The effect of dispersal and neighbourhood in games of cooperation

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ABSTRACT

The prisoner's dilemma (PD) and the snowdrift (SD) games are paradigmatic tools to investigate the origin of cooperation. Whereas spatial structure (e.g. nonrandom spatial distribution of strategies) present in the spatially explicit models facilitates the emergence of cooperation in the PD game, recent investigations have suggested that spatial structure can be unfavourable for cooperation in the SD game. The frequency of cooperators in a spatially explicit SD game can be lower than it would be in an infinitely large well-mixed population. However, the source of this effect cannot be identified with certainty as spatially explicit games differ from well-mixed games in two aspects: (i) they introduce spatial correlations, (ii) and limited neighbourhood. Here we extend earlier investigations to identify the source of this effect, and thus accordingly we study a spatially explicit version of the PD and SD games with varying degrees of dispersal and neighbourhood size. It was found that dispersal favours selfish individuals in both games. We calculated the frequency of cooperators at strong dispersal limit, which in concordance with the numerical results shows that it is the short range of interactions (i.e. limited neighbourhood) and not spatial correlations that decreases the frequency of cooperators in spatially explicit models of populations. Our results demonstrate that spatial correlations are always beneficial to cooperators in both the PD and SD games. We explain the opposite effect of dispersal and neighbourhood structure, and discuss the relevance of distinguishing the two effects in general.

1. Introduction

The origin of cooperation has been one of the hot spots in evolutionary biology for decades (Axelrod and Hamilton, 1981; Maynard Smith and Szathmáry, 1995; Dugatkin, 1997). The classical theoretical framework for studying cooperation of unrelated individuals is the prisoner's dilemma (PD) game (Trivers, 1971), in which partners can choose either a selfish (defective) or a cooperative strategy. If both partners defect, they get a smaller fitness than if both cooperate, but a defector gets an even higher fitness value when its opponent cooperates. However, the defector receives the smallest fitness of all if its opponent is a defector (Table 1). Consequently, although mutual cooperation would result a higher fitness, defection is the only evolutionarily stable state in this model. Defectors can invade and destroy cooperation in a cooperative population while cooperators cannot spread in a defective population (Trivers, 1971; Axelrod and Hamilton, 1981).

Some years ago Nowak and May (1992) introduced a spatially explicit model of a population to study the evolution of cooperators in the PD game. They considered a 2D (rectangular) grid one individual living on each grid point. Individuals interact only with their nearest neighbours and thus the fitness of this local interaction determines the success of the individuals. Since successful strategies can invade only to their neighborhood, dispersal (or mixing) of individuals is very limited. They pointed out that the cooperative strategy can coexist with the defector one in this model since spatial aggregation of cooperators can defend themselves from the invasion of defectors. For convenience we refer this spatially explicit model as grid model, and use the abbreviation GM. Nowak and May's seminal paper catalysed a large number of investigations on different variants of the original model (see e.g. Nowak and May, 1993; Nowak et al., 1994; Hubermann and Glance, 1993; Killingback et al., 1999; Nowak and Sigmund, 2004; Szabó and Fáth, 2007), which strengthened further the conclusion that spatial structure promotes cooperation.

For comparison we emphasise that the classical dynamical view of game theory is based on replicator dynamics (Hofbauer and Sigmund, 1998). Replicator dynamics assumes an infinitely large "well-mixed" population. Since every individual feels the average frequencies of strategies living in the population, it is assumed indirectly that not only the population size (N) but also the number of neighbours of an individual (m) tend to infinity in...
this model. At the same time interactions have to be local compared to the population size, thus $m/M \to 0$. Since these set of assumptions is well known in statistical physics as thermodynamic limit, we denote this model as population in thermodynamic limit, and use the abbreviation PTL in the future.

Recently, Hauert and Doebeli (2004) have suggested the so-called snowdrift (SD) instead of the PD game to describe a social dilemma of cooperation. We have again a cooperative (C) and a defective strategy (D) in the SD game. Cooperation yields a benefit $b$ to the cooperator and its opponent as well. Cooperation has a cost $c$ which is paid by the cooperator if the opponent defects, but this cost is halved if the opponent cooperates. If both players defect then there is no cost and no benefit. Table 2 summarises this situation in the payoff matrix. (This game behaves like to the famous hawk–dove game in the case when the cost of injury is high relative to the rewards of victory.) Both strategies can invade when rare, resulting a polymorphic evolutionarily stable state at which the proportion of cooperators is $1 - c/(2b - c)$ in PTL model (Maynard Smith, 1982; Hofbauer and Sigmund, 1998). Hauert and Doebeli (2004) observed that proportion of cooperators is generally below $1 - c/(2b - c)$ in GM, thus they argue that “spatial structure” (spatial patterns) of the GM can often inhibit the evolution of cooperation in the SD game. These results suggest that spatial structure has opposite effect on the evolution of cooperation in the PD and SD games. It can be seen, however, from their Fig. 1, that the detrimental effect of “spatial structure” becomes less pronounced as the neighbourhood size increases. Thus it can be suspected that beside the spatial correlations the limited neighbourhood size has a key effect in explaining the observed patterns. Thus we think that their conclusion is limited neghbourhood size has a key effect in explaining the observed patterns. Thus we think that their conclusion is

### Table 1

The payoff matrix of the PD game ($b > c > 0$)

<table>
<thead>
<tr>
<th></th>
<th>Defect</th>
<th>Cooperate</th>
</tr>
</thead>
<tbody>
<tr>
<td>Defect</td>
<td>$0$</td>
<td>$b$</td>
</tr>
<tr>
<td>Cooperate</td>
<td>$-c$</td>
<td>$b - c$</td>
</tr>
</tbody>
</table>

Assuming that $b > c > 0$ the matrix describes a SD game, but for high cost $(2b > c > b)$ the game converts to a PD game situation.

### Table 2

The payoff matrix of the SD game

<table>
<thead>
<tr>
<th></th>
<th>Defect</th>
<th>Cooperate</th>
</tr>
</thead>
<tbody>
<tr>
<td>Defect</td>
<td>$0$</td>
<td>$b$</td>
</tr>
<tr>
<td>Cooperate</td>
<td>$b - c$</td>
<td>$b - c/2$</td>
</tr>
</tbody>
</table>

To do so we repeat the grid models of the PD and SD games with the same update technique by which the main results of Hauert and Doebeli (2004) and Doebeli and Hauert (2005) were obtained but with an added mixing (dispersal) effect and varied neighborhood size. We make a semi-analytical calculation for the equilibrium level of cooperators at the strong dispersal limit, and compare our findings with the numerical results.

### 2. Method and results

We investigate a spatially explicit version of the PD and SD games, where each player is situated on a 2D lattice. Four different lattice types were used with neighbourhods $(k)$ of $k = 3, 4, 6, 8$. There is a population of $n = 100 \times 100$ individuals, each individual plays either the PD or the SD game with its neighbours, and the lattice update is the function of the payoffs that the players achieve. An asynchronous update was used in which a pairwise comparison is made between the fitness of the focal individual (PC rule) and the fitness of one of its neighbours randomly chosen. The neighbour $y$ takes over the site of the focal individual $x$ with probability $w_y = f(P_y - P_x)$, where $P_y - P_x$ is the payoff difference between strategies $y$ and $x$. If $P_y - P_x > 0$ then $f(P_y - P_x) = (P_y - P_x)/b$, otherwise $f() = 0$ (Hauert and Doebeli, 2004; Doebeli and Hauert, 2005). Alternatively, the so called birth–death (BD), death–birth (DB) and imitation (IM) rules can be used for the update (Hauert and Doebeli, 2004; Ohtsuki and Nowak, 2006). For BD rule an individual selected for reproduction from the focal individual and its neighbourhood proportional to the fitness. For DB update, a randomly selected individual dies, and its neighbours compete for this empty site proportional to fitness. In the case of IM update a random individual revises its strategy by comparing their fitness to the neighbours and imitates one of its neighbours proportional to fitness. We emphasise that the behaviour of spatial games and games on graphs are sensitive to the applied update rule: for example the DB and IM rules favour the evolution of cooperation while BD, and the PC rules are against it (Hauert, 2006; Kun et al., 2006; Ohtsuki and Nowak, 2006; Ohtsuki et al., 2006). For the better comparison we use the same rule (that is PC) which was applied by Hauert and Doebeli (2004) and Doebeli and Hauert (2005).

To investigate the effect of dispersal we randomised the structure of the population after the $m$th update (where $m$ can take values from 1 to $10^3$). This randomisation is achieved with a pairwise mixing algorithm in which the position of randomly chosen adjacent individuals is transposed. The value $m = 1$ represents the well-mixed case, since every update step is followed by a mixing step here, and increasing $m$ decreases the level of mixing. Also, to allow comparison we have run the simulations without mixing, thus reproducing the original findings (Hauert and Doebeli, 2004; Doebeli and Hauert, 2005).

#### 2.1. The PD game

Defection is the only evolutionarily stable state in the PD game in PTL. In a GM, however, there is a small-region of cost/benefit ratio where cooperators and defectors can coexist on the long term if we use the payoff matrix presented in Table 1 (Nowak and May, 1992; Doebeli and Hauert, 2005). The presence of cooperators, however, is not robust with regard of dispersal. Even a small amount of mixing can disrupt patches formed by cooperators, leading to the complete disappearance of cooperators from the population. We found that cooperators cannot coexist with defectors even when $1/m$ set to be approximately greater than $10^{-8}$ (Fig. 1). Coexistence can be observed only if dispersal is practically zero, and $c$ is very close to $b$ (for comparison see
Doebeli and Hauert, 2005). Further we can observe that increasing neighborhood size increases the level of cooperation and the interval of cost and benefit ratio \( r = c/(2b - c) \) in the figure) where cooperative strategy is present (Fig. 1). If we use matrix of 2 with the \( 2b > c > b \) assumptions, then cooperation was not observed at all. Supporting this numerical result it can be shown easily that \( 2 \times 2 \) or \( 3 \times 3 \) fundamental clusters of cooperators are never stable again the invasion of defectors in this case (Hauert, 2001).

### 2.2. The SD game

The SD game is different from the previous PD game that there is a polymorphic evolutionarily stable state even in the PTL (Maynard Smith, 1982; Hofbauer and Sigmund, 1998). A previous study suggested that spatial structure of the grid models—unlike in the PD game—might hinder cooperation in the SD game (Hauert and Doebeli, 2004). Fig. 2. shows the frequency of cooperators as a function of the cost-to-benefit ratio \( r = c/(2b - c) \) in the SD game. The figure depicts the analytical result (asterisk) valid in PTL (Hofbauer and Sigmund, 1998), the frequencies of cooperators in GM without mixing (open squares, i.e. the results of Hauert and Doebeli, 2004) and with mixing of \( m = n \) (full circles) for four different \( k \) values (\( k = 3, 4, 6, 8 \)). First, as it can be seen from the figure the full circles are always below the symbols corresponding to both the analytical results and the results of Hauert and Doebeli (2004). This shows again that mixing (dispersal) favours selfish behaviour in GM. Second, increasing the value of \( k \) decreases the difference between the analytical results (asterisk) and between the result achieved with moderate mixing (\( m = n \), full circles). That is, increasing the radius of interactions will reduce the effect of mixing.

Why does mixing favour selfish behaviour and what is the effect of varying \( m \)? To answer these questions we have run the simulations with a fixed pair of \( r \) and \( k \) parameters changing only the value of \( m \). Also, we have calculated the average of local frequency of cooperators as observed by cooperators compared to the global frequency of cooperators \( P'(C) = P_{loc}(C)/P_{glob}(C) \) that is we measured the local spatial correlations of them Fig. 3(a) depicts the frequency of cooperators for the values of \( r = 0.45 \) and \( k = 3 \) as a function of \( 1/m \) on a log scale. It shows that the frequency of cooperators decreases monotonically as the frequency of mixing increases. Fig. 3(b) shows the value of \( P'(C) \) for the same range of \( m \); insets also show the probability of having zero, one, two and three cooperation partners for cooperators and for selfish individuals, respectively, for three different values of dispersal \( (1/m = 10^{-2}, 1/m = 10^{-3}, 1/m = 10^{-4}) \). It can be seen that for a high value of mixing \( (1/m = 10^{-2}) \) the observed distribution gives a perfect fit to the binomial distribution, thus distribution of strategies are random. Consequently, population is well mixed at this level of mixing. However for moderate and low values of mixing there are differences. For a moderate value \( (1/m = 10^{-3}) \), the probability of having one or two cooperation neighbours is higher than predicted by the binomial distribution for cooperators; and for low mixing \( (1/m = 10^{-4}) \) all three probabilities of having more than one cooperation neighbours are higher than expected in the random case. It is interesting to note that the most dramatic change in Fig. 3(a) corresponds to the maximum of the correlation function of \( P'(C) \) (see Fig. 3(b)). Fig. 4 depicts the typical spatial patterns for the same values of \( m \) (\( k = 3 \)). These patterns confirm the same trend depicted by the previous figure (Fig. 3(b)). At low and moderate mixing \( (1/m = 10^{-2}, 10^{-3}, \text{respectively}) \) the “filament structure” of cooperators can be observed as described by Hauert and Doebeli (2004). However, at high mixing \( (1/m = 10^{-4}) \) the pattern seems to be random, and indeed it is, as the distribution of cooperation neighbours confirms it (see Fig. 3(b)).

### 2.3. The strong mixing limit

Knowing that the spatial distribution of strategies is binomial at strong mixing limit we can derive the equilibrium
frequency of cooperators analytically in this case. For the SD game (Table 2):\

\[ p(k) = 1 - \frac{k + 1}{k} r \quad (1) \]

where \( p \) denotes the equilibrium frequency of cooperators as a function of neighbourhood \( (k) \), and \( r = c/(2b - c) \) as before (see Appendix).

Further, it is clear from Eq. (1) that the frequency of cooperators is smaller in this finite well-mixed population than it would be in an infinitely large well-mixed population. For every finite \( k \). Further, to get the analytical result valid for infinitely large well-mixed populations, not only the population size but also the neighbourhood size must tend to infinity \( (p(k) \to 1 - r \text{ as } k \to \infty) \). Comparing (1) with Fig. 2, we can see that simulations fit exactly to the analysis for \( k = 3, 4 \) (our simulated values lie at \( 1 - 2r \) and \( 1 - \frac{7}{6}r \) lines, respectively). There is only a small difference between the numerical and analytical results for \( k = 6, 8 \). The reason why our analysis is less precise for higher values of \( k \) is as follows: there is no common neighbour of adjacent individuals if \( k = 3, 4 \) thus \( W(C|D) \) and \( W(D|C) \) can be calculated independently from each other. However, when the two adjacent individuals have common neighbours such as in the case of \( k = 6, 8 \) the neighbourhood configurations among the two individuals are correlated, and as a result this simple calculation becomes only an approximation for these cases. All in all, the calculation is exact if the clustering coefficient of the grid is zero (Newman, 2003). In the case of the PD game either \( r > 1 \) in Table 2 thus \( p(k) \) would be smaller than zero or by using Table 1 invading defectors always win over cooperators (see Appendix), which means that only defectors remain at the equilibrium.

3. Discussion

We studied the PD and SD games in a spatially explicit population model. We expanded the earlier investigations studying both the effect of neighbourhood size and dispersion in these games. Note that the effect of dispersion (or mixing) on spatially extended games was generally neglected before, or at least simplified to limiting cases (very low mixing Hauert and Doebeli, 2004) and complete mixing (Killingback and Doebeli, 1999; Doebeli and Knowlton, 1998; Kerr et al., 2002). There are only few counterexamples where the effect of dispersion on a game dynamics is studied systematically (van Baalen and Rand, 1998; Koella, 2000; Szabo et al., 2002; Károlyi et al., 2005; Reichenbach et al., 2007). Recently, some studies investigated the effect of preferential linking dynamics on the evolution of cooperation in complex networks (Pacheco et al., 2006; Santos et al., 2006). They pointed out that if linking dynamics was defined to prefer links among satisfied individuals (e.g. between cooperators) and rewiring is more pronounced among dissatisfied ones (e.g. between defectors or between cooperators and defectors), then graph dynamics helps the evolution of cooperators.

Our simulations show that increasing dispersal favours the selfish strategy and thus decreases the frequency of cooperators in the population. It also shows that this effect is decreasing with increasing range of interactions (i.e. with increasing neighbourhood size). This result is due to the fact that in the PD and SD games both defectors and cooperators are better off in the neighbourhood of cooperators. Thus, it is easy to see that allowing cooperators to form spatially homogeneous groups in the long term increases their average fitness and thus their frequency. All in all, one can conclude that mixing works the same way in the PD and SD games, it favours those strategies that benefit better from the company of different strategies than from themselves.
(like defectors in the PD and SD games). It is important to note, however, that in a spatial PD game where not all the local sites are occupied by the individuals, dispersal can increase the proportion of cooperative strategy (Vainstein et al., 2007) indicating that our conclusions are valid only in the presented model framework.

While “spatial structure” promotes cooperation in the PD game, the situation is just the reverse in SD game according to Hauert and Doebeli: “Our results show that spatial extension generally fails to promote cooperative behaviour in the hawk–dove or snowdrift game. In fact, with the exception of small cost-to-benefit ratios, spatial structure tends to reduce the level of cooperation.” (Hauert and Doebeli, 2004). Our results suggest that the picture is a bit more complex than that. Hauert and Doebeli (2004) argue that the key of the problem is the different spatial pattern of the two games: big cluster of cooperators in the PD game vs. fine filaments in the SD game. They argue further that the reason behind these different spatial patterns is the different payoff structure of the two games: namely in the PD game a cooperator cannot invade a patch of defectors while in the SD game it can.

We agree that the different payoff structure of the SD and PD games is the reason behind the observed difference in spatial patterns; however, we emphasise that it is the limited nature of the range of interactions that causes the decreasing of the frequency of cooperators in the spatial version of the SD game.

Fig. 3. The effect of dispersal. (a) The equilibrium frequency of cooperators as a function of dispersal ($1/m$) for a fixed value of $r$ and $k$ ($r = 0.45, k = 3$). (b) The local frequency of cooperators ($P_{\text{loc}}(C)$) compared to the expected frequency ($P_{\text{glob}}(C)$) as a function of dispersal ($P^*(C) = P_{\text{loc}}(C)/P_{\text{glob}}(C), r = 0.45, k = 3$). The small insets shows the probability of having zero, one, and three cooperator neighbours for cooperators and for selfish individuals, respectively, for three different values of dispersal ($1/m = 10^{-2}, 1/m = 10^{-3}, 1/m = 10^{-4}$).
This conclusion is supported by two observations. (i) On the one hand, increasing the level of mixing, which decreases the spatial correlations decreases the frequency of cooperators as well (see Figs. 1 and 2). Consequently, allowing spatial correlations to take effect, that is allowing cooperators to form patches (by decreasing dispersal) increases their frequency within the population. (ii) On the other hand, increasing the neighbourhood size decreases the difference between the PTL and GM model even in moderate dispersal level in the SD game (Fig. 2). We show that GM indeed gives back to the results of PTL if population is "well mixed" and interaction range tend to infinity (see Eq. (1)).

Investigation of the PD game supports further our logic. In single shot interactions defection is the only ESS (Maynard Smith, 1982) or the only asymptotically stable equilibrium of replicator dynamics (Hofbauer and Sigmund, 1998) in PTL. It is well known that cooperation can be maintained at reasonably high levels in spatially explicit PD game (Nowak and May, 1992; Doebeli and Hauert, 2005). However, even a very limited level of dispersal leads to the extinction of cooperators in these models. It is indeed the existence of spatial correlations that maintains cooperation in the PD game in our 2D grid models. Note that the existence of these correlations also favours cooperation in the SD game regardless of differences in spatial patterns! The frequency of cooperators is higher at low mixing (where filament like structures can be found, see Fig. 4) than at high mixing (where cooperators is higher at low mixing (where filament like structures, while dispersal destroys them. Cooperators can feel only safe if they get the opportunity to stick together, and this opportunity benefits them in both PD and SD games.

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Appendix

The equilibrium frequency of cooperators can be calculated analytically as follows. Let \( p(k) \) be the frequency of the cooperators in the population, assuming that there are \( k \) neighbours for every individual. A change in the frequency of the different strategies in the spatial game is only possible if a given individual has a neighbour that has a higher fitness and plays the opposite strategy. This, our aim to calculate the average fitness of a cooperator having at least one defector neighbour, and the average fitness of defector having at least one cooperator neighbour. If these fitness values are equal then the system is in dynamical equilibrium. Since the analysis is not limited to the PD or SD game, let us denote the elements of a general \( 2 \times 2 \) payoff matrix by \( E(C, C), E(C, D), E(D, C), \) and \( E(D, D) \) where \( E(x,y) \) denotes the payoff of strategy \( x \) playing against strategy \( y \). The average fitness of the cooperator if it has at least one non-cooperator neighbour is

\[
W(C|D) = \sum_{i=0}^{k-1} \binom{k-1}{i} p(k)^i (1-p(k))^{k-1-i} \times [ (k-i)E(C, D) + iE(C, C)]
\]

Similarly, the average fitness of a non-cooperator if it has at least one cooperator neighbour is as follows:

\[
W(D|C) = \sum_{i=0}^{k-1} \binom{k-1}{i} p(k)^i (1-p(k))^{k-1-i} \times [(i+1)E(D, C) + (k-1-i)E(D, D)]
\]
There is equilibrium if \( W(C|1D) = W(D|1C) \), which leads to:

\[
kE(C, D) - E(D, C) - (k - 1)E(D, D) + [E(C, C) + E(D, D) - E(C, D) - E(D, C)](k - 1)p(k) = 0
\]

After rearranging (4) to get the equilibrium.

\[
p(k) = \frac{E(D, C) + (k - 1)E(D, D) - kE(C, D)}{(k - 1)[E(C, C) + E(D, D) - E(C, D) - E(D, C)]}
\]

Substituting the payoff matrix of the SD game (Table 2) into (5) we obtain

\[
p(k) = 1 - \frac{k + 1}{k - 1}r
\]

where \( r = c/(2b - c) \) as before.

For the PD game (Table 1) \( [E(C, C) + E(D, D) - E(C, D) - E(D, C)] = 0 \), thus defectors can always invade, and \( p(k) \) is zero in the equilibrium.

References


