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The effect of dispersal and neighbourhood in games of cooperation

Szabolcs Számadó [a,*], Ferenc Szalai [b], István Scheuring [a]

[a] Department of Plant Taxonomy and Ecology, Research Group of Theoretical Biology and Ecology, Eötvös Loránd University and the Hungarian Academy of Sciences, Pázmány Péter sétány, 1/c, H-1117 Budapest, Hungary
[b] Research Institute for Solid State Physics and Optics, Hungarian Academy of Sciences, P.O. Box 49, H-1525 Budapest, Hungary

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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 cooperator 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 defective 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

* Corresponding author. Tel.: +36 1 381 2187; fax: +36 1 381 2188.
E-mail address: szamszab@ludens.elte.hu (S. Számadó).

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Table 1
The payoff matrix of the PD game ($b>c>0$)

	Defect	Cooperate
Defect	0	b
Cooperate	$-c$	$b-c$

Table 2
The payoff matrix of the SD game

	Defect	Cooperate
Defect	0	b
Cooperate	$b-c$	$b-c/2$

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.

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 know 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 neghbourhood size has a key effect in explaining the observed patterns. Thus we think that their conclusion is premature and need further studies.

As we indicated above GM has two important characteristics which are missing in PTL:

(1) Limited dispersal: because of limited dispersal spatial distribution of strategies are nonrandom. That is, patterns of cooperators and defectors are spatially correlated.
(2) Limited neighbourhood: since every individual interacts with a finite number of other individuals in the GM, and because of probabilistic update rules there is a variance among the success of a strategy within the population. (This is true even if extensive dispersal makes spatial distribution to be random.)

The effect of these two differences present between PTL and GM can be studied separately if the level of dispersal and neighborhood size varies independently.

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 neighbourhoods (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 $f(\cdot) = 0$ (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 mth update (where m can take values from 1 to 10^7). 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