

# Sorting out the effect of spatial structure on the emergence of cooperation

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## Abstract

The positive effect on cooperation of the spatial structure of a population is currently regarded as a well established principle in evolutionary game theory. Since Nowak and May's report of a promotion of cooperation in the Prisoner's Dilemma, the most demanding binary game, many subsequent studies have supported this conclusion. Some recent results, however, seem to refute it. The present situation is that this question remains basically unresolved, as it has not been investigated systematically and with enough detail, considering different social dilemmas and rules for the update of strategies. Moreover, the time evolution of these models has hardly been studied, with the result that a convincing explanation of the effect of spatial structure is not available. We have addressed these issues to provide a complete picture of the effect of spatial structure on the evolution of cooperation, as well as the identification of the underlying dynamical mechanisms. We have found that spatial structure, in general, only promotes cooperation on coordination games, like Stag Hunt, and that the positive effect on Prisoner's Dilemma occurs only with a particular non-stochastic rule. We explain all these effects in terms of the local densities of each strategy and the structure of equilibria of the game. As a result, the asymmetry between the effects on coordination and anti-coordination games arises as a fundamental feature of these evolutionary models.

Keywords: evolution of cooperation; game theory; spatial structure; social networks.

Abbreviations: HG, Harmony game; PD, Prisoner's Dilemma; SH, Stag Hunt game; SD, Snowdrift game.

Cooperation is a key force in evolution, present in all scales of organization, from unicellular organisms to complex modern human societies [Maynard-Smith & Szathmáry 1998]. For this reason the elucidation of the emergence and stabilization of cooperative behavior has become a core problem in biology, economics and sociology. Evolutionary game theory has proven to be one of the most fruitful approaches to investigate this problem, using evolutionary models based on so-called social dilemmas [Maynard-Smith 1982; Axelrod 1984; Nowak 2006]. Among the mechanisms proposed to enhance cooperation, the structure of the population stands out as one of the most relevant. The presence of structure means that each individual does not interact with every other, but with a limited subset of the

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population that constitutes his neighborhood, arranged according to an underlying network of connections. This idea was very successfully introduced by Nowak and May in their seminal paper [Nowak & May 1992], stimulating a wealth of work that continues to date (see [Szabó & Fáth 2007] for a review, and references therein).

The current view on the influence of spatial structure, as a particular case of population structure, is that in general it promotes cooperation, given its positive effects on the most demanding social game (Prisoner’s Dilemma) [Nowak & May 1992], with the only exception of anti-coordination games such as Hawk-Dove or Snowdrift [Hauert & Doebeli 2004; Sysi-Aho et al 2005]. However, very little evidence has been provided for the generality of this conclusion. Most studies have concentrated on a particular parameterization of Prisoner’s Dilemma, and the influence of the rule used for the update of strategies has not been systematically discussed. In addition, research has focused on the asymptotic states, paying practically no attention to the time evolution. As a consequence, the understanding of the effect of spatial structure has not gone beyond the formation of clusters of cooperators already reported in [Nowak & May 1992].

To provide a definitive answer to these questions, we have performed a thorough and systematic computational study, taking into account the most relevant  $2 \times 2$  games and update rules. To assess the influence of a given spatial structure, we have defined a quantitative measure for the cooperation achieved on each kind of game, and we have compared results not only with the unstructured population (well-mixed), but also with the corresponding homogeneous (single degree) random population. Besides, we have considered in detail the time evolution, both under synchronous and asynchronous update schemes, in order to understand the fundamental mechanisms involved.

We show that the effect of spatial structure on the evolution of cooperation has been misunderstood. We prove that, in general, spatial structure only promotes cooperation in coordination games, like Stag-Hunt [Skyrms 2003], and that this promotion is significant only if the spatial structure has high transitivity (clustering coefficient) [Newman 2003]. Furthermore, the rules for the update of strategies play a crucial role. The fostering of cooperation in Prisoner’s Dilemma is actually a singular case, that results from the lack of stochasticity of a particular update rule, namely unconditional imitation. We explain these effects in terms of the local densities of cooperators and defectors and how they relate to the structure of equilibria of the game. In addition, the comparison of results with weak selection models yields a fundamental difference, as the asymmetry between the effects on coordination and anti-coordination games that we have found in our results is lost in the case of weak selection pressure.

## 1 Evolutionary Games

Let us consider a symmetric  $2 \times 2$  game, a game with 2 players who choose between 2 strategies and with no difference in role. Each player obtains a payoff given by the following matrix

$$\begin{array}{cc} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \left( \begin{array}{cc} 1 & S \\ T & 0 \end{array} \right). \end{array} \quad (1)$$

The rows represent the strategy of the player who obtains the payoff and the columns that of her opponent.

The strategies are labeled as C and D for cooperate and defect, because we interpret the game as a social dilemma. Indeed, certain values of  $S$  and  $T$  undermine a hypothetical situation of mutual cooperation. If  $S < 0$  a cooperator faces the risk of losing if the other player defects, performing worse than with mutual defection. If  $T > 1$  a cooperator has the temptation to defect and obtain a payoff larger than that of mutual cooperation. Both tensions determine the social dilemmas represented by symmetric  $2 \times 2$  games [Macy & Flache 2002]. Restricting the values of the coefficients within the intervals  $-1 < S < 1$  and  $0 < T < 2$ , we have the Harmony game [Licht 1999]

(HG,  $0 < S, T < 1$ ) and three classic social dilemmas: the Prisoner's Dilemma [Axelrod & Hamilton 1981] (PD,  $-1 < S < 0, 1 < T < 2$ ), the Stag-Hunt game [Skyrms 2003] (SH,  $-1 < S < 0 < T < 1$ ), and the Hawk-Dove [Maynard-Smith & Pride 1973] or Snowdrift game [Sudgen 2004] (SD,  $0 < S < 1 < T < 2$ ). Each game corresponds, thus, to a quadrant in the  $ST$ -plane.

To study the competition between cooperation and defection from an evolutionary perspective, the payoffs obtained by playing the game are considered as fitness and a darwinian dynamics is introduced to promote the fittest strategy. The classic framework to do so is the replicator dynamics [Hofbauer & Sigmund 1998; Gintis 2000], which assumes an infinite and well-mixed population, i.e. a population with no structure, where each individual plays with every other. Let  $x$  be the density of cooperators, and  $f_c$  and  $f_d$  the fitness of a cooperator and a defector, respectively. The replicator dynamics states that  $x$  evolves as [Hofbauer & Sigmund 1998]

$$\dot{x} = x(1-x)(f_c - f_d). \quad (2)$$

Then, if cooperators are doing better than defectors their density rises accordingly, and the opposite occurs if they are doing worse. Provided that the initial density of cooperators  $x^0$  is different from 0 and 1, the asymptotic state of this dynamical system is, for each game ( $x^*$  represents the asymptotic density of cooperators) [Hofbauer & Sigmund 1998]: HG, full cooperation,  $x^* = 1$ ; PD, full defection,  $x^* = 0$ ; SH, full cooperation if  $x^0 > x_e$ , or full defection if  $x^0 < x_e$ ; SD, mixed population with  $x^* = x_e$ , regardless of the initial density  $x^0$ . Both in SH and SD the coexistence equilibrium has a probability of cooperation  $x_e = S/(S + T - 1)$ . It is important to note that the outcome of these four games encompasses all the possible cases for any symmetric  $2 \times 2$  game [Rapoport & Guyer 1996; Roca et al 2006].

The standard equivalent version of this evolutionary model, for finite populations and discrete time, is built by connecting the population with a complete network and by making use of the following rule for the update of strategies, known as the replicator update rule [Hofbauer & Sigmund 1998; Gintis 2000]. Let  $i = 1 \dots N$  label the individuals in the population. Let  $s_i$  be the strategy of player  $i$ ,  $\pi_i$  her payoff and  $N_i$  her neighborhood. With the replicator update rule one neighbor  $j$  of player  $i$  is chosen at random,  $j \in N_i$ . The probability of player  $i$  adopting the strategy of player  $j$  is given by

$$p_{ij}^t \equiv \mathcal{P}\{s_j^t \rightarrow s_i^{t+1}\} = \begin{cases} (\pi_j^t - \pi_i^t)/\Phi & : \pi_j^t > \pi_i^t \\ 0 & : \pi_j^t \leq \pi_i^t \end{cases}, \quad (3)$$

with  $\Phi = k(\max(1, T) - \min(0, S))$  to ensure  $\mathcal{P} \in [0, 1]$ .

Figure 1 shows the simulation results for this setting, which, as expected, are in complete agreement with the evolutionary outcome predicted by (2) in an infinite well-mixed population. It constitutes the standard scenario against which the effect on cooperation of a given population structure will be assessed. Additionally, we introduce a quantitative measure  $\mathcal{C}_G$  for the overall asymptotic cooperation in game  $G$  ( $=$  HG, PD, SH, SD), given by the integral of  $x^*$  over the corresponding region in the  $ST$ -plane. This global index of cooperation has a range  $\mathcal{C}_G \in [0, 1]$  and appears on the graphs by the quadrant of each game.

Besides the replicator update rule, we have considered other local non-innovative rules that have received attention in previous research [Szabó & Fath 2007]: multiple replicator, Moran and unconditional imitation.

The multiple replicator update rule is similar to the replicator rule, with the difference of checking simultaneously all the neighborhood and thus making more probable a strategy change. Then, the probability that player  $i$  maintains her strategy is

$$\mathcal{P}\{s_i^t \rightarrow s_i^{t+1}\} = \prod_{j \in N_i} (1 - p_{ij}^t), \quad (4)$$

with  $p_{ij}^t$  given by (3). In case the strategy update takes place, the neighbor  $j$  whose strategy is adopted by player  $i$  is selected with probability proportional to  $p_{ij}^t$ .

With the Moran update rule, a player chooses the strategy of one of her neighbors, or herself's, with a probability proportional to the payoffs. Because the payoffs may be negative in PD and SH, the constant  $\Psi = -k \min(0, S)$  is added to them. With this rule a player can adopt, with low probability, the strategy of a neighbor that has done worse than herself. This is the only rule among those studied in this work that has this property.

Finally, unconditional imitation makes each player choose the strategy of the neighbor with largest payoff, provided this payoff is greater than the player's. This is a deterministic rule, in contrast to the previous ones, which are all stochastic.

## 2 Results

### 2.1 Homogeneous Random Topology

To address the effect of spatial structure in the evolution of cooperation, it is illuminating to study the influence of the homogeneous random topology, where all individuals have exactly the same number of neighbors, randomly distributed over the population. Our aim is to discern what can be attributed to the spatial distribution of links and what to the mere limitation of the size of the neighborhoods.

Figures 2 A-C show the simulation results for homogeneous random networks of degree  $k = 4, 6$  and  $8$ , using the replicator update rule. Comparing with Figure 1, it is clear that this topology has a weak effect on the evolution of cooperation, the weaker the larger the degree. The only remarkable differences are a small promotion of cooperation in SH, because of the advance of the transition line between full cooperation and defection, and a small inhibition in SD, given the contraction of the asymptotic equilibrium density  $x^*$ . This can be regarded as a continuous mapping of the domains in the  $ST$ -plane between the results of the complete network and those of the homogeneous random one, with the corresponding displacement of the effective equilibria of the underlying dynamical system. This interpretation could be thought of as a transformation of the payoff matrix, similar to that found in the different context of weak selection pressure [Ohtsuki & Nowak 2006].

Changing the update rule to the multiple replicator one does not alter qualitatively the evolutionary outcome. In this case, the promotion of cooperation in SH is somewhat stronger and the inhibition in SD is a bit weaker (see Figures SI 1 A-C). The results with the Moran update rule exhibit even weaker effects on the evolution of cooperation, with the difference of a reversal of the influence: a small inhibition in SH and a small promotion in SD (see Figures SI 2 A-C). Remarkably, in all cases the effect on cooperation in SH is opposite to that in SD.

### 2.2 Spatial Structure

Spatially structured populations are defined by means of regular lattices. Following standard practice [Szabó & Fáth 2007] we have studied the topologies that correspond to a two-dimensional square lattice, with 4 or 8 neighbors, also known as von Neumann and Moore neighborhoods, respectively. Additionally, we have included in our analysis the 6-neighbor topology based on a triangular lattice. An important property of this kind of networks is their transitivity or clustering coefficient  $C$ , which for our purposes can be defined as the probability that any two neighbors of a given individual are also neighbors themselves [Newman 2003]. For degree  $k = 4$ ,  $C = 0$ , but for  $k = 6$ ,  $C = 2/5 = 0.4$  and for  $k = 8$ ,  $C = 3/7 \approx 0.43$ .

Figures 2 D-F show the results for populations on regular lattices, with the replicator update rule. The comparison with Figures 2 A-C yields, for each degree, the effect of the spatial structure. The only major overall difference is found in SH, for degrees  $k = 6$  and  $8$ , with a substantial reinforcement of the cooperative strategy. Therefore, it is only for this game and for these degrees that the spatial arrangement of links has a strong effect on the evolution of cooperation. It is important to note that these degrees correspond to the networks with high clustering coefficient. For  $k = 4$ , the promotion of cooperation in SH is much weaker: the mean cooperation in SH has a relative increase of less than 10 %, compared to values well above 40 % for  $k = 6$  and  $8$ .

In SD the spatial structure further inhibits cooperation as compared to the homogeneous random topology, specially for small  $S$ . Again the effects in SH and SD are opposite. Finally, HG and PD remain unchanged.

The multiple replicator update rule leads to the same results (see Figures SI 1 D-F), slightly intensified. As for the Moran rule, the influence of spatial structure is in general very weak (see Figures SI 2 D-F). The only remarkable effect is the change in SH from a small inhibition with the homogeneous random network to a small promotion with the regular lattice.

### 2.3 Unconditional Imitation

Figures 3 A-C display the results with this update rule on a population with random homogeneous topology. For all the degrees considered cooperation is strongly enforced in SH and inhibited in SD. Even a noticeable promotion of cooperation occurs in PD. The effects do not decrease as the degree increases and, specially for the lowest degree  $k = 4$ , there are sharp transitions (i.e., discontinuities) in the asymptotic density of cooperators  $x^*$ . That means that the idea of a continuous mapping in the  $ST$ -plane does not hold in this case.

These results are a first example of the dramatic difference between models with unconditional imitation as update rule and those updated via stochastic rules. With the latter we have a weak effect on the evolution of cooperation for homogeneous random topologies, with just a slight promotion in SH and a slight inhibition in SD, or vice versa. With unconditional imitation, however, we find a strong promotion of cooperation in SH and positive effects on PD.

Finally, Figures 3 D-F display the results for regular lattices with unconditional imitation. As with the other update rules, the results for  $k = 4$  are very similar to that of the regular random topology, but, in contrast, for lattices with high clustering coefficient ( $k = 6$  and  $8$ ) there is a large difference. The spatial structure of the population produces again in those cases a southeast displacement of the transition line, which in this case goes well into the region with  $T > 1$ . As a consequence, cooperation is not only promoted in SH, where it is virtually complete, but also reaches high levels in SD and PD.

Summarizing the results obtained for populations with spatial structure, we have to point out, in the first place, that the effect has a great dependence on the update rule. Letting aside the Moran update rule, because of its negligible influence, another key conclusion is that, in general, spatial structure has a clear effect on the evolution of cooperation only when the clustering coefficient is high. The scope of this effect, i.e. the games it affects and how, depends crucially on the update rule. For the replicator and multiple replicator rules, it simply consists in a high promotion of cooperation in SH. For unconditional imitation, however, spatial structure produces almost full cooperation in SH and a significant promotion in SD and PD. Therefore, it is the combination of spatial structure and unconditional imitation that produces such an extraordinary fostering of cooperative behavior. Interestingly, it is the only case where cooperation is significantly promoted in PD.

## 2.4 Small-World Networks

As a way to check the robustness of our conclusions about the effect of spatial structure on the evolution of cooperation, and also for the intrinsic interest of this network topology, we have included small-world networks in our systematic simulations. We have used the algorithm devised by [Watts & Strogatz 1998], which starts from a regular lattice and performs, with low probability, a random reshuffling of links preserving the degree of the nodes, with the aim of lowering the mean distance between nodes while maintaining the high clustering coefficient.

In our case, we have started from the two-dimensional lattices used in the previous section, so we can consider the resulting network as a slightly disordered lattice, which maintains, however, its key local property of large clustering. Figure SI 3 shows a comparison between the results obtained with the small-world topology and the corresponding initial regular network, for all four update rules. The evolutionary outcomes are almost identical, and the tiny quantitative differences can only be noticed by means of the mean cooperation index associated with each game. Consequently, a small number of defects in the spatial structure of a lattice does not alter its effect on the evolutionary outcome. Considering this result from another point of view, we conclude that the influence on the evolution of cooperation of the Watts-Strogatz small-world topology is simply that of the underlying regular lattice.

## 2.5 Synchronous vs Asynchronous Updating

All the results presented so far have used a synchronous update: after playing, all the individuals compare their payoff with their neighborhood and update simultaneously their strategy. Another option is to employ an asynchronous scheme, where one individual, chosen at random, plays and updates its strategy while the rest of the population remains the same.

We have simulated all the previous evolutionary models, changing the update scheme from synchronous to asynchronous. With stochastic update rules the results are virtually identical, whereas for unconditional imitation the overall outcome and the main transitions are preserved, but some differences appear for specific values of the parameters  $S$  and  $T$  (see Figure SI 4 for an example of each case). Moreover, we have found that, with the appropriate scaling, even the time evolution is practically the same (stochastic rules) or quite similar (unconditional imitation). As an illustration of this property, Figure SI 5 shows some comparisons of the time evolution using both types of updating.

# 3 Discussion

## 3.1 Local Densities and Time Evolution

We have shown compelling evidence that for stochastic update rules the influence of spatial structure on cooperation is only significant in SH and SD, and that it has opposite signs (promotion or inhibition) in both games.

To understand this result, let us consider a population with no structure, i.e. connected by a complete network. A cooperator and a defector obtain the following payoffs

$$\pi_c = (n_c - 1) + n_d S \approx N(x + (1 - x)S), \quad (5)$$

$$\pi_d = n_c T = NxT, \quad (6)$$

$N$  being the population size,  $n_c$  and  $n_d$  the total number of cooperators and defectors, and  $x$  the global fraction of cooperators.

With a structured population, however, each individual only plays with her neighbors. Then, the payoffs are

$$\pi_c = \hat{n}_c + \hat{n}_d S = k(\hat{x} + (1 - \hat{x})S), \quad (7)$$

$$\pi_d = \hat{n}_c T = k\hat{x}T, \quad (8)$$

$\hat{n}_c$  and  $\hat{n}_d$  being the number of cooperators and defectors that the player is connected to, and  $\hat{x}$  the local fraction of cooperators in the player's neighborhood. Note that  $x$  is a global variable, shared by all players, whereas  $\hat{x}$  is defined for every player. As a result, the effect of the population structure can be understood as the replacement of the global density  $x$  by the player-dependent local densities  $\hat{x}$ .

Let us now assume that the effect of a given population structure consists in an increase of the local densities  $\hat{x}$  with respect to the global density  $x$ . Considering SH in the first place, for a given initial condition  $x^0$  there must be a subregion of the SH quadrant in which  $x_e$  verifies  $x^0 < x_e < \hat{x}^0$ . For these games a complete network would produce an outcome of  $x^* = 0$ , whereas the structured population would yield  $x^* = 1$ , with the subsequent promotion of cooperation. On the other hand, for SD, the increase of  $\hat{x}$  will drive the population to a lower global cooperator density so that the local densities are at the stable equilibrium, i.e.  $x^* < \hat{x}^* = x_e$ , with the corresponding inhibition of cooperation.

This mechanism explains the opposite effects on SH and SD, and the absence of any effect when the game has only one equilibrium, which is the case with HG and PD. The increase in the local densities is caused by the correlations that appear as a result of the spatial structure of the population. For homogeneous random networks and lattices with low clustering coefficient correlations are weak, and hence their influence on cooperation is hardly noticeable. Lattices with large clustering, however, allow strong correlations to develop, raising the local densities to such an extent that cooperation is heavily promoted in SH. Considering the time evolution in this case, the local densities fluctuate over the population in the initial random condition, with cooperators more or less connected to other cooperators. Those with small  $\hat{x}$  eventually disappear, while those with large  $\hat{x}$  convert, with high probability, their defective neighbors to cooperators. This is the point when the large clustering plays its crucial role: newly converted cooperators will be connected not only to the cooperator whose strategy they have just adopted, but also to some of his neighbors (because of the network clustering), which are, with high probability, cooperators as well (because of the high  $\hat{x}$  of the initial cooperator). Hence the new cooperator will also have a large local density of cooperators. This process continues until the population reaches full cooperation.

In other words, for SH the large clustering of the network allows the peaks in the local density caused by random fluctuations in the initial condition to propagate all over the population. This is the reason why, in the range of parameters where the population structure is critical for the prevailing of cooperation, mesoscopic structures develop in the form of compact clusters of cooperators. It is at the interfaces of these clusters that the explained mechanism takes place. See Figure SI 6 for some snapshots of a typical example of this phenomenon, and also Figure SI 7 for a movie with the full evolution.

In the case of SD, cooperators tend to aggregate as well, but this immediately raises the payoff of the surrounding defectors more than that of the cooperators, which makes them switch to defection, thus disintegrating the embryonic cluster. The overall effect is a decrease in the global cooperator density. Besides, as the clustering effect does not develop beyond its initial stages, the inhibition in SD is not as strong as the promotion in SH.

Nevertheless, unconditional imitation does promote cooperation in SD and even in PD on lattices with large clustering. Obviously, the effect of the network topology is basically the same as with the stochastic update rules. The sharp difference in the results lies in the lack of stochasticity of unconditional imitation, which makes the

cluster interfaces advance uniformly, as Figures SI 8 and SI 9 exemplify. As a consequence, the dynamics of flat interfaces takes on a special importance in this case, determining the evolutionary outcome. For example, computing the payoff balance between cooperators and defectors arranged on both sides on a flat interface yields the most important transition line between full cooperation and full defection in the  $ST$ -plane (see Figures 3 E-F):  $T - S = 2$  for  $k = 6$ , and  $T - S = 5/3$  for  $k = 8$  [Nowak & May 1992].

### 3.2 Previous Results

The seminal paper by [Nowak & May 1992] studied the effect of spatial structure on the borderline between SD and PD, using unconditional imitation as update rule, and reported a very significant promotion of cooperation. Our work points out that the choice of the update rule is essential for obtaining this result. In general, i.e. considering also stochastic update rules, spatial structure only promotes cooperation in SH, and only significantly when the network has a high clustering coefficient.

Remarkably, [Huberman & Glance 1993] questioned the generality of the conclusions of [Nowak & May 1992] considering the time scheme employed for the update of strategies. They argued that if the update was done asynchronously, instead of synchronously, the promotion of cooperation disappeared. We have found that such an influence of the update scheme only occurs with unconditional imitation and for particular regions in the  $ST$ -plane. Our results show that, in general, the feature is the insensitivity to the kind of updating, not only for the evolutionary outcome but also for the time evolution.

An interesting “rule of thumb” to estimate the fate of cooperation on a spatially structured population has been proposed by [Hauert 2002]: cooperation emergence is directly related to the stability and growth of  $3 \times 3$  clusters. We confirm this rule for unconditional imitation and  $k = 8$ , because in that case the growing conditions of a  $3 \times 3$  cluster are exactly the same as the advance conditions of a flat interface mentioned above. However, for stochastic update rules this rule of thumb does not apply: not only it overestimates the promotion of cooperation, but also, and more importantly, it implies an independence of the evolutionary outcome from the initial density of cooperators  $x^0$ , which does not hold. If it did, for almost any  $x^0$ , as long as there were in the initial population at least a  $3 \times 3$  or bigger cluster, the population would reach the same asymptotic state. This occurs, as expected, with unconditional imitation, but not with the replicator rule, as Figure SI 7 reveals. The dependence on the initial density of cooperators in the case of stochastic update rules means that there is not one or a small subset of privileged configurations that determine the evolutionary outcome. This fact suggests that techniques such as pair approximation methods [Van Baalen 2000] are more appropriate to obtain estimations in this case [Roca et al 2008].

One of the works that has reported inhibition of cooperation in SD with spatially structured populations is that of [Hauert & Doebeli 2004]. The authors compared this inhibition with the promotion of cooperation in PD reported by [Nowak & May 1992]. Their result is intriguing if one takes into account that SD has a equilibrium structure more favorable to cooperation. Nevertheless, the authors overlooked the crucial role of the update rule, because Nowak and May used unconditional imitation, which also promotes cooperation in SD, whereas they employed the replicator rule, which has no effect on PD. Our results prove that spatial structure, for any given update rule, either promotes cooperation in SD and PD, or does not in any of them. More importantly, we have shown extensively that, for stochastic update rules (like the replicator rule), the conclusion is the contrast between the effects on SH and SD, not between PD and SD.

This far, we have investigated the effect of spatial structure in the case of strong selection pressure, which means that the fitness of individuals is totally determined by the payoffs obtained from the game. Another possibility is weak selection, where the payoffs are only a small contribution to the fitness. In general, the fitness can be expressed as  $f = 1 - w + w\pi$ . The parameter  $w$  determines the selection pressure, with limit values of  $w = 1$  (strong selection)



and  $w \rightarrow 0$  (weak selection). [Ohtsuki & Nowak 2006] have studied the influence of the homogeneous random topology with weak selection pressure, finding that for all the update rules they consider the effect is symmetric between SH and SD, i.e. the homogeneous population structure equally promotes or inhibits cooperation in both games. Moreover, with the update rule that yields the most similar results to ours, they obtain a null global effect on both games. These results contrast strongly with ours, where the asymmetry of effects on SH and SD appears as a recurrent and essential feature not only for homogeneous random networks, but also for regular lattices. That means that there is a fundamental difference between the strong and weak selection limits, which is caused by the different way correlations develop in both models. See the Supporting Information for a detailed discussion on this issue.

## 4 Conclusions

Our work provides the complete picture of the influence of spatial structure on the evolution of cooperation, in the essential setting of binary games and local non-innovative update rules. It brings about a major clarification of the conclusions provided by previous research, as well as new insights on these evolutionary models.

Thus, we have established that the spatial structure of a population only has a significant effect on cooperation when the clustering coefficient is high, by comparing with homogeneous random networks of the same degree. This property holds for all the update rules we have considered and also explains the effect of Watts-Strogatz small-world networks on cooperative games, ruling out the influence of the small-world property itself.

We have shown the crucial dependence that the outcome of these evolutionary models has on the update rules. Only for coordination games, like SH, we have found a promotion of cooperation which holds for every update rule. For other games, as for example PD or SD, there is not such a generic influence on cooperation. Therefore it is necessary in these cases to classify the results according to the update rules.

Unconditional imitation stands out as a very singular update rule, which yields the highest promotion of cooperation because of its deterministic character. This rule promotes cooperation in SH even with homogeneous random networks, and it is the only rule that is able to substantially sustain cooperation in PD and SD. On the other hand, for stochastic update rules, like the replicator rule, the effect on cooperation concentrates on SH and SD. In this case, the most relevant effect is the promotion of cooperation in SH for regular lattices with high clustering coefficient.

We have explained these effects in terms of how the local densities of cooperators in each neighborhood relate to the structure of equilibria of the game, in contrast to the global densities, which determine the outcome for well-mixed populations. This argument has allowed us to understand why clusters of cooperators develop in SH but not in SD, thus going further than the mere observation of cluster formation reported by previous research. We have also pointed out that flat interfaces are key to explain the outcome with unconditional imitation.

Additionally, we have compared our results, which corresponds to strong selection pressure, to those of weak selection, finding fundamental differences related to the symmetry or asymmetry of results in SH and SD. Weak selection has the advantage of being analytically tractable, but our findings cast serious doubts on its ability to give insights into evolutionary models with strong selection.

Finally, from a more methodological point of view, our work highlights the importance of the following procedures: the study of a full region in the  $ST$ -plane that includes the most significant games, instead of a particular one-dimensional parameterization of a single game; the analysis of several update rules, stochastic and deterministic; the consideration of the time evolution of the population, not only the asymptotic states, and the use of quantitative measures to assess the influence on cooperation for a given game. Otherwise, in view of our conclusions, it seems

hardly feasible to gain a deep understanding of this kind of evolutionary models, given its inherent complexity and rich behavior. Currently, we are carrying out further research to extend our systematic and comprehensive approach to heterogeneous networks [Santos et al 2006] and innovative update rules [Sysi-Aho et al 2005].

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## A Methods Information

All the simulations were performed for a population size of  $N = 10000$ . The initial density of cooperators was  $x^0 = 0.5$  unless otherwise stated. The update scheme was synchronous, with a convergence time of 10000 steps, with the exception of Figures SI 4 and SI 5.

With the synchronous update of strategies, all the individuals in the population play the game once with all their neighbors, compare payoff with them and decide the new strategy for the next time step. Then, they all update their strategy at once and their payoff is set to zero before the next step. With the asynchronous update, an individual is chosen at random. She and her neighbors play the game once, each one with all her neighbors, so that they earn the same payoff than they would have earned with a synchronous update. Then, the chosen individual compares payoff with her neighbors and updates her strategy accordingly. Finally, the payoff of all the individuals is set to zero before the next time step.

The time of convergence in the simulations was  $T = 10000$  steps for synchronous update and  $T = N \times 10000$  for asynchronous ( $N$  is the population size). This way the total number of update events was the same for both schemes. If the population did not reach full cooperation or defection, an average of the cooperator density during the last tenth of the time evolution was used to obtain the asymptotic cooperator density. Figure SI 5 shows that this time of convergence is enough to reach a steady state. In contrast, some previous research [Hauert 2002] used much smaller times of convergence, namely a total of 48 time steps for a population of 2601 individuals, which is clearly insufficient considering the typical convergence times in Figure SI 5 for our population size of  $N = 10000$ , less than four times bigger.

The studied region in the  $ST$ -plane was sampled in steps of 0.05. For each point in the resulting  $41 \times 41$  grid, which corresponds to a concrete game, 100 realizations were performed to obtain a final average value for the asymptotic density of cooperators. The cited work [Hauert 2002] used a sampling step of 0.2, too large a value to discern important differences in the results, specially around the key point  $(S, T) = (0, 1)$ .

Each realization started from a newly generated population, with strategies randomly assigned and the network, when applicable, also randomly built.

The global measure of cooperation in each game was numerically calculated from the simulation results using the standard composite Simpson's rule for two variables.

The homogeneous random networks were constructed directly, assigning links randomly to the population, while ensuring an equal number of links for every individual. All the regular lattices were built with periodic boundary conditions. For the Small-World networks, the standard value of  $p = 0.01$  was used for the rewiring probability of the underlying regular lattice [Watts & Strogatz 1998].

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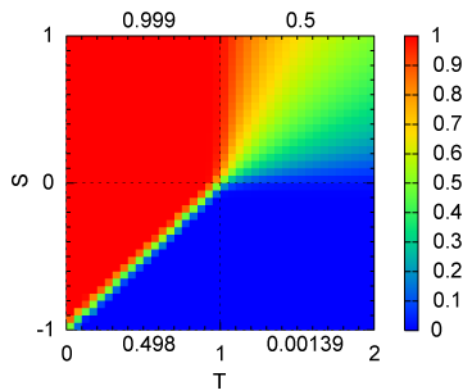


Figure 1: Asymptotic density of cooperators  $x^*$  in a complete network with the replicator update rule, starting with an initial density of cooperators  $x^0 = 0.5$ . Each quadrant correspond to a game: HG upper-left, PD lower-right, SH lower-left, SD upper-right. The outcome is the same as that of the standard replicator dynamics on a well-mixed population (see text). Note the values of the global measures of cooperation, which are shown by each game quadrant.

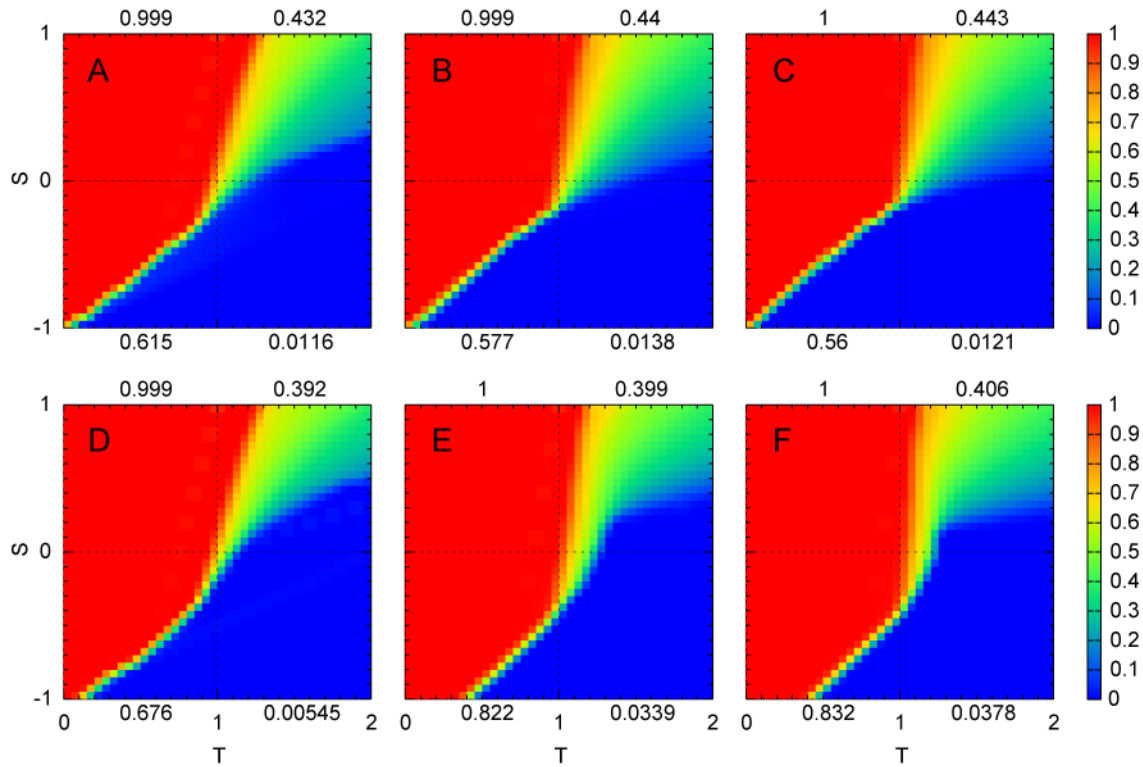


Figure 2: Asymptotic density of cooperators  $x^*$  in homogeneous random networks (upper row, A to C) compared to regular lattices (lower row, D to F), with degrees  $k = 4$  (A, D), 6 (B, E) and 8 (C, F). The update rule is the replicator rule and the initial density of cooperators is  $x^0 = 0.5$ . The values of the global indexes of cooperation in the upper row display the weak effect of homogeneous random networks, which is opposite in SH (lower-left quadrants) and SD (upper-right). Comparing both rows, the differences are only significant in SH for  $k = 6$  and 8, because of the strong promotion of cooperation caused by the regular lattices with large clustering (see text). The influence on HG and PD is negligible in all cases.

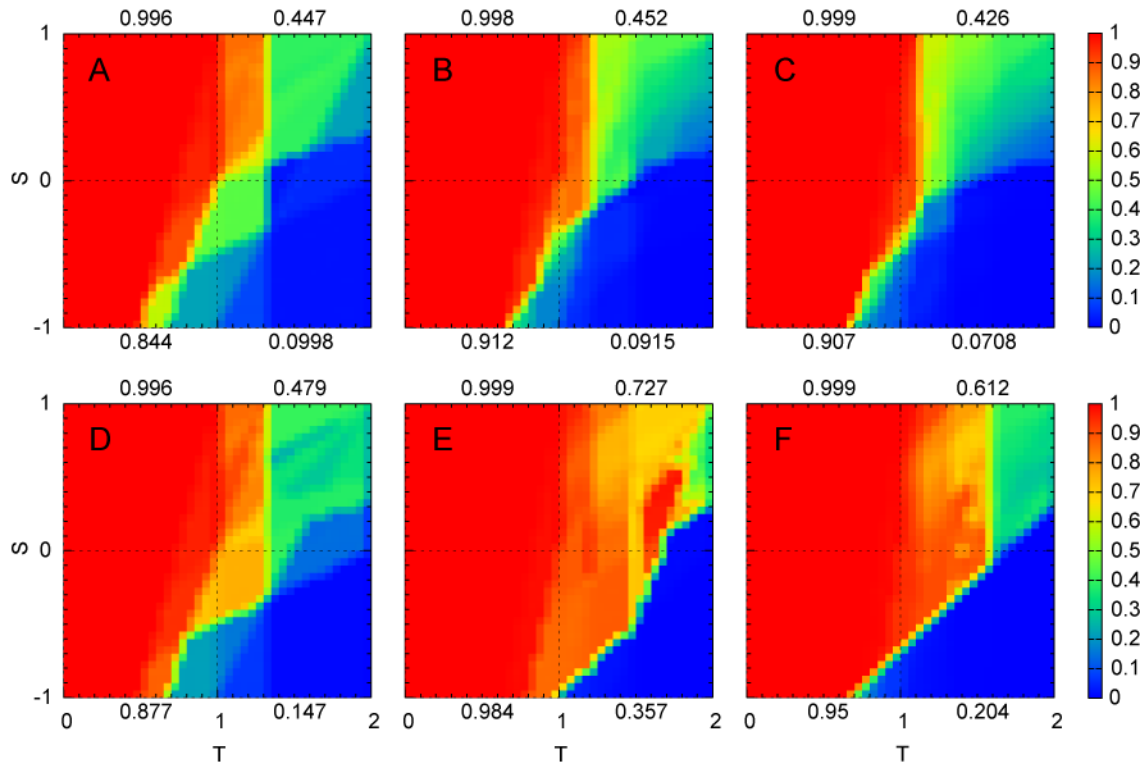


Figure 3: Asymptotic density of cooperators  $x^*$  in homogeneous random networks (upper row, A to C) compared to regular lattices (lower row, D to F), with degrees  $k = 4$  (A, D), 6 (B, E) and 8 (C, F). The update rule is unconditional imitation and the initial density of cooperators is  $x^0 = 0.5$ . Cooperation is fostered in SH in all cases. As in Figure 2, the differences between homogeneous random networks and regular lattices of the same degree are significant only when the regular lattices have large clustering ( $k = 6$  and 8). In those cases the promotion of cooperation extends to SD and PD. Note that for  $k = 4$  the transitions in the outcome with regular lattices [Schweitzer et al 2002] are the same as with homogeneous random networks.

## B Additional figures

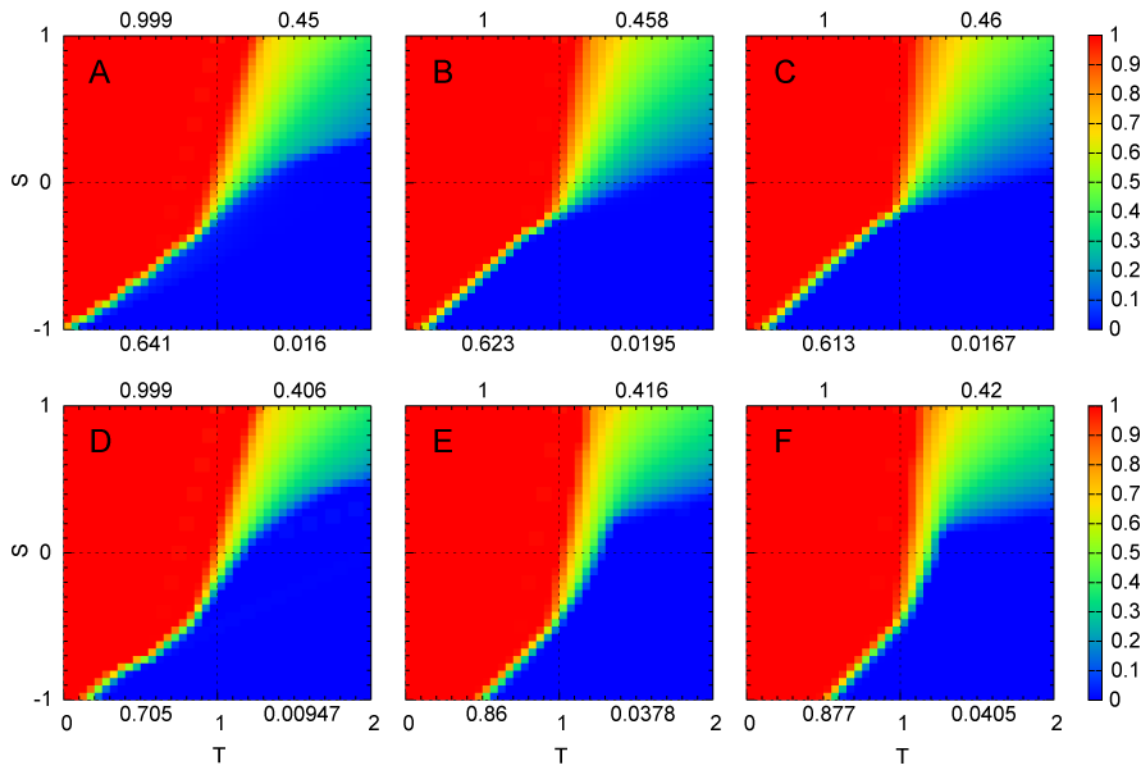


Figure 4: Asymptotic density of cooperators  $x^*$  in homogeneous random networks (upper row, A to C) compared to regular lattices (D to F), with degrees  $k = 4$  (A, D), 6 (B, E) and 8 (C, F). The update rule is the multiple replicator rule and the initial density of cooperators is  $x^0 = 0.5$ . The results are very similar to those of the replicator update rule, just slightly reinforced (see Figure 2 in main text). Thus, the most important effect of spatial structure is again the promotion of cooperation on SH when the clustering coefficient is large. Note also the asymmetry of the effects on SH and SD, in all cases.



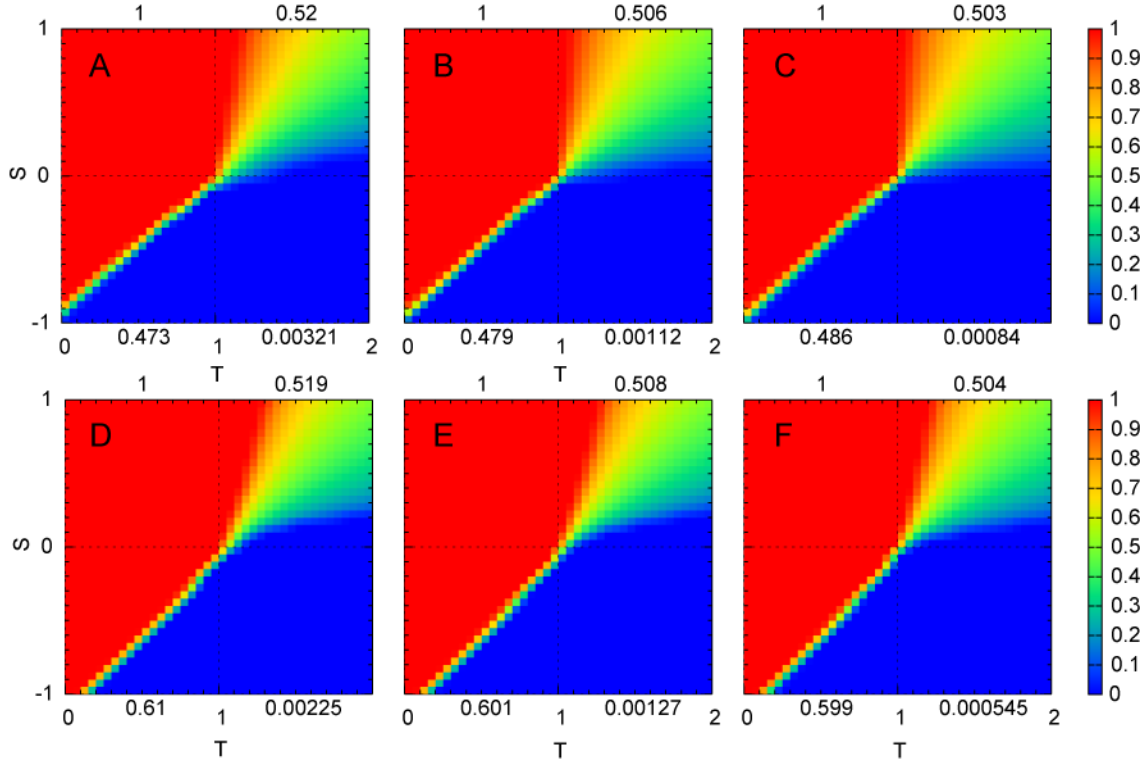


Figure 5: Asymptotic density of cooperators  $x^*$  in homogeneous random networks (A to C) compared to regular lattices (D to F), with degrees  $k = 4$  (A, D), 6 (B, E) and 8 (C, F). The update rule is the Moran rule and the initial density of cooperators is  $x^0 = 0.5$ . With this update rule the effect is very small, in comparison with the other stochastic rules (see Figures 1, in main text, and SI 1). The asymmetry of effects on SH and SD is maintained in the random lattices (A to C) but, remarkably, is inverted with respect to the other stochastic rules, producing in this case an inhibition of cooperation on SH and a promotion on SD. The effect of spatial structure (D to F) is again a promotion of cooperation on SH.

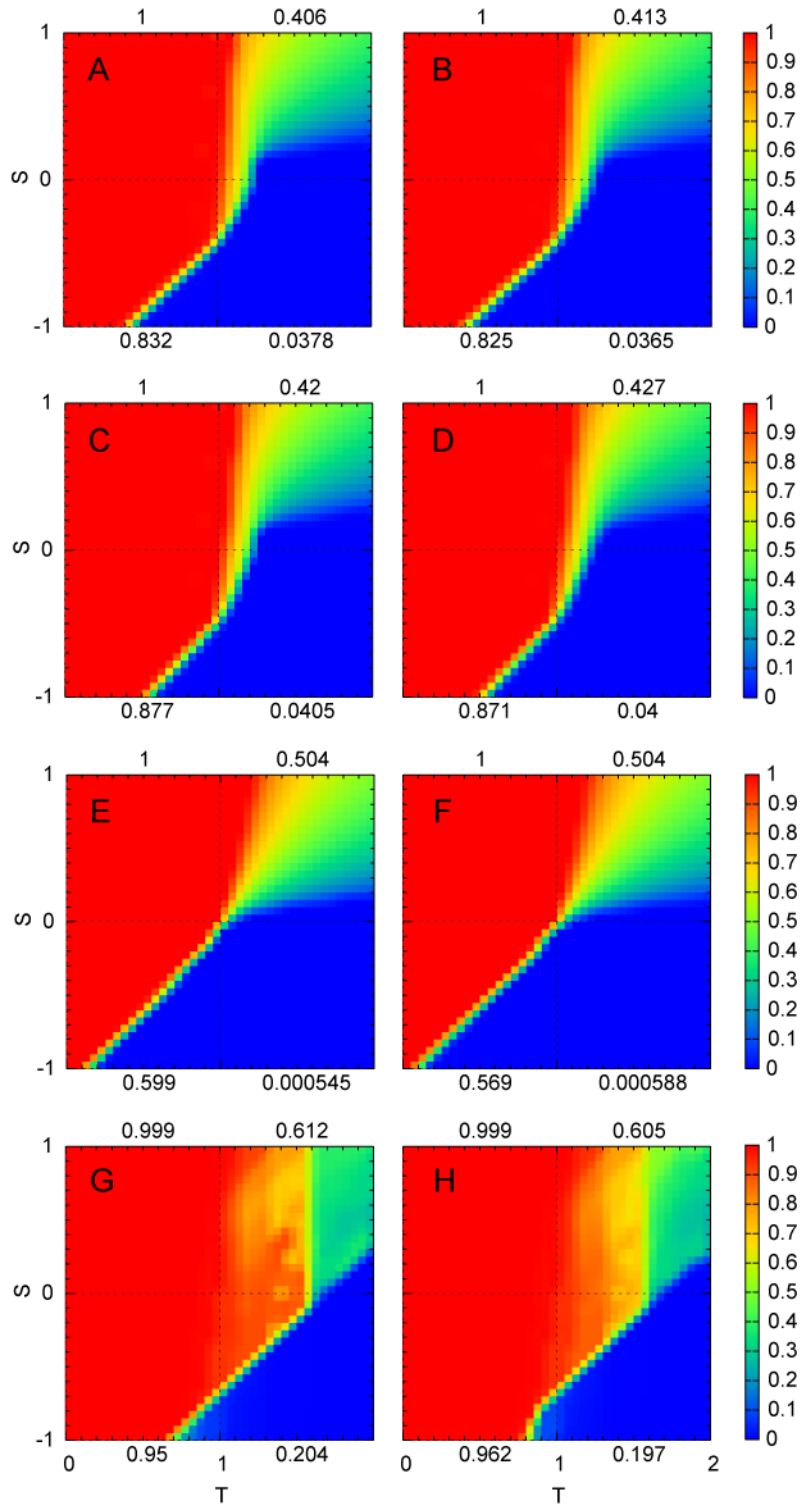


Figure 6: Asymptotic density of cooperators  $x^*$  in small-world networks (left column) compared to regular lattices (right column), all with degree  $k = 8$ . The update rules are: replicator rule (A, B), multiple replicator rule (C, D), Moran rule (E, F) and unconditional imitation (G, H). The initial density of cooperators is  $x^0 = 0.5$ . The evolutionary outcomes are practically identical for all the update rules, showing that the effect of small-world networks is due to the high clustering of the initial regular lattices used to generate them.

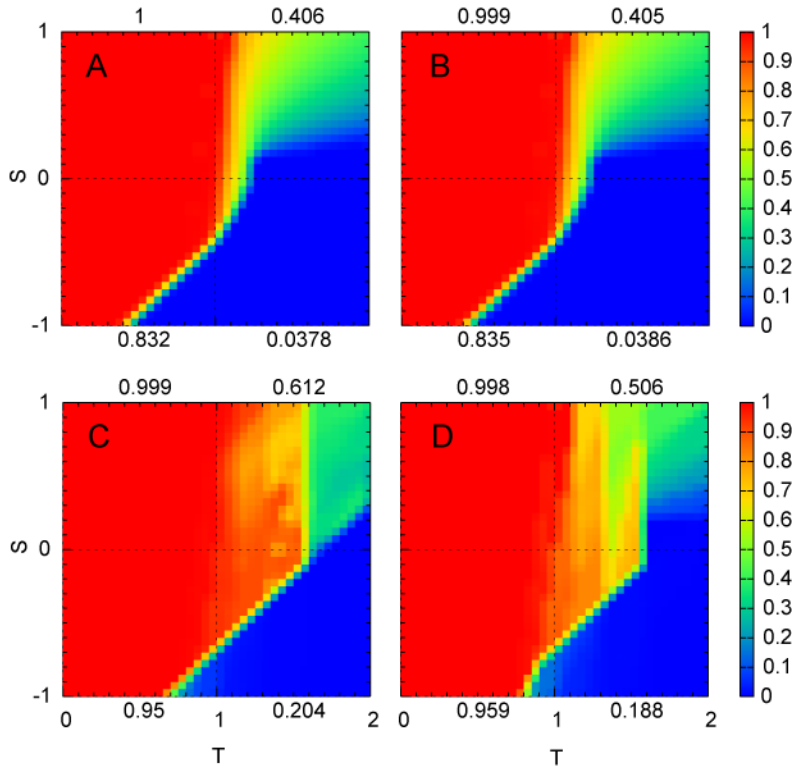


Figure 7: Asymptotic density of cooperators  $x^*$  in the regular lattice of degree  $k = 8$ , with synchronous updating (left column) compared to asynchronous (right column). The update rules are the replicator rule (upper row) and unconditional imitation (lower row). The initial density of cooperators is  $x^0 = 0.5$ . For the replicator rule, the results are virtually identical, showing the lack of influence of the kind of updating on the evolutionary outcome. In the case of unconditional imitation the results are very similar, but there are differences for some points, specially those in SD with  $S \lesssim 0.3$  and  $T > 5/3 \approx 1.67$ . The particular game studied by [Huberman & Glance 1993], which reported an inhibition of cooperation due to the asynchronous updating, belongs to this region.

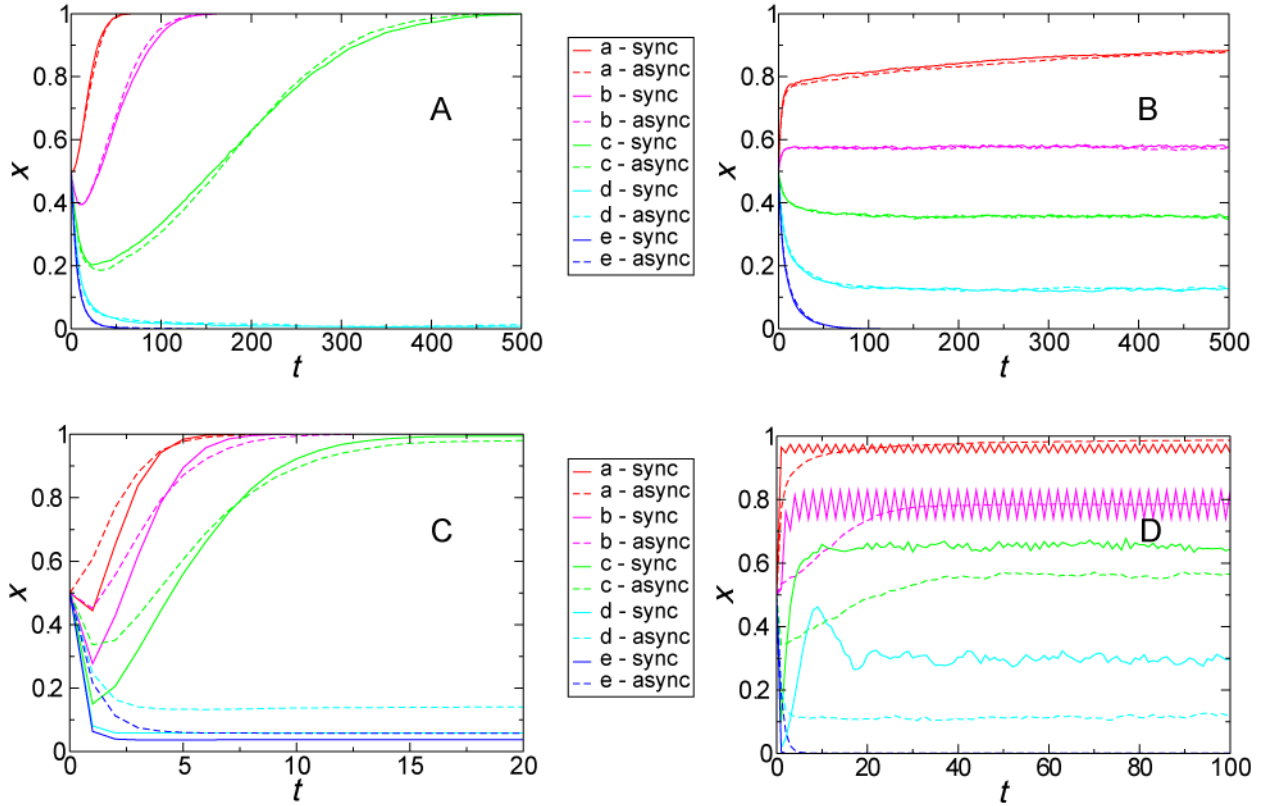


Figure 8: Time evolution of the density of cooperators  $x$  in a regular lattice of degree  $k = 8$ , for typical realizations of SH (left column) and SD (right column), with synchronous (continuous lines) or asynchronous (dashed lines) updating. The update rules are the replicator rule (upper row) and unconditional imitation (lower row). The SH games for the replicator rule (A) are: a,  $S = -0.4, T = 0.4$ ; b,  $S = -0.5, T = 0.5$ ; c,  $S = -0.6, T = 0.6$ ; d,  $S = -0.7, T = 0.7$ ; e,  $S = -0.8, T = 0.8$ . For unconditional imitation the SH games (C) are: a,  $S = -0.6, T = 0.6$ ; b,  $S = -0.7, T = 0.7$ ; c,  $S = -0.8, T = 0.8$ ; d,  $S = -0.9, T = 0.9$ ; e,  $S = -1.0, T = 1.0$ . The SD games are, for both update rules (B, D): a,  $S = 0.9, T = 1.1$ ; b,  $S = 0.7, T = 1.3$ ; c,  $S = 0.5, T = 1.5$ ; d,  $S = 0.3, T = 1.7$ ; e,  $S = 0.1, T = 1.9$ . The initial density of cooperators is  $x^0 = 0.5$ . The time scale of the asynchronous realizations has been rescaled by the size of the population  $N = 10000$ , so that for both kinds of updating a time step represents the same number of update events in the population. Figures A and B show that, in the case of the stochastic rule, not only the outcome but also the time evolution is independent of the kind of updating. With unconditional imitation the results are also very similar for SH (C), but not so much in SD (D), displaying the influence of the type of updating in this region. Note that unconditional imitation causes a much faster evolution than the replicator rule, in all cases.

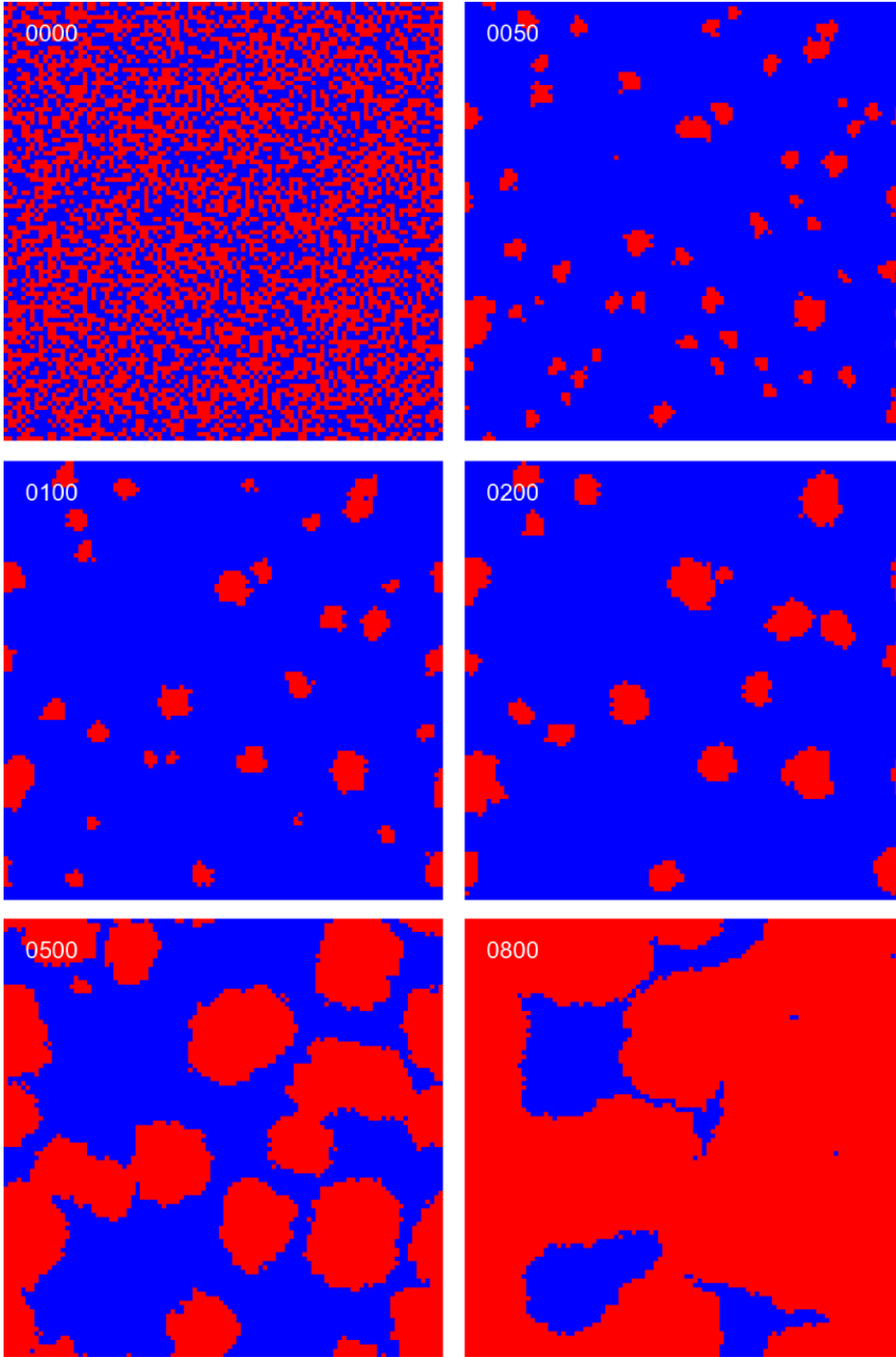
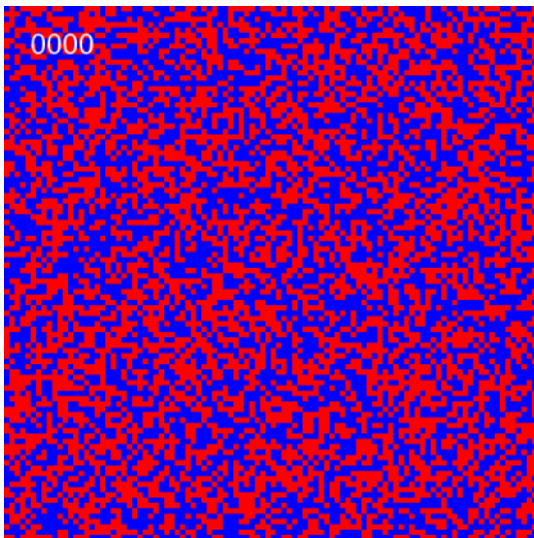


Figure 9: Snapshots of the evolution of a population on a regular lattice of degree  $k = 8$ , playing a SH game ( $S = -0.65$  and  $T = 0.65$ ). Cooperators are displayed in red and defectors in blue. The update rule is the replicator rule and the initial density of cooperators is  $x^0 = 0.5$ . The upper left label shows the time step  $t$ . During the initial steps, the cooperators with low local density of cooperators  $\hat{x}$  disappear, meanwhile those with high local density grow into the clusters that eventually take up the full population.



( <http://gisc.uc3m.es/~cproca/spatial-structure/mov1.gif> )

Figure 10: Full evolution of the population of Figure SI 9.

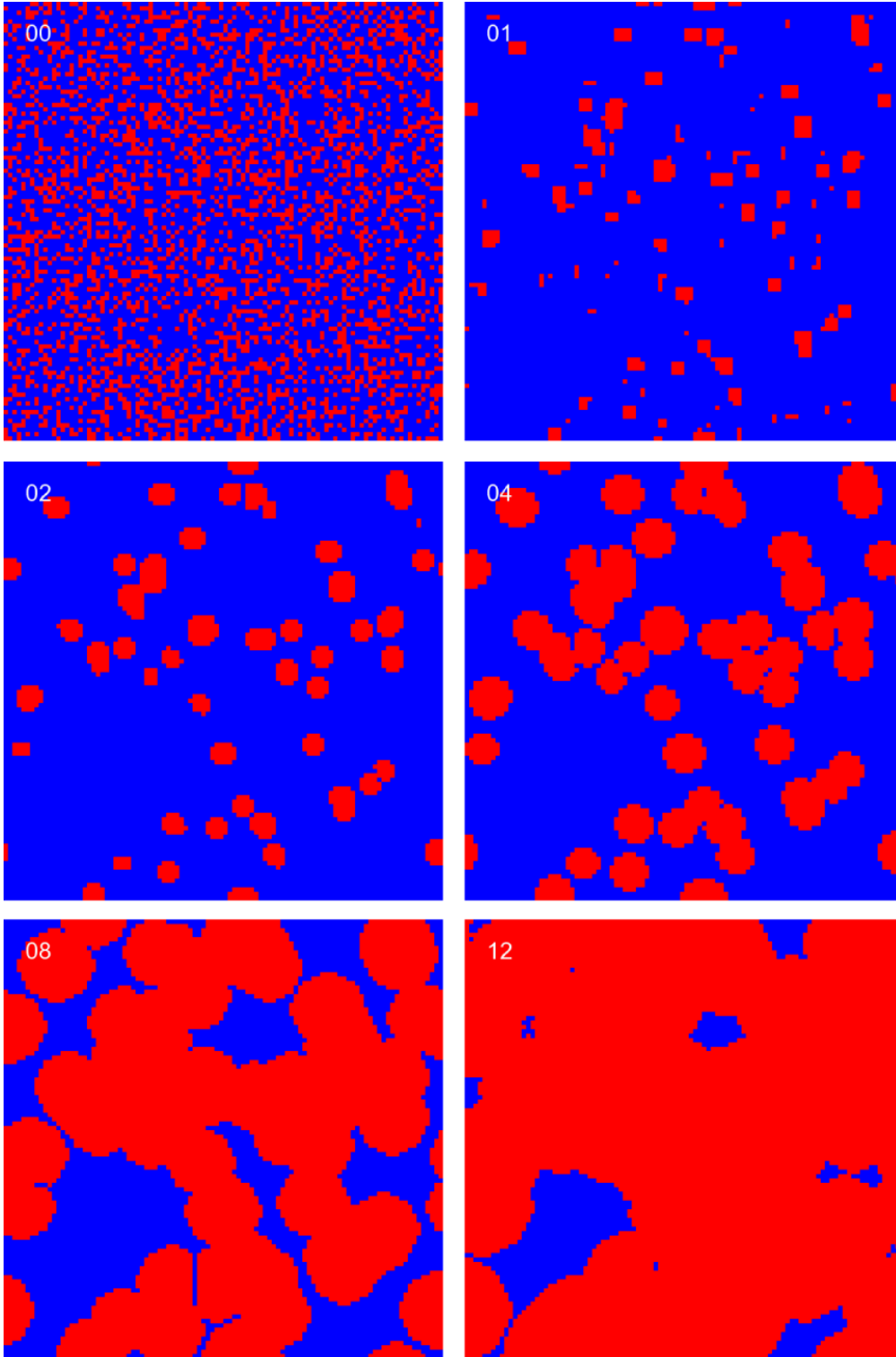
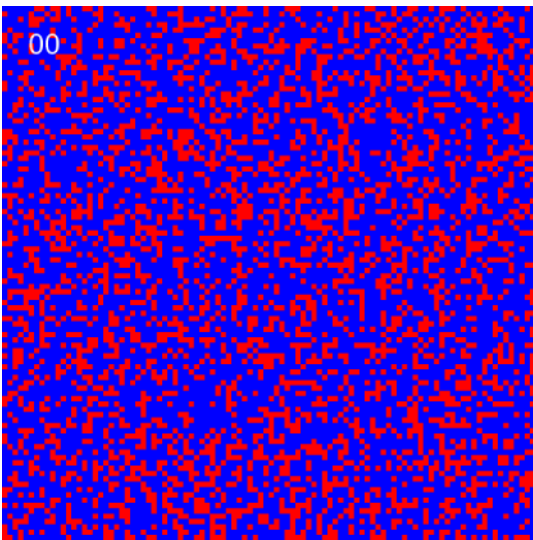


Figure 11: Snapshots of the evolution of a population on a regular lattice of degree  $k = 8$ , playing a SH game ( $S = -0.65$  and  $T = 0.65$ ). Cooperators are displayed in red and defectors in blue. The update rule is unconditional imitation and the initial density of cooperators is  $x^0 = 1/3$  (this lower value than that of Figure SI 9 has been used to make the evolution longer and thus more easily observable). The upper left label shows the time step  $t$ . As with the replicator update rule (see Figure SI 9), during the initial time steps clusters emerge from cooperators with high local density of cooperators  $\hat{x}$ . In this case, the interfaces advance deterministically at each time step, thus producing a much more rapid evolution than with the replicator rule (compare the time labels with those of Figure SI 9)



( <http://gisc.uc3m.es/~cproca/spatial-structure/mov2.gif> )

Figure 12: Full evolution of the population of Figure SI 11.



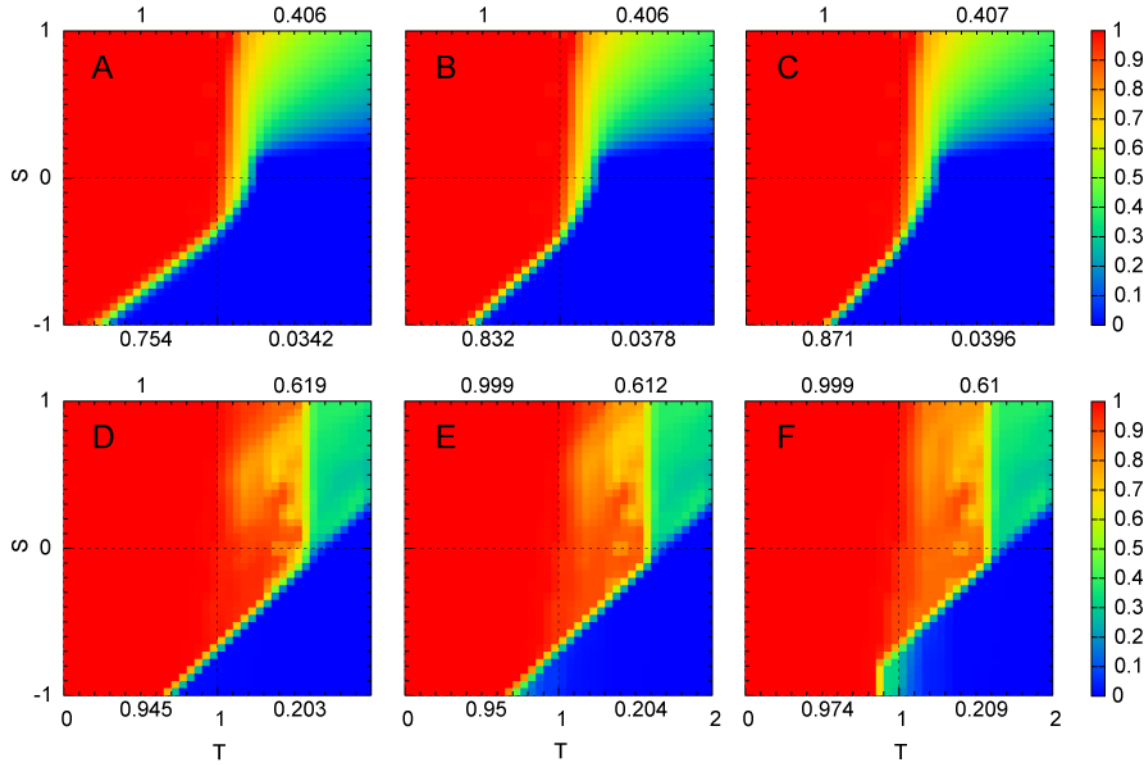


Figure 13: Asymptotic density of cooperators  $x^*$  in a regular lattice of degree  $k = 8$ , for different initial densities of cooperators  $x^0 = 1/3$  (A, D),  $1/2$  (B, E) and  $2/3$  (C, F). The update rules are the replicator rule (upper row, A to C) and unconditional imitation (lower row, D to F). With the replicator rule, the evolutionary outcome in SH depends on the initial condition, as is revealed by the displacement of the transition line between full cooperation and full defection. However, with unconditional imitation this transition line remains in the same position, thus showing the insensitivity to the initial condition. In this case, the outcome is determined by the presence of small clusters of cooperators in the starting random population, which is ensured for a large range of values of the initial densities of cooperators  $x^0$ .

## C Comparison with results for weak selection pressure

Ohtsuki and Nowak take advantage of an analytical approach in the case of weak selection pressure with homogeneous random networks [Ohtsuki & Nowak 2006]. They find that the effect of the network is equivalent to considering a modified payoff matrix on a complete network. Translating their results into our notation and normalization, the new payoff matrix would be

$$A' = \begin{pmatrix} 1 & S + \Delta \\ T - \Delta & 0 \end{pmatrix}. \quad (9)$$

The effect of the network is given by  $\Delta$ , which depends on the rule used for the update of strategies. It corresponds to a displacement of the game on the  $ST$ -plane, given by the vector  $(\Delta, -\Delta)$ . With respect to the influence on cooperation, this displacement admits a very straightforward interpretation: if the game starts and ends as HG or PD, there is no influence; otherwise, cooperation is fostered if  $\Delta > 0$  and inhibited if  $\Delta < 0$ .

Unfortunately, there is not an exact correspondence between their update rules and ours, but there are two, Pairwise Comparison (PC) and Death-Birth (DB), which are quite close to our replicator and Moran rules, respectively. For them,

$$\Delta_{PC} = \frac{S - (T - 1)}{k - 2} \quad (10)$$

$$\Delta_{DB} = \frac{k + 3(S - (T - 1))}{(k + 3)(k - 2)}. \quad (11)$$

For both update rules  $\Delta$  is invariant with respect to a displacement in the  $ST$ -plane along the direction of the line  $S = T$ . Thus the effect of the network in SH and SD is symmetric with weak selection pressure.

Comparing with our results for strong selection, there is some qualitative agreement between weak selection with Pairwise Comparison and strong selection with the replicator update rule, as Figures SI 14 and SI 15 show. For both selection pressures there is no influence on HG and PD. For SD and SH with weak selection, the effect is positive for  $S > T - 1$  and negative for  $S < T - 1$ , resulting in a null overall effect. This is not the case, however, with strong selection, where there is a net promotion of cooperation in SH and an inhibition in SD.

This asymmetry of results between SH and SD has revealed in our work as one of the fundamental features of the effect of homogeneous random networks and regular lattices on the evolution of cooperation, with strong selection pressure. This asymmetry is caused by the different influence that the developing correlations have on each kind of game. With strong selection these correlations follow the changes of the local densities in each neighborhood. Nevertheless, the correlations that arise with weak selection are of a completely different nature. They are the result of the locality of the update rules and the global densities of cooperators and defectors. For weak selection, the changes in the local densities that the game causes diffuse over the population, without affecting directly the fate of the original neighborhood in the following evolution steps. In other words, with weak selection pressure the local densities are decoupled from the game, in contrast with what occurs with strong selection. Therefore, as correlations take part in the basic mechanisms that determine the fate of cooperation, such a difference in the development of correlations causes substantially different evolutionary outcomes.

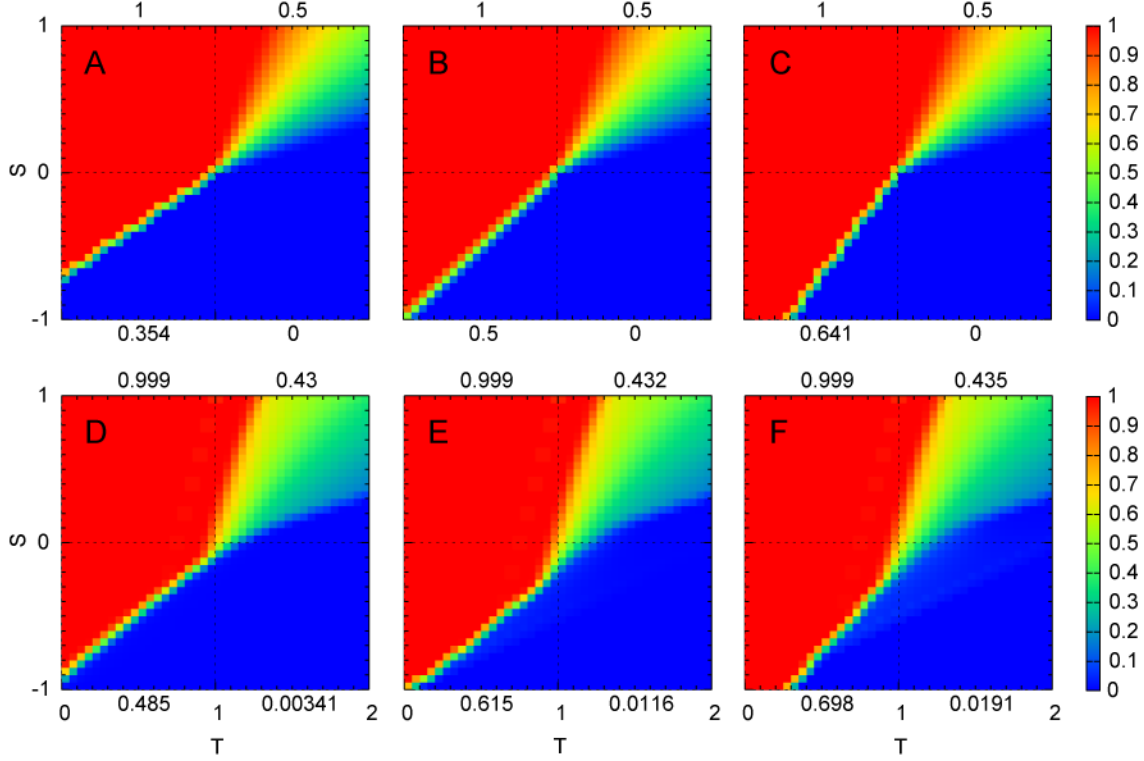


Figure 14: Asymptotic density of cooperators  $x^*$  in a homogeneous random network of degree  $k = 4$ , with weak selection with Pairwise Comparison as update rule [Ohtsuki & Nowak 2006] (upper row, A to C) compared to strong selection with the replicator rule (lower row, D to F). The initial density of cooperators is  $x^0 = 1/3$  (A, D),  $1/2$  (B, E) and  $2/3$  (C, F). The results for weak selection were calculated, while those of strong selection come from simulations. With weak selection, the results in SH for the initial condition  $x^0 = 1/3$  (A) are opposite to those obtained for  $x^0 = 2/3$  (C), whereas the results for  $x^0 = 1/2$  (B) are the same as Figure 1 in main text. Specifically, cooperation is promoted in SH with  $x^0 = 1/3$  to the same extent that it is inhibited with  $x^0 = 2/3$ . The same effect is observed in SD, as cooperation is enforced near the point  $(S, T) = (1, 1)$  and hindered near  $(S, T) = (0, 2)$ . In contrast, strong selection produces a global promotion of cooperation in SH and a global inhibition in SD. Note that the transition between full cooperation and full defection in SH depends on the initial density of cooperators  $x^0$ , and that for a complete network this transition is given by  $S/(S + T - 1) = x^0$  (see main text).

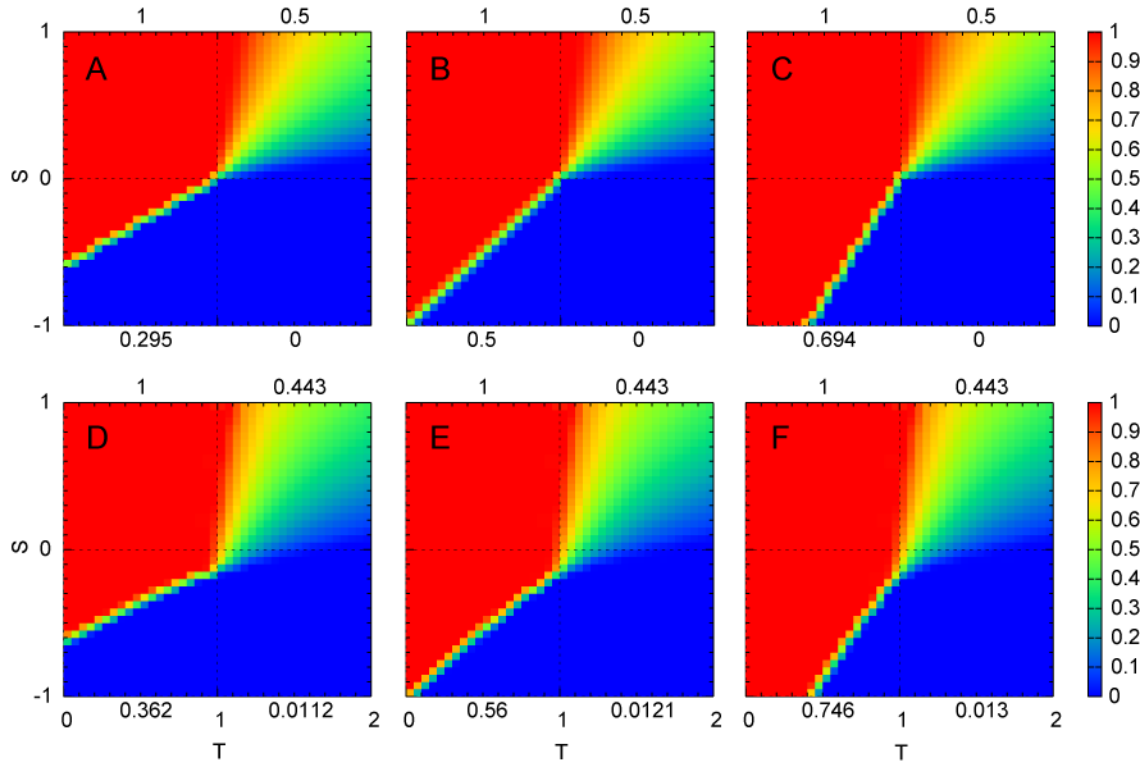


Figure 15: Asymptotic density of cooperators  $x^*$  in a homogeneous random network of degree  $k = 8$ , with the rest of conditions equal to those of Figure SI 14. The results are similar to those of  $k = 4$ , with the only difference of a smaller effect on cooperation.