

# Spatial effects in social dilemmas

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Received 8 August 2005; received in revised form 27 October 2005; accepted 31 October 2005

Available online 13 December 2005

## Abstract

Social dilemmas and the evolutionary conundrum of cooperation are traditionally studied through various kinds of game theoretical models such as the prisoner's dilemma, public goods games, snowdrift games or by-product mutualism. All of them exemplify situations which are characterized by different degrees of conflicting interests between the individuals and the community. In groups of interacting individuals, cooperators produce a common good benefitting the entire group at some cost to themselves, whereas defectors attempt to exploit the resource by avoiding the costly contributions. Based on synergistic or discounted accumulation of cooperative benefits a unifying theoretical framework was recently introduced that encompasses all games that have traditionally been studied separately (Hauert, Michor, Nowak, Doebeli, 2005. Synergy and discounting of cooperation in social dilemmas. *J. Theor. Biol.*, in press.). Within this framework we investigate the effects of spatial structure with limited local interactions on the evolutionary fate of cooperators and defectors. The quantitative effects of space turn out to be quite sensitive to the underlying microscopic update mechanisms but, more general, we demonstrate that in prisoner's dilemma type interactions spatial structure benefits cooperation—although the parameter range is quite limited—whereas in snowdrift type interactions spatial structure may be beneficial too, but often turns out to be detrimental to cooperation.

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*Keywords:* Cooperation; Social dilemmas; Spatial games; Evolutionary game theory; Prisoner's dilemma; Snowdrift game; Public goods game

## 1. Introduction

Social dilemmas capture the fundamental puzzle of the evolution of cooperation. Ever since Darwin (1859) the evolution and maintenance of cooperation has been a major challenge in evolutionary biology and behavioral sciences. In spite of the inherent risk of exploitation by cheaters, cooperation is abundant in nature and, in fact, it can be argued that all major transitions in evolution (Maynard Smith and Szathmáry, 1995) can be reduced to successful resolutions of social dilemmas under Darwinian selection.

Social dilemmas occur whenever conflicts of interest arise between the preferences of individuals as compared to the preferences of the community (Dawes, 1980). The simplest and most general definition of a social dilemma consists of two conditions imposed on situations where

cooperators produce a valuable and publicly accessible public good  $b$  at some cost  $c$  to themselves with  $b > c$  while defectors attempt to free ride on the benefits of the common resource without bearing the costs of cooperation:

- (i) Groups of cooperators outperform groups of defectors because the former profits from the public good whereas the latter foregoes the opportunity of mutually beneficial interactions.
- (ii) In every mixed group, defectors outperform cooperators because they avoid the costs of cooperation.

Condition (i) states that from the community perspective it is clearly advantageous to cooperate but condition (ii) dictates that individuals should opt for defection in order to maximize their profit. Hence the dilemma. Situations that meet these two conditions are abundant in nature and range from bacterial colonies to human interactions (Dugatkin, 1997). For example, yeast cells secrete an enzyme that lyses their environment, thus creating a

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publicly available food resource. Naturally, this resource can be exploited by other cells that do not produce the enzyme (Greig and Travisano, 2004). Other famous examples include alarm calls in meerkats (Clutton-Brock et al., 1999), predator inspection behavior in fish (Milinski, 1987), blood sharing in vampire bats (Wilkinson, 1984) or public goods experiments with students (Fehr and Gächter, 2002).

Evolutionary game theory has long established as powerful mathematical framework to analyse social dilemmas (Maynard Smith and Price, 1973; Nowak and Sigmund, 2004). The single most famous mathematical metaphor for a social dilemma denotes the prisoner's dilemma (Axelrod and Hamilton, 1981). Other well studied models include public goods games (Kagel and Roth, 1995), which essentially represent a generalization of the pairwise prisoner's dilemma to interactions in groups of arbitrary size (Hauert and Szabó, 2003), the snowdrift game (Hauert and Doebeli, 2004; Sugden, 1986) (or chicken or hawk–dove game, Maynard Smith, 1982) as well as by-product mutualism (Connor, 1995). All these models address the problem of cooperation under different biologically plausible conditions and all are aiming at removing the apparent dilemma in social dilemmas.

Over the last decades several mechanisms have been proposed to successfully overcome the dilemma. Pioneering work goes back to Hamilton's kin selection theory (Hamilton, 1964) and Trivers' concept of reciprocal altruism or direct reciprocity (Trivers, 1971). Boosted by Axelrod's computer tournaments (Axelrod, 1984) direct reciprocity attracted most attention. Only more recently alternative approaches are gaining momentum. This includes models of conditional strategies based on reputation which can establish cooperation either through indirect reciprocity (Nowak and Sigmund, 1998) or through punishment (Boyd and Richerson, 1992; Fehr and Gächter, 2002; Henrich et al., 2001; Sigmund et al., 2001), voluntary participation in social dilemmas (Hauert et al., 2002) or by introducing structured populations e.g. to account for spatial extensions (Nowak and May, 1992).

This last scenario represents the main topic of this article applied to a generalized framework of cooperation that embeds all the above models for social dilemmas. This emphasizes the common underlying structure of the different approaches and demonstrates the continuous transitions from one scenario to another when varying biologically meaningful parameters. In accordance with earlier results it turns out that spatial structure is not necessarily beneficial for cooperation and, in fact, often turns out to be detrimental as compared to well-mixed populations with random encounters.

## 2. Model

Recently a generalized theoretical framework to model any kind of social dilemmas in arbitrarily sized groups of  $N$  interacting individuals was introduced (Hauert et al.,

2005). A summary of this framework follows to set the stage for investigations on effects arising in spatially structured populations. Each cooperator produces a benefit  $b$  that is equally shared among all  $N$  members of the group (including the individual itself). However, in groups containing several cooperators, the actual value of the accumulated benefits must not necessarily increase linearly with increasing numbers of cooperators. Instead, each additional benefit may be discounted or synergistically enhanced by a factor  $w$ . More precisely, assuming that

$$P_D(k) = \frac{b}{N}(1 + w + w^2 + \dots + w^{k-1}) \\ = \frac{b}{N} \frac{1 - w^k}{1 - w}, \quad (1a)$$

$$P_C(k) = P_D(k) - c \quad (1b)$$

states that the first cooperator provides a benefit  $b/N$  to everyone, the second increases the value of everyone's benefit by  $wb/N$  and so on to the last cooperator  $k$  augmenting the value by  $w^{k-1}b/N$ . Note that for defectors  $k$  runs from zero to  $N - 1$ , whereas for cooperators  $k$  runs from one to  $N$ . If  $w = 1$ , all cooperators provide the same benefit  $b/N$ . For  $w < 1$ , the value of additional provisions of benefits is discounted. For example, in the aforementioned yeast cells, the food resource provided by the first cooperator may be vital for the survival for all group members but in particular for the cooperator itself. However, the value of additional food decreases until further increases become essentially useless because of the cell's limited capabilities of food intake. Conversely, if  $w > 1$ , the value of additional benefits is synergistically enhanced. This occurs, for example, in situations where cooperators produce substances for chemical reactions. The efficiency of the reaction is generally sensitive to the concentration of reactive compounds and can increase faster than linear (Fersht, 1977; Hammes, 1982). In nature, such situations can occur not only in foraging yeast and chemical reactions but essentially whenever individuals create any kind of common good (see e.g. Doebeli and Hauert, 2005), be it in the form of replication enzymes in viruses (Huang and Baltimore, 1977) or in the form of information gained from predator inspection behavior in fish (Magurran and Higham, 1988).

In well-mixed populations, interaction groups of size  $N$  are randomly formed according to binomial sampling such that the fitness of cooperators and defectors becomes

$$f_C = \frac{b}{N(1-w)}(1 - w(1-x+wx)^{N-1}) - c, \quad (2a)$$

$$f_D = \frac{b}{N(1-w)}(1 - (1-x+wx)^{N-1}), \quad (2b)$$

where  $x$  denotes the frequency of cooperators (Hauert et al., 2005). The growth (or decline) of cooperators is then given by the replicator dynamics (Hofbauer and Sigmund, 1998)

$$\dot{x} = x(f_C - \bar{f}),$$

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