Evolutionary diversity and spatiotemporal dynamics of a spatial game

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ABSTRACT

In this paper, the evolution of cooperation is studied by a spatially structured evolutionary game model in which the players are located on a two-dimensional square lattice. Each player can choose one of the following strategies: "always defect" (ALLD), "tit-for-tat" (TFT), and "always cooperate" (ALLC). Players merely interact with four immediate neighbors at first and adjust strategies according to their rewards. First, the evolutionary dynamics of the three strategies in non-spatial population is investigated, and the results indicate that cooperation is not favored in most settings without spatial structure. Next, an analytical method, which is based on comparing the local payoff structures, is introduced for the spatial game model. Using the conditions derived from the method as criteria, the parameter plane for two major parameters of the spatial game model is divided and nine representative regions are identified. In each parameter region, a distinct spatiotemporal dynamics is characterized. The spatiotemporal dynamics not only verify that the spatial structure promote the evolution of cooperation but also reveal how cooperation is favored. Our results show that spatial structure is the keystone of the evolution of intraspecific diversity.

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1. Introduction

Cooperation, which is ubiquitous on many levels of biological organization in nature, is essential for evolution to construct new levels of biological organization (Doebeli and Hauert, 2005; Nowak, 2006, and references therein). Genomes, cells, multicellular organisms, social insects, and human society are all based on cooperation (Nowak, 2006). However, within the classic Darwinian framework of evolutionary theory (the struggle for life and survival of the fittest), cooperation may be difficult to achieve under the natural selection. Cooperators have to succeed in the struggle for survival with defectors, who by definition have a certain fitness advantage (Nowak and May, 1993). So the question of how natural selection can lead to cooperation has fascinated evolutionary biologists for a long time. Maynard Smith and Price (1973) ingeniously related the economic concept of players to biological individuals and payoff function of a player to evolutionary fitness that describes the survivability and fecundity of an individual. Their seminal work thus signified the advent of an entirely new game theoretical approach to evolutionary ecology that evoked numerous investigations successively (Doebeli and Hauert, 2005). In particu-

lar, evolutionary game theory has been used as a standard tool in understanding the evolution of cooperation (Maynard Smith, 1982; Weibull, 1995; Hofbauer and Sigmund, 1998; Nowak and Sigmund, 2004; Nowak, 2006; Doebeli and Hauert, 2005). Over the past few decades, several mechanisms have been proposed to explain the problem of cooperation. Nowak (2006) reviewed the related studies and categorized these mechanisms as five rules: kin selection, group selection, direct reciprocity, indirect reciprocity and network reciprocity.

Since the pioneering work of Trivers (1971), direct reciprocity was embedded into evolutionary game theory by Axelrod and Hamilton (1981). Their models are based on the Prisoner's Dilemma (PD) game, perhaps the single most famous metaphor for the problem of cooperation (Doebeli and Hauert, 2005 and references therein). The original PD includes two players, each of which may choose either to cooperate (C), or to defect (D) in any encounter. If both players cooperate, they will be rewarded with R points. If they both defect, they get the punishment P. If one player defects while the other cooperates, the defector gets the temptation payoff T, while the other gets the sucker's payoff S. Now, with $T > R > P > S$ and $2R > T + S$ we have an obvious dilemma, in any round, the strategy D is unbeatable no matter what the opponent does. The original PD has four parameters, which can be reduced for the purpose of analytical simplicity. Particularly, they can be reduced as $R = 1$, $T = b(1 < b < 2)$, $S = 0$, $P = 0$, where only one parame-

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ter b retains, and the parameter b characterizes the advantage of defectors against cooperators (Nowak and May, 1992, 1993). This parameter setting preserves the essentials of the PD, and is widely accepted as its simplicity and generality.

The game theoretic framework of direct reciprocity is the repeated Prisoner's Dilemma game (repeated PD), which is one type of solution to the dilemma. Repeated PD is based on the memories of an individual who remembers opponents' actions in previous encounters and on the probability $w > 0$ of encountering similar actions again in the next round (Axelrod and Hamilton, 1981; Axelrod, 1984; Axelrod and Dion, 1988; Nowak and Sigmund, 1992, 1993, 1994), thus cooperation may evolve in the context in which future behavior may be determined by current payoff. The most famous strategy of this type is "Tit-for-Tat" (TFT), the most basic conditional strategy, which consists of cooperating in the first round of the interaction, and taking the opponent's strategy in the previous round. In Axelrod's seminal computer tournaments (1984), TFT was proven as the only successful strategy against a range of other strategies, such as the two extreme unconditional strategies, "always cooperate" (ALLC) and "always defect" (ALLD). However, TFT does not always perform well when erroneous behaviors are incorporated (Doebeli and Hauert, 2005). Needless to say, there are a variety of modified versions of TFT strategies to improve its robustness. But we will not want to mention all of them in this study. It is believed that the interplay of the three most basic strategies, ALLC, ALLD, and TFT captures an essential aspect of the evolutionary dynamics of cooperation, and of our instinct for direct reciprocation. At the same time, we have known that in well-mixed populations, ALLC is dominated by ALLD, ALLD is bistable with TFT if average number of rounds is sufficiently high, TFT and ALLC are neutral if there is no noise (Nowak and Sigmund, 2004).

During the history of finding solutions to the dilemma, spatial structure of the interacting populations is also another an absolutely ineligible factor. In contrary to classical evolutionary game model, spatially structured evolutionary game model can be interpreted as, individuals only play against their nearest neighbors but not against random opponents (Brauchli et al., 1999). The biological interpretation of spatial game model corresponds to the issue of kin selection and more generally group selection (Frank, 1998; Sober and Wilson, 1998). Axelrod (1984) had already pointed out the potential role of spatial structure, but it was really the seminal paper by Nowak and May (1992) that spawned a large number of investigations of "games on grids" (Nowak and Sigmund, 2000), i.e. evolutionary games that are played in populations having a spatial structure, whose individuals located on a lattice only play locally with their neighbors (sometimes include themselves) (Nowak and May, 1992). Payoffs obtained are then used to update the lattice, i.e. to create subsequent generations in the evolutionary process. The propagation of successful strategies to neighboring sites may be interpreted either in terms of reproduction, or in terms of imitation and learning (Nowak and Sigmund, 2004). An ambiguous conclusion that has been reached from studies of the different types of the spatial PD is that spatial structure promotes cooperation (Nowak and May, 1992, 1993; Huberman and Glance, 1993; Nowak et al., 1994; Killingback et al., 1999). Nowak and May (1992) have shown that a simplified spatial structure enables the maintenance of cooperation for the simple PD, in contrast to the classical, spatially unstructured PD where defection is always favored. And they observed the perpetual coexistence of cooperative and defective players for a range of parameters, forming constantly changing spatial patterns. An interesting combination of repeated games and spatial structure, was studied by Lindgren and Nordahl (1994). Not only did they find that in structured populations there is more cooperation, but also that different strategies are successful in spatially structured populations than in non-structured populations

Table 1
Payoff matrix of the three strategies ALLD, TFT and ALLC in repeated PD.

	ALLD	TFT	ALLC
ALLD	$P/(1-w)$	$T + wP/(1-w)$	$T/(1-w)$
TFT	$S + wP/(1-w)$	$R/(1-w)$	$R/(1-w)$
ALLC	$S/(1-w)$	$R/(1-w)$	$R/(1-w)$

In the two players PD game, if both cooperate, they get a payoff of magnitude R, if both defect they get P. If one player defects while the other cooperates, the defector gets the payoff T, while cooperator gets S, w is the probability that the same two players interact in the following step as well. In our study, the parameters are: $R = 1$, $T = b(1 < b < 2)$, $S = 0$, $P = 0$ (Nowak and May, 1992, 1993).

(Brauchli et al., 1999). Actually, there are plenty of spatial evolutionary game models and we cannot list and review all of them. To the best of our knowledge, the spatial effect on the evolutionary game dynamics of the three strategies ALLD, TFT, and ALLC has not been extensively investigated, and a systematic analysis about the influences of parameters on the spatiotemporal dynamics is still lack.

The aim of this study is to give a thorough analysis of the spatiotemporal dynamics of the spatial evolutionary game, where three types of players ALLD, TFT, and ALLC are included. The ultimate goal is to answer the question, how spatial structure influences the evolution of cooperation and what impact it has on the evolutionary dynamics of a spatially structured model. Before that, we will first present the replicator dynamics of the three strategies in completely well-mixed populations. The replicator equation and mathematical analysis will be shown in Section 2. In Section 3, the spatial evolutionary game model will be constructed, where ALLD, TFT, and ALLC players are placed on a regular spatial lattice. A systematic mathematical analysis for this model will be given. Particularly, we will focus on two major parameters b and w, then the plane of parameters $b - w$ will be divided based on comparing local occupation patterns, and the corresponding spatiotemporal dynamics will be identified by computer simulations. Lastly, the main results will be concluded, and a short discussion will be given within the framework of Nowak's five rules leading to cooperation.

2. Replicator dynamics of non-spatial game models

Traditionally, evolutionary game model always assumes randomly interacting populations, it does not include the effect of spatial structure of populations. Replicator equation is introduced as a corresponding mathematical tool to describe evolutionary game dynamics in the deterministic limit of an infinitely large and well-mixed population (Taylor and Jonker, 1978; Hofbauer et al., 1979; Zeeman, 1980; Weibull, 1995; Hofbauer and Sigmund, 1998, 2003). Since w is the probability that the same two players interact in the following step as well, then $w^{n-1}(1 - w)$ will be the probability that they interact exactly n times ($n = 1, 2, 3 \ldots$). The expected number of times that the two players interact is $1/(1 - w)$ (Nakamaru et al., 1997). The expected total payoff matrix is shown in Table 1. For facility of comparison, we also assume that parameters are $R = 1$, $T = b(1 < b < 2)$, $S = 0$, $P = 0$ and setting $P = \epsilon$ with ϵ positive but significantly below unity (so that $T > R > P > S$ is strictly satisfied) does not qualitatively change the analytical results. In the following, the parameter setting keeps constant except special declaration. Denoting $\{x_1, x_2, x_3\}$ ($0 \leq x_i \leq 1, i = 1, 2, 3$) as the fractions of ALLD, TFT and ALLC, respectively, then the replicator dynamics are restricted in the simplex $x_1 + x_2 + x_3 = 1$. Substituting the payoff matrix into the classical replicator equation (Taylor and Jonker, 1978; Hofbauer et al., 1979; Zeeman, 1980; Weibull, 1995; Hofbauer and Sigmund, 1998, 2003), we get the following dynamic system: