC})^{\tau_d - 1}$. Thus the distribution densities of both strategies permanence times are exponentially decreasing. For

example, at $\varepsilon = 0$, i.e. at the border between the PD and the HD game, if one further assumes that the relative size $\mu(\mathcal{F})$ of the component $\mathcal{F}$ is large enough, i.e. $\mu(\mathcal{F}) \to 1$, and $\mu(\mathcal{C}) \to 0$, one obtains that the stationary solution of Eq. (5) behaves as $c^* \simeq (b+1)^{-1}$ near the limit $\mu(\mathcal{F}) \to 1$. The distribution density $P(\tau_c)$ of the cooperation permanence times of a fluctuating node, as a function of the parameter b is thus

$$P(\tau_c) = (2b+1)^{-1}\left(\frac{2b+1}{2b+2}\right)^{\tau_c}, \tag{7}$$

and the distribution density $P(\tau_d)$ of defection permanence times

$$P(\tau_d) = (2b(b+1)-1)^{-1}\left(\frac{2b(b+1)-1}{2b(b+1)}\right)^{\tau_d}. \tag{8}$$

For SF networks, one expects that the permanence times at the fluctuating nodes show some correlation with the node's degree. The upper panel of Fig. 4 represents the average permanence time, $\tau_c^{(k)}$, that fluctuating nodes of degree k remain as cooperators as a function of b and k, for observation times of 10^4 generations. We see that cooperation permanence times are strongly correlated with degree: highest τ_c's occur along the line $k^*(b)$ of maximal degree in the fluctuating set.

As noted before, the heterogeneity of social contacts in SF networks provides local environments where cooperation has a distinctive selective advantage at high degree nodes. This not only enhances the size of the subpopulation where fixation of cooperation occurs, but also enlarges the average total fraction of time of cooperation in the fluctuating subpopulation.

Moreover, the picture emerging from the strategists' partition in heterogeneous graphs indicates that individuals are effectively organized in such a way that a fraction of pure cooperators is isolated from contacts with the fluctuating population, and thus safe from invasion. This "Eden of cooperation", provides a safe source of benefits to those highly connected pure cooperators in the frontier (Gómez-Gardeñes et al., 2007), reinforcing the resilience to invasion and providing a stabilizing feedback mechanism for the survival of cooperation. Hence, heterogeneity of social contacts enhances the lattice reciprocity, thus preventing the fixation of the defection strategy even when cooperation is expensive.

4. Conclusions

In this paper, we have further analyzed the dynamical organization of strategies when the strategists are coupled through heterogeneous topologies. We have presented analytical insights derived from a model network that mimics the competition for invasion of two highly connected nodes where strategies have reached fixation. Under the hypothesis that the players imitate a neighbor with a higher payoff proportionally to the payoff differences, we have shown that fixation of any strategy in the whole population is an impossible event when there is some degree of heterogeneity in the network of contacts. Furthermore, the strategists' partition into three sets for SF networks has been shown to be correlated with structural properties such as the degree of the nodes. Nodes with higher degree are mainly occupied by pure cooperators or fluctuating strategists who spend

most of the time cooperating. In this way, the overall dynamical picture that emerges is that of a set of pure cooperators placed on highly degree classes interacting with members of the fluctuating set that on its turns occupy lower levels in the degree hierarchy of the network. In all, this provides cooperation with a stabilizing mechanism that does not allow defection to be fixated in the whole population.

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