



Examining the role of individual movement in promoting coexistence in a spatially explicit prisoner's dilemma



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ARTICLE INFO

Keywords:

Spatial games
Random motion
Chemotaxis
Prisoner's dilemma
Spatial patterning

ABSTRACT

The emergence of cooperation is a major conundrum of evolutionary biology. To unravel this evolutionary riddle, several models have been developed within the theoretical framework of spatial game theory, focussing on the interactions between two general classes of player, “cooperators” and “defectors”. Generally, explicit movement in the spatial domain is not considered in these models, with strategies moving via imitation or through colonisation of neighbouring sites. We present here a spatially explicit stochastic individual-based model in which pure cooperators and defectors undergo random motion via diffusion and also chemotaxis guided by the gradient of a semiochemical. Individual movement rules are derived from an underlying system of reaction-diffusion-taxis partial differential equations which describes the dynamics of the local number of individuals and the concentration of the semiochemical. Local interactions are governed by the payoff matrix of the classical prisoner's dilemma, and accumulated payoffs are translated into offspring. We investigate the cases of both synchronous and non-synchronous generations. Focussing on an ecological scenario where defectors are parasitic on cooperators, we find that random motion and semiochemical sensing bring about self-generated patterns in which resident cooperators and parasitic defectors can coexist in proportions that fluctuate about non-zero values. Remarkably, coexistence emerges as a genuine consequence of the natural tendency of cooperators to aggregate into clusters, without the need for them to find physical shelter or outrun the parasitic defectors. This provides further evidence that spatial clustering enhances the benefits of mutual cooperation and plays a crucial role in preserving cooperative behaviours.

1. Introduction

An enduring puzzle in a wide range of biological disciplines is to identify the principles underpinning the evolution of cooperation. In this regard, much attention has been given to the prisoner's dilemma as a possible conceptual apparatus to shed some light on the way cooperative behaviours emerge and are maintained (Roca et al., 2009).

In the classical prisoner's dilemma, individuals belonging to a well-mixed population interact through a two-player game in which each individual can adopt one of two strategies: Cooperator (C) or Defector (D). The outcome of the game is determined by the following payoff matrix

$$\begin{array}{cc} & \begin{array}{c} C \\ D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{array}{cc} R & S \\ T & P \end{array} \end{array} \quad (1.1)$$

If both players cooperate, they get the ‘reward’ (R) payoff. If one player defects while the other cooperates, the former gets the ‘temptation’ (T) payoff and the latter gets the ‘sucker's’ (S) payoff. Finally, if the two players defect they both get the ‘punishment’ (P) payoff. If $T > R > P > S$, defectors will necessarily outcompete cooperators. In fact, whether an opponent decides to cooperate or defect, the strategy D is unbeatable, by virtue of the fact that $T > R$ and $P > S$. However, if both players choose to defect they will end up with the payoff P , which is lower than the payoff R that they would get by playing the strategy C.

In their pioneering papers published in the nineties (Nowak et al., 1994a, 1994b; Nowak and May, 1992, 1993), Nowak & May developed the idea, first suggested by Axelrod (1984), of extending game theory, in general, and the standard version of the prisoner's dilemma, in particular, to include spatial interactions between the players. Using a cellular-automaton approach in which individual players are distrib-

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uted over a two-dimensional array, they demonstrated that cooperators and defectors can coexist in the prisoner's dilemma, even if $T > R > P > S$, on condition that a spatial structure is introduced.

Several models have been considered within this theoretical framework since the original works proposed by Nowak and May [vid., for instance, Alonso-Sanz (2014), Fogarty et al. (2012), Fu et al. (2010), Gianetto and Heydari (2015), Grim (1997), Grujić et al. (2014), Kirchkamp (2000), Qin et al. (2008), Lindgren and Nordahl (1994), Nakamaru et al. (1997), Oliphant (1994), Pereira et al. (2008), Roca et al. (2009), Schweitzer et al. (2002), Szabó and Fath (2007), Vainstein and Arenzo (2001), Xia et al. (2015)]. Traditionally, explicit motion is not included in these models, with strategies moving via imitation or colonisation of neighbouring sites. More recently, increasing attention has been given to models that incorporate individual movement. For instance, Dugatkin and Wilson (1991) and Enquist and Leimar (1993) allowed individuals to migrate between patches without spatial structure. Diffusion-based dispersal of offspring was considered in Hamilton and Taborsky (2005), Koella (2000), Ferriere and Dieckmann, (2005), van Baalen and Rand (1998). Ferriere and Michod (1995) studied an explicit diffusive process in the context of the replicator equation, and then extended their approach by including a diffusive term (Ferriere and Michod, 1996). Stochastic cellular-automaton models in which individuals can jump to a nearest empty site were developed in Jian-Yue et al. (2007), Sicardi et al. (2009), Vainstein et al. (2007). A dynamical system of reaction-diffusion type was investigated by Durrett and Levin (1994). Aktipis (2004) proposed a walk-away strategy to avoid repeated interactions with defectors. In de Andrade et al. (2009), a conditional mobility model on a lattice was presented in the context of the Chicken Game. Helbing and Yu (2008) introduced a model of success-driven migration, where individuals move to the sites with the highest estimated payoffs. Chen et al. (2011) explored the effects of mobility when individuals interact with neighbours within a prescribed view radius. The case of heterogenous view radii was analysed by Zhang et al. (2011). An aspiration-induced migration mechanism – inducing individuals to move to new sites if their payoffs are under their aspiration level – was investigated by Yang et al. (2010) and Lin et al. (2011). Meloni et al. (2009) focused on the case where individuals are situated on a two-dimensional plane, and each individual moves to a randomly chosen position with a certain speed.

To complement these earlier studies, in this paper we present a spatially explicit stochastic individual-based model in which pure cooperators and defectors diffuse through space and follow semiochemical cues. We believe these two generalisations to be important, because many common biological situations involve diffusion-based dispersal and/or chemotaxis guided by semiochemical gradients. In our model, individuals occupying the same position can undergo binary interactions. When interacting, they play a round of the prisoner's dilemma game, and are awarded a payoff according to their strategy. The accumulated payoff determines the reproductive fitness of individuals, and thus the number of their offspring. We investigate the case of synchronous and non-synchronous generations. Following the modelling strategy that Schofield et al., (2002, 2005) developed from the original approach proposed by Anderson and Chaplain (1998), we derive the individual movement rules from a system of parabolic equations describing the dynamics of the local number of individuals and the dynamics of the concentration of a semiochemical. This is a further novelty that distinguishes our work from the existing literature on spatial games.

To carry out numerical simulations, we consider a form of the prisoner's dilemma in which defectors are parasitic on cooperators – i.e., the S entry of the payoff matrix (1.1) is set to zero and defectors invade a resident population of cooperators. Our main results show that allowing individuals to diffuse through space, and move up semiochemical gradients, brings about self-organised patterns in which resident cooperators and parasitic defectors can coexist in proportions that fluctuate about non-zero values. This is in stark contrast to the

expected catastrophic effect that the introduction of even a small contingent of pure defectors into a population of pure cooperators would have in a well-mixed scenario. In our spatial model, coexistence has its roots firmly in spontaneous spatial organisation, without the need for individuals to remember past encounters or play elaborate strategies. This makes the results of our study applicable to a broad range of real organisms.

2. The model

We study the interaction dynamics between pure cooperators and defectors which move in a square domain $\Omega := [-\ell, \ell] \times [-\ell, \ell]$. Individual movement is seen as the superposition of spatial diffusion and chemotaxis. The former is due to random motion, whilst the latter is guided by the gradient of a semiochemical emitted by individuals themselves. Individuals occupying the same position can interact with each other and the outcome of interactions is determined by the payoff matrix (1.1). To keep the model as simple as possible, we make the *prima facie* assumption that individuals cannot keep memory of past interactions. Moreover, we assume that the semiochemical is equally released from and sensed by cooperators and defectors. Despite these simplifications, the model captures a wide spectrum of biological scenarios.

2.1. Individual movement rules

At each time instant $t \geq 0$, the concentration of semiochemical and the number of individuals at position $(x, y) \in \Omega$ are characterised by the functions $K(t, x, y) \geq 0$ and $I(t, x, y) \geq 0$, respectively. The evolution of $K(t, x, y)$ is governed by the following reaction-diffusion equation

$$\frac{\partial K}{\partial t} = \beta_K \nabla^2 K + \nu I - \gamma K \tag{2.1}$$

along with no-flux boundary conditions. Eq. (2.1) relies on the assumptions that the semiochemical is produced by all individuals at the same rate $\nu \geq 0$, undergoes a linear decay process at rate $\gamma > 0$, and diffuses with diffusion coefficient $\beta_K > 0$.

To describe the movement of cooperators and defectors, we make use of the following strategy:

- (i) We introduce the taxis-diffusion equation below

$$\frac{\partial I}{\partial t} = \beta_I \nabla^2 I - \chi \nabla \cdot (I \nabla K), \tag{2.2}$$

along with reflective (no-flux) boundary conditions. In Eq. (2.2), the diffusion term models the tendency of individuals to diffuse through space with motility $\beta_I > 0$. The advection term accounts for the fact that both cooperators and defectors move up the semiochemical gradient, and the parameter $\chi > 0$ is the chemotactic sensitivity coefficient.

- (ii) We fix a time step Δt and set $t_n = n \Delta t$, we discretise the square Ω with a uniform mesh as

$$\Delta x = \frac{\ell}{L}, \quad x_i = i \Delta x, \quad i \in [-L, L] \subset \mathbb{Z}, \tag{2.3}$$

$$\Delta y = \frac{\ell}{L}, \quad y_j = j \Delta y, \quad j \in [-L, L] \subset \mathbb{Z}, \tag{2.4}$$

and thereafter we approximate $K(t_n, x_i, y_j)$ and $I(t_n, x_i, y_j)$ by discrete values $K_{i,j}^n$ and $I_{i,j}^n$, respectively.

- (iii) Following Schofield et al. (2002, 2005), we discretise Eq. (2.2) by using an explicit five-point central difference scheme to obtain the following algebraic equation for $I_{i,j}^{n+1}$, i.e., the number of individuals at grid-point (x_i, y_j) at the time step $n + 1$:

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