Conformity hinders the evolution of cooperation on scale-free networks

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We study the effects of conformity, the tendency of humans to imitate locally common behaviors, in the evolution of cooperation when individuals occupy the vertices of a graph and engage in the one-shot prisoner's dilemma or the snowdrift game with their neighbors. Two different graphs are studied: rings (one-dimensional lattices with cyclic boundary conditions) and scale-free networks of the Barabási-Albert type. The proposed evolutionary-graph model is studied both by means of Monte Carlo simulations and an extended pair-approximation technique. We find improved levels of cooperation when evolution is carried on rings and individuals imitate according to both the traditional payoff bias and a conformist bias. More importantly, we show that scale-free networks are no longer powerful amplifiers of cooperation when fair amounts of conformity are introduced in the imitation rules of the players. Such weakening of the cooperation-promoting abilities of scale-free networks is the result of a less biased flow of information in scale-free topologies, making hubs more susceptible of being influenced by less-connected neighbors.

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I. INTRODUCTION

Understanding the emergence and stability of cooperation is a central problem in many fields of both natural and social sciences. Researchers have traditionally adopted evolutionary game theory [1] as common formal framework for studying the dynamics of strategy change and games such as the prisoner's dilemma (PD) and the snowdrift game (SG) as metaphors for the tension between group welfare and individual selfishness. The PD and the SG (also known as chicken or hawks-doves) are two-person symmetric games in which a given player can be, at each time step, either a cooperator (C) or a defector (D). Cs are willing to engage in cooperative tasks, while Ds prefer not to, thus exploiting Cs. If two individuals of the same type interact, they both get the reward for mutual cooperation R if they cooperate or the punishment for mutual defection P if they defect. If a D and a C interact, the D receives the temptation to defect T and the C receives the sucker's payoff S. In the PD, the payoffs are ordered such that T > R > P > S with 2R > T + S. Since T >R and P>S, the only Nash equilibrium of the game is the pure strategy (D,D). In this case, the dilemma is caused both by "greed" (or the temptation to cheat) and "fear" that the other player cheats. In the SG, the order of P and S is reversed, yielding T > R > S > P. Thus, when both players defect they get the lowest possible payoff. The pairs of pure strategies (C,D) and (D,C) are Nash equilibria of the game. There is also a third equilibrium in mixed strategies in which strategy D is played with probability p and strategy C with probability 1-p, where p depends on the actual payoff val-

Conventional evolutionary game theoretical models assume an infinite population in which pairs of randomly drawn individuals interact according to a given game. Selection is strictly payoff biased, which implies that fitter individuals reproduce more (genetic evolution) or successful individuals tend to be imitated more frequently (cultural evolution). In both genetic and cultural evolutions, the evolutionary process can be analytically described by a set of equations called the replicator dynamics [1]. In the SG, the only stable equilibrium of such equations is an internal one, corresponding to the mixed strategy of classical game theory, while the two pure equilibria are unstable. In the PD, the only stable rest point occurs when the population is entirely composed of Ds: Cs are doomed to extinction in this game.

Given these unfavorable predictions for the evolution of cooperation, several mechanisms have been invoked in order to explain why altruism can actually emerge, such as kin selection, group selection, direct reciprocity, indirect reciprocity, and network reciprocity [2]. Network reciprocity [3–6] arises when individuals occupy the vertices of a graph (modeling spatially subdivided populations or social networks) such that interactions are constrained to direct neighbors. When the population of players possesses such a structure, Cs can survive in clusters of related individuals for certain ranges of the game parameters, as it has been known since the pioneering work by Nowak and May [3]. Among the different conceivable population topologies, scale-free networks have received particular attention since they have been found to promote cooperation to a point that Cs dominate Ds in a significant portion of the parameters' space [4].

In addition to positing infinite well-mixed populations, the replicator dynamics relies on the assumption that selection is entirely payoff biased. Such a premise, although natural to

ues. The dilemma in this game is caused only by greed, i.e., players have a strong incentive to threat their opponent by playing D, which is harmful for both parties if the outcome happens to be (D,D).

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posit in genetic evolution, is less straightforward to postulate in cultural evolution where information is transmitted by means of imitation. Humans not only have a bias for imitating more successful people but also are prone to conform or to show a disproportionate tendency to copy the behavior of the majority [7]. Recent empirical research has shown that conformity is an important bias in our social learning psychology [8,9] and that it can partially account for the results obtained in laboratory experiments on social dilemmas [10,11]. Theoretical research has also shown that conformity can promote cooperation in the PD. In the standard case of a large well-mixed population, the dynamics can lead either to full defection or to bistability, depending on the amount of conformity [12–14]. In [13] the case of square lattices was studied by simulation, with the result that conformity stabilizes cooperation in such population topologies, a result confirmed for rings in [15] and, in a more detailed way, in the work presented here.

In this paper we investigate the evolution of cooperation when individuals imitate with a given amount of conformity and both interaction and imitation are constrained to nearest neighbors in a network. In order to extend previous work [3,4,13,16–18] and to study the influence of the network topology, we use rings and Barabási-Albert scale-free networks as examples of simple degree-homogeneous (i.e., regular) and highly degree-heterogeneous graphs, respectively. It will be shown that, while conformity reinforces the cooperationpromoting advantages of network reciprocity in rings, the very same mechanism may strongly hinder the evolution of cooperation when the network topology is scale-free. Indeed, when Cs are not initially in the majority and imitation is partly conformist, scale-free networks are no longer the powerful amplifiers of cooperation expected from the results of previous studies. There is thus an interesting interplay between conformity and network reciprocity so that the cooperation-promoting effects of conformity depend on the particular type of networks on which evolutionary dynamics are played.

II. MODEL

We consider a population of size N where the ith individual is represented by the vertex v_i of an undirected simple graph G(V,E). The neighborhood of i, $\Gamma(i)$, is the set of all individuals j such that there is an edge $e_{ij} \in E$. The number of neighbors of i is thus the degree k_i of vertex v_i .

At each time step, each individual is either a C or a D. The system evolves by the successive application of interaction and imitation phases. During the interaction phase, individuals simultaneously engage in a single round of the game with their neighbors. As a result, individual i collects an accumulated payoff $\Pi_i = \sum_{l \in \Gamma(i)} \pi_{il}$, where π_{il} is the payoff player i receives when interacting with player l (e.g., T, R, P, or S). During the imitation phase, each individual randomly chooses one of its neighbors as its *cultural model*. Let us denote by j the cultural model of player i. We consider two update rules for the cultural evolutionary dynamics: payoff biased imitation and conformist imitation. (i) For payoff biased imitation, i copies j's strategy with a probability given

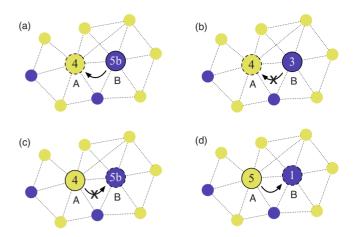


FIG. 1. (Color online) Individuals imitate following two different update rules, each reflecting a different bias of our social learning psychology: payoff based imitation and conformist imitation. Cooperators are shown in light yellow; defectors are shown in dark blue. Social interaction is modeled by a rescaled prisoner's dilemma with T=b>1, R=1, and P=S=0. (a) Successful payoff biased transmission. When applying a payoff biased rule of imitation, A can copy B's strategy and become a defector since B's payoff is greater than A's. (b) Unsuccessful conformist transmission. If A was to imitate B according to conformity, no transmission would take place since defectors are in the minority of A's neighborhood (three defectors vs four cooperators). (c) Unsuccessful payoff biased transmission. B will not copy A's strategy under a payoff biased rule since A's payoff is smaller than B's. (d) Successful conformist transmission. Conformist transmission from A to B can take place because cooperators constitute the majority in B's neighborhood (five cooperators vs one defector).

by $f((\Pi_i - \Pi_i)/(\theta k_>))$, where f(x) is equal to x if x > 0 and 0 otherwise, $k = \max\{k_i, k_i\}, \ \theta = T - S$ in the PD, and $\theta = T - P$ in the SG. This update rule is a local finite population analog of the replicator dynamics, commonly used in the literature [4,16]. (ii) For conformist imitation the probability that icopies j's strategy is given by $f((n_{i|i}-n_{i|i})/k_i)$, where $n_{l|i}$ is the number of i's neighbors with the same strategy as l. This update rule is related to the majority rule and to the voter model, commonly used in interdisciplinary physics studies [19]. In our model individuals imitate according to a payoff bias with probability $1-\alpha$ and according to a conformist bias with probability α . Thus, the parameter α represents the amount of conformity in the individuals' behavior and gives the average proportion of players imitating according to the conformity rule at each time step. When $\alpha=0$ our local dynamics reduce to the strictly payoff biased imitation rule used in previous studies [4,16]. Figure 1 gives some illustrative examples of the imitation dynamics of the proposed model.

In order to allow comparison with previous studies, we focus on the commonly used rescaled version of the PD [3,4], for which T=b, $1 \le b \le 2$, R=1, and P=S=0. The parameter b represents the advantage of defectors over cooperators. For the SG we make, as in [4], $T=\beta > 1$, $R=\beta -1/2$, $S=\beta-1$, and P=0, such that the cost-to-benefit ratio of mutual cooperation is given by $r=1/(2\beta-1)$. It is worth noting that, in degree-inhomogeneous networks, the local

replicator dynamics using accumulated payoff is not invariant with respect to affine transformations of the payoff matrix [20,21]. Although this fact invalidates generalizations of the obtained results to the extended parameter space, it allows us to compare our results with relevant previous work.

Before studying our model with actual network models (rings and scale-free networks) by means of numerical simulation, we briefly present analytical results obtained using the mean-field method and the pair approximation. Such analytical results are important in order to identify the dynamical regions of the system and to serve as starting point for comparisons with the dynamics on actual networks studied in Sec. IV.

III. ANALYTICAL RESULTS

A. Mean-field approach

Within the framework of the traditional mean-field approach [6] network locality is ignored and the system is assumed to have an infinite size, leading to an infinite well-mixed population. In this case, it is easy to show that the time evolution of the fraction of Cs, ρ , is ruled by the following equation:

$$\dot{\rho} = \rho(1 - \rho) \{ \gamma [\pi_{\rm C} - \pi_{\rm D}] + \alpha(2\rho - 1) \},$$
 (1)

where $\pi_C = \rho R + (1-\rho)S$ and $\pi_D = \rho T + (1-\rho)P$ are the average payoffs to Cs and Ds and $\gamma = (1-\alpha)/\theta$. Equation (1) (or a similar formula) has been derived in related work on cultural transmission processes including both payoff biased imitation and conformist imitation [10,12–14,22]. The dynamics has the two trivial fixed points $\rho_0^* = 0$ and $\rho_1^* = 1$, as well as (possibly) one internal nontrivial equilibrium given by

$$\rho^* = \frac{\gamma(P-S) + \alpha}{\gamma\{R-T+P-S\} + 2\alpha}.$$

For α =0 (pure payoff biased transmission), Eq. (1) recovers the standard replicator dynamics of the original game, whereas for α =1 (pure conformist transmission), Eq. (1) is equivalent to the replicator dynamics of a pure coordination game with internal (unstable) equilibrium ρ^* =1/2. For 0 < α <1, variations in the amount of conformity and the entries of the payoff matrix can change the evolutionary dynamics of the social dilemma. In particular, the global behavior of the system depends on the two critical values, α_D =(S-P)/(θ +S-P) and α_C =(T-R)/(θ +T-R), so that the system is in one of the following four dynamical regions:

- (1) Dominant defection $(\alpha > \alpha_D \land \alpha < \alpha_C)$: $\rho_0^* = 0$ is the only stable equilibrium. In this case, Cs are doomed to extinction regardless of their initial frequency in the population.
- (2) Coexistence ($\alpha < \alpha_{\rm D} \land \alpha < \alpha_{\rm C}$): only the internal equilibrium ρ^* is stable. Cs and Ds coexist in equilibrium at proportions given by ρ^* and $1-\rho^*$, respectively.
- (3) Bistability $(\alpha > \alpha_D \land \alpha > \alpha_C)$: both $\rho_0^* = 0$ and $\rho_1^* = 1$ are stable, whereas the internal fixed point ρ^* is unstable. In this case, the evolutionary dynamics depends on the initial frequency of Cs, $\rho(0)$. For $\rho(0) > \rho^*$ cooperation prevails, whereas it vanishes for $\rho(0) < \rho^*$.

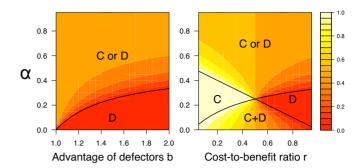


FIG. 2. (Color online) Phase diagrams of the mean-field solutions for the PD with conformity on the b- α plane (left) and for the SG with conformity on the r- α plane (right). For the PD, the system can be in the dominant defection (D) or the bistability (C or D) region. For the SG, dominant cooperation (C) and coexistence (C + D) are also possible outcomes. Darker colors indicate more defection in the average. In the C or D region, colors indicate the size of the basin of attraction for the cooperative equilibrium. In the C + D region, colors indicate the equilibrium proportion of Cs.

(4) Dominant cooperation ($\alpha < \alpha_D \land \alpha > \alpha_C$): $\rho_1^* = 1$ is the only stable equilibrium; Cs get fixed regardless of their initial frequency in the population.

These regimes can be seen in Fig. 2, which shows the phase diagrams of the two rescaled games. In the PD with conformity, $S < P \Rightarrow \alpha_D < 0$, so that only dominant defection and bistability are possible. In particular, for the rescaled version of the game, conformity can make the system bistable if $\alpha > (b-1)/(2b-1)$. However, for all values of b in the bistability region, the basin of attraction of ρ_0^* is greater than the basin of attraction of ρ_1^* , i.e., Cs initially in the minority are doomed to extinction regardless of their initial proportion and the values of b and α . In the SG with conformity, the four dynamical regions above described are possible, with $\alpha_D = (1-r)/2$ and $\alpha_C = r/(1+2r)$. In the coexistence region, the equilibrium proportion of Cs is larger than what is expected in the α =0 case when r<1/2 and smaller when r > 1/2. In the bistability region, the basin of attraction of ρ_1^* is greater than the basin of attraction of ρ_0^* for r

In summary, conformity can promote cooperation in the PD to a certain degree in the mean-field limit. If in the majority (and if conformity is strong enough) Cs now have a chance of surviving invasion from Ds and eventually take over the whole population [13]. In the SG, whether conformity helps or hinders the evolution of cooperation actually depends on the cost-to-benefit ratio r. Cs are favored for r < 1/2 and disfavored for r > 1/2.

B. Pair approximation

Pair approximation [23,24] improves over the traditional mean-field approach for structured populations by considering the frequency of strategy pairs (i.e., C-C, C-D, and D-D). Since the technique assumes regular graphs without loops, it only applies to Bethe lattices in a strict sense [25]. However, pair approximation has been used to predict evolutionary dynamics on more general regular graphs with considerable

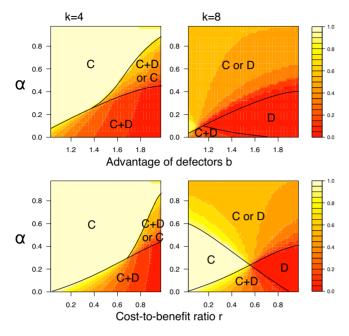


FIG. 3. (Color online) Phase diagrams of the pair approximations for the PD with conformity on the b- α plane (top row) and the SG with conformity on the r- α plane (bottom row). The first column shows the results for k=4 and the second column for k=8. The system exhibits different dynamical regimes depending on the game: dominant cooperation (C), dominant defection (D), coexistence (C+D), and bistability (C or D and C+D or C). In the C+D or C region, the system can stabilize in a mixed state or in pure cooperation. Darker colors indicate more defection in the average.

success [16,25]. We extended the pair-dynamics model presented in the supplementary information in Ref. [16] to investigate the cultural evolutionary dynamics of social dilemmas on graphs. The pair approximation of our model leads to a system of ordinary differential equations, tracking changes in the proportions $p_{c,c}$, $p_{c,d}$, and $p_{d,d}$ of the C-C, C-D, and D-D links in the population graph, respectively. The resulting system, although impossible to solve analytically due to the nonlinearity of the equations, can be solved numerically after specifying suitable initial conditions.

Figure 3 shows the phase diagrams of the pair approximation of our model for regular graphs with degrees k=4 and k=8. The figures were constructed by numerically integrating the equations under different initial proportions of Cs $[\rho(0)=\{0.1,0.2,\ldots,0.9\}]$ and averaging over all initial conditions. Pure spatial effects can be seen when α =0. For the PD, the dynamical regime of the game is no longer of dominant defection but of coexistence. Locality of interactions thus favors Cs by allowing them to survive extinction. In addition to this classical result, for k=4 conformity is largely favorable to Cs. Indeed, augmenting α increases the proportion of Cs in the coexistence region and, depending on the value of b, can shift the system to the region of dominant cooperation. In the SG with k=4 conformity has similar effects, resulting in an analogous dynamic picture. The fact that the SG represents a less stringent dilemma makes larger the area of dominant cooperation. For k=8, phase diagrams get closer to those predicted by the mean-field method (see Fig. 2), but important levels of cooperation are still sustained. In the PD, for instance, the basins of attraction of the cooperative equilibrium in the bistability region are larger than those expected in a well-mixed population (compare the top right panel of Fig. 3 with the left panel of Fig. 2).

In a nutshell, when the population of players possesses local structure, a given amount of conformity in the imitation rules of the players is able to foster cooperation at least for low values of the mean degree k. The reason for this is the easier formation of clusters of individuals playing the same strategy induced by conformist imitation.

IV. SIMULATION RESULTS

We now turn our attention to actual networks as population topologies, in particular (i) rings (regular one-dimensional lattices with cyclic boundary conditions) with degrees k=4, k=8, and k=16 and (ii) Barabási-Albert scale-free networks [26] with average degrees $\bar{k}=4$, $\bar{k}=8$, and $\bar{k}=16$. For both types of networks we generated graphs of size $N=10^4$. In the case of rings, graphs are constructed by arranging the nodes on a circle and connecting each node to the k most-neighboring nodes.

We study the model by Monte Carlo simulations in populations randomly initialized with 50% Cs and 50% Ds (but see Sec. IV C for other initial conditions). The probability α of conformist transmission was set to $\alpha \in [0,0.5]$ in steps of 0.1. We privilege values of $\alpha \le 0.5$ so that dynamics are primarily driven by payoff differences in the competing strategies. However, we also study the limiting case $\alpha = 1$ in Sec. IV D and the case $0 \le \alpha \le 1$ in Sec. IV C. The advantage of defectors b (PD) and the cost-to-benefit ratio r (SG) were varied in steps of 0.05. We carried out 50 runs for each couple of values of α and the game parameter. For the scale-free networks, we used a fresh graph realization in each run. The average final frequency of Cs, $\hat{\rho}$, was obtained by averaging over 10^3 time steps after a relaxation time of 10^4 time steps.

A. Results for rings

Figure 4 summarizes the results obtained for the PD and the SG on rings with k=4. These plots confirm the results previously obtained for the standard α =0 case on these population topologies [4,18], which in turn are qualitatively similar to those obtained for square lattices [3,16]. In the PD, Cs are able to survive for low values of b by forming clusters wherein they interact more often with their own strategy than what is expected in well-mixed populations. Cs can thus benefit from mutual cooperation and counterbalance the exploitation of Ds at the borders of the clusters [17]. In the SG, spatial structure hinders the evolution of cooperation [16], such that only for small values of r (i.e., r < 0.3) the final fraction of Cs is higher than what is expected in a wellmixed population. As it is evident from our results, conformity enhances cooperation in rings, moving rightward the critical value b^* for which $\hat{\rho}=0$ in the PD and the value r^* for which $\hat{\rho}$ becomes smaller than the corresponding proportion in a well-mixed population in the SG. Furthermore, the different curves are ordered in a way that the higher the α , the

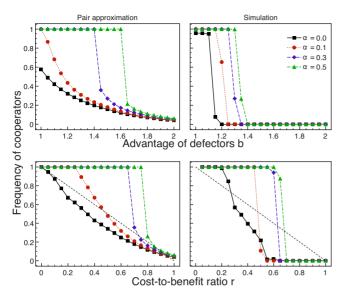


FIG. 4. (Color online) Final average frequency of Cs on rings with k=4 for the PD (upper panels) and the SG (lower panels) as a function of b or r for different values of the propensity to conform α . Results by Monte Carlo simulations are shown in the right panels while predictions by pair approximation are shown in the left panels. Mean-field approximations for the SG without conformity (α =0) are shown with dotted lines.

higher $\hat{\rho}$ for all values of b and r (except for the SG, r = 0.5, $\alpha = 0.1$) and the larger the critical values b^* and r^* .

Figure 5 plots the results for rings with k=8. In the PD, conformity enhances cooperation even more pronouncedly than in the k=4 case. Indeed, the threshold b^* has moved rightward for every value of α . Such trend is still present in

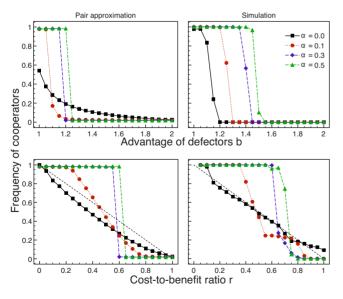


FIG. 5. (Color online) Final average frequency of Cs on rings with k=8 for the PD (upper panels) and the SG (lower panels) as a function of b or r for different values of the propensity to conform α . Results by Monte Carlo simulations are shown in the right panels while predictions by pair approximation are shown in the left panels. Mean-field approximations for the SG and $\alpha=0$ are shown with dotted lines.

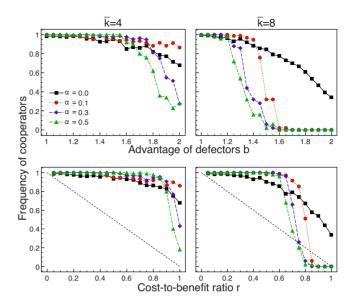


FIG. 6. (Color online) Final average frequency of Cs on scale-free networks for the PD (upper panels) and the SG (lower panels) as a function of b (PD) or r (SG) for different values of the propensity to conform α . Results are shown for \overline{k} =4 (left panels) and \overline{k} =8 (right panels). Mean-field approximations for the SG without conformity (α =0) are shown with dotted lines.

the results obtained for rings with k=16 (not shown here to avoid cluttering the figures). In the SG, the increase in the degree of the graph makes conformity cooperation-enhancing up to a threshold value \hat{r} (where a curve with $\alpha > 0$ crosses the curve with $\alpha = 0$) but detrimental afterward. As b^* in the PD, also \hat{r} moves rightward as α increases.

With respect to simulation results, pair approximation tends to underestimate cooperation for low values of α and bor r and to overestimate it for medium to large values of these parameters. In the PD with conformity, results for k =8 are rather pessimistic and are much closer to what we have obtained for random graphs (data not shown here). This is not surprising since random graphs are locally similar to Bethe lattices [27]. Notice, however, that pair approximation predicts reasonably well the cooperation-enhancing effects of conformity in the PD and the ordering of the curves for different values of α . Also, for the SG, pair approximation accurately predicts the fact that the curves with conformity $(\alpha > 0)$ are above the curve without conformity $(\alpha = 0)$ when k=4 (lower panels of Fig. 4), but that they cross it when k =8 (lower panels of Fig. 5). This means that pair approximation correctly predicts the fact that, for k=8, there is a point up to which conformity helps Cs but beyond which Ds are favored with respect to the standard case without conformity.

B. Results for scale-free graphs

Let us now turn our attention to the results obtained for scale-free networks (Fig. 6). When imitation is strictly payoff biased (α =0) these degree-heterogeneous graphs importantly foster cooperation in both the PD and the SG with respect to what is obtained in rings and other degree-homogeneous graphs [4]. As an aside, we note that the higher the average

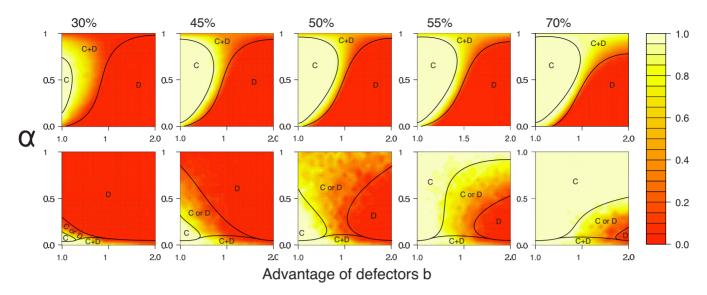


FIG. 7. (Color online) Phase diagrams for the PD game on rings with k=8 (top row) and on scale-free graphs with $\bar{k}=8$ (bottom row) as a function of b and α . The images are for increasing initial fractions of cooperation $\rho(0)$ from left to right.

degree \overline{k} , the lower the gains in cooperation [28]. The addition of conformity has important consequences in the evolution of cooperation on scale-free graphs. In the PD, conformity improves $\hat{\rho}$ for all values of b only for a scale-free topology with \bar{k} =4 and α <0.3. For the other cases, conformity does not hamper cooperation for small values of b but is detrimental for medium to large values of the game parameter. Furthermore, the threshold value \hat{b} above which $\hat{\rho}$ is higher than in the case without conformity is a monotonically decreasing function of both α and \bar{k} , such that the higher the amount of conformity and the average connectivity of the graph, the smaller the value of \hat{b} . Particularly, for scale-free networks with \bar{k} =8 and $\alpha \ge 0.2$, conformity weakens the advantage of these graphs in promoting cooperation to a point that $\hat{\rho}$ becomes comparable to the corresponding fraction obtained in rings (compare the right upper panels of Figs. 5 and 6).

Results for the SG on scale-free networks (lower panels of Fig. 6) are qualitatively similar to those obtained for the PD. Again, conformity is beneficial for cooperation for all values of the game parameter r only for $\bar{k}=4$ and $\alpha<0.3$. For the remaining cases, there is a threshold value \hat{r} of the cost-to-benefit ratio above which $\hat{\rho}$ is smaller than the corresponding frequency of Cs in the $\alpha=0$ case. We note again the fact that the higher the value of α , the lower the value of \hat{r} . Finally, and as in the PD, for $\bar{k}=8$ and $\alpha\geq0.2$ there are no important quantitative differences in $\hat{\rho}$ between rings and scale-free networks: scale-free networks have again lost the cooperation-enhancing capabilities they feature when imitation is strictly payoff biased. For $\bar{k}=8$ and high values of r, the addition of conformity can even make Cs go extinct, which would not happen in the nonconformist case.

C. Dependence on the initial conditions

In order to investigate the robustness of cooperation and to study the influence of the initial fraction of Cs $\rho(0)$ we

have also run simulations for the PD on rings and scale-free graphs for \bar{k} =8 starting from values of $\rho(0)$ other than 0.5 and on an extended range of values of α going from 0 to 1. Results are shown in Fig. 7 in the form of phase diagrams for each initial condition. In contrast to the notion of bistability in a system of ordinary differential equations (such as those resulting from the mean-field approach and the pair approximation), here we define bistability as the ability of the system to reach either full cooperation or full defection starting from the same *global* initial conditions due to its stochastic dynamics and finite size.

Not unexpectedly, initial conditions influence the final outcomes of the simulations, so that the strategy initially in the majority is always favored with respect to the case when $\rho(0)=0.5$. Notice, however, that the effects of conformity are still qualitatively different for each of the two types of networks considered in this study. On these phase diagrams the transition from the region of dominant cooperation (C) to dominant defection (D) is steeper on rings, where the two zones with monomorphic populations are divided by a narrow region of coexistence (C+D). On scale-free networks a large region of bistability (C or D) tends to be formed in the middle of the parameter's space, being the largest for $\rho(0)$ close to 50%. Indeed, the cultural evolutionary dynamics are much more sensitive to the initial conditions when applied on top of scale-free networks than when they are played on top of rings. For rings, conformity favor Cs even if they are initially in the minority, such that, in general, the higher the value of α the higher the final fraction of Cs in the population. For scale-free networks, conformity can be favorable to cooperation when Cs are initially in the majority but decidedly detrimental if they are in the minority. The remarkable observation is that in scale-free networks even a small change in the initial fraction of Cs can drastically change the final outcome [see the second and fourth images in the lower row of Fig. 7 for $\rho(0)=0.45$ and $\rho(0)=0.55$]. It would be tempting to compare the numerical results for scale-free graphs with those obtained analytically in the mean-field

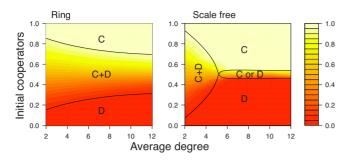


FIG. 8. (Color online) Final population composition as a function of the average degree \bar{k} and the initial proportion of cooperators when imitation is purely conformist (α =1).

case and with the pair approximation (Figs. 2 and 3). However, this cannot be done as both the mean-field and pair approximation approaches give poor results in highly degree-inhomogeneous networks.

D. Pure conformist dynamics

We briefly comment on the case with $\alpha=1$ which is special as the dynamics is completely driven by the majority rule and games' payoffs play no role. Figure 8 shows what happens in this case as a function of the network's average degree \bar{k} and the initial proportion of Cs. For $\bar{k}=2$ there is a large coexistence region for both graphs, and the pure equilibria have relatively small basins of attraction. With increasing \bar{k} , the coexistence region decreases so that a greater connectivity favors fixation in a monomorphic population. Whereas in rings coexistence is still reached for \bar{k} as large as 12, for scale-free networks such regime disappears for \bar{k} >5. For these networks, only in the narrow central strip around $\rho(0)=0.5$ may bistability arise. Note that in this case the C and D labels indicating cooperators or defectors are purely conventional as payoffs (and so the behavioral strategies of the individuals) are completely ignored.

V. DISCUSSION

Conformity and network reciprocity are able to act together and foster cooperation in degree-homogeneous graphs for social dilemmas such as the PD and the SG. The basic principle behind network reciprocity is the formation of clusters of related individuals leading to assortative interactions that favor Cs. Conformity further helps such cluster formation, thus improving the efficiency of cooperative behavior in a network of interacting individuals.

More interestingly, conformity may hinder the evolution of cooperation on the otherwise cooperation-promoting scale-free networks. The different dynamical organization of cooperation in degree-heterogeneous graphs with conformity can explain the reason of such phenomenon. When individuals imitate exclusively according to a payoff bias, Cs and Ds coexist in quasiequilibrium, with some nodes fixed in cooperative or defective behavior and others where there is no

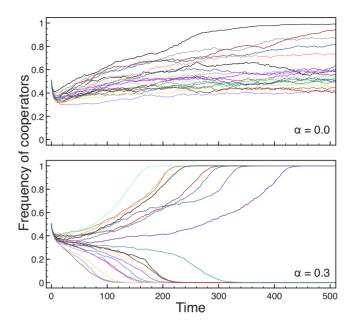


FIG. 9. (Color online) Evolution of the frequency of Cs on scale-free networks (\bar{k} =8) during the first 500 time steps for the PD, without conformity (upper panel) and with conformity (lower panel). In both figures, b=1.35. Twenty distinct curves are shown.

fixation and cycles of invasion follow indefinitely [29]. Thus, the gradual drop in cooperation seen in Fig. 6 for the case α =0 is mostly due to fluctuating individuals spending less and less time engaging in cooperative behavior. This dynamical picture changes when individuals imitate not only according to a payoff bias but also to conformity. In this case, for $\bar{k}=8$, the population always reaches one of the two absorbing states, so that in the limit only one strategy gets fixed: Cs for low values of b, Cs or Ds (with a certain probability) for intermediate values of b, and Ds for large values of b (see also the bottom row of Fig. 7). In general and contrary to what happens without conformity, intermediate levels of cooperation for $\alpha > 0$ (when averaging over several runs) are not the result of the coexistence or fluctuation of different strategies but of the fact that, for an interval of values of b, whose length increases with α , the system sometimes converges to the cooperative equilibrium and some others to the defective equilibrium (see bottom row of Fig. 7, central image). Additionally, evolutionary dynamics develop much faster in the presence of conformity. Figure 9 illustrates these observations for the case of scale-free networks with $\overline{k}=8$ and b=1.35. Without conformity (upper panel of Fig. 9) the fraction of Cs for each run slowly increases during the initial part of the simulation until, eventually, it stabilizes around 0.9. Conversely, with conformity (lower panel of Fig. 9), very early in the evolutionary process the population goes either to full cooperation or to full defection.

We can gain an insight into the interplay between network reciprocity and conformity by making use of the notion of the temperature of players [5,30]. Hot players are those who play more since they have a large number of neighbors, whereas cold players are those who have few neighbors and, consequently, play less games. By playing more often and provided that payoffs are positively biased (i.e., $S \ge 0$ in the

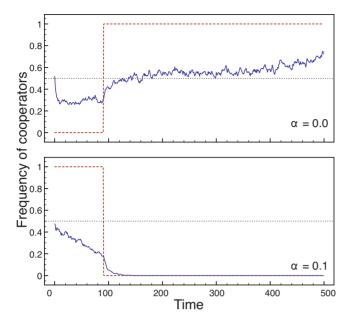


FIG. 10. (Color online) Evolution of cooperation around the most connected hub of a scale-free network with $\bar{k}=8$. The game is a rescaled PD with b=1.35 for $\alpha=0$ (upper panel) and $\alpha=0.1$ (lower panel). The fraction of C neighbors is shown in solid lines and the strategy of the hub in dashed lines (D corresponds to 0; C to 1). As a reference, the level of 50% cooperation is depicted in dotted lines. The most connected hub is initially set to D (upper panel) or to C (lower panel). The rest of the population is initialized to around 50% Cs.

PD), hot players get higher accumulated payoffs than cold players. Under pure payoff biased imitation (α =0) this implies that hot players are also more successful in being imitated and in disseminating their strategies [30].

Both Cs and Ds do better when they are surrounded by Cs. By spreading defective behavior, hot Ds become less and less successful since the number of their C neighbors decreases. Hot Cs, on the contrary, see their payoff increased by spreading their own strategy. The more hot Cs are imitated the more they earn and the more difficult it is for a surrounding D to invade. A typical example of such "hub dynamics" is illustrated in Fig. 10 (upper panel) for the most connected hub of a scale-free network. The hub is D at the beginning of the simulation, while the rest of the population is initialized to around 50% Cs. Many C neighbors imitate the defective hub (or other surrounding Ds) during the first steps of simulation, so that the proportion of C neighbors is reduced to approximately 30%. As a consequence, the total payoff of the hub is reduced, and the hub becomes vulnerable to invasion from a neighboring C. When the hub becomes a C, more and more of its D neighbors also switch their strategies. Consequently, the proportion of C neighbors (and the total payoff to the hub) increases and is maintained at a high level afterward. The presence of such positive feedback mechanism, and the fact that it only works for Cs, greatly enhances cooperation in degree-heterogeneous graphs and, particularly, in scale-free networks [31].

The introduction of conformity decreases the bias in the flow of information in degree-heterogeneous graphs, making hubs vulnerable to invasion from their cold neighbors. While hubs are unlikely to imitate their low connected neighbors when using a payoff biased rule, nothing prevents them from imitating a cold surrounding player if it holds the strategy of the local majority [see Fig. 1(d)]. Since the fraction of Cs generally decreases at the outset of the simulation (see the first time steps of the curves shown in Fig. 9), conformity further favors Ds, which become predominant in the population. An example of this dynamics is shown in Fig. 10 (lower panel). Initially, the hub is a C. Many of the hub's neighbors turn to defection during the first time steps, making cooperation the less common strategy in the hub's neighborhood. Around the 100th time step, the hub imitates by conformity one of its defector neighbors, leading to a quicker decrease in the proportion of Cs in its neighborhood. Shortly after, Cs completely vanish around the most connected hub. During those first time steps, hubs imitating according to a conformist bias will have many chances of becoming Ds. When Cs are not initially in the large majority, such initial asymmetry in the strategies of the hubs can account for the negative effects of conformity in the evolution of cooperation in scale-free networks. Conformity partly reverses the flow of information on degree-heterogeneous networks so that hubs no longer conduct the dynamics and instead quickly conform to the general trend of the whole population.

VI. CONCLUSIONS

To sum up, we have investigated the effects of conformity in the evolution of cooperation on regular one-dimensional lattices (rings) and scale-free networks. This was done by proposing an updating rule that is a stochastic average of the traditional local replicator dynamics, which models payoff biased imitation, and a conformist biased rule of transmission favoring the most common variants around focal individuals. We explored rings and scale-free networks with different average degrees, as well as different values of the propensity to conform α . Two games representing social dilemmas were studied: the rescaled versions of the PD and the SG. In addition to Monte Carlo simulations, we also used an extended pair-dynamics model to predict the average fraction of cooperators in equilibrium and compare them with the results obtained from our simulations.

The results presented in this paper show that whether conformity strengthens or weakens the evolution of cooperation depends on the intrinsic characteristics of the underlying graph. In the PD, conformity favors cooperation on rings by allowing clusters of Cs forming more easily. Conversely, it can hinder cooperation in scale-free networks for medium to large values of b due to the exposure of hubs to the opinions of the local majority in their neighborhoods. In particular and already for small amounts of conformity in the imitation rules of the players, scale-free networks do not show the great improvement over regular structures that has been previously reported in the literature. In the SG, conformity fosters cooperation on rings in the case k=4 for all values of the cost-to-benefit ratio r and for low to medium values of r in

the case k=8. In scale-free networks, conformity is rather detrimental for large values of r. Thus, for both the PD and the SG, conformity often hinders the evolution of cooperation on scale-free networks for the cultural evolutionary dynamics described in this paper.

It is worth pointing out that other factors dismissing the advantage of scale-free networks in the evolution of cooperation have been identified, such as participation costs [30], other positive affine transformations of the payoff matrix [20,21], and the use of average instead of accumulated payoffs [32]. While these factors are extrinsic to the imitation rules of the agents, conformity is a simple mechanism undoubtedly present in our social learning psychology and central to better understand cultural dynamics and the way cooperation evolves on real social networks.

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APPENDIX: PAIR APPROXIMATION

An analytical approximation of the dynamics of evolutionary games on graphs can be obtained by means of pair approximation [23,24]. For detailed surveys of this technique and its applications to games on graphs, we refer the interested reader to Refs. [6,16,25]. We limit ourselves to briefly introduce the pair approximation and to explain how we have extended it for taking into account conformity in the imitation rules of the players.

Pair approximation is a method for constructing a system of ordinary differential equations for the global frequencies of strategies by tracking the changes in the frequencies of strategy pairs. In our case, we are interested in determining the global frequency ρ of Cs by tracking the fluctuations in $p_{c,c}$, $p_{c,d}$, $p_{d,c}$, and $p_{d,d}$, where $p_{s,s'}$ is the probability of having an individual playing strategy s connected to an individual playing strategy s'. For pair approximation to be consistent with the mean-field approach, it is assumed that p_s $=\sum_{s'}p_{s,s'}$. Furthermore, and in order to "close" the set of equations, configurations of triplets and more complicated configurations are approximated by the configuration probabilities of strategy pairs. For example, the configuration probability of the triplet s, s', s'' is approximated by $p_{s,s',s''}$ $=p_{s,s'}p_{s',s''}/p_{s'}$. It is important to note that pair approximation (i) requires regular graphs and (ii) corrections arising from loops are ignored. Finally, note that the predictions of the pair approximation for any two regular graphs with the same degree k are exactly the same. This allows us to compare our results to those in [16] when $\alpha=0$.

Let us consider individuals sitting on the vertices of a graph of degree k. Whenever a randomly chosen site A up-

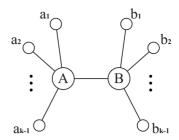


FIG. 11. A generic configuration for pair approximation. A is the focal individual, B is A's cultural model, $a_1, a_2, \ldots, a_{k-1}$ are A's neighbors other than B, and $a_1, a_2, \ldots, a_{k-1}$ are B's neighbors other than A. A and B are assumed to have no common neighbors, i.e., triangles and loops are neglected.

dates its strategy, a random neighbor B is selected as A's cultural model. Common neighbors of any pair of vertices are considered to be independent by pair approximation (i.e., loops are neglected). Thus, let us denote by a_1, \ldots, a_{k-1} (b_1, \ldots, b_{k-1}) the k-1 the neighbors of A (B) other than B (A). The probability of a generic configuration (see Fig. 11) is given by

$$\prod_{i=1}^{k-1} p_{a_i,A} p_{b_i,B} \\ p_{A,B} \frac{1}{p_A^{k-1} p_A^{k-1}}.$$

The probability that the pair A, B becomes B, B is calculated by multiplying the transition probability $\sigma_{A \to B}$ by the configuration probability and summing over all possible configurations, so that

$$p_{A,B \to B,B} = \sum_{a_1, \dots, a_{k-1}} \sum_{b_1, \dots, b_{k-1}} \sigma_{A \to B} \times p_{A,B} \frac{\prod_{i=1}^{k-1} p_{a_i,A} p_{b_i,B}}{p_A^{k-1} p_B^{k-1}}.$$

In our model, the transition probability $\sigma_{A \to B}$ depends not only on the payoffs of A and B but also on α (the probability to imitate according to a conformist bias) and on the number of players among a_1, \ldots, a_{k-1} playing the same strategy of A and B. The transition probability is given by

$$\sigma_{A \to B} = (1 - \alpha) f\left(\frac{\Pi_B(b_1, \dots, b_{k-1}) - \Pi_A(a_1, \dots, a_{k-1})}{k\theta}\right)$$
$$+ \alpha f\left(\frac{n_B(a_1, \dots, a_{k-1}, B) - n_A(a_1, \dots, a_{k-1}, B)}{k}\right).$$

where $\Pi_B(x_1,\ldots,x_{k-1})$, $\Pi_A(x_1,\ldots,x_{k-1})$ denote the payoffs of B(A) interacting with x_1,\ldots,x_{k-1} plus A(B), and $n_B(a_1,\ldots,a_{k-1},B)$, $n_A(a_1,\ldots,a_{k-1},B)$ specify the number of players with strategy B(A) among a_1,\ldots,a_{k-1} and B. The definitions of the parameter θ and the function f are given in Sec. II

Whenever A imitates B, the pair configuration probabilities change so that $p_{B,B}, p_{B,a_i}, \ldots, p_{B,a_{k-1}}$ increase, while $p_{A,B}, p_{A,a_i}, \ldots, p_{A,a_{k-1}}$ decrease. All these changes lead to a set of ordinary differential equations governing the dynamics of the system,

$$\begin{split} \dot{p}_{c,c} &= \sum_{a_1,\ldots,a_{k-1}} [n_c(a_1,\ldots,a_{k-1})+1] \prod_{i=1}^{k-1} p_{d,a_i} \sum_{b_1,\ldots,b_{k-1}} \prod_{j=1}^{k-1} p_{c,b_j} \\ &\times \left\{ (1-\alpha)f \bigg(\frac{\Pi_c(b_1,\ldots,b_{k-1})-\Pi_d(a_1,\ldots,a_{k-1})}{k\theta} \bigg) + \alpha f \bigg(\frac{2n_c(a_1,\ldots,a_{k-1})+2-k}{k} \bigg) \right\} \\ &- \sum_{a_1,\ldots,a_{k-1}} n_c(a_1,\ldots,a_{k-1}) \prod_{i=1}^{k-1} p_{c,a_i} \sum_{b_1,\ldots,b_{k-1}} \prod_{j=1}^{k-1} p_{d,b_j} \\ &\times \left\{ (1-\alpha)f \bigg(\frac{\Pi_d(b_1,\ldots,b_{k-1})-\Pi_c(a_1,\ldots,a_{k-1})}{k\theta} \bigg) + \alpha f \bigg(\frac{k-n_c(a_1,\ldots,a_{k-1})}{k} \bigg) \right\}, \end{split}$$

$$\dot{p}_{c,d} &= \sum_{a_1,\ldots,a_{k-1}} \bigg(\frac{k}{2} - 1 - n_c(a_1,\ldots,a_{k-1}) \bigg) \prod_{i=1}^{k-1} p_{d,a_i} \sum_{b_1,\ldots,b_{k-1}} \prod_{j=1}^{k-1} p_{c,b_j} \\ &\times \left\{ (1-\alpha)f \bigg(\frac{\Pi_c(b_1,\ldots,b_{k-1})-\Pi_d(a_1,\ldots,a_{k-1})}{k\theta} \bigg) + \alpha f \bigg(\frac{2n_c(a_1,\ldots,a_{k-1})+2-k}{k} \bigg) \right\} \\ &- \sum_{a_1,\ldots,a_{k-1}} \bigg(\frac{k}{2} - n_c(a_1,\ldots,a_{k-1}) \bigg) \prod_{i=1}^{k-1} p_{c,a_i} \sum_{b_1,\ldots,b_{k-1}} \prod_{j=1}^{k-1} p_{d,b_j} \\ &\times \left\{ (1-\alpha)f \bigg(\frac{\Pi_d(b_1,\ldots,b_{k-1})-\Pi_c(a_1,\ldots,a_{k-1})}{k\theta} \bigg) + \alpha f \bigg(\frac{k-n_c(a_1,\ldots,a_{k-1})}{k} \bigg) \right\}, \end{split}$$

where $n_c(a_1, \ldots, a_{k-1})$ gives the number of Cs among a_1, \ldots, a_{k-1} and $\Pi_c(x_1, \ldots, x_{k-1})$, $\Pi_d(x_1, \ldots, x_{k-1})$ denote the payoffs of a C (D) interacting with x_1, \ldots, x_{k-1} plus a D (C). Because of the symmetry condition $p_{c,d} = p_{d,c}$ and the constraint $p_{c,c} + p_{c,d} + p_{d,c} + p_{d,d} = 1$ these two differential equations are sufficient to describe the system. Note that whenever $\alpha = 0$ the system of equations is equivalent to that derived in the supplementary information in Ref. [16] and in

the Appendix in Ref. [25]. Following those works, the above equations also omit the common factor $2p_{c,d}/(\rho^{k-1}p_d^{k-1})$, which has no influence in the equilibria of the system. The equilibrium values $\hat{p}_{c,c}$, $\hat{p}_{c,d}$ were obtained by numerically integrating the equations for 10^{10} time steps after specifying initial conditions. In all cases, $p_{c,c}(0) = [\rho(0)]^2$, $p_{c,d}(0) = \rho(0)[1-\rho(0)]$. The equilibrium frequency of Cs was then approximated by $\hat{p}_c = \hat{p}_{c,c} + \hat{p}_{c,d}$.

- J. W. Weibull, Evolutionary Game Theory (MIT Press, Cambridge, MA, 1995).
- [2] M. A. Nowak, Science 314, 1560 (2006).
- [3] M. A. Nowak and R. M. May, Nature (London) 359, 826 (1992).
- [4] F. C. Santos and J. M. Pacheco, Phys. Rev. Lett. 95, 098104 (2005).
- [5] E. Lieberman, C. Hauert, and M. A. Nowak, Nature (London) 433, 312 (2005).
- [6] G. Szabó and G. Fáth, Phys. Rep. 446, 97 (2007).
- [7] R. Boyd and P. J. Richerson, *Culture and the Evolutionary Process* (University of Chicago Press, Chicago, 1985).
- [8] J. C. Coultas, Group Process. Intergroup Relat. 7, 317 (2004).
- [9] C. Efferson, R. Lalive, P. J. Richerson, R. McElreath, and M. Lubell, Evol. Hum. Behav. 29, 56 (2008).
- [10] J. P. Carpenter, J. Socio-Economics 33, 395 (2004).
- [11] N. Bardsley and R. Sausgruber, J. Econ. Psychol. 26, 664 (2005).

- [12] J. Henrich, Am. Anthropol. **103**, 992 (2001).
- [13] J. Peña, Proceedings of Artificial Life (MIT Press, Cambridge, MA, 2008), Vol. XI, pp. 458–465.
- [14] J. Henrich and R. Boyd, J. Theor. Biol. **208**, 79 (2001).
- [15] F. Mengel, J. Evol. Econ. 19, 397 (2009).
- [16] C. Hauert and M. Doebeli, Nature (London) 428, 643 (2004).
- [17] M. Doebeli and C. Hauert, Ecol. Lett. 8, 748 (2005).
- [18] M. Tomassini, L. Luthi, and M. Giacobini, Phys. Rev. E 73, 016132 (2006).
- [19] J. T. Cox and R. Durrett, in *Random Walks, Brownian Motion, and Interacting Particle Systems*, edited by R. Durrett and H. Kesten (Birkhauser, Boston, 1991), pp. 189–202.
- [20] M. Tomassini, E. Pestelacci, and L. Luthi, Int. J. Mod. Phys. C 18, 1173 (2007).
- [21] L. Luthi, M. Tomassini, and E. Pestelacci, BioSystems **96**, 213 (2009).
- [22] B. Skyrms, Monist 88, 259 (2005).
- [23] H. Matsuda, N. Ogita, A. Sasaki, and K. Sato, Prog. Theor.

- Phys. 88, 1035 (1992).
- [24] M. van Baalen and D. A. Rand, J. Theor. Biol. 193, 631 (1998).
- [25] C. Hauert and G. Szabó, Am. J. Phys. 73, 405 (2005).
- [26] R. Albert and A.-L. Barabási, Rev. Mod. Phys. **74**, 47 (2002).
- [27] B. Bollobás, *Random Graphs* (Academic Press, New York, 1995).
- [28] When comparing our results with those in [4], note that the
- curves are in the wrong order in [4] as cooperation should decrease with increasing mean degree for scale-free networks.
- [29] J. Gómez-Gardeñes, M. Campillo, L. M. Floría, and Y. Moreno, Phys. Rev. Lett. 98, 108103 (2007).
- [30] N. Masuda, Proc. R. Soc. London, Ser. B 274, 1815 (2007).
- [31] F. C. Santos, J. F. Rodrigues, and J. M. Pacheco, Proc. R. Soc. London, Ser. B 273, 51 (2006).
- [32] F. C. Santos and J. M. Pacheco, J. Evol. Biol. 19, 726 (2006).