Epidemic spreading and cooperation dynamics on homogeneous small-world networks

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We introduce a class of small-world networks—homogeneous small-worlds—which, in contrast with the well-known Watts-Strogatz small-worlds, exhibit a homogeneous connectivity distribution, in the sense that all nodes have the same number of connections. This feature allows the investigation of pure small-world effects, detached from any associated heterogeneity. Furthermore, we use at profit the remarkable similarity between the properties of homogeneous small worlds and the heterogeneous small-worlds of Watts-Strogatz to assess the separate roles of heterogeneity and small-world effects. We investigate the dependence on these two mechanisms of the threshold for epidemic outbreaks and also of the coevolution of cooperators and defectors under natural selection. With respect to the well-studied regular homogeneous limits, we find a subtle interplay between these mechanisms. While they both contribute to reduce the threshold for an epidemic outburst, they exhibit opposite behavior in the evolution of cooperation, such that the overall results mask the true nature of their individual contribution to this process.

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I. INTRODUCTION

The study of networks pervades all of science, and the recent and spectacular developments in computers and communication networks made it easier to understand that the world in which we live and which we create and shape is in fact a huge web of networks of different kinds, some of which were recently found to obey scaling laws. In fact, only very recently [1,2] such features have been recognized as playing a ubiquitous role on many processes taking place in different types of communities. These can be typically mapped onto networks, in which community members occupy the nodes and their interactions are represented by the links between nodes. Moreover, networks often portray the coexistence of local connections (spatial structure) with nonlocal connections (or shortcuts). The celebrated Watts-Strogatz [3] small-world (SW) networks proved instrumental to understand and characterize such network features. As a result, many studies originating from diverse areas of science have been carried out to investigate the impact of SW effects on the static and dynamic properties of phenomena taking place on networks. As a rule, such impact of SW effects has been sought by comparing the behavior of the system with that known from analytical studies typically carried out at a mean-field level, or in spatially homogeneous layouts. However, in contrast with spatial configurations and mean-field models, in which the homogeneity of node connectivity translates into a degree distribution characterized by a welldefined, single peak, most SW networks studied so far are inherently heterogeneous (for an exception, cf. Ref. [4]), with associated multipeaked degree distributions [for a network with N nodes, the degree distribution is defined as $d(k) = N_k/N$, where N_k gives the number of nodes with k links]. In other words, the systematic study of the role of "pure" SW effects devoid of any associated heterogeneity has not been carried out, precluding a clear understanding of the role of such SW effects. For instance, it has been recently shown [5] how computer networks exhibiting the ubiquitous scale-free degree distributions $d(k) \approx k^{-3}$ are extremely fragile to epidemic outbreaks, such that in the limit of infinite size, these networks show no threshold for such outbreaks. This result, extended to other epidemiological contexts in Ref. [6], was shown to result from the divergence of the second moment of the degree distribution in the limit of infinite size, a typical heterogeneity effect. As such, the specific contribution of SW effects to the characterization of epidemic thresholds remains unclear.

On the following, we start by defining a class of SW networks—homogeneous SW (HoSW)—which exhibit SW features without giving up the homogeneity of the associated degree distribution. These networks will prove very useful in our subsequent investigations of the contributions of SW effects and of network heterogeneity to phenomena taking place on networks.

Inspired by the algorithm developed in Ref. [3]. to generate Watts-Strogatz heterogeneous SW (HeSW), we generate HoSW starting from a (undirected) regular graph with average connectivity z and size N, which fixes the number of edges E=Nz/2. We introduce a dimensionless parameter f which gives the fraction of edges to be randomly rewired: for f=0 we have a regular graph, whereas for f=1 all edges are randomly rewired. We adopt, however, a rewiring mechanism which does not change the degree distribution [7]. The algorithm resumes to repeat the following two-step circular procedure until fE edges are successfully rewired: (i) choose—randomly and independently—two (different) edges which have not been used yet in step (ii) and (ii) swap the ends of the two edges if no duplicate connections arise.

The procedure of edge-swapping, as is well-known [7], does not change the overall degree distribution. On the other



FIG. 1. (Color online) HoSW versus HeSW. The cluster coefficient C and average path length L, divided by their values for regular networks (C_0 and L_0 , respectively), are shown as a function of ffor the HoSW proposed in this work, and of the SW rewiring probability p for HeSW. We divided the domains of f and p in two subregions, which were found to be associated with different regimes for the processes studied here. On the left panel (in a log scale) we detail the behavior for the region in which L changes significantly while C remains nearly constant. The remaining domain, shown in the right panel, is dominated by changes in C while changes in L are very small.

hand, since the edges are randomly chosen, by swapping the ends of each pair of edges one is actually introducing shortcuts in the original regular graph, in this way strongly affecting the properties of the associated network. Indeed, and similarly to the HeSW rewiring probability p, the parameter f has a strong nonlinear impact on both local and global properties of the resulting network. In Fig. 1 a comparison is shown between key features of HoSW and HeSW as functions of f and p, respectively. Specifically, we plot the average path length L and cluster coefficient C [1], for both HoSW and HeSW, divided by the corresponding values at f=p=0. The networks are characterized by $N=10^4$ and z =8 (although the qualitative behavior shown in both panels of Fig. 1 does not depend on the precise value of z), and Fig. 1 shows that, in spite of the fact that for HoSW the degree distribution is independent of f, the behavior of L and C for both types of networks is remarkably similar. In other words, heterogeneity constitutes the main distinctive feature of HeSW when compared to HoSW. What is the contribution of each of these mechanisms to a given dynamical process taking place on networks? The answer will depend on the process under study. Here we select two examples of complex phenomena in which the individual contributions of each mechanism turn out to be of different magnitude and sign: The threshold for epidemic outbreaks, within the simple susceptible-infected-susceptible (SIS) model [5] and the evolution of cooperation, for which we adopt the single-round Prisoner's dilemma (PD), a model which has been recently studied in different types of networks [8–15].

A. Threshold for epidemic outbreaks

Following Ref. [5], we adopt the susceptible-infectedsusceptible (SIS) model to describe epidemic spreading in a



FIG. 2. (Color online) Different contributions to the threshold of epidemic outbreaks. The threshold for the occurrence of an epidemic outbreak λ_c has been computed on HoSW and HeSW of size $N=10^4$ and z=4. The dependence in terms of f for HoSW and p for HeSW is plotted with solid squares and solid circles, respectively (a logarithmic scale is used for f and p). For f=p=1, where all edges have been randomized, the reduction in the threshold for epidemic out-breaks is $\approx 36\%$ in homogeneous networks with respect to regular networks. On the other hand, heterogeneity adds to the previous effects, further reducing by $\approx 10\%$ the value of λ_c at p=1.

(computer) network, in which computers occupy the nodes and their connections are represented by the links between nodes. The status of each node evolves in time according to the following update rules [5]: An infected node at time t recovers and becomes susceptible at time t+1. A susceptible node at time t may become infected with probability λ if it is linked to at least one infected node. We carry out extensive computer simulations and compute the critical value λ_c above which infected nodes persist in the stationary regime. Initially, an equal percentage of infected and susceptible is randomly distributed among the nodes of the network. After a transient time, a stationary state is reached, in which we compute the prevalence of infected individuals. For given values of f and p, and for $N=10^4$ and z=4, we determined the critical value λ_c . We have checked that the results shown here remain valid for N > 1000, the differences between HoSW and HeSW becoming smaller with increasing z. We carried out 100 runs for each value of f, p, and λ . The results are shown in Fig. 2. For small values of $f=p \le 0.01$ (left panel of Fig. 1), for which small-world effects occur (associated with the coexistence of large values of C with small values of L) the behavior of both curves is very similar. This is so in spite of the fact that in this interval range L has dropped by over one order of magnitude from its value at f=p=0, indicating an insensitivity of λ_c with respect to L. This is also the region in which the dependence of L is more dissimilar between the two models. For larger values of f and p, the two curves increasingly deviate from each other up to f=p=1. This is the region in which C undergoes its major changes, indicating that the threshold for epidemic outbreaks is more sensitive to C than to L. We obtain a sizable reduction of the critical value, up to a total of $\approx 36\%$ in the homogeneous random limit (f=1), when compared to the ho-

TABLE I. Finite-size effects in uncorrelated networks. The value for the epidemic threshold λ_c is tabulated for different network sizes, for HoSW with f=1 and HeSW with p=1. The analytical value corresponding to the mean-field approximation is given [17] by $\lambda_c = 1/z = 0.25$ (z=4). The results tabulated show the interference between heterogeneity and finite-size effects, such that for $N=10^4$ the mean-field result is accidentally reached, in spite of the fact that, as expected, the limit of λ_c in HeSW whenever $N \rightarrow \infty$ is lower than the mean-field limit, which corresponds to the limit obtainable in HoSW.

N	λ_c (HoSW)	λ_c (HeSW)
10 ³	0.290	0.265
10^{4}	0.279	0.250
10^{5}	0.276	0.245

mogeneous regular network. On the other hand, heterogeneity adds to the previous effects, further reducing the value of λ_c by $\approx 10\%$ (p=1). Clearly, the major contribution to such a reduction arises exclusively from the increasing randomization of the edges (taking place with increasing f) heterogeneity providing a minor contribution. For f=p=1, the value of C is very small, comparable to the values typical for random scale-free networks [1]. Therefore, as heterogeneity continues to increase, we expect it to become the dominant mechanism, such that on extreme heterogeneous networks the effects on λ_c associated with the introduction of shortcuts will be washed out by heterogeneity effects. This is exactly what comes out of the results of Refs. [5,6].

On the other hand, the results shown in Fig. 2 illustrate how finite-size effects should not be overlooked whenever the limiting behavior of processes taking place in networks is at stake. As is well-known [16], the mean-field approximation assumes that networks are of infinite size, the pattern of connectivity is uncorrelated, and all nodes share the same number of connections [17] (homogeneous ansatz). In other words, in order to compare simulation results with the (analytical) mean-field results of Ref. [17] one should adopt HoSW with f=1 and $N \rightarrow \infty$. Indeed, simulations on such networks for f=1 deviate from the mean-field approximation only to the extent that they must be carried out in finite-sized networks. HeSW, on the other hand, deviate more from the mean-field approximation, since heterogeneity translates into different nodes exhibiting a different number of connections. The results shown in Fig. 2 (and, for that sake, the results in Ref. [17]) seem to indicate, however, that HeSW lead to an excellent agreement when compared to the analytical value $\lambda_c = 1/z$, actually better than those associated with HoSW, a feature which seems paradoxical in view of the present discussion. This is clearly a finite-size effect, as tabulated in Table I, which shows how λ_c changes as we change the size of the network. Clearly, while for $N \approx 10^3$ both values overestimate the mean-field limit, λ_c already underestimates the mean-field limit for $N \approx 10^5$ in HeSW, whereas λ_c continues the slow, monotonic convergence toward the mean-field limit in HoSW.

B. Evolution of cooperation

The ongoing challenge [18] of understanding the emergence of cooperation in the context of Darwinian evolution is traditionally addressed in the framework of evolutionary game theory [19], combined with games such as the PD, used as metaphors of cooperation between unrelated individuals [19]. In the simple, single-round PD, individuals are either *cooperators* or *defectors*, acting accordingly whenever two of them interact. They both receive R upon mutual cooperation and P upon mutual defection. A defector exploiting a cooperator gets an amount T and the exploited cooperator receives S, such that T > R > P > S. On the foregoing, we shall follow common practice [8-15] and adopt the simplest parametrization for the PD, making 2 > T = b > R = 1 > P = S=0, where b represents the temptation to defect. In infinite, well-mixed populations, evolution under replicator dynamics favors defectors over cooperators. However, whenever cooperators and defectors are spatially arranged on a regular, homogeneous network for which $z \ll N$ [13] cooperators are now able to dominate defectors for small values of the temptation to defect b. This dominance is significantly enhanced [13] whenever the populations are mapped onto HeSW, being maximal for p=1 (for fixed z), although the origin of this enhancement remains to be clarified (see below).

The sensitivity of cooperation to the underlying population structure has prompted a series of work on the subject. Both the simple PD game considered here [8–15] as well as the more complex repeated PD game [21,22] have been studied in networks which resemble those used in this work. Indeed, Watts-Strogatz small-world ring networks have been investigated in Ref. [10] under deterministic imitation dynamics, in two-dimensional lattices in [20–22] or in random homogeneous and heterogeneous networks in [9,14,21,22]. Moreover, disorder in the environment has been mimicked by introducing site-diluted graphs in Ref. [11].

Here we simulate evolution in HoSW and HeSW by implementing the finite population analog of replicator dynamics [13,19], which converges to replicator dynamics in the limit of infinite, well-mixed populations: In each generation, all pairs of individuals x and y, directly connected, engage in a single round of the PD, their accumulated payoffs being stored as P_x and P_y , respectively. Whenever a site x is updated, a neighbor y is drawn at random among all k_x neighbors; whenever $P_y > P_x$ the chosen neighbor takes over site x with probability given by $(P_y - P_x)/(Dk_>)$, where $k_>$ is the largest between k_x and k_y and D=T-S, ensuring the proper normalization of the probability. Such a stochastic update rule is different from the deterministic rule used in other studies of the PD [8-12,14] and, as shown recently, the specific update rules used [23] lead to different evolutionary dynamics both for finite as well as for infinite populations. The framework adopted here corresponds to the so-called synchronous updating. We have checked that no qualitative changes of the results are obtained if asynchronous updating is used instead. Initially, an equal percentage of strategies (*cooperators* or *defectors*) is randomly distributed among the elements of the population. Evolution undergoes a transient period before a stationary regime is reached, in which we compute the equilibrium frequencies of cooperators and defectors. As a result, we determine the dependence of the equilibrium frequency of cooperators on the temptation to defect b.

In Fig. 3 we show the results of extensive computer simulations carried out both for HoSW (upper panel) and for



FIG. 3. (Color online) Evolution of cooperation in HoSW (upper panel) and HeSW (lower panel). We computed the fraction of cooperators who survive evolution, as a function of the PD parameter b, for selected values of the SW parameters f and p. All networks have size $N=10^4$ and z=4. Comparison between the two panels shows that while the range of b values for which cooperators resist invasion by defectors results from SW effects associated with the increase of shortcuts, the overall fraction of cooperators that survives evolution is sizably enhanced via heterogeneity effects, which completely mask the hindrance of cooperation induced by the previous effects for small values of b.

HeSW (lower panel). In all cases, we make z=4 and $N = 10^4$, although the results we obtain here are robust both for larger populations as well as for smaller communities and other values of *z*. Each data point in Fig. 3 results from an average over 100 simulations, resulting from 10 different realizations of each type of network, and 10 runs for each network realization.

The solution corresponding to the evolution of cooperation on homogeneous regular graphs (f=p=0) is shown with a solid line in both panels. The behavior of cooperation remains unchanged with respect to the regular limit up to f $= p \approx 0.005$, at which point we have, on average, 0.5% of the edges randomly rewired, and L has decreased typically one order of magnitude from its value for f=p=0, indicating that the overall incidence of cooperators is again insensitive to L. For f=p=0.01, one obtains small changes as a function of b. Comparison between the results for HoSW and HeSW show no qualitative difference, however, which means that the effects responsible for this change do not rely on heterogeneity effects (cf. Fig. 1). f=p=0.01 marks the onset of a more rapid change of C, whereas most of the variation in L has already taken place, which indicates that cooperation may be more sensitive to changes in C. This is indeed what happens, as shown in Fig. 3. For f=p=0.1, a sizable change of behavior is obtained, being also markedly different for *both* types of networks. Indeed, cooperators are now able to resist invasion by defectors up to values of $b \approx 1.35$ in both networks. The fact that the onset of survival for cooperators is essentially identical in both types of networks indicates that the increasing randomization of the edges is responsible for this enhancement of the survivability of cooperators, independently of any heterogeneity effects. These effects alone, however, lead to a sizable reduction of the fraction of cooperators for small *b*. Larger values of $f \leq 0.5$ lead to an amplification of both behaviors, whereas for f > 0.5 no further qualitative changes take place. It is noteworthy that *C* still changes significantly as *f* varies from f=0.5 to f=1, suggesting that above a certain value, *C* plays no additional role.

Comparison between the two panels in Fig. 3 for p=f ≥ 0.1 also shows the effect of "adding" heterogeneity: Overall, the fraction of cooperators who survive evolution in HeSW is considerably enhanced. Moreover, both curves in Fig. 3 show how heterogeneity counterbalances those effects associated with the occurrence of shortcuts such that, for small b, the levels of cooperation now overshoot those obtained on regular networks. For larger values of b, cooperation is also sizably enhanced. These nontrivial effects demonstrate the detailed interplay between these mechanisms taking place in the evolutionary dynamics of cooperation. In HeSW individuals do not interact the same number of times per generation. As such, cooperators have a better chance of increasing their relative fitness by "placing themselves" on the nodes with larger connectivity. Indeed, heterogeneity increasingly assumes a dominant role such that, on scale-free networks, cooperation may become the dominating trait for all values of b, a result which extends to other symmetric two-person games [15].

To summarize, the present results show that "conventional" SW effects result from the concurrent contributions of heterogeneity and "pure" SW effects, associated with the substitution of regular links by shortcuts. These two mechanisms, depending of the process being studied, may exhibit constructive or destructive interference. In what concerns the spread of viruses taking place on networks, for small values of the heterogeneity, the increasing randomness associated with large f values in HoSW provides the dominant contribution to the sizable reduction of the threshold for epidemic outbursts obtained. However, as heterogeneity grows, it becomes the dominating effect [5,17]. In what concerns the evolution of cooperation, SW effects play a more subtle role. On one hand, SW effects (and for large f, the increasing randomness of the network) increase the survivability of cooperators up to larger values of the temptation to defect b. On the other hand, the overall incidence of cooperators decreases whenever the temptation to defect is small. Heterogeneous effects, in turn, lead to an overall enhancement of cooperation for all values of b which, even for the moderate heterogeneity considered here, completely mask the modifications induced by SW effects, notably the reduction of the incidence of cooperators for small values of b.

The possibility to separate heterogeneity and "pure" SW effects may provide further insights into the detailed dynamics of complex phenomena taking place on networks. Work along these lines is in progress.

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