



Random mobility and spatial structure often enhance cooperation

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ABSTRACT

The effects of an unconditional move rule in the spatial Prisoner's Dilemma, Snowdrift and Stag Hunt games are studied. Spatial structure by itself is known to modify the outcome of many games when compared with a randomly mixed population, sometimes promoting, sometimes inhibiting cooperation. Here we show that random dilution and mobility may suppress the inhibiting factors of the spatial structure in the Snowdrift game, while enhancing the already larger cooperation found in the Prisoner's dilemma and Stag Hunt games.

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1. Introduction

Competition and cooperation are two inseparable sides of the same coin. While competition is a key concept in Darwin's theory of evolution, cooperation is rather puzzling, yet ubiquitous in nature (Maynard Smith and Szathmari, 1997). How cooperative behavior evolved among self-interested individuals is an important open question in biology and social sciences, along with the issue of how cooperation contends with competition in order to achieve global and individual optima. A powerful tool to analyze these problems is evolutionary game theory (Hofbauer and Sigmund, 1998; Maynard Smith, 1982; Weibull, 1995), an application of the mathematical theory of games to biological contexts. Of particular relevance are two-player games where each player has a strategy space containing two possible actions (2×2 games), to cooperate (C) or to defect (D). The payoff of a player depends on its action and on the one of its co-player. Assuming pairwise, symmetric interaction between the players, there are four possible values for this payoff. Cooperation involves a cost to the provider and a benefit to the recipient. Two cooperators thus get a reward R while two defectors get a punishment P . The trade between a cooperator and a defector gives the temptation T for the latter, while the former receives the sucker's payoff, S . We renormalize all values such that $R = 1$ and $P = 0$. The ranking of the above quantities defines the game they are playing. The

paradigmatic example is the Prisoner's Dilemma (PD) game in which the four payoffs are ranked as $T > R > P > S$. It clearly pays more to defect whatever the opponent's strategy: the gain will be $T > R$ if the other cooperates and $P > S$ if he defects. The dilemma appears since if both play D they get P , what is worse than the reward R they would have obtained had they both played C. The PD is related with two other social dilemma games (Liebrand, 1983; Poundstone, 1992). In most animal contests (in particular those involving escalating conflicts), mutual defection is the worst possible outcome for both players, and the damage exceeds the cost of being exploited, i.e. $T > R > S > P$. This game is called Chicken (Rapoport, 1966) or Snowdrift (SD). On the other hand, when the reward surpasses the temptation to defect, i.e. $R > T > P > S$, the game becomes the Stag Hunt (SH) (Skyrms, 2004). The coordination of slime molds is an example of animal behavior that has been described as an SH (Strassman et al., 2000). When individual amoebae of *Dictyostelium discoideum* are starving, they aggregate to form one large body whose reproductive success depends on the cooperation of many individuals. Here, we consider for $T > 1$ the PD ($S < 0$) and the SD ($S > 0$), whose interface ($S = 0$) is known as the weak form of the PD game, with $S = P = 0$. The SH game is obtained for $S < 0$ and $T < 1$.

Classical evolutionary game theory constitutes a mean-field-like approximation which does not include the effect of spatial, correlated structures of populations. Axelrod (1984) suggested to place the agents on a two-dimensional spatial array interacting with their neighbors. This cellular automaton was explored by Nowak and May (1992), who found that such spatial structure allows cooperators to build clusters in which the benefits of

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mutual cooperation can outweigh losses against defectors, thus enabling cooperation to be sustained, in contrast with the spatially unstructured game, where defection is always favored. The original Nowak–May model was extended and modified in several different ways (see Szabó and Fath, 2007 and references therein). Related to the present work, the effects of dilution and mobility were recently studied in Vainstein and Arenzon (2001) and Vainstein et al. (2007) in the weak form of the PD game.

Mobility effects are difficult to anticipate. When non-assortative movements are included, the effective number of neighbors increases (towards the random mixing limit). Moreover, those clusters so necessary to sustain cooperation may now evaporate. Both these effects promote defection and the number of cooperators is expected to decrease. On the other hand, dilution (Alizon and Taylor, 2008) and mobility decrease the competition for local resources and help to avoid retaliation and abuse (although that may require more contingent movements), thus tending to increase cooperation. In the evolutionary game context, diffusion was studied by several authors, sometimes as a cost to wander between patches without spatial structure (Dugatkin and Wilson, 1991; Enquist and Leimar, 1993) or as a trait connected with laying offspring within a given dispersal range (Hamilton and Taborsky, 2005; Koella, 2000; Le Galliard et al., 2005; van Baalen and Rand, 1998). An explicit diffusive process was studied in the framework of the replicator equation (Hofbauer and Sigmund, 1998), extended to include a diffusive term (Ferrière and Michod, 1995, 1996); however, the interactions were still mean field like. Aktipis (2004) considered contingent movement of cooperators with a “win-stay, lose-move” rule, allowing them to invade a population of defectors and resist further invasions. Models with alternating viscosities, which reflect different stages of development that can benefit from the clusterization of cooperators or from dispersal, have also been considered and promote altruism, since the high viscosity phase allows interactions between close relatives and the low viscosity phase reduces the disadvantages of local competition among related individuals. In cases of populations with only a highly viscous phase, the effects of interactions among relatives and competition for local resources tend to balance and thus the evolution of altruistic behavior is inhibited (Taylor, 1992; Wilson et al., 1992). Differently from previous works, Vainstein et al. (2007) considered a diluted version of Nowak–May’s spatial PD model where individuals are able to perform random walks on the lattice when there is enough free space (the non-assortative “always-move” strategy). Specifically, the setting was the simplest possible: random diffusion of simple, memoryless, unconditional, non-retaliating, strategy-pure agents. Under these conditions, cooperation was found not only to be possible and robust but, for a broad range of the parameters (density, viscosity, etc.), often enhanced when compared to the strongly viscous (no mobility) case. The parameters chosen put the model at the interface between the PD and the SD, and a natural question is how robust is the behavior when $S < P$, that is, in a genuine PD game? Moreover, how does mobility affect other games, like the SD or the SH? Recently, Jian-Yue et al. (2007) extended the results of Vainstein et al. (2007) for the SD game and COD dynamics (see next section), but with a restricted choice of S and T . Another relevant question regards the existence of any fundamental difference between those games when mobility is introduced. In particular, in those cases where the spatial structure is known to inhibit cooperation (Hauert and Doebeli, 2004), does mobility change this picture?

Our objective here is to present a more comprehensive analysis and extend our previous study in several directions, trying to shed some light on the above questions. The paper is organized as follows. The next section describes the details of the model and simulation. Then, we present the results for two possible

implementations depending on the order of the diffusive and offspring steps. Finally, we present our conclusions and discuss some implications of the results.

2. The model

The model is a two-dimensional stochastic cellular automaton in which cells are either occupied by unconditional players (cooperators or not) or vacant. At time t , the variable $S_i(t)$ is 0 if the corresponding lattice cell is empty, or ± 1 depending on whether the agent at that site cooperates (1) or defects (-1). The relevant quantity is the normalized fraction of cooperators, ρ_c , after the stationary state is attained, defined as $\rho_c = (1 + M/\rho)/2$, where M is the “magnetization” $M = N^{-1} \sum_i S_i(\infty)$, N is the system size and $\rho \neq 0$ is the fraction of occupied sites, that is kept fixed at all times (when $\rho \neq 1$, we call the system diluted). The symbol $\langle \dots \rangle$ stands for an average over the ensemble of initial configurations. We call “active” a site that has changed strategy since the previous step. At each time step, all individuals play

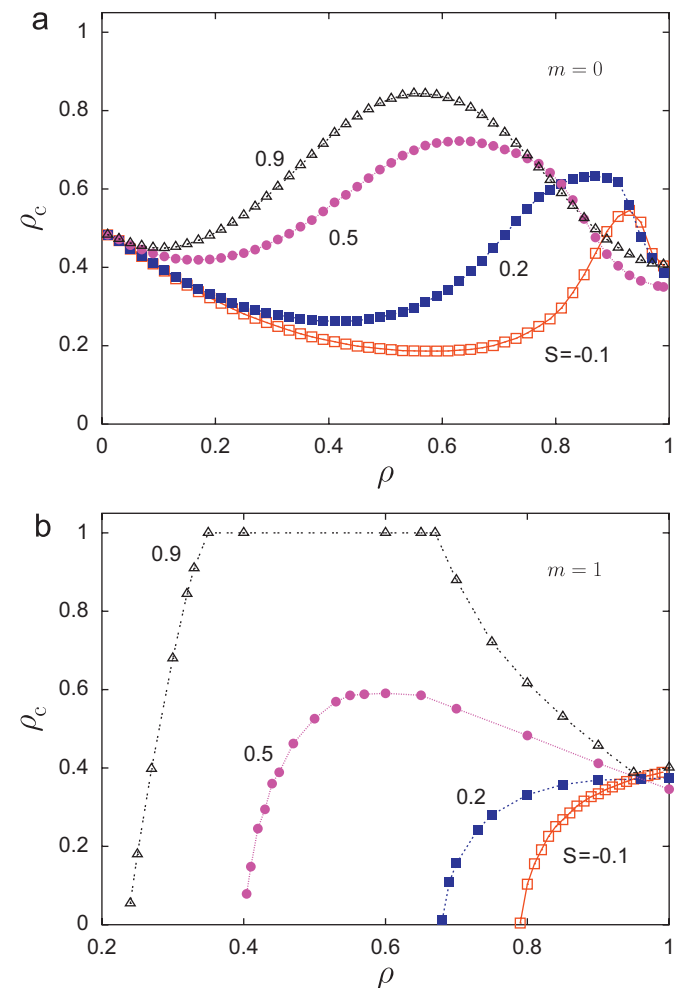


Fig. 1. Average fraction of cooperating individuals ρ_c for mobilities $m = 0$ (top) and 1 (bottom), $P = 0$, $R = 1$, $T = 1.4$ and several values of S in the COD case. The case $S = -0.1$ is representative of the whole interval around the weak PD point $S = 0$ ($-0.2 < S < 2/15$). Indeed, all curves in this interval collapse. Notice also that near $\rho = 1$, negative responses occur and ρ_c may decrease as S gets larger, the effect being stronger for $m = 0$ (see text). At small densities, mobility is detrimental to cooperators: isolated clusters of cooperators, that could survive for $m = 0$, can be predated by mobile defectors once mobility is considered. At intermediate densities, mobility can strongly increase the amount of cooperation.

against all its four nearest neighbors (if present), collecting the payoff from the combats. After that, it may either move or try to generate its offspring. We consider a best-takes-all reproduction: each player compares its total payoff with those of its nearest neighbors and changes strategy following the one (including itself) with the greatest payoff among them. This strategy changing updating rule preserves the total number of individuals, thus keeping ρ constant. If a tie among some of the neighbors occurs, one of them is randomly chosen. During the diffusive part, each agent makes an attempt to jump to a nearest neighbor site chosen randomly, that is accepted, provided the site is empty, with a probability given by the mobility parameter m . Notice that m does not measure the effective mobility, that depends on both m and ρ , but only a tendency to move, space allowing. However, different combinations of both parameters could give the same effective mobility (measured, for example, through the mean square displacement), but that parameter alone would not suffice to characterize the game, since spatial correlations are determined by ρ . Among the several ways of implementing the reproductive and diffusive steps, here we

consider two possibilities, named contest-offspring-diffusion (COD) and contest-diffusion-offspring (CDO). In the former, as the name says, each step consists of combats followed by the generation of offspring done in parallel, and then diffusion, while in the latter, the diffusion and offspring steps are reversed. Of course, the stochasticity introduced by the mobility disappears under some conditions (e.g., $\rho = 1$ or $m = 0$), and the final outcome may now depend on the initial conditions.

We explore many choices of the payoff parameters T and S while P and R are kept fixed at 0 and 1, respectively, and compare the effects of diffusion with those obtained either for the related spatial weak version (Vainstein et al., 2007) or for the randomly mixed limit. Square lattices of sizes ranging from 100×100 to 500×500 with periodic boundary conditions are used. Averages are performed over at least 100 samples and equilibrium is usually attained before 1000 network sweeps are completed, although in some cases not even 10^7 sweeps are enough to bring the system to an equilibrium state. The initial configuration has ρN individuals placed randomly on the lattice, equally distributed among cooperators and defectors.

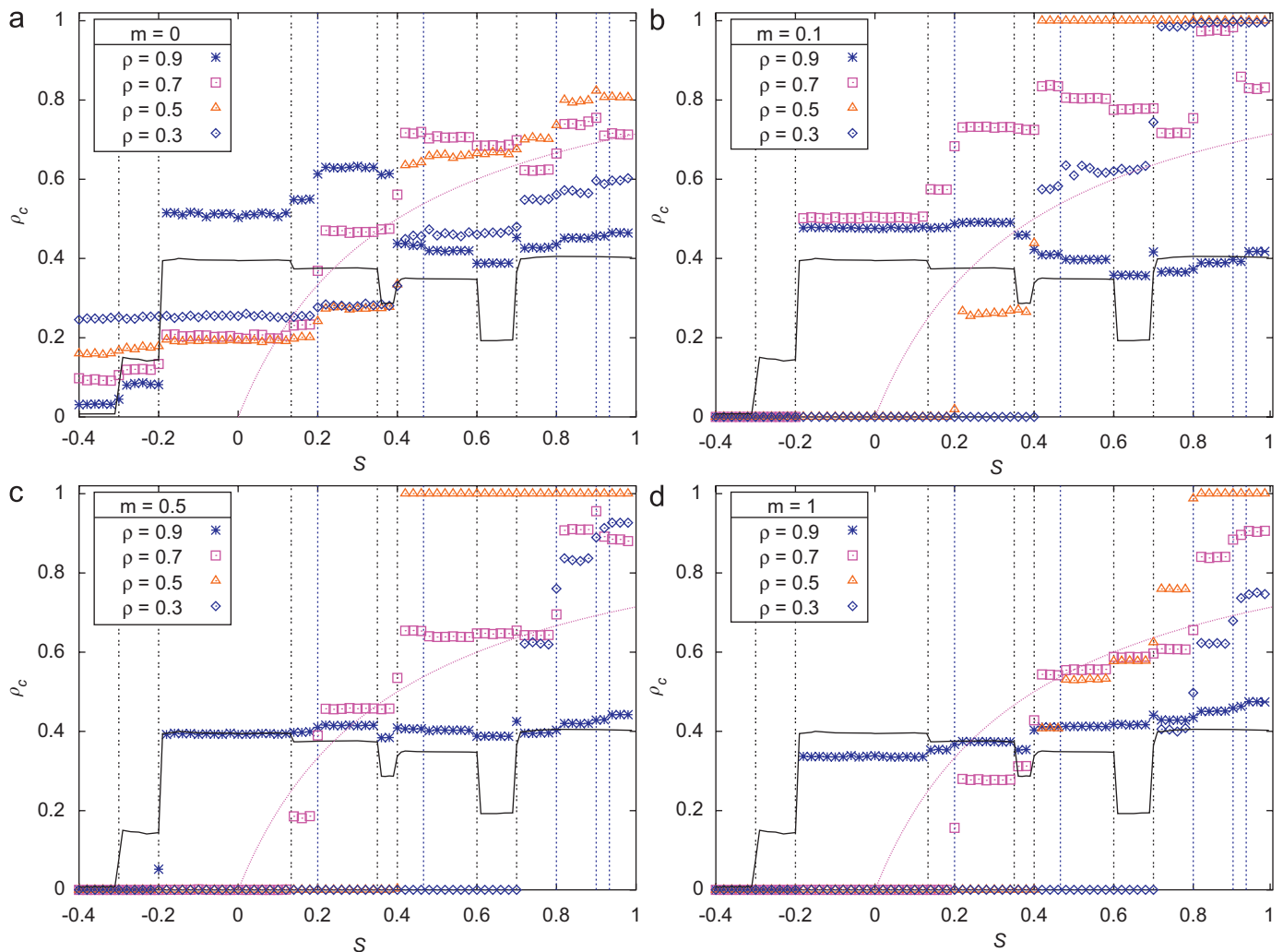


Fig. 2. Average fraction of cooperating individuals ρ_c versus S ($T = 1.4$, $R = 1$ and $P = 0$) in the SD ($S > 0$) and PD ($S < 0$) games with COD dynamics for different values of the mobility and ρ . The solid black line is the case $\rho = 1$. The vertical dashed lines locate the transition points for $\rho = 1$ ($S = -0.3, -0.2, 2/15, 0.35, 0.4, 0.6$ and 0.7) and the vertical dotted lines locate a few more when $\rho < 1$ ($S = 0.2, 7/15, 0.8, 0.9$ and $14/15$), as explained in the text. The curved line is the expected result for random mixing ($\rho_c = 0$ for the PD game, $S < 0$ and Eq. 1 for the SD game, $S > 0$). The point $S = 0.6$ corresponds to the standard parametrization $T = 1 + r = 1.4$, $R = 1$, $S = 1 - r = 0.6$ and $P = 0$ for the SD game, considered in Jian-Yue et al. (2007). For comparison, the case without mobility ($m = 0$), whose results are obviously independent of the diffusion dynamics, is also shown. No new transitions appear due to mobility besides those already present when $m = 0$ for the COD dynamics (Vainstein and Arenzon, 2008).

3. Results

Vainstein et al. (2007) considered only the weak limit $P = S = 0$ of the PD game for $T = 1.4$ and $R = 1$, that is, inside the region where, for $\rho = 1$, both strategies coexist along with active sites. When $S \neq 0$, this region may comprise values of S both in the PD and in the SD regimes, that is, $S < 0$ and $S > 0$, respectively. Figs. 1 and 2 show that the results found in Vainstein et al. (2007) with the COD dynamics remain unchanged for $2T - 3 < S < (T - 1)/3$. Indeed, the line labeled $S = -0.1$ in Fig. 1 exactly superposes with the results for all values of S in this interval, $S = 0$ included. This can be more clearly seen in Fig. 2, where ρ , m and S are varied, and a plateau in the interval $(-0.2, 2/15)$ (Hauert, 2001) is observed (although the value of ρ_c in the plateau depends on both ρ and m). Besides this active phase, the system presents a large number of different phases, with sharp transitions between them. For comparison, the no mobility case (Vainstein and Arenzon, 2008), $m = 0$, is also included, as well as the cooperators density when $\rho = 1$ (solid black line). The transition points, calculated considering the several possible local neighborhoods (Vainstein and Arenzon, 2008), are represented by vertical dashed and dotted lines located at the points where S equals to $(T + 3P)/2 - R = -0.3$, $2T + 2P - 3R = -0.2$, $(T + 3P - R)/3 = 2/15$, $(T + 3P)/4 = 0.35$, $T + P - R = 0.4$, $(2P + 2T - R)/3 = 0.6$ and $P + T/2 = 0.7$. In addition to these transitions, a few more are introduced when the system is diluted (vertical dotted lines), $\rho < 1$, each phase being characterized by the fraction of cooperators and by the way they organize spatially (Vainstein and Arenzon, 2008). When mobility is introduced after the offspring generation (COD dynamics), no new transition appears. Dilution (without mobility) allows cooperation for small values of S ($S < -0.3$), which is absent with $\rho = 1$. For low densities in particular, clusters are small and isolated; therefore, depending on the initial condition, cooperators succeed in forming pure clusters. However, as soon as mobility is introduced, this disorder driven phase disappears since small cooperative clusters are easily predated by wandering defectors. In this low density situation, cooperation is only sustained when the exploitation is not too strong (larger values of S), as can be seen in the case $\rho = 0.3$ and $m = 1$, where cooperation exists only for $S > 0.7$. For intermediate densities, some phases may coalesce, like the large S region for $\rho = 0.5$ where $\rho_c = 1$. Interestingly, mobility has a non-trivial effect in the negative response that is already present at $\rho = 1$ or

$m = 0$. When the sucker's payoff S increases (less exploitation), one expects higher levels of cooperation. But the opposite behavior is sometimes observed, and the number of cooperators may also decrease. An example occurs when $\rho = 1$ as S increases beyond the transition point 0.6, and ρ_c attains a new plateau, far below the previous one. However, with mobility such effect may be enhanced, attenuated or reverted. Fig. 2 depicts many examples of such behavior. Moreover, for a fixed ρ , mobility affects different phases in diverse ways. For example, for $\rho = 0.5$, when m changes from 0.1 to 0.5, the cooperative phase at $0.2 < S < 0.4$ disappears, while the one for $0.4 < S < 1$ suffers no alteration. When $m = 1$, instead, this region splits into five smaller regions. Therefore, whether large or small mobility is better for cooperators strongly depends on both m and ρ . For example, for $\rho = 0.9$, ρ_c increases with m when S is large and decreases for smaller values. The behavior of ρ_c as a function of the mobility is shown in Fig. 3. In some cases cooperation is an increasing function of the mobility and the optimal value is thus $m = 1$. On the other hand, it may also be detrimental for cooperation, and ρ_c steadily decreases with m . In this latter case, a non-zero but very small mobility gives the optimal value.

The most important result is obtained when we compare the simulations with what one would obtain in a large randomly mixed population. A simple mean field (Hauert, 2001; Hofbauer

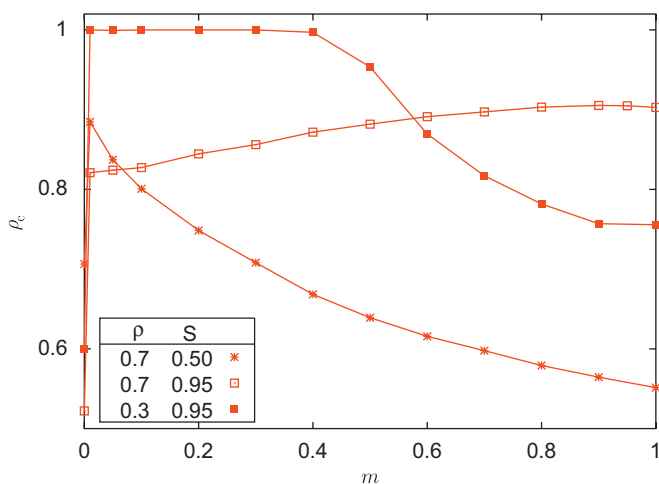


Fig. 3. Average fraction of cooperating agents ρ_c as a function of the mobility m for several values of ρ and S . Notice that ρ_c may either increase ($m = 1$ is optimal) or decrease (a small, but non-zero, m is optimal), depending on the parameters, and that there is a discontinuity at $m = 0$.

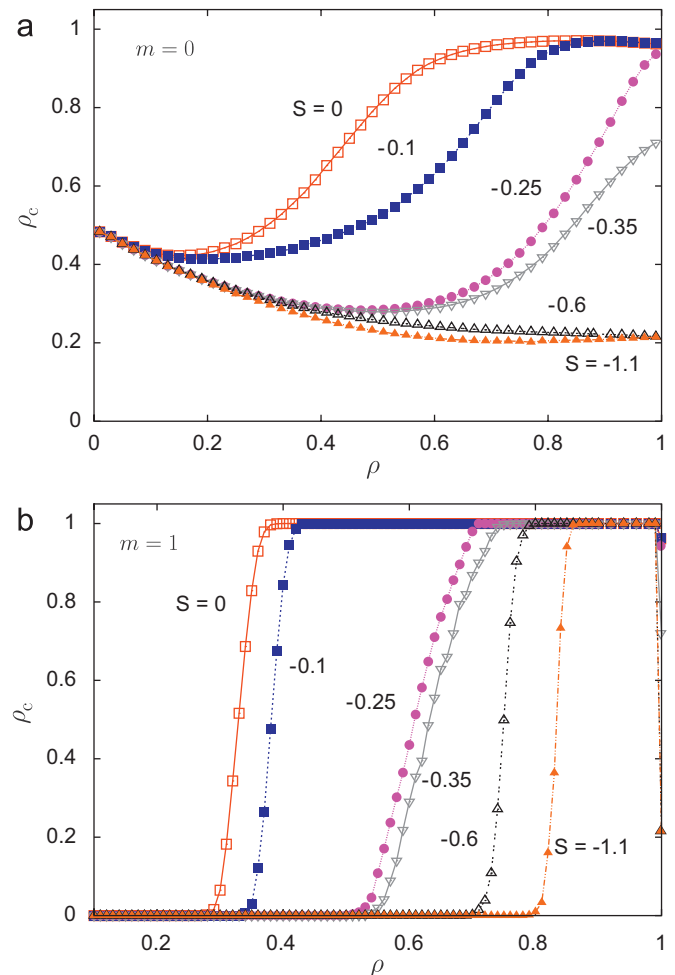


Fig. 4. Average fraction of cooperating individuals ρ_c for mobilities $m = 0$ (top) and $m = 1$ (bottom), $P = 0$, $R = 1$, $T = 0.9$ and several values of S with COD dynamics for the SH game. Notice the strong effect of the inclusion of mobility. The chosen values correspond to the different plateaux seen in Fig. 5. The density of cooperators is a monotonically increasing function of the total density for $m \neq 0$, while it is either non-monotonic or monotonically decreasing for $m = 0$.

and Sigmund, 1998) calculation leads to three possible solutions: two absorbing states, $\rho_c = 0$ and 1, and a mixed case with

$$\rho_c = \frac{S}{S+T-1}, \quad (1)$$

where we have already considered $R = 1$ and $P = 0$. Depending on the values of S and T , one of these solutions may become the stable one. In the mean-field PD case, there is no cooperation and $\rho_c = 0$ is the stable solution. For the SH, the stable solution depends also on the initial density of cooperators ρ_c^0 and Eq. (1) delimits the basin of attraction of each solution: $\rho_c = 0$ if $\rho_c^0 < S/(S+T-1)$ and 1 otherwise. The solution given by Eq. (1), shown in Fig. 2 as a curved line, is only stable in the SD game. It has been known that a structured spatial distribution of agents often inhibits cooperation (Hauert and Doebeli, 2004) in the SD game, as opposed to what happens in the PD and SH games. Nevertheless, when both dilution and mobility are introduced, cooperation is not so often inhibited. Indeed, in Fig. 2 one can see that in many cases the spatially distributed population outperforms the randomly mixed population in terms of cooperative behavior.

Besides the PD and SD games, we also studied the effect of mobility in the SH game. Fig. 4 shows the normalized fraction of

cooperators as a function of the total density for several values of $S < 0$ and $T = 0.9 < R = 1$ when the mobility is either high ($m = 1$) or absent ($m = 0$). Without mobility, isolated clusters of cooperators are able to survive and even at very low densities cooperation is sustained. Once mobility is included, cooperation at low densities is destroyed as small cooperator clusters are easily predated by mobile defectors. On the other hand, at higher densities cooperation is strongly enhanced and $\rho_c = 1$ for all values of $S < 0$. It is interesting to notice that mobility also changes the dependence on the density: with $m = 1$ all curves are monotonically increasing functions of ρ , while for $m = 0$ they are always decreasing for low S and non-monotonic for larger values. The general dependence on S , for several values of the mobility can be observed in Fig. 5. No negative response appears and the amount of cooperation increases with S , as expected.

When the diffusion step is performed before the offspring laying (CDO dynamics), the amount of cooperation is often strongly enhanced, as can be observed in Fig. 6. Cooperators close to defectors have low payoff; therefore, if they do not move, in the next step their strategy will be replaced by D. On the other hand, if they do move away, there is a probability of surviving depending

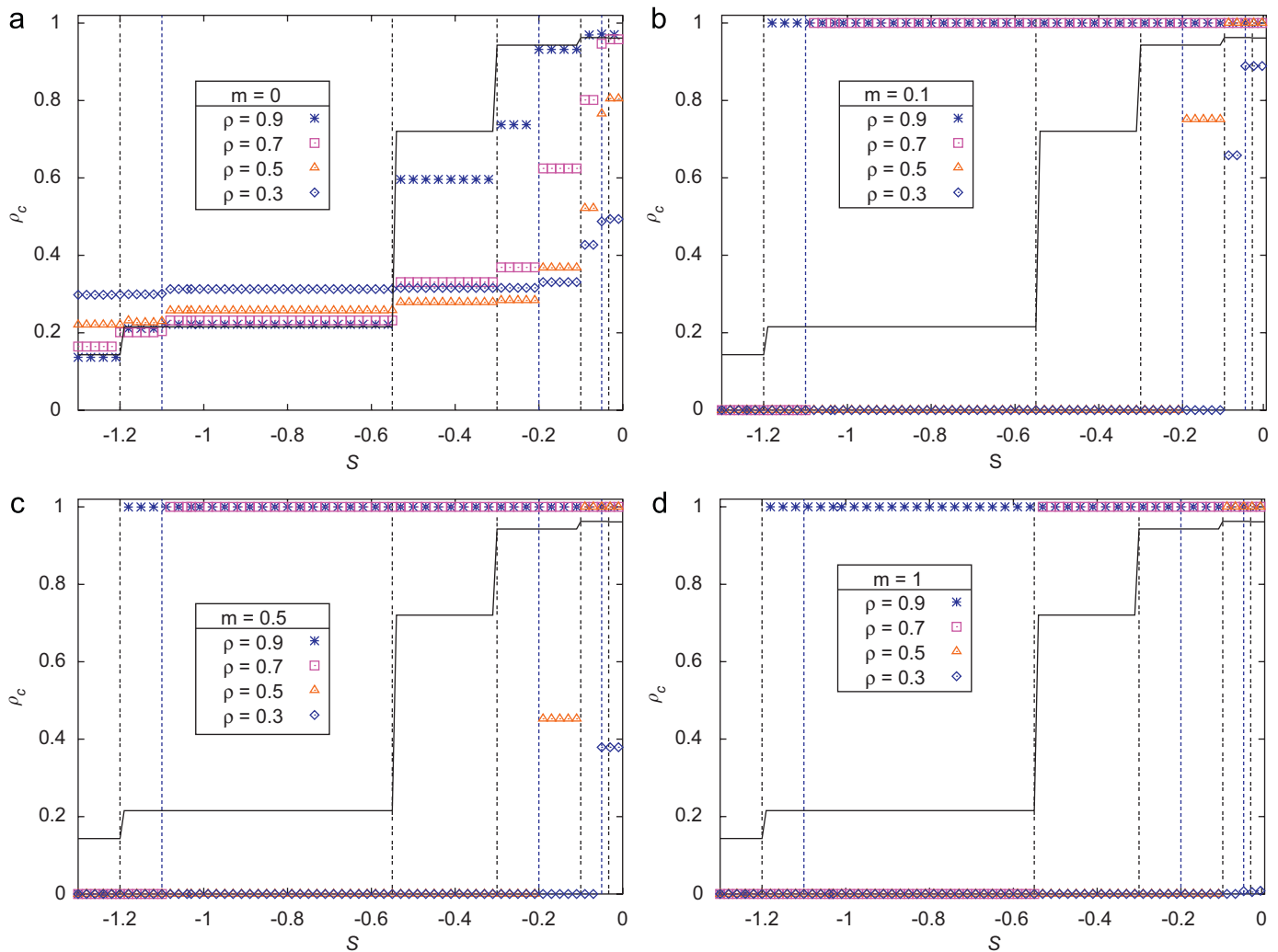


Fig. 5. Average fraction of cooperating individuals ρ_c versus S ($T = 0.9$, $R = 1$ and $P = 0$) for different values of the mobility and ρ in the SH game with COD dynamics. The solid black line is the case $\rho = 1$, while the vertical dashed lines locate the transition points for $\rho = 1$ ($S = -1.2, -0.55, -0.3, -0.1$ and $-1/30$) and the vertical dotted lines locate a few more when $\rho < 1$ ($S = -1.1, -0.2$ and -0.05), as explained in the text. For comparison, the case without mobility ($m = 0$), whose results are obviously independent of the diffusion dynamics, is also shown. No new transition appears due to mobility for the COD dynamics besides those already present when $m = 0$.

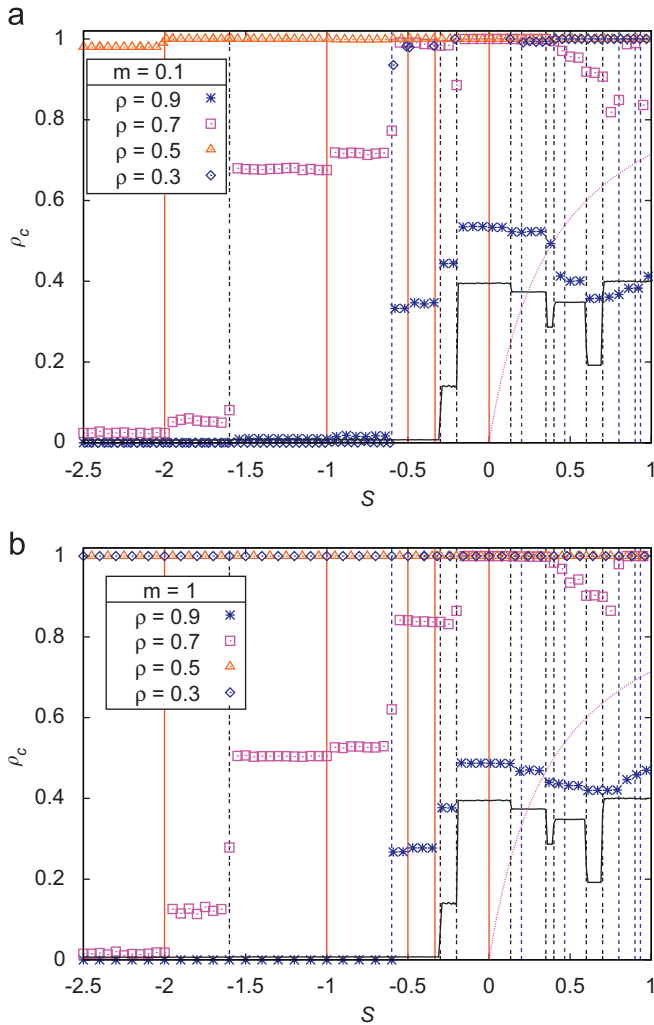


Fig. 6. Average fraction of cooperating individuals ρ_c versus S ($T = 1.4$, $R = 1$ and $P = 0$) for different values of the mobility and ρ in the CDO case. The solid black line is the case $\rho = 1$, while the vertical ones locate the transition points for both $\rho = 1$ and $\rho < 1$ (see Fig. 2 and text). Differently from the COD case, mobility introduces new transitions (indicated by vertical solid lines) at $S = -3$, -2 , -1 , $-1/2$, $-1/3$ and 0 .

on the new neighborhood they encounter (at low densities, for example, they may be isolated after the move, and thus survive). Moreover, cooperators that detach from a cooperative neighborhood have high payoff and may replace the defectors they find. Indeed, for many values of the parameters ρ and m , cooperators fully dominate the system, even in the region of small S values where the COD dynamics allows no cooperators to survive. While all phases appearing in the COD dynamics were already present when $m = 0$, in the CDO case a few new phases appear. These mobility driven transitions can be seen in Fig. 6 and are marked by solid vertical lines at $S = -3$, -2 , -1 , $-1/2$, $-1/3$ and 0 . In particular, a new transition appears at $S = 0$ and, differently from all other cases where the weak PD behavior was representative of a wide range of values of S , in this case, although the weak and the strict PD ($S < P$) still behave in the same way, the small- S SD becomes different. Even though the density of the two phases is very similar, they are in fact different since the final configurations are slightly different even if we prepare two systems (for example, one with $S = -0.01$ and the other with $S = 0.01$) with identical initial conditions and subject to the same sequence of random numbers.

4. Discussion and final comments

The main question posed at the beginning was how mobility affects the outcome of different games beyond the weak dilemma at the frontier between the PD and the SD studied in Vainstein et al. (2007). A main novelty emerges in the context of the SD game: mobility restores the enhancing factor of the spatial structure also found in the PD game, at variance with the $m = 0$ case where cooperation is usually lower than the fully mixed case (Hauert and Doebeli, 2004). In general, when agents are able to randomly diffuse on the lattice, unmatched levels of cooperation can be attained for wide ranges of the parameters. Moreover, differently from the PD and SH games, the spatial SD presents negative responses when the value of S increases: instead of enhancing the amount of cooperation as one would expect, ρ_c sometimes decreases. This effect, absent in the fully mixed case, is also observed even in the absence of mobility, something that has not been previously noticed. Cooperators are spatially organized in different ways depending on the game they play. For example, the clusters may be more compact or filamentous. This spatial structure rules the effect that mobility has on the fate of the game.

We considered three regions of interest in the T and S plane, the genuine PD game ($T > 1$ and $S < 0$), the SD game ($T > 1$ and $S > 0$) and the SH game ($T < 1$ and $S < 0$). Let us analyze what happens for each of the three games separately. We start with the genuine PD where qualitative differences with respect to the weak dilemma occur only for values of S below a threshold S^* , a region in which cooperation is completely extinguished in the presence of mobility. This is reasonable since by increasing the penalization for the sucker's behavior (decreasing S) one finally reaches a point below which C agents perform badly and cannot overcome the filter of selection. For the COD variant at $T = 1.4$, $S^* = -0.2$ no matter the density ρ and for all $m > 0$ considered. On the other hand, for the CDO variant, S^* depends strongly on ρ . It is remarkable that, even for very severe sucker's penalizations (down to $S = -2.5$ in the figure, but whatever smaller value will do, and since there is no further transition below $S = -3$, even any negatively large one), for intermediate values of ρ (e.g., $\rho = 0.5$), the universal cooperation state ($\rho_c = 1$), or a state very close to that, can still be attained.

In less severe dilemmas than the PD—mutual defection pays less than the sucker's payoff in the SD, and mutual cooperation pays more than cheating in the SH—cooperation is, as one would have expected, in general higher. In the case of the SD, cooperation is often enhanced with respect to the weak dilemma with COD dynamics, while an unprecedented state of universal cooperation ($\rho_c = 1$) can be sometimes reached with the CDO one. Hauert and Doebeli (2004) noticed that cooperation is often inhibited by spatial structure with ρ_c being usually lower than its value in a randomly mixed population, where for large systems one of the three solutions $\rho_c = S/(T + S - 1)$, 0 or 1 is stable. Dilution and mobility change dramatically this scenario. When only dilution (but no mobility) is present, cooperation in a spatially distributed system is higher than in the random mixed limit either for intermediate densities or small values of S . When mobility is added, only high densities follow the behavior of the $\rho = 1$ situation where spatial structure inhibits cooperation. On the contrary, for not so high densities cooperation is enhanced in the SD game when $m \neq 0$. In this way, in the presence of mobile agents, it is again possible to make the general statement that spatial structure promotes cooperation. In the COD SH, the combination of mobility and large density ($\rho \geq 0.7$) leads to a boost in ρ_c or even to universal cooperation. On the other hand, for smaller values of ρ , provided the sucker's payoff S is also small, ρ_c is lower. So a crucial difference is that, for a given mobility, the level of

cooperation grows with the density of agents, different from the behavior at $m = 0$.

Accessing the actual payoff involved in real situations is not an easy task, and it has been suggested that many examples that have been interpreted as realizations of the PD are also compatible with the SD and the SH games (see Hauert and Doebeli, 2004; Skyrms, 2004 and references therein). In addition to this, mobility effects on the cooperation of real organisms are still largely unknown, as they are difficult to isolate from other factors and, as the theoretical results presented here have shown, even a tiny amount of mobility is able to produce very strong changes in the final result. Although mobility may have an effect similar to noise, allowing shallow basins to be avoided, they are not equivalent. For example, in Hauert and Doebeli (2004), several different dynamics, with and without noise, gave consistent results for the inhibition of cooperation in the SD game with spatial structure, while mobility drastically changes this outcome. Since the results seem to strongly depend on the chosen dynamics (although we have only considered “best-takes-over” updatings, it has two possible variants, CDO and COD), an important, yet open, question concerns the existence of an unifying principle, in Hamilton’s sense (Hamilton, 1964; Nowak, 2006), relating the parameters of the game, that tells us when cooperative behavior might be expected when mobile agents are present.

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