Does mobility decrease cooperation?

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Abstract

We explore the minimal conditions for sustainable cooperation on a spatially distributed population of memoryless, unconditional strategies (cooperators and defectors) in presence of unbiased, non-contingent mobility in the context of the Prisoner's Dilemma game. We find that cooperative behavior is not only possible but may even be enhanced by such an "always-move" rule, when compared with the strongly viscous ("never-move") case. In addition, mobility also increases the capability of cooperation to emerge and invade a population of defectors, what may have a fundamental role in the problem of the onset of cooperation.
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1. Introduction

The onset and sustainability of cooperation in social and non-social populations is still an open and challenging problem (Maynard Smith, 1982; Axelrod, 1984; Dugatkin and Reeve, 1998; Hauert and Szabó, 2005; Szabó and Fath, 2006) that has been tackled with tools from different fields, ranging from psychological and social sciences to statistical physics. Although involving a cost to the performer, cooperative behavior is ubiquitous in biological populations. Even more tantalizing is its presence in groups of extremely simple individuals (Turner and Chao, 1999; Crespi, 2001; Vulic and Kolter, 2001; Frick and Schuster, 2003; Rainey and Rainey, 2003; Velicer and Yu, 2003; Griffin et al., 2004; Greig and Travisano, 2004; Wolf et al., 2005; Fiegna et al., 2006; Mehdiabadi et al., 2006), where a mechanism other than direct or indirect reciprocity due to memory of previous encounters or kinship relations should apply. Indeed, cooperative behavior is found to occur when dispersal is very limited (high viscosity), what increases the probability of future encounters among close neighbors (the so-called shadow of the future), albeit decreasing the

propagation rate of the strategies. Axelrod (1984) was perhaps the first to consider the effects of territoriality in the spread of strategies in the Prisoner's Dilemma game (see definition below), either by colonization or imitation, but without explicit migration. Differently from the standard, random mixing population, spatial localization allows a continuing interaction within the local neighborhood. The reasons for this are manyfold: individuals usually occupy well-defined territorial regions, they do not move far from their places of birth (population viscosity, Hamilton, 1964), interactions occur in places where animals usually meet such as water ponds, etc. That preliminary study was later extended by Nowak and May (1992, 1993) who showed that geographical fixation enhances the probability of further interaction in such a way that even simple nice rules like unconditional cooperation are able to survive. In these structured populations, cooperative strategies can build clusters in which the benefits of mutual cooperation can outweight losses against defectors, maintaining the population of cooperators stable. These spatial games, where the interactions are localized and non-random, have been studied and extended in many ways (see, for example, Nowak et al., 1994a,b; Lindgren and Nordahl, 1994; Grim, 1995; Killingback and Doebeli, 1996; Nakamaru et al., 1997;

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Szabó and Töke, 1998; Brauchli et al., 1999; Killingback et al., 1999; Szabó et al., 2000; Vainstein and Arenzon, 2001; Abramson and Kuperman, 2001; Hauert, 2002, 2006; Kim et al., 2002; Miekisz, 2004; Aktipis, 2004; Hauert and Doebeli, 2004; Fort and Viola, 2005; Santos and Pacheco, 2005; Durán and Mulet, 2005; Eguiluz et al., 2005; Soares and Martinez, 2006; Santos et al., 2006; Hammond and Axelrod, 2006). Once the population is spatially structured, a natural question concerns the effects of mobility that, along with other important biological factors, is often neglected (Houston, 1993): is it possible to evolve and sustain cooperation in a population of mobile agents, where retaliation can be avoided by moving away from the former partner? In particular, do we need explicit assortment, contingent movements or any behaviorally complex strategy, or is it possible to have a finite density of unconditional cooperators with unbiased, random mobility? By increasing the effective range of interactions, the introduction of mobility increases the random mixing and gets the system closer to the mean field situation, in which every agent interacts randomly with the whole population, and defection is known to prevail. Thus, one might naively think that by dissipating the shadow of the future, mobility becomes a limiting factor for cooperation.

Here we provide some insight on this issue by explicitly considering individual random diffusion in the framework of a locally, non-randomly interacting spatial game, where simple, memoryless, strategy-pure agents coexist. This is important as it helps to settle the minimal conditions under which cooperative behavior might emerge. Although there is no simple answer to the above question since motion can both destroy and enhance the altruistic behavior, we show that there are broad conditions under which even a blind pattern of mobility, without anticipating the future neighborhood (no assortment) and without considering the accumulated payoff, may have a positive effect in the amount of cooperation. In other words, although mobility decreases the shadow of the future for nearest neighbors by diminishing the probability of a future encounter, it also increases it for more distant ones, that may now be visited.

Dugatkin and Wilson (1991) and Enquist and Leimar (1993) showed that a randomly interacting population of fixed cooperators (playing Tit-for-Tat, TFT) could be invaded by mobile defectors that avoid retaliation by moving in search of new cooperators to exploit. Mobility was introduced as a cost to wander between patches without spatial structure, not as an explicit diffusive process. By letting both mobility and cooperative traits evolve together, Koella (2000) (see also van Baalen and Rand, 1998; Hamilton and Taborsky, 2005; Le Galliard et al., 2005) obtained low dispersive altruists and highly dispersive egoists which enhanced the stability of local clusters. Again, there was no explicit diffusive behavior as mobility was introduced by generating offspring within a given dispersal range. Diffusion was considered by Ferrière and Michod (1995, 1996) by including a diffusive term in the replicator equation (Hofbauer and Sigmund, 1998).

Two strategies, TFT and unconditional defection (D), were allowed to move in a one-dimensional system with local, non-random interactions, mobility again involving a cost. This system may sustain cooperation when both strategies have a minimum mobility, and retaliation by TFTs was found to be an important ingredient. More recently, Aktipis (2004) considered contingent movement of cooperators: once a defection occurred in the previous movement, they walk away. This win-stay, lose-move strategy can invade a population of defectors and resists further invasions. Hamilton and Taborsky (2005) and Le Galliard et al. (2005) (and Koella, 2000 as well) considered the coevolution of mobility and cooperation traits. However, both models are a kind of mean field approach as there is no spatial structure and interactions are random. Models with alternating viscosities, reflecting different stages of development that benefit both from the clusterization of cooperators and dispersal, have also been considered (Wilson et al., 1992; Taylor, 1992), showing that local competition for resources balances the benefits of kinship cooperation, inhibiting cooperation. The present work differs from all these in several aspects: we consider non-random interactions on a two-dimensional structure, mobility traits do not evolve and movements are Brownian, non-contingent, and not under the control of the agents, both strategies considered are simple, unconditional and non-retaliating, with no memory of previous steps. In other words, we are considering the simplest possible scenario for cooperation.

We addressed in earlier work (Vainstein and Arenzon, 2001) the question of the robustness of cooperation in spatial games in the presence of heterogeneous environments. By introducing quenched disorder in the lattice (random dilution) each individual would sense a locally varying social environment as the number of neighbors becomes site dependent: optimal cooperation can be achieved for weak disorder as the defects (or inaccessible regions) act as pinning fields for the strategy transition waves that cross the system, keeping the clusters of cooperators more protected from invasions. Thus, an irregular landscape may enhance cooperation by introducing natural defenses against invasions of defectors. Now we allow this disorder to be annealed: the vacant sites are no longer fixed and may become occupied by a neighbor agent with a probability that depends on the populational viscosity. Only random, unbiased diffusion is considered here, although extensions to contingent rules may be also devised. The detailed outcome of the game will depend on the precise implementation of the dynamics. For example, the order in which combats, offspring generation and diffusion occur leads to qualitative differences in the population.

2. The spatial Prisoner's Dilemma

The Prisoner's Dilemma game is the archetypal model for reciprocal altruism. In any round, each of the two

players either cooperates (C) or defects (D), without knowledge of the opponent's strategy. The result depends on the mutual choice and is given by the payoff matrix whose elements are: a reward R (punishment P) if both cooperate (defect), S (sucker's payoff) and T (temptation) if one cooperates and the other defects, respectively. Moreover, these quantities should satisfy the inequalities $T > R > P > S$ and $2R > T + S$. In a random mating, infinite population of asexual (haploid) elements, where two pure strategies are present (cooperators C and defectors D), defecting will be the most rewarding strategy, independently of the opponent's choice. Nonetheless, more complex rules (with memory of previous encounters) have been devised (Axelrod, 1984) if the agents are to meet again in the future. Here we will take a simplified version of the payoff matrix (Nowak and May, 1992): $R = 1$, $P = S = 0$ and $T = b > 1$, reducing the matrix to only one free parameter. Initially, an equal number of cooperators and defectors are randomly placed on a two-dimensional square lattice of length size L and periodic boundary conditions, such that the total density is ρ. Each individual combats with all its four closest neighbors (if any), accumulates the corresponding payoff and then may either move or try to generate its offspring. In the reproduction step, each player compares its total payoff with the ones of its neighbors and changes strategy, following the one with the greatest payoff among them. This strategy changing updating rule preserves the total amount of individuals, thus keeping ρ constant. Results, averaged over 30–130 samples, are shown for $L = 100$ and $b = 1.4$, where the original model ($\rho = 1$) is known to sustain cooperation along with a finite fraction of strategy changing, active sites. As mentioned in the introduction, different values of ρ can be used to mimic heterogeneous environments by allowing the number of connections to vary from site to site due to dilution (Vainstein and Arenzon, 2001).

There are several ways of implementing an unbiased random walk along with the PD interactions. Here we consider two possibilities, named combat–offspring–diffusion (COD) and combat–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 later, the diffusion and offspring steps are reversed. During the diffusive step, each agent makes an attempt to jump to a site chosen randomly within its four nearest neighbors, what is accepted, provided the site is empty, with a probability m. Here we only consider local steps with a reduced dispersal range (one lattice site), m thus measuring the mobility of the agents ($m = 0$ reduces to the case studied in Vainstein and Arenzon, 2001).

3. Results

Figs. 1 and 2, where the average temporal evolution of the cooperators density ρ_c is shown for different values of the viscosity parameter m, exemplify the rich behavior presented by the model once mobility is introduced. Under
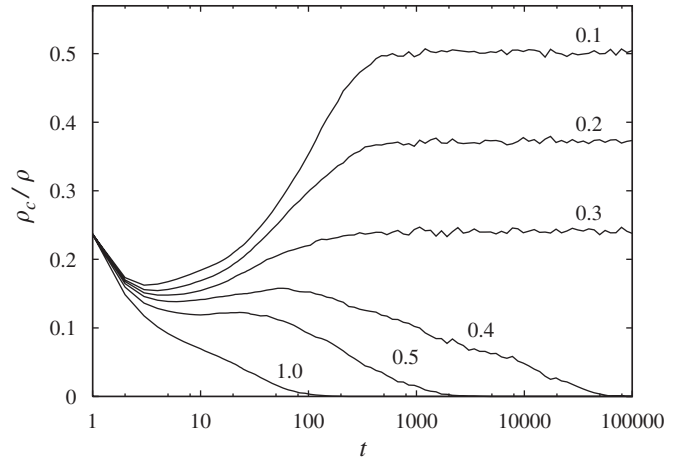

Fig. 1. Average fraction of cooperators ρ_c/ρ as a function of time for several values of m for the COD dynamics at $\rho = 0.7$ in a semi-log plot. In all cases there is an initial decrease in the cooperators density since cooperators are not yet coordinated and only form small groups, being easily predated. Depending on the mobility, at later times the existing cooperator clusters may either disappear or grow, leading to extinction or a stable, mixed population, respectively. For values of $m \gtrsim 0.33$, mobility leads to extinction of cooperation, even if sometimes very slowly. Indeed, close to the transition point, the extinction time seems to diverge. On the other hand, for low mobility, $m \lesssim 0.33$, after the initial decrease common to all values of m, cooperation resumes and a plateau is attained at intermediate values of ρ_c, with cooperators and defectors coexisting. Notice also that for $m = 0$, $\rho_c/\rho \simeq 0.2$ (not shown) (Vainstein and Arenzon, 2001): the behavior, for $m = 0$ and $m \to 0^+$, is quite different.
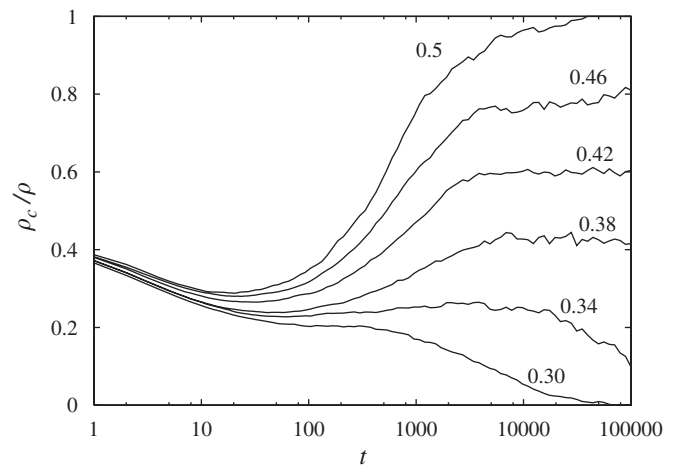

Fig. 2. Average fraction of cooperators ρ_c/ρ as a function of time for $\rho = 0.24$ and several values of m for the CDO dynamics near the transition from an all-D to an all-C phase. Analogously to Fig. 1, after the common initial decrease in the amount of cooperation, at late times the existing cooperator clusters may either disappear or increase their sizes, depending on the mobility m. On the other hand, in this case cooperators may fully invade the population and $\rho_c = \rho$.

thinning or thickening, the ultimate fate of a population depends on the total density (and probably on the initial state), as is exemplified in these figures: while in the COD dynamics of Fig. 1 the asymptotic density of cooperators decreases as m increases, in the CDO case of Fig. 2, on the contrary, ρ_c may increase with m for some values of ρ. The

short time behavior is similar in both cases: the density of cooperators initially decreases since they are not yet coordinated (the initial state is random) forming only small groups, what does not prevent the exploitation by neighboring defectors.

Fig. 3, for COD dynamics, shows both the density of cooperators and strategy-changing individuals (active sites, ρ_a), as a function of the total lattice occupation ρ, after the system attained a stationary state where both quantities fluctuate around their average values. Also shown, for comparison, are the results from Vainstein and Arenzon (2001) for the extremely viscous case $m = 0$. Cooperation only appears above a minimum, m-dependent, density; below this point, defectors dominate ($\rho_c = 0$). At low densities, any mobility destroys cooperation ($\rho_c = 0$): for $m = 0$, isolated all-cooperating clusters are able to survive, but as soon as $m > 0$ the existence of free riders will invade these small clusters. Although cooperation is possible for large mobilities (e.g. $m = 1$), cooperators perform better when nobody moves, $\rho_c(m = 0) > \rho_c(m = 1)$, for all ρ. Interestingly, for intermediate values of the mobility (e.g. $m = 0.1$) cooperation is enhanced when compared with the viscous case: for a broad range of densities, $\rho_c(m = 0.1) > \rho_c(m = 0)$. Thus, two immediate conclusions are: first, cooperation is possible in the presence of mobility

when the available space is somewhat reduced and, second, intermediate mobilities enhance cooperation! Indeed, for intermediate mobilities, there is a maximum in the fraction of cooperators (e.g. for $m = 0.1$, the maximum occurs at $\rho \simeq 0.75$), differently from the $m = 1$ case where this maximum occurs at $\rho = 1$, where no movement is allowed. The transition from the region with $\rho_c = 0$ to the cooperative one seems to be continuous and the finite fraction of active sites indicates that when $\rho_c \neq 0$, both strategies, C and D, coexist. Remarkably, the fall of cooperation after the maximum seems not to be associated with any particular behavior of active sites, whose fraction keeps growing with the total density. Thus, although no particular sign is observed in ρ_a around the maximum of ρ_c, the decrease of cooperation after the maximum is related to a smaller number of empty sites that act as pinning points that slow the dynamics or even prevent that some regions of cooperators be predated, as was observed in Vainstein and Arenzon (2001). Fig. 4 shows the fraction of cooperators as a function of m for two different densities, 0.7 and 0.9. For both densities, mobility decreases cooperation, and in the former, even destroys it completely above a threshold (close to it, the relaxation becomes too slow and longer runs should be performed in order to decide whether the transition is continuous or not). Both cases also differ on the role played by the active sites, much more prominent for $\rho = 0.9$ because the smaller the number of empty sites (pinning points), the larger the number of active sites.
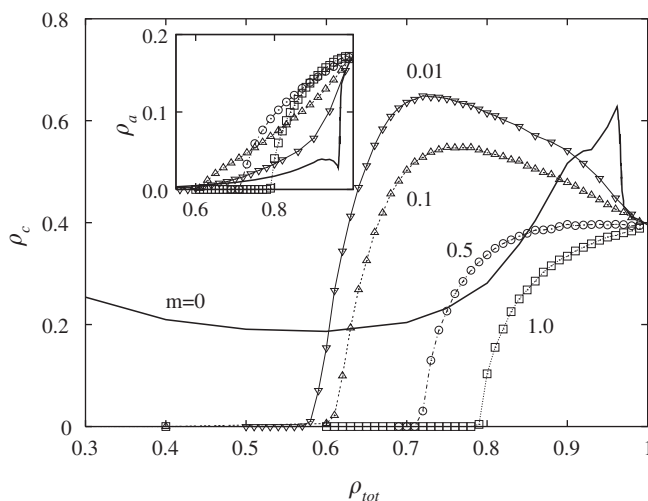

Fig. 3. Average fraction of cooperating individuals ρ_c/ρ and active sites ρ_a/ρ (inset) for the COD dynamics and different values of the mobility, from $m = 0$ (solid line) to 1. Different from the CDO case (see Fig. 5), here there is not a defector-free phase (ρ_c/ρ is always lower than 1) at intermediate densities, although their presence is reduced. For small mobilities (smaller than 0.5 in the figure) there is an optimal density where the relative amount of cooperators is maximized. This maximum increases as m decreases. Notice that as soon as there are cooperators, there are also active sites: there is no frozen mixed configurations in this case. Thus, as was exemplified in Fig. 1, for a fixed density, a very tiny mobility is usually the best scenario at intermediate densities. For small and high values of ρ, the viscous, "never-move" case performs better. In particular, the $m = 1$ always has less cooperators than the immobile case ($m = 0$). In the inset, the corresponding fraction of active sites are plotted: the mixed state where Cs and Ds coexist is also an active phase. Differently from the $m = 0$ case, mobility, even if in small amounts, helps to unpin the strategy-flipping waves that roam the system.
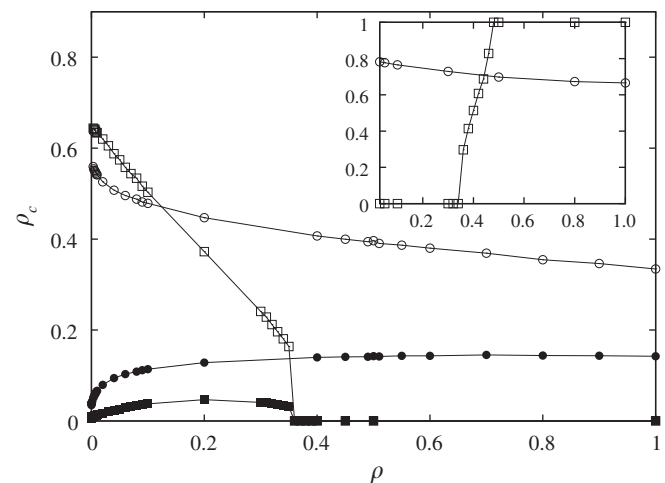

Fig. 4. Average fraction of cooperating individuals (empty symbols) and active sites (filled symbols) for the COD dynamics and densities $\rho = 0.7$ (squares) and 0.9 (circles). For comparison, the values of ρ_c/ρ for $m = 0$ are: 0.2 ($\rho = 0.7$) and 0.52 ($\rho = 0.9$). For all values of ρ, the amount of cooperation is a decreasing function of the mobility. Whether cooperative behavior exist depends, however, on the value of ρ: while for $\rho = 0.9$ cooperators exist in the whole region, for $\rho = 0.7$ a critical value of m (around 0.33) exists above which defectors dominate. In analogy with some physical systems, the dynamics close to this point slows down and long time simulations are needed in order to extract the correct location and order of the transition. Inset: the same as above but for the CDO dynamics. Notice that in this case, the cooperation increases with m for some values of ρ (e.g. 0.24, squares), and decreases for others (0.8, circles).
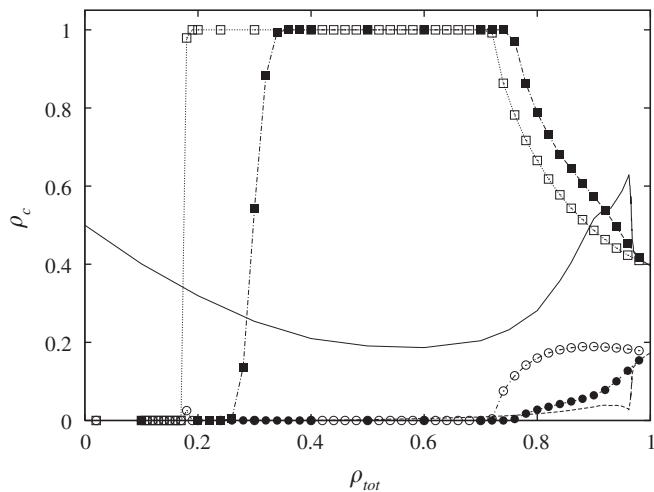
Fig. 5. Average fraction of cooperating individuals, ρ_c/ρ (squares), and active sites (circles), ρ_a/ρ, for the CDO dynamics and several values of the mobility: $m = 0$ (solid line), 1 (hollow symbols) and 0.1 (filled symbols). Notice the three regimes: defector dominated ($\rho_c = 0$, at low ρ), cooperator dominated ($\rho_c = 1$, at intermediate ρ) and a mixed one ($0 < \rho_c < 1$, at greater values of ρ). They are separated by two transitions, discontinuous and continuous, respectively. Notice also that active sites, those that change strategy at a given time, have non-neglectable densities only at large densities (roughly above $\rho \simeq 0.7$), where there is a mixed phase with both strategies coexisting ($0 < \rho_c < 1$). Again, in analogy with the COD case, mobility enhances cooperation for intermediate values of densities. However, higher mobilities increase the range of ρ of the all-C phase.

Fig. 6. Probability of invasion of a population of defectors by cooperators, as a function of ρ, when an initial patch with two cooperators is immersed in a whole population of defectors. We consider several values of m and CDO dynamics. Notice that the larger the mobility is, the greater is the probability of invasion. This effect is absent in the corresponding viscous case ($m = 0$), where this small patch is not enough for invasion to occur.

Fig. 5 presents the long time behavior of the density of cooperators shown in Fig. 2 for the CDO dynamics, as a function of the total lattice occupation ρ, along with the fraction of active sites ρ_a. Again, the overall picture remains the same: mobility destroys cooperation for low densities, while enhances it for higher densities. This effect is even stronger here than in the COD case: besides occurring in a wider range of ρ (compare Figs. 3 and 5), cooperators can invade completely the population ($\rho_c = \rho$, for some ρ, in Fig. 5 and $\rho_c < \rho$, for all ρ, in Fig. 3). Also, when compared with the viscous $m = 0$ case, this dynamics outperforms it, except very close to $\rho = 1$. The origin of the difference between CDO and COD dynamics is that, whenever $m \neq 0$, it is always good for the cooperators to move away from its partner, whatever its strategy, what favors the CDO dynamics. Differently from the previous case, here there are two transitions: a sharp one from a D-dominated ($\rho_c = 0$) to a C-dominated ($\rho_c = \rho$), followed by a continuous one to an active phase (both strategies coexist and $\rho_a \neq 0$). Moreover, for a given ρ, the dependence on mobility is more complex than the previous case, as shown in the inset of Fig. 4: for large densities, the behavior is analogous to the COD dynamics, while the behavior for intermediate densities is unexpected, as the system passes from an all-D to an all-C state as m increases. Although we do not deal in this paper with the question of invadability of a population by a different strategy, we present in Fig. 6, an example of when an initial patch with only two cooperators completely replaces the sea of defectors in
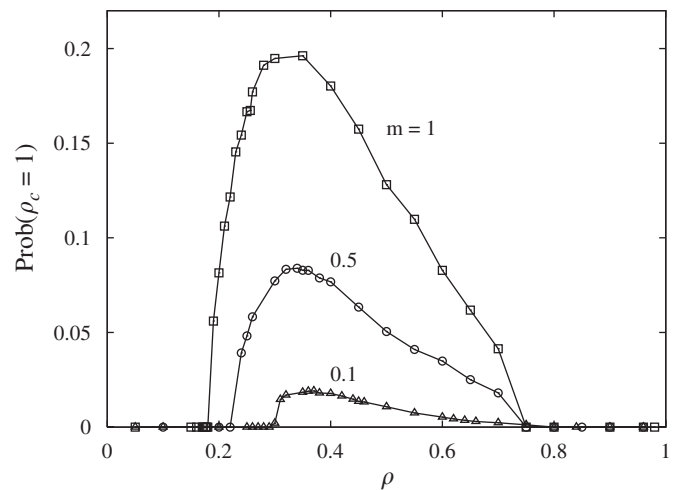
which they are immersed. Again, in this case the mobility enhances the effect (unless the density is so high that movements are prevented), and the larger m is, the greater is the probability of cooperators to invade the population. In comparison, this has a very small probability of happening when $m \simeq 0$.

4. Discussion and conclusions

High population viscosity, or very limited dispersal (low mobility), is a possible mechanism for the emergence and maintenance of cooperation, even in a population of very simple, non-retaliating, strategy-pure, agents (Nowak and May, 1992). The cluster organization prevents defectors from completely overtaking the population because the payoff from the bulk cooperators outwin the exploitation at the borders. A fundamental problem consists in obtaining the minimal conditions under which cooperation is present in a population. In particular, in this paper, we tried to shed some light in the role of mobility, a usually neglected factor. On one hand, besides helping to spread clusters of cooperators, mobility may allow defectors to escape retaliation from a former partner and helps to increase the random mixing of a population by increasing the range of interaction. Once memoryless agents are considered (no recognition process is involved), the probability of future encounters (the so-called shadow of the future) increases when the mobility is small, and spatial correlations are strong. Moreover, when increasing the mobility, the effective range of interactions increases proportionally to it and the probability of sharing the same opponent decreases, thus dissipating the shadow of the future. In this case, defection is expected. On the other

hand, contingent mobility is expected to enhance cooperation by avoiding continued exploitation or defector rich regions. In between, when diffusion is unbiased and the strategies, unconditional, it is not obvious what would be the effect of mobility.

Here we presented results for a simple spatial game where the patched environment allows explicit, although random, movement of agents whose strategies are pure, non-retaliating (unconditional). The diffusion is Brownian, not relying on any type of explicit, genotypic or phenotypic assortment. Moreover, in our model there is no correlation between mobility and altruism: all rules are equally mobile. Whether a given strategy is able or not to invade another population would strongly depend on how viscous a population is, the global density and the chosen dynamics. However, some universal conclusions can be stated. First of all, cooperation is possible under the above conditions, thus enlarging the limits for cooperative behavior. Second, for a broad range of the parameters (density, viscosity, etc.), cooperation is enhanced in respect to the viscous case. Third, a rule like always-move, regardless of the opponent strategy, may increase the capability of cooperators to invade and overtake a population of defectors. In this sense, mobility may have a fundamental role in the problem of the onset of cooperation. Once mobility is incorporated within a population, it may evolve to more contingent forms, perhaps under the control of the agents, and be strategy, payoff or partner dependent. A possible realization of such diffusion scenario may occur in organisms with extracellular metabolism, as is the case of some yeast cells (Greig and Travisano, 2004). Sugar is processed outside the cell by a secreted enzyme called invertase, creating a common resource for all surrounding cells. This offers the opportunity for defection as some cells may not have the cost of producing the enzyme but yet benefit from that produced by others. To what extent the cooperative behavior observed in such simple organisms is a sole effect of the underlying spatial structure or whether there is an enhancement factor due to diffusion is an open and interesting question. Moreover, in systems that present polarized motion (chemotaxis), depending on the concentration of cooperators a gradient of nutrients may be present and both cooperators and defectors can migrate towards (away) high cooperator (defector) density regions. Thus, a possible rule in this case can be: "cooperators attract–defectors repell", but many others can be devised. Such non-random rules may also develop cooperative swarming, relevant for evolving higher levels of biological organization, and is already found to occur in bacteria (Velicer and Yu, 2003). Also interesting is the effect of these more complex dynamical rules as well as the consequences of random mobility in other regions of the strategy space, in particular, when involving TFT players.

The mobility m is an intrinsic parameter that indicates the individual capability of performing walks (with unitary step). As so, data for the same density ρ but different mobilities m can be directly compared in Figs. 3 and 5, and this information is summarized in Fig. 4. However, this parameter alone is not a measure of the effective dispersal since, as the density increases, movements are prevented by the lack of empty space. Unfortunately there is not a general prescription for this effective dispersal and an actual measure would be necessary. This is an important point, that will be addressed in a forthcoming publication along with the question of how the diffusivity of individuals change, for a given m and ρ, when changing the displacement rule from the random case considered here to a more biased choice. Even for the simple unbiased case of this work some preliminary results indicate that the effective mobility is not a simple function of these parameters as the dynamics may become very slow, due both to the presence of defects or critical slowing down, analogous to those observed in glassy systems and close to a continuous transition, respectively.

The PD is not the only possible framework in which social dilemmas can be studied. For example, the snowdrift game (Szabó and Fath, 2006; Doebeli and Hauert, 2005), where $P < S$ (while $P > S$ in the PD), is also biologically relevant and may lead to persistent cooperative behavior. The payoff matrix considers that cooperation involves a benefit b to those involved and a cost c to the performer, while defection involves no costs or benefits. When both cooperate, they receive $R = b - c/2$, sharing the cost, while if they both defect they receive $P = 0$. When one cooperates and the other defects, the later receives $T = b$ while the former is penalized with the total cost $S = b - c$. Although $b > c > 0$ and $P < S$, if we allow higher costs, $b < c < 2b$, we have $P > S$, recovering the PD ranking. Interestingly, when taking the spatial structure into account in the snowdrift game, the amount of cooperation may be reduced, depending on the cost to benefit ratio $c/(2b - c)$ (Hauert and Doebeli, 2004). It would be interesting to extend our results and study the effects of dilution and mobility in the snowdrift game, and different updating rules, stochastic or deterministic, synchronous or not, as well. The parametrization considered in our work, proposed in the original work of Nowak and May (1992), is at the borderline between these two games as it considers $b = c$. There are, however, other possible one-parameter matrixes, still keeping the ranking of the PD game, for example, $T = 1 + r$, $R = 1$, $P = 0$ and $S = -r$, with $r = c/(b - c)$.

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