BioSystems 113 (2013) 81–90

Contents lists available at SciVerse ScienceDirect

BioSystems

journal homepage: www.elsevier.com/locate/biosystems

Invasion of cooperators in lattice populations: Linear and non-linear public good games

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ARTICLE INFO

Article history:
Received 8 January 2013
Received in revised form 30 April 2013
Accepted 13 May 2013

Keywords:
Social dilemma
Stochastic dynamics
Probability of invasion
Publicgoods
Volunteer's dilemma game

ABSTRACT

A generalized version of the N-person volunteer's dilemma (NVD) Game has been suggested recently for illustrating the problem of N-person social dilemmas. Using standard replicator dynamics it can be shown that coexistence of cooperators and defectors is typical in this model. However, the question of how a rare mutant cooperator could invade a population of defectors is still open.

Here we examined the dynamics of individual based stochastic models of the NVD. We analyze the dynamics in well-mixed and viscous populations. We show in both cases that coexistence between cooperators and defectors is possible; moreover, spatial aggregation of types in viscous populations can easily lead to pure cooperation. Furthermore we analyze the invasion of cooperators in populations consisting predominantly of defectors. In accordance with analytical results, in deterministic systems, we found the invasion of cooperators successful in the well-mixed case only if their initial concentration was higher than a critical threshold, defined by the replicator dynamics of the NVD. In the viscous case, however, not the initial concentration but the initial number determines the success of invasion. We show that even a single mutant cooperator can invade with a high probability, because the local density of aggregated cooperators exceeds the threshold defined by the game. Comparing the results to models using different benefit functions (linear or sigmoid), we show that the role of the benefit function is much more important in the well-mixed than in the viscous case.

1. Introduction

Social dilemmas, that is situations in which collective and private interest conflict, are frequently experienced in nature and human societies. Well-known examples include cooperation of unicellular organisms, hunting in groups, tax paying, the open source software movement, etc. (Chuang et al., 2009; Johnson, 2002; Kollock, 1998; MacLean et al., 2010; Packer et al., 1990; Wilson, 2011). Concerning these dilemmas, two key questions emerge:

(1) What kind of mechanism maintains cooperative or altruistic behavior in situations where selfishness seems more beneficial?

And an even more challenging question:

(2) How can cooperation invade populations where selfishness is dominant?

In the literature of theoretical work treating social dilemmas, there is a weakening but still apparent dominance of 2-person game theory models with two strategies, cooperation (C) and defection (D). The most popular ones, the prisoner's dilemma (PD) (Hamilton, 1971; Axelrod and Hamilton, 1981) and the snowdrift game (SD) (Sugden, 1986; Doebeli and Hauert, 2005) are simple models that capture some key attributes of the problem. Due to decades of research on the PD, it is common knowledge now that well-mixed populations are dominated by defection, but in the case of structured, spatial, or socially inhomogenous populations, the stable coexistence of cooperation and defection or even the dominance of cooperation can occur. (Nowak, 2006; Nowak and May, 1992; Perc and Szolnoki, 2010; Szabó and Fáth, 2007). However, in most social conflicts, like the abovementioned (and many others), there are many more than $N = 2$ players simultaneously active. Thus, using N-person games is a much more desirable way of modelling social dilemmas.

Indeed, a rapidly growing body of experimental research (Chuang et al., 2009; Damore and Gore, 2012; Lee et al., 2008; MacLean et al., 2010; Packer et al., 1990; Rainey and Rainey, 2003; Wilson, 2011; Yip et al., 2008) has recently invigorated interest in game-theoretical models of N-person social dilemmas (Archetti,

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http://dx.doi.org/10.1016/j.biosystems.2013.05.003

2009; Archetti and Scheuring, 2011, 2012; Chen et al., 2012, 2012b; Damore and Gore, 2012; Hauert et al., 2006a; Motro, 1991; Pacheco et al., 2009; Peña, 2012; Perc et al., 2013; Szolnoki and Perc, 2010; Souza et al., 2009; Zheng et al., 2007). Although the models have moved from 2- to the biologically more relevant N-object interactions, the key questions, that is how stability and invasion of cooperative behavior can be explained, have not altered. Let us outline briefly the main results obtained from the simplest and most frequently used models of N-person social dilemmas. Consider an infinite well-mixed population with strategies C and D, where selection is studied by replicator dynamics (Hofbauer and Sigmung, 1998). In the model framework for N-person SD (NSD) games, the coexistence of cooperators and defectors is the only stable fixed point of replicator dynamics. However, the frequency of cooperators decreases with $1/N$ at equilibrium (Souza et al., 2009; Zheng et al., 2007). In the N-person PD (NPD) game, which builds on the 2-person PD game, cooperation disappears if $c/b > 1/N$ where c is the cost and b is the benefit of the cooperative act (for details see Appendix A). It is generally argued that this relation is valid for most biologically reasonable situations (Archetti and Scheuring, 2012; Hauert et al., 2006a). To summarize, the frequency of cooperators is marginally low or zero in large well-mixed populations where individuals play the NSD or the NPD games in larger groups. These results sharply contradict the numerous observations of cooperation in groups of bacteria, animals, and in human communities (Kollock, 1998; Lee et al., 2008; Rainey and Rainey, 2003; Yip et al., 2008).

Naturally, the condition of a large well-mixed population does not necessarily hold for real situations, because, in many cases, there is some kind of positive assortment among cooperators (e.g. colonies of bacteria or groups of cooperative animals or humans, etc.). Positive assortment or relatedness, giving opportunity for kin-selection to act, enables cooperators to outcompete or coexist stably with defectors even in NPD-like situations (Hamilton, 1964, 1971; van Baalen and Rand, 1998; Nowak, 2006; Nowak and May, 1992; Perc et al., 2013). Thus, the literature gives us the impression that positive assortment (or relatedness) is necessary for cooperation to persist in NPD/NSD-like situations. However, in addition to positive assortment, there is another candidate mechanism that can explain how the production of public goods exists stably in well-mixed, natural systems, which is to apply an alternative and more adequate N-person game to the NSD or the NPD (Archetti, 2009; Archetti and Scheuring, 2012; Hauert et al., 2006a; Motro, 1991; Pacheco et al., 2009). One of these alternatives is the N-person volunteer's dilemma (NVD) Game (or Threshold Public Goods Game) (Bach et al., 2006; Diekmann, 1985; Archetti, 2009; Archetti and Scheuring, 2011).

The crucial difference between the NPD and the NVD games is the shape of the public goods function they use. In the NPD, the public good increases *linearly* with the number of cooperators i (Fig. 1). However, in real biological systems, this linearity is at most a rare exception, and certainly not the rule. The well-documented case of cooperative hunting in groups is a good example, in which per capita success and benefit change non-linearly with the number of participants (Bednarz, 1988; Creel and Creel, 1995; Packer et al., 1990; Stander, 1992; Yip et al., 2008). Similarly, cooperative nesting and breeding of vertebrates (Rabenold, 1984) and the fruiting body formation of social amoebas (Bonner, 2008) are examples of non-linear public goods games. In microbial communities, where the public good is based on specific molecules like replication enzymes (Turner and Chao, 2003), adhesive polymers produced by viruses (Rainey and Rainey, 2003), antibiotic resistance in bacteria (Lee et al., 2008) or invertase enzyme in yeast (Gore et al., 2009), the effect of enzyme production, and thus the amount of obtainable common good must generally be a saturating function of the molecule concentration (Eungdamrong and Iyengar, 2004; Hemker and Hemker, 1969; Mendes, 1997; Ricard and Noet, 1986). Following this train of thought, the public goods function ($B(i)$) used when modelling these kind of dilemmas should be a monotonously saturating curve with an inflection point somewhere, i.e. a sigmoid one (Fig. 1). It is quite a challenge to analyze a model with this benefit function instead of the linear NPD. In ordeer to simplify the problem, specific $B(i)$ functions are defined (Archetti, 2009; Bach et al., 2006; Hauert et al., 2006b; Motro, 1991).

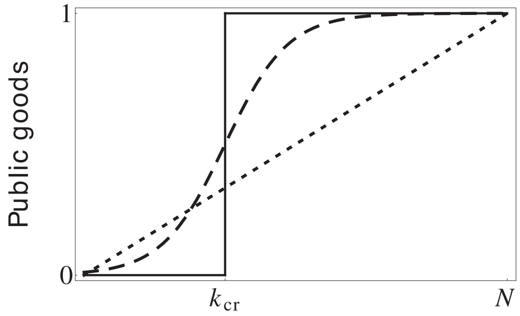

Fig. 1. Schematic picture of characteristically different public goods as a function of number of cooperators. A general saturating non-linear $B(i)$ function with inflection point at k_{cr} (dashed line), the linear N-person prisoner's dilemma game (dotted line) and the N-person volunteer's dilemma game with threshold at k_{cr} (continuous line).

It is biologically realistic to assume that the transition phase from accelerating to discounting is steep at the inflection point, and, thus, as a specific model, we can use a step function for $B(i)$ (Archetti, 2009):

$$B(i) = \begin{cases} 0 & \text{if } i < k_{cr} \le N \\ b & \text{otherwise,} \end{cases}$$

which defines the generalized N-person volunteer's dilemma game (Archetti, 2009; Diekmann, 1985). That is, at least k_{cr} cooperators (volunteers) are needed for the high benefit, otherwise cooperation does not achieve net benefit (in the classical NVD game $k_{cr} = 1$). This model is more tractable, and its dynamical behavior remains qualitatively the same as it would be for smooth but similar functions of $B(i)$ (Fig. 1) (Archetti and Scheuring, 2012). We note here that the problem of a collective action in public goods game with non-linear benefit functions is a classical one in sociology and political science (e.g. Hardin, 1982; Maxwell and Oliver, 1993; Oliver, 1993; Ostrom, 2003). However, studying this problem in the framework of evolutionary game theory has become an important issue only recently.

Assuming that N interacting individuals are selected randomly from an infinitely large well-mixed population and using the replicator dynamics for the NVD game, it can be shown that if $c/b > 1/r^*$, then complete defection ($x^* = 0$ if x denotes the frequency of cooperators) is the only stable state of the dynamics, while if $c/b < 1/r^*$, then $x^* = 0$ and $x^* = x_s < 1$ are the stable fixed points, and $x^* = x_u < x_s$ and $x^* = 1$ are the unstable fixed points of (A.4) (Archetti and Scheuring, 2011, 2012) (for details, see Appendix A). Naturally, if the population structure allows positive assortment for cooperators and the social dilemma is described by the NVD, cooperators coexist or dominate structured populations even more easily (Boza and Számadó, 2010; Szolnoki and Perc, 2010; Perc et al., 2013).

It is important that r^* (which is a complex function of b/c and N) can be much smaller than N for the NVD and for similar games with smooth but highly nonlinear benefit functions, so stable coexistence of D and C strategies at x_s is a typical solution of these non-linear public goods games (Archetti and Scheuring, 2011, 2012). We have to note here, that the cooperative state is evolutionary unstable if investment (that is, c and $b = rc$) is an evolvable parameter of the NVD, but remains stable for smooth sigmoid