Evolutionary diversity and spatiotemporal dynamics of a spatial game

Hui Zhang[a], Feng Zhang[b], Zizhen Li[a,c,*], Meng Gao[d], Wenlong Li[e,*]

[a] *Institute of Bioinformatics, School of Mathematics and Statistics, Lanzhou University, Lanzhou 730000, People's Republic of China*
[b] *Department of Mathematics, College of Science, Gansu Agricultural University, Lanzhou 730000, People's Republic of China*
[c] *Key Laboratory of Arid and Grassland Agroecology of the Ministry of Education, Lanzhou University, Lanzhou 730000, People's Republic of China*
[d] *Yantai Institute of Coastal Zone for Sustainable Development, Yantai 264003, People's Republic of China*
[e] *School of Pastoral Agriculture Science and Technology, Lanzhou University, Lanzhou 730000, People's Republic of China*

ARTICLE INFO

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.

© 2009 Elsevier B.V. All rights reserved.

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-

* Corresponding authors at: State Key Laboratory of Arid Agroecology, Lanzhou University, Lanzhou 730000, People's Republic of China. Tel.: +86 931 8913370.
E-mail address: zizhenlee@lzu.edu.cn (Z. Li).

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 $\{x_1, x_2, x_3\}$ ($0 \le x_i \le 1, i = 1, 2, 3$) 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:

Table 2
The stability of the equilibria of the replicator dynamics

Equilibrium	$b(1-w) > 1$	$b(1-w) < 1$
$x_2 + x_3 = 0$	Stable	Higher order odd points
$x_2 + x_3 = 1$ $\left(x_2 > \frac{b-1}{bw} \right)$	Unstable	Stable
$x_2 + x_3 = 1$ $\left(x_2 < \frac{b-1}{bw} \right)$	Unstable	Unstable
$x_3 = \frac{1 - b(1-w)x_2}{b-1}$	Non-equilibria	Fixed points

If the parameters chosen satisfy $b(1-w) > 1$, the evolutionary stable state is ALLD, whereas satisfy $b(1-w) < 1$, the evolutionary dynamics is a bistable case depending on initial state, except ALLD is still the evolutionary stable state, the mixed state of TFT and ALLC is also evolutionary stable while $x_2 > (b-1)x_3/(1-b+bw)$ (x_2 and x_3 indicate the frequencies of TFT and ALLC, respectively).

$$\frac{dx_1}{dt} = x_1 \left[bx_1 + \frac{b}{1-w}x_3 - x_1 \left(bx_2 + \frac{b}{1-w}x_3 \right) - \frac{1}{1-w}(x_2 + x_3)^2 \right]$$

$$\frac{dx_2}{dt} = x_2 \left[\frac{1}{1-w}(x_2 + x_3) - x_1 \left(bx_2 + \frac{b}{1-w}x_3 \right) - \frac{1}{1-w}(x_2 + x_3)^2 \right]$$

$$\frac{dx_3}{dt} = x_3 \left[\frac{1}{1-w}(x_2 + x_3) - x_1 \left(bx_2 + \frac{b}{1-w}x_3 \right) - \frac{1}{1-w}(x_2 + x_3)^2 \right]$$

$$(1)$$

With the restriction $x_1 + x_2 + x_3 = 1$, system (1) can be reduced into a two-dimensional Lotka–Volterra system. Using the classic analytical method of dynamic system, we can easily find that the edge $x_1 = 0$ consists of fixed points only. Clearly, a population of ALLC and TFT players will always cooperate, and none of the two strategies is favored. When $b > 1/(1-w)$, if a random shock introduces a small amount of ALLD, they will take over the whole population (some details have been shown in Appendix A). For $b < 1/(1-w)$, there is another invariant line $(1 - b + bw)x_2/(b-1) - x_3 = 0$. Once $x_2 > (b-1)x_3/(1-b+bw)$, then ALLD will forthwith be eliminated, and ALLC and TFT players will coexist finally. Thus the dynamics is bistable, and the evolutionary stable states depend on the initial condition. Since $(b-1)x_3/(1-b+bw)$ is small when w is close to 1, it means that a small TFT cluster is able to invade a population of defectors. This is due to a sufficiently large w, which is interpreted as the "shadow of the future" (Axelrod and Hamilton, 1981). Table 2 concludes the results of the dynamics of system (1). As one example, Fig. 1 illustrates the evolutionary dynamics of the three strategies on the phase plane.

3. The spatial game model and analysis

3.1. Spatial game model

Compared with non-spatial model, the most remarkable characteristic of spatially structured model is that individuals will interact with neighbors selectively or assortatively, which is more realistic for many ecological and social phenomena (Hui et al., 2005; Zhang et al., 2006; Xiao et al., 2007). Spatial structure might influence the evolutionary outcome, therefore, evolutionary games in spatially structured populations have attracted the interest of evolutionary biologists (Nowak and May, 1992; Hauert and Doebeli, 2004; Doebeli and Hauert, 2005 and references therein). Our spatial game model is actually a cellular automaton (e.g. Balzter et al., 1998; Ruxton and Saravia, 1998; Berec, 2002), where ALLD, TFT or ALLC players are arranged on a two-dimensional spatial lattice using a deterministic and synchronized updating rule (Nowak and May, 1992). That is, in each round, every individual "plays the game" with the immediate neighbors; after this, the individual player will either insists its strategy or imitates one of its neighbor's depending on who scores the highest total payoff, everyone's total payoff is measured by adding up the score from all encounters in that round; and so to the next round of the game. The biological interpretation of this updating rule is related to reproductive success, where
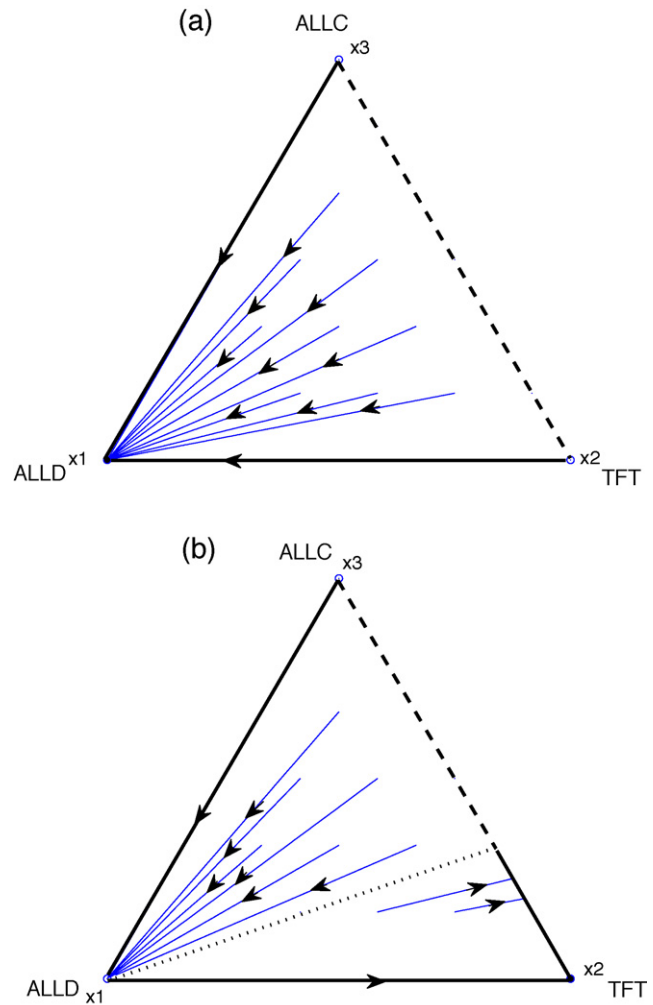
Fig. 1. The replicator dynamics of the three strategies in the completely well-mixed population. (a) Parameters are $b = 9/5$, $w = 1/3$, and $b > 1/(1-w)$; (b) parameters are $b = 9/5$, $w = 2/3$, and $b < 1/(1-w)$. The lines with arrows are the trajectories, where the arrows indicate the direction of the trajectories. The solid lines without arrows are stable fixed sets, while the dashed lines are unstable manifold. The dotted line is an invariant set in (b).

more successful strategies have more offsprings. In this study, we assume that each player only plays with its four immediate neighbors, which is referred to as "Neumann" neighborhood. Using the terminology of cellular automata, the lattices represent the players and the strategies are termed as states. In the following of this study, we will not distinguish the appellations strictly.

3.2. Analysis

3.2.1. Payoffs for local configurations

As pointed out in the previous section, the change of player's "behavior" depends on the payoff of the players in the immediate neighborhood, which in turn depends on the local occupation. In order to derive the analytical conditions for the transition of state, we thus have to look more closely at the local occupation patterns, which includes the focal player and its four immediate neighbors. We denote the local occupation pattern as $K_\theta^{s,p}$. Here $\theta \in \{0, 1, 2\}$ represents the state of the focal player, where 0, 1 and 2 correspond to ALLD, TFT and ALLC, respectively, and $s, p \in \{0, 1, 2, 3, 4\}$ give the total numbers of TFT, ALLC in the nearest neighborhood, respectively. According to the above definition of local occupation pattern, we can see that the relative positions of neighbors does not affect the payoff of a focal player.

For each possible realization of $K_\theta^{s,p}$, the payoff of the focal player, $a_\theta^{s,p}$ can be calculated. The results are given by Eq. (2) in terms of an analytical expression and for a particular realization of the payoff matrix in the Table 1.

$$a_0^{s,p} = sb + \frac{pb}{1-w}, \quad a_1^{s,p} = \frac{s+p}{1-w}, \quad a_2^{s,p} = \frac{s+p}{1-w} \qquad (2)$$

We notice that the payoff $a_\theta^{s,p}$ increases with the number of TFT players or ALLC players in the neighborhood, i.e., for a particular θ

$$a_\theta^{s,p} > a_\theta^{s-1,p}(s \in \{1,2,3,4\}, s+p \leq 4) \qquad (3a)$$

$$a_\theta^{s,p} > a_\theta^{s,p-1}(p \in \{1,2,3,4\}, s+p \leq 4) \qquad (3b)$$

Furthermore, we have

$$a_1^{s,p} = a_2^{s,p}(s, p \in \{1,2,3,4\}) \qquad (4a)$$

$$a_0^{t,q} > a_0^{s,p}(s, p \in \{1,2,3,4\}, s+p = t+q, s > t) \qquad (4b)$$

$$a_0^{0,4} = \max\{a_0^{s,p}, a_1^{s,p}, a_2^{s,p}\}(s, p \in 1,2,3,4) \qquad (4c)$$

$$a_1^{0,0} = a_2^{0,0} = \min\{a_0^{s,p}, a_1^{s,p}, a_2^{s,p}\}(s, p \in 1,2,3,4). \qquad (4d)$$

Based on these general considerations, we will discuss different conditions that arise in the spatial case for the invasion or the coexistence of the three strategies ALLD, ALLC and TFT.

3.2.2. Conditions for invasion and coexistence

To derive the conditions for invasion and coexistence, it is necessary to concentrate on the border region between the domains of ALLD players, TFT players and ALLC players. To elucidate the dynamics at the border, we will independently discuss the two possible cases, (i) configurations $K_0^{s,p}$ "owned" by ALLD players invade into neighboring configurations $K_1^{s,p}$ "owned" by TFT players and $K_2^{s,p}$ "owned" by ALLC players. In this study, we should only pay attention to that $K_0^{s,p}$ invade into $K_1^{s,p}$ since the equality shown in Eq.

(4a); (ii) configurations $K_1^{s,p}$ ($K_2^{s,p}$) invade into neighboring configurations $K_0^{s,p}$, $K_2^{s,p}$ ($K_1^{s,p}$), respectively. Note that the ALLD player and TFT (ALLC) player are always on the adjacent sites. Some results are explained below.

The ALLD players can definitely invade the whole spatial population, if the lowest possible payoff of ALLD player is larger than the highest possible payoff for collaborators. According to Eqs. (3a) and (3b), this leads to the necessary condition for the complete invasion of ALLD player into the domain of TFT player, $a_0^{1,0} > \max_{(s+p=4)}\{a_1^{s,p}\}$. Actually, the payoff $a_0^{0,0}$ can be ignored here, because in the configuration $K_0^{0,0}$, there is no TFT player left to adopt the ALLD strategy. It is also required that $a_0^{0,1} > \max_{(s+p=4)}\{a_2^{s,p}\}$ as the same reason. Then all the above inequalities are concluded as the necessary condition for the complete invasion of ALLD behavior, $\min\{a_0^{1,0}, a_0^{0,1}\} > \max_{(s+p=4)}\{a_1^{s,p}, a_2^{s,p}\}$. That is $b > 4/(1-w)$. Obviously, it contradicts to our requirement $1 < b < 2$, $0 < w < 1$. Similarly, the TFT behavior can definitely invade the whole spatial population, if $\min\{a_1^{0,0}, a_1^{0,1}\} > \max_{(s+p=4)}\{a_0^{0,4}, a_2^{s,p}\}$. And, for the ALLC players, the condition is $\min\{a_2^{0,0}, a_2^{1,0}\} > \max_{(s+p=4)}\{a_0^{0,4}, a_1^{s,p}\}$. Both of the two equalities contradict to the requirement referred above. Combined with the analysis of ALLD behavior, we derive the conclusion that there is no strategy can invade the whole spatial population, if the three strategies all initially exist. It is obvious that TFT player and ALLC player are neutral without ALLD player according to Eq. (4a).

The above analysis is only a sketch illustration to the invasion process, however, some detailed analyses are also required. For example, for the ALLD strategy, we notice that $K_0^{s,p}$ could always $(s+p=3)$ invade neighboring configurations $K_1^{s,p}$ or $K_2^{s,p}$ because the $(s+p\leq3)$ $(s+p\leq3)$ necessary condition $\min_{(s+p=3)}\{a_0^{s,p}\} > \max_{(s+p\leq3)}\{a_1^{s,p}, a_2^{s,p}\}$ always holds $(3b > 3/(1-w))$. But this kind of invasion does not happen, if
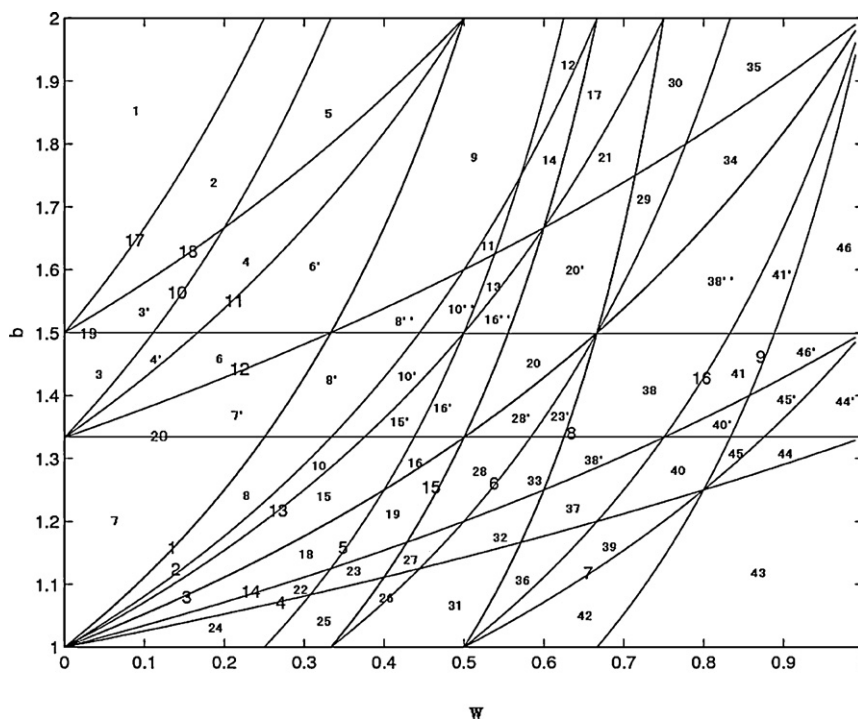

Fig. 2. The parameter plane of $\{w, b\}$ can be separated into 65 small areas according to the possible payoffs of the three strategies. The horizontal axis is w and the vertical axis is b. The definition of all the 20 lines indexed are shown in Appendix B.

max $\{a_0^{s,p}\} < 4/(1-w)$ is valid. In contrast, the configuration $(s+p=3)$ $K_0^{s,p}$ cannot invade neighboring configurations $K_1^{s,p}$ or $K_2^{s,p}$ $(s+p=3)$ $(s+p\leq3)$ $(s+p\leq3)$ because of the higher payoff of configuration $K_1^{s,p}$ or $K_2^{s,p}$ that $(s+p=4)$ $(s+p=4)$ "backs" them from the other side, so the border remains at its current position. However, to fully analyze the invasion and coexistence patterns is a difficult task because the local occupation configurations are intricate. Whereas we know that the change of player's behavior only depends on the payoffs of the players in the immediate neighborhood, and the possible payoff $a_\theta^{s,p}$ only depends on the two variables w and b, therefore, we will mainly focus on these two parameters. The mathematical analysis will divide the parameter plane according to the different payoff conditions. Moreover, as the payoffs $a_\theta^{s,p}$ in Eq. (2) is known, we can derive all of the conditions and list them in Appendix B (the same equation has been deleted). Additionally, we always have $0 < w < 1$ and $1 < b < 2$. As long as the spatiotemporal dynamics, it need further computer simulations. The detailed division and results are shown in the next section.

3.3. Results

The $\{w, b\}$ parameter plane can be divided into 65 areas (Fig. 2), where all lines coincide with front restrictions marking the different boundaries between areas. One the other hand, what really interests us is the spatiotemporal dynamics in these different areas. We carry on computer simulations for different parameters selected in each area, the lattice size is $N = 100 \times 100$ with fixed boundary conditions (the qualitative character of our results is unchanged if we instead choose periodic boundary conditions), the initial frequency of strategies is equal and individuals are randomly distributed. In order to introduce a time scale, we define a generation G to be the time in which each player has interacted with its four nearest neighbors one time (also referred to as a one-shot game). Through an extensive simulation and careful identifications, nine different dynamic regions, each characterized by a distinct spatiotemporal

dynamics and a corresponding final distribution, are confirmed (see Fig. 3). Next, we will introduce all of them one by one. And each will be summarized in the following subtitles in bold.

Case 1. There is stable coexistence state with large domains of ALLD players in a background of TFT players and ALLC players.

$\{(w, b)|3/(2 - 2w) < b\} \cap \{(w, b)|0 < w < 1/4, 2/3 < b < 2\}$.

The above set is denoted as region **1** in Fig. 3. For parameters located in this region, ALLD players cluster with static large domains in the sea of TFT players and ALLC players. The frequency of the three strategies is approximately stable within a very short time, and the values are $f(0) = 0.6$, $f(1) = 0.2$ and $f(2) = 0.2$, respectively. These results are robust and are not sensitive to the initial distribution.

Case 2. ALLC players form stable small domains, but movement at the boundary between clusters of ALLD players and TFT players can always be observed.

$\{(w, b)|4/(3 - 3w) < b < 3/(2 - 2w)\} \cap \{(w, b)|3/2 < b < 2\}$.

The above set is denoted as region **2** in Fig. 3. The movement at the boundary between clusters of TFT players and ALLD players can always be observed, therefore, the frequencies of ALLD players and TFT players will fluctuate slightly all the time. There will be a few small compact clusters of ALLC players that like islands in the sea of ALLD players, and the relative frequency of ALLC players will reach a stationary state after a short transient period. The spatiotemporal dynamics of TFT players is similar to ALLC players but the relative frequency will be higher. We give an example in Fig. 4(a)–(c).

Case 3. There is unstable coexistence state between large domains of ALLD players and the background of ALLC players. And TFT players will disappear. Spatiotemporal chaos arises.

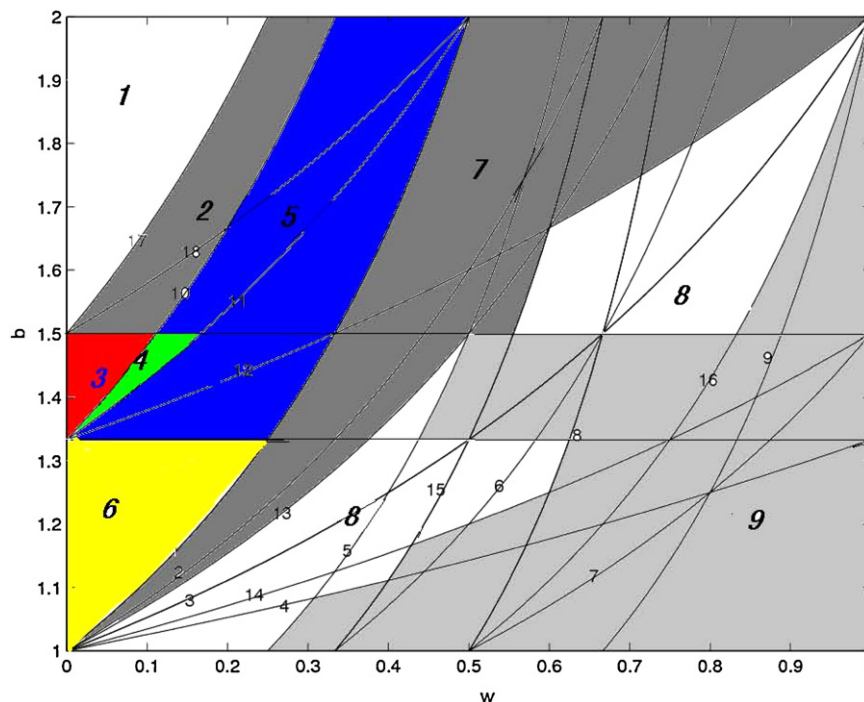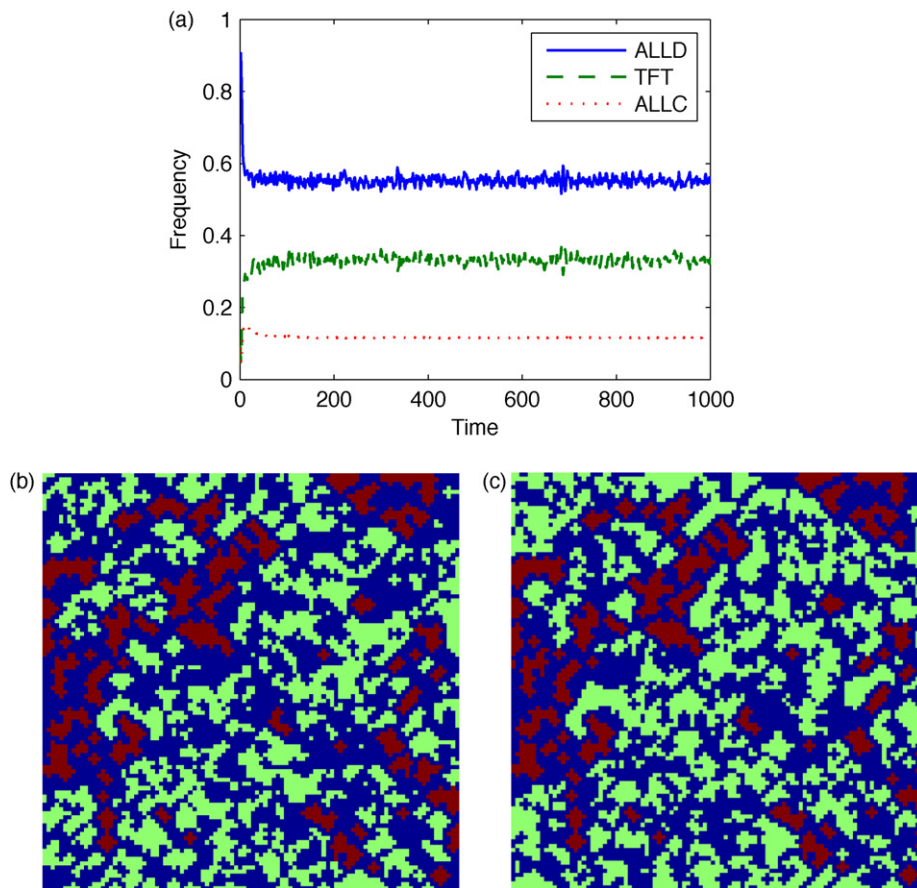$\{(w, b)|4/(3 - 3w) < b\} \cap \{(w, b)|0 < w < 1/9, 4/3 < b < 3/2\}$.

Fig. 3. Based on computer simulation, we can summarize the 65 parameter areas in Fig. 2 into 9 different dynamic regions, each characterized by a distinct spatiotemporal dynamics and a corresponding final distribution. The horizontal axis is w and the vertical axis is b. All the nine regions are indicated in bold numbers.

Fig. 4. The spatial game can generate nine qualitatively different spatiotemporal dynamics, depending on the parameters b and w. Simulations are performed on a 100×100 square lattice with fixed boundary conditions, and start with 1/3 ALLD, 1/3 TFT, and 1/3 ALLC players located randomly. This figure shows an example for $b = 1.6$, $w = 0.1$ in region **2**, and the following others give examples in some other regions. (a) The temporal dynamics of frequencies of the three strategies over 1000 generations, solid line indicates ALLD, dashed line indicates TFT and dotted line indicates ALLC. (b) and (c) The spatial patterns at generations $G = 100$ and $G = 1000$, respectively. The color coding is as follows: blue is an ALLD, green is a TFT, and red is an ALLC player. (For interpretation of the references to color in these figure legend, the reader is referred to the web version of the article.)

The above set is denoted as region **3** in Fig. 3. Parameters in this region correspond to mutual invasion process between ALLD players and TFT players, or between ALLD players and ALLC players. TFT and ALLC players can easily form big clusters only after a short period. These initial clusters of ALLC players then split up into smaller clusters, which grow, split up again and may disappear. As these TFT clusters grow, they will collide and joint as a large cluster. In the following steps, these smaller clusters of TFT will be taken over by ALLD, and bigger clusters of TFT will become smaller because of the neutrality with ALLC, and the more ALLC players surround a ALLD player, the bigger payoff of the ALLD player gets according to Eq. (4b). All these reasons cause to the extinction of TFT players. After TFT player disappears, the frequency of ALLD players still shows light fluctuations, so does that of ALLC players (see Fig. 5(a)). And we always observe the spatial domains of ALLD players are separated by regions of ALLC players. This leads to a non-stationary spatial distribution even in the long run, it has been already argued by Nowak and May (1992) that this region can be characterized as spatiotemporal chaos. A fixed configuration of the system is shown in Fig. 5(b) and (c).

Case 4. There is stable percolation network of ALLD players in a background of TFT players, ALLC players either form few small clusters or disappear.

$$\{(w, b)|4/(3 - 2w) < b < 4/(3 - 3w)\} \cap \{(w, b)|4/3 < b < 3/2\}.$$

The above set is denoted as region **4** in Fig. 3. ALLC players either form few small clusters or disappear for parameters located in this region. And ALLD player can invade the domain of TFT players along diagonal direction, or then form a pattern of glider (stable propagating structures) (Nowak and May, 1993) in the background of TFT players. An irregular but static pattern that percolation network of ALLD players occurring in a background of TFT players takes on as illustrated in Fig. 6.

Case 5. There is stable coexistence state with a majority of TFT players and a minority of ALLC players.

$$\{(w, b)|(3b - 4)/2b < w < (b - 1)/b, 4/3 < b < 2\}$$

$$\cup\{(w, b)|(3b - 4)/3b < w < (3b - 4)/2b, 3/2 < b < 2\}.$$

The above set is denoted as region **5** in Fig. 3. For parameters located in this region, ALLD players invade TFT players along diagonal direction, then a long strip of ALLD players arises on the grid, or they occur as a single cell, or two or three isolated cells in a background of TFT players. We can also find four or five ALLD cells form a cross or types of glider in the sea of TFT players. aggregated ALLC players are encircled by ALLD players with relative fixed borders and most of them distribute on the boundary of grid. The time needed to reach stable state decreases with increasing of b. And the final spatial patterns bear a strong resemblance to region **4**, it always shows stable coexistence state of the three kind players with a majority of TFT players and a minority of ALLC players.
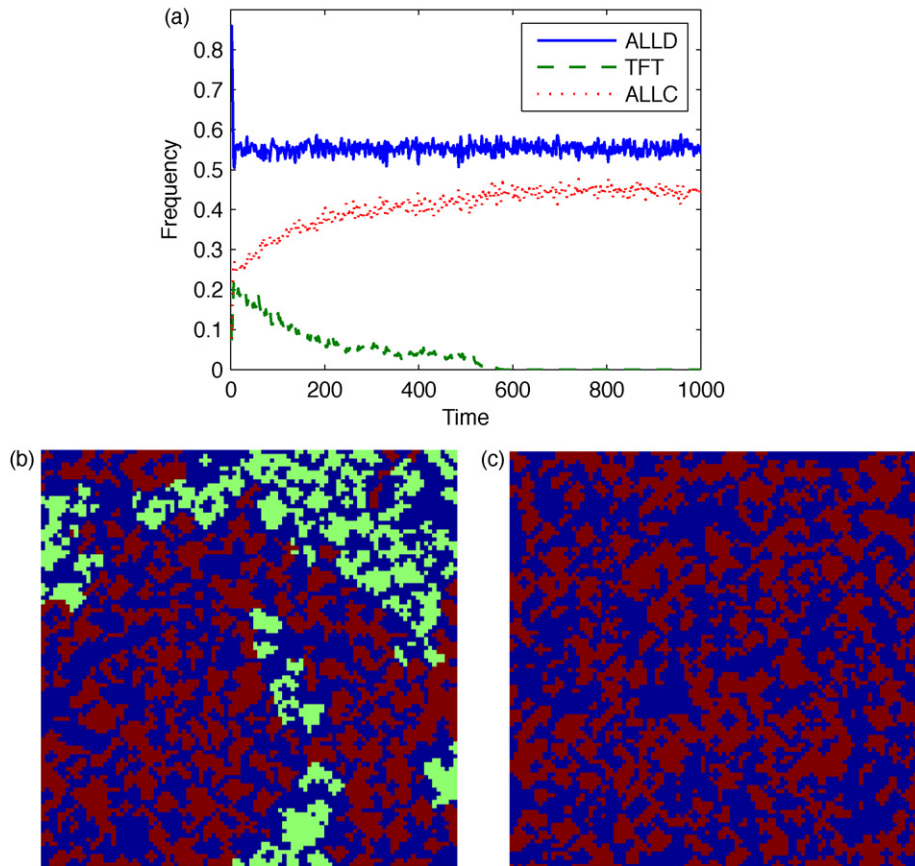
Fig. 5. Spatiotemporal dynamics for $b = 1.45$, $w = 0.08$ in region **3**. (a) The temporal dynamics of frequencies of the three strategies over 1000 generations, the representation of lines is the same as in Fig. 4(and throughout this paper). (b) and (c) The spatial patterns at $G = 100$ and $G = 1000$, respectively. Spatiotemporal chaos characterizes this region. The color coding is the same as in Fig. 4(and throughout this paper).

Case 6. There is unstable coexistence state with both a majority of TFT and ALLC players. "Evolutionary kaleidoscope" arises.

$$\{(w, b)|1/(1 - w) < b\} \cap \{(w, b)|0 < w < 1/4, 1 < b < 4/3\}.$$

The above set is denoted as region **6** in Fig. 3. ALLD players form stable squares or stripes in the background of TFT players and ALLC players within extremely short generations. The movement
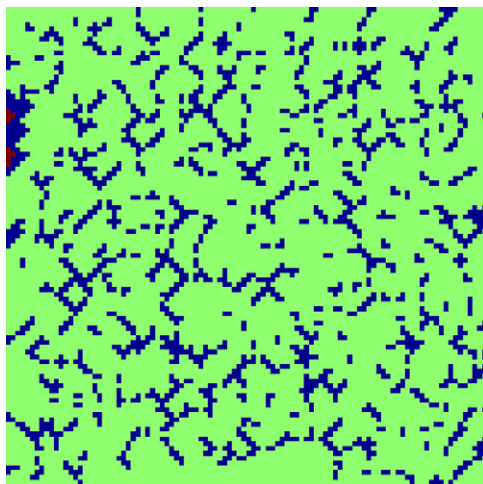
Fig. 6. Stable percolation network characterizes region **4**. The spatial pattern of the three strategies at $G = 1000$ for $b = 1.45$, $w = 0.1$ in this region.

between the border in clusters of TFT players and ALLC players can be observed, and the small cluster of TFT players will be replaced by ALLC players. Eventually most cells will be occupied by TFT and ALLC players. Fig. 7(a) gives us an illustration of the temporal dynamics. The spatial game can generate an "evolutionary kaleidoscope" such as shown in Fig. 7(b) and (c). This spatial structure evolves forever, single-players domains appear and grow indefinitely, and the process exhibits coarsening. In other words, equilibrium is never attained, instead, an irregular network of domains develops. And the domain patterns are self-similar, i.e., the structures differ only by a global change of scale between at later times and at earlier times. Such a behavior is a signature of dynamical scaling.

Case 7. There is unstable coexist state with both a minority of ALLD players and ALLC players. Irregular frozen state (with some ALLC enclosed by ALLD players) arises.

$$\{(w, b)|1/2 < w < 1, 4/(3 - w) < b < 1/(1 - w)\}$$
$$\cup \{(w, b)|(b - 1)/b < w < 3(b - 1)/2b, 1 < b < 3/2\}$$
$$\cup \{(w, b)|(3b - 4)/b < w < (3b - 2)/3b, 3/2 < b < 2\}.$$

The above set is denoted as region **7** in Fig. 3. If parameters are chosen in this region, we can observe that isolated ALLD players and clusters of ALLC players appear in TFT players. Eventually most cells will be occupied by TFT players. Irregular frozen state (Lindgren and Nordahl, 1994) will be observed with some ALLC enclosed by ALLD players. Fig. 8(a) and (b) show us a specific case.
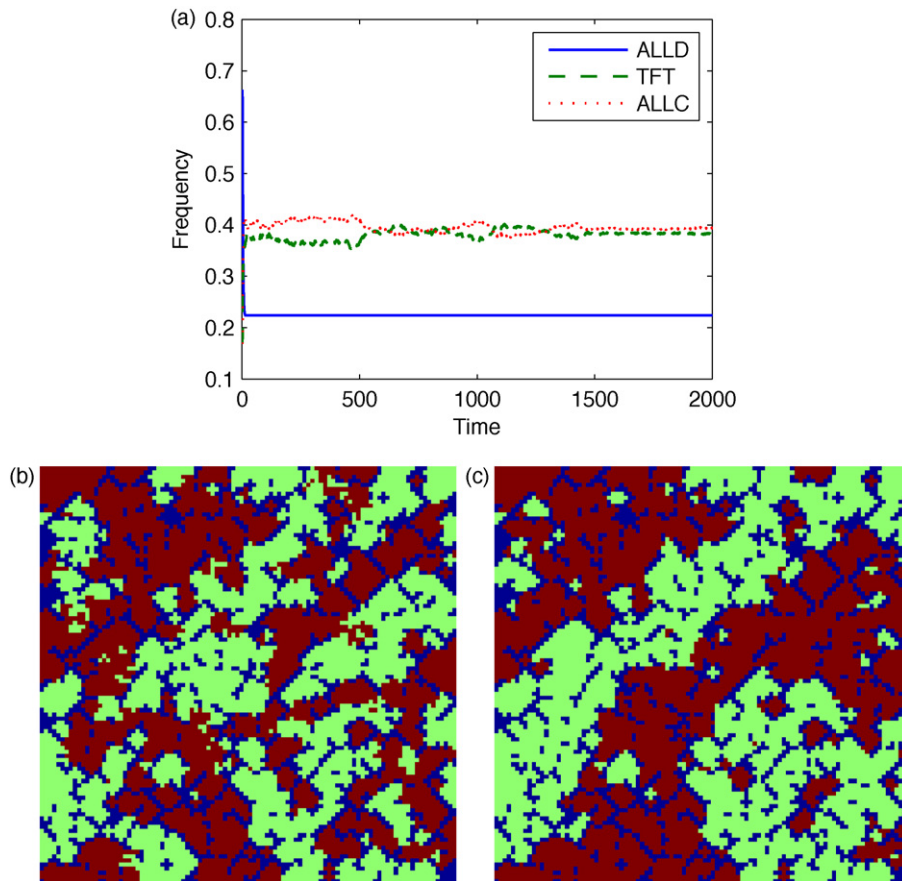
Fig. 7. Spatiotemporal dynamics for $b = 1.2$, $w = 0.1$ in region **6**. (a) the temporal dynamics of frequencies of the three strategies over 2000 generations. (b) and (c) are the spatial patterns at $G = 100$ and $G = 2000$, respectively. "Evolutionary kaleidoscope" characterizes this region.
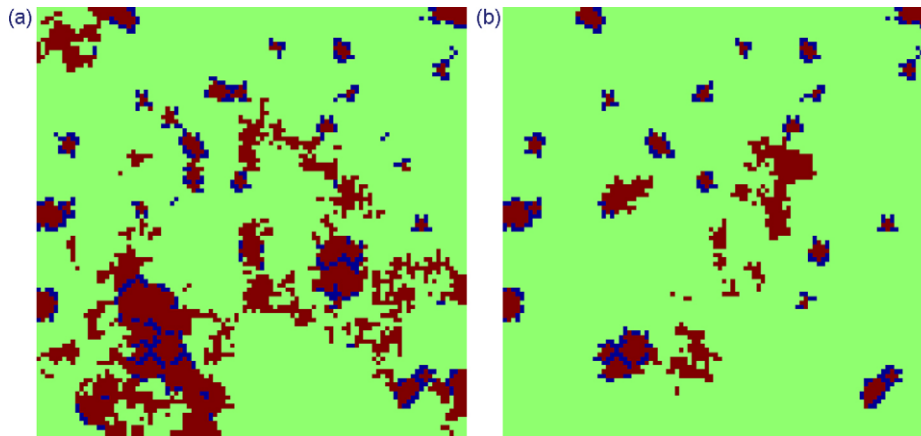

Fig. 8. Irregular frozen state (with some ALLC enclosed by ALLD players) characterizes region **7**. (a) and (b) the spatial patterns at $G = 100$ and $G = 1000$, respectively for $b = 1.3$, $w = 0.25$ in this region.

Case 8. ALLD players may disappear or exist with only few regular small stable domains or single cells.

$\{(w, b)|3(b-1)/2b < w < (4b-3)/4b, 1 < b < 2/3\}$

$\cup \{(w, b)|(3b-2)/3b < w < (3b-2)/2b, 3/2 < b < 4/(3-w)\}$

$\cup \{(w, b)|(4b-3)/4b < w < (3b-2)/3b, 4/(4-w) < b < 4/3\}$

$\cup \{(w, b)|(3b-2)/3b < w < (2b-1)/2b, 3/(3-w) < b < 4/3\}$.

The above set is denoted as region **8** in Fig. 3. ALLD players may disappear or exist with only few regular small stable domains and single cells in this region. Fig. 9 gives us an example that ALLD players enclose some clusters of ALLC players in their border regions.

Case 9. ALLD players disappear.

$\{(w, b)|(3b-2)/3b < w < 1, 3/2 < b < 2\} \cup \{(w, b)|(2b-1)/2b$

$< w < 1, 1 < b < 4/3\} \cup \{(w, b)|(4b-3)/4b < w < 1, 4/3$

$< b < 3/2\} \cup \{(w, b)|(3b-2)/3b < w < (2b-1)/2b, 1 < b$

$< 3/(3-w)\} \cup \{(w, b)|(4b-3)/4b < w < (3b-2)/3b, 1$

$< b < 4/(4-w)\}$.
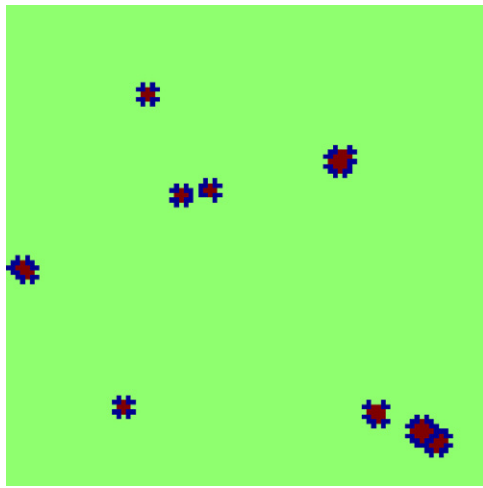
Fig. 9. The spatial pattern of the three strategies at $G = 1000$ for $b = 1.65$, $w = 0.7$ in region **8**.

The above set is denoted as region **9** in Fig. 3. ALLD players disappear in this region. And it can be taken as the homogeneity of cooperative state because of neutrality between TFT and ALLC strategy.

And we always observe that ALLD players take over a lot of cells after one generation no matter what parameter region is in the simulations. There are only single ALLC player, single TFT player, small square of ALLC players, and small square of TFT players left. The single ALLC players and single TFT players almost disappear while $G = 2$, but the small square of ALLC players and small square of TFT players which have formed in $G = 1$ tend to grow bigger in the following generations. Different parameter regions own different transient period for clustering. For example, it is obvious that ALLC and TFT players form clusters much faster in regions **7** and **8** than the others. And we notice stationary spatial configuration appears once clusters of ALLC players are all enclosed by ALLD players. Although ALLC is dominated by ALLD in well-mixed populations, ALLC players can build clusters which resist invasion of ALLD while only considering local spatial interactions. Otherwise, non-stationary spatial state emerges once ALLC players surpass the enclosure. On the one hand, ALLD player would invade these disadvantageous ALLC players, on the other hand, ALLD players can be indirectly invaded by TFT players who seems far from them now, but these TFT players may approach them sooner or later due to the neutrality between ALLC and TFT.

So far, we have investigated the spatiotemporal dynamics in these nine pure parameter regions, however, the question arising is how the system behaves if we choose parameters on the border between two regions. From the above conclusions, we have already known that there must be some border regions which mark the transition from stable coexistence to invasion thus leads to the non-stationary state (such as the transitional border **5**|**6** from region **5** to region **6**). Next, we also give some investigation to them. And we notice not both frequencies and spatial patterns of a border all hold the same dynamics as one of its neighboring regions. For instance, in the case of **1**|**2** border, the frequencies are the same as in region **1** once reaching stationary state. But spatial dynamics always only show the movement between the border domains of ALLD players and TFT players, while the light invasion dynamics between ALLD player and ALLC player in region **1** can not arise. In the case of **2**|**5** border, the movement between the border domains of ALLD players and TFT players like region **2** can be observed, but the final spatial pattern is similar to region **5**, that the respective separated domains

of their's own cannot be seen. A strange phenomenon arises in the **2**|**3** border where ALLC players disappear instead of TFT players, which seems counter-intuition because it is TFT players disappear in region **3**. Actually, the outcome in the border is expected because there is only a minority of ALLC players in the region **2**. Thus, the **2**|**3** border gives an obvious segregation between the two regions. **5**|**7** and **6**|**7** hold the analogous dynamics to their common neighboring region **7**, but a much faster invasion speed of TFT players in the **6**|**7** border can be observed. We also find the frequencies and spatial pattern of **5**|**6** are all the same as in region **6**. There are still other border regions but we do not list all of them one after another, since their behavior are trivial and not worthy of interest.

Furthermore, we know Nowak and May (1992, 1993) have obtained the detailed division for their unique parameter b based on the simple spatial PD by means of computer simulations. Let $w = 0$ and make only cooperator and defector left in the initial populations, our work can be verified with theirs, and the consistent conclusions can be obtained clearly.

4. Conclusions and discussion

Repeated Prisoner's Dilemma is the game theoretic framework of reciprocity (Trivers, 1971), which is a mechanism for the evolution of cooperation. While network reciprocity is another mechanism for the evolution of cooperation, and it is actually the generalization of spatial reciprocity (Nowak and May, 1992) to evolutionary graph theory (Lieberman et al., 2005). In this paper, we have constructed a spatial game model combining direct and spatial reciprocity together to investigate how evolution of cooperation is influenced in spatially structured populations. The spatiotemporal dynamics of the three strategies ALLD, TFT, and ALLC were investigated by both mathematical analysis and computer simulations. Remarkably, our results confirm that spatial structure promotes cooperation, echoing Nowak and May (1992, 1993), Huberman and Glance (1993), Nowak et al. (1994), Killingback et al. (1999). In line with some previous studies, it was observed that the survival of cooperators was based on forming clusters, which allowed them to persist despite exploitation by defectors along the cluster boundaries (Doebeli and Hauert, 2005). Meanwhile, nine different spatiotemporal dynamic regimes were concluded with the division of parameter plane. The spatial game model gave rise to amazing evolutionary diversity where cooperation could be promoted.

First, we will focus our interest on the differences between non-spatial and spatial game models. From analysis in well-mixed populations in Section 2, we can easily obtain that, under the initial equal frequency condition, the parameter groups which satisfy $b < 2/(2 - w)$ coincide with the evolutionary end points of cooperation, whereas it will be defection if inverse parameter conditions were chosen. Hence, the third line $b = 2/(2 - w)$ in Fig. 2 forms the boundary between the two evolutionary stable state. If parameters are chosen above it in non-spatial game, the evolutionary outcome is ALLD, otherwise is cooperation under it. But for the spatial game, we have obtained some new findings comparing with the non-spatial game model. The most important is that the state where all individuals adopting ALLD strategy can be fully eliminated for each parameter setting while only considering the local spatial interactions. Refer to Fig. 3, the spatiotemporal dynamics can give rise to coexistence with defectors (see regions **1**–**7** above the third line). For example, this could happen if the system goes to a fixed point containing stable spatial domains of cooperators, or through space-time chaos. Then we clearly obtain cooperation is prompted in regions **1** –**7** under the spatial setting. Region **9** (below the third line) still shows pure cooperation state in spatial setting. Therefore, space no longer plays a role in the determination of the evolutionary state if parameter values are chosen from region

9, that is the same regardless of whether interaction occurs only between nearest neighbors or between all players in the system. The transition region **8** (from coexistence state to the homogeneous cooperator state) which takes on ALLD disappear or exist with only a few of single cells, is a special case, not all of the areas included in is above or under the third line. Why? It is only the stochasticity in finite population size. All in all, the fact that spatial structure facilitates evolution of cooperation can be verified in our study. And spatial structure tends to allow more diversity than prevails in well-mixed populations (Nowak and Sigmund, 2004), which can also be realized once again. These different coexistence patterns of multiple strategies can be interpreted as the evolution of intraspecific diversity (meaning here players with different behavior strategies).

From the above discussion, we have known the spatial structure facilitates the evolution of cooperation in our model, and the question arising naturally is that how cooperation is promoted in spatially structured populations. There has been a common view about the main effect of spatial structure is that cooperative strategies can build clusters of similar individuals due to local reproduction in which the benefits of mutual cooperation outweigh losses against defectors. Thus, clusters of cooperative players can invade into populations of defectors that constitute an evolutionary stable strategy (ESS) in non-spatial populations (Axelrod and Hamilton, 1981; Nowak and May, 1992; Killingback and Doebeli, 1996; Brauchli et al., 1999). No doubt, our study is not an exception. But the significance of our study is not merely to confirm some previous common view but to reveal the impact of geometry of cluster formation to the spatiotemporal dynamics in spatially structured population. In particular, simulations have shown the coexistence of strategies might be achieved by forming stable spatial domains. It was observed that cooperative TFT and ALLC players could form scattered domains and survive in the background of ALLD players. In general, any compact domain formation would be preferable for TFT players and ALLC players, however, the ALLD players make them become rare. Domain formation is inevitably changed by competition between these mutual invasion processes of the three kinds of players, which varies in different regions of parameter space. For example, the TFT players and ALLC players can invade the territory of ALLD players along straight borderlines, while ALLD players gain along irregular boundaries for some given intervals of b and w, due to the discrete nature of total payoffs. Visualizing the time-dependent configurations, we can observe how the domains try to spread out. Domain walls move randomly. Their center, size, shape and location change continuously and a segregated domain may disappear without any trace. Two domains can unite which provides a better opportunity for their survival. Or inversely, a domain can be separated into two (or more) parts. While the same procedure repeatedly, stable domains may gradually organize if there is a trade-off between these competition strength, thus coexistence state becomes true. And it will be shown that the transitions from the active state (coexistence of the three kinds of players) to the absorbing ones (homogenous cooperators) exhibit universal behavior.

Finally but very importantly, Doebeli and Hauert (2005) reviewed that most models of spatial evolutionary game theory are generally difficult to obtain analytical results, because they can exhibit very complicated dynamics (e.g. Killingback and Doebeli, 1998; Hauert, 2001). Some analytical results have been obtained through geometrical arguments about cluster formation analysis (Nowak and May, 1992; Killingback et al., 1999; Hauert, 2001). Recently, Schweitzer et al. (2002) derived the critical conditions for the invasion or the spatial coexistence of cooperators and defectors. Meanwhile, interesting phase transitions can occur between the different dynamic regimes of spatial games, which were reported in some previous studies (Szabo and Toke, 1998; Szabo and Hauert,

2002). In this study, the idea of local payoff structures analysis is similar to that of Schweitzer et al. (2002). However, it is not easy to derive similar analytical results as Schweitzer et al. (2002) since three strategies game is much more complex than the original PD. Fortunately, we find that the critical conditions for invasion and coexistence are only determined by the payoff structure. Then the problem can be solved by comparing the payoff differences of local patterns. A rough partition for the plane of parameters $b - w$ can be obtained firstly. Then based on extensive computer simulations that reveal the distinct spatiotemporal dynamics and the corresponding final spatial patterns, the parameter plane can be divided and each of them can be identified. Although the method does suffer the drawback of time consuming, but its accuracy and usefulness to the partition of the parameter region is undoubted.

Nowak and May (1992) have shockingly revealed that simple, and purely deterministic spatial version of the PD can generate chaotically changing spatial patterns, in which cooperators and defectors both persist indefinitely. In their following work (Nowak and May, 1993), they found that spatial chaos and dynamic fractals were typical features of spatial evolutionary game (i.e., evolutionary games played with neighbors on spatial lattices). Through analysis based on the fate of a single isolated defector or cooperator and combined with computer simulations, they did more extensively and carefully investigations for different spatial geometry structure and local interaction neighborhood structures. However, it should be kept in mind that, individual cells do not have memory or elaborate strategies in their models. And, another parameter w arises naturally while considering direct reciprocity in our work. Thus, the dynamics depends on the two parameters w and b. Specifically, Nowak and May (1993) also derived the parameter division of b for the four neighborhood structure which was investigated in this paper. They are, respectively, coexistence with large domains of cooperators if $1 < b < 4/3$; coexistence with spatial chaos if $4/3 < b < 3/2$; and coexistence with small clusters of cooperators if $3/2 < b < 2$. As illustrated in Fig. 2, the lines 19 and 20 indicate $b = 3/2$ and $b = 4/3$, respectively. It clearly gives the phase division as shown in Fig. 3. We find parameters in regions **1–6** where w close to zero (can be approximately taken as the simple PD) produce nearly the same spatiotemporal dynamics. For instance, the interesting region **3** also represents spatial chaos which satisfies $4/3 < b < 3/2$. Therefore, the accuracy of the method can be verified again.

Doebeli and Hauert (2005) have pointed out, the overall conclusion that spatial structure is beneficial for the evolution of cooperation has been obtained mainly for the PD model in which spatial structure was incorporated by using regular square lattices, in which interaction and reproduction (imitation) was limited to either the four or the eight nearest neighbors. However, so far as we know, regular square lattices, the nearest local interaction and reproduction neighborhood structure are not necessary. Some research results have indicated that the lattice topology does affect the dynamics of cooperation, and interestingly, relaxing the rigid purely local neighborhood structure of lattices seems to benefit cooperation (Abramson and Kuperman, 2001; Masuda and Aihara, 2003; Ifti et al., 2004; Hauert and Szabo, 2005). And much attention has been given to "evolutionary graph theory" recently, which aims at investigating the impact of graph topology on the evolution of cooperation (Lieberman et al., 2005; Ohtsuki and Nowak, 2006; Ohtsuki et al., 2006; Grafen, 2007; Lehmann et al., 2007; Taylor et al., 2007). For example, Santos et al. (2006a) have demonstrated that cooperation can be favored in heterogeneous populations, such heterogeneity can result from the joint evolution of graph topology and cooperation (Santos et al., 2006b, c). In this paper, we only investigated four neighborhood structure using deterministic synchronous updating. In fact, many variants are possible in terms of lattice geometry neighborhood structure, deterministic or stochas-

tic updating, synchronous or asynchronous, and so on. It deserves further investigation in future.

Appendix A.

$$\frac{dx_2}{dt} = x_2(1 - x_2 - x_3)\left[\frac{1}{1-w}(x_2+x_3) - (bx_2 + \frac{b}{1-w}x_3)\right] = x_2(1-x_2-x_3)P$$

$$\frac{dx_3}{dt} = x_3(1 - x_2 - x_3)\left[\frac{1}{1-w}(x_2+x_3) - (bx_2 + \frac{b}{1-w}x_3)\right] = x_3(1-x_2-x_3)P$$

The points on the invariant line $x_2 + x_3 = 1$ are not hyperbolic because one of the eigenvalue of the jacobian matrix is zero. Therefore, the linearization tells us nothing about the stability properties of these fixed points in the original system. We can consider the relative entropy function $V = 1 - (x_2 + x_3)$, defined for allowable states of the system close to these points $\bar{x} = (x_2, x_3)$ with $x_2 + x_3 = 1$. Such that, $V(\bar{x}) = 0$, $V(\bar{x}) > 0$ for any points $x \in O(\bar{x})$.

$$\frac{dV}{dt} = -(\dot{x}_2 + \dot{x}_3)$$

The derivative of V about t is

$$\begin{aligned}\frac{dV}{dt} &= -\{x_2(1-x_2-x_3)\left[\frac{1}{1-w}(x_2+x_3) - (bx_2 + \frac{b}{1-w}x_3)\right] \\ &\quad + x_3(1-x_2-x_3)\left[\frac{1}{1-w}(x_2+x_3) - (bx_2 + \frac{b}{1-w}x_3)\right]\} \\ &= -\{(x_2+x_3)(1-x_2-x_3)\left[\frac{1}{1-w}(x_2+x_3) - (bx_2 + \frac{b}{1-w}x_3)\right]\} \\ &> -\{(x_2+x_3)(1-x_2-x_3)\left[\frac{1}{1-w}(x_2+x_3) - (bx_2 + bx_3)\right]\} \\ &= (b - \frac{1}{1-w})(x_2+x_3)^2(1-x_2-x_3)\end{aligned}$$

Since $0 < x_2 < 1$, $0 < x_3 < 1$, $1 < b < 2$, $0 < w < 1$, therefore, when $b(1-w) > 1$, we have $dV/dt > 0$ for any points $x \in O(\bar{x})$. Thus we can obtain that $x_2 + x_3 = 1$ is an unstable manifold.

Appendix B.

$1: \quad 4b \gtrless \frac{4}{1-w} \Rightarrow b = \frac{4}{4-4w}$

$2: \quad 3b + \frac{b}{1-w} \gtrless \frac{4}{1-w} \Rightarrow b = \frac{4}{4-3w}$

$3: \quad 2b + \frac{2b}{1-w} \gtrless \frac{4}{1-w} \Rightarrow b = \frac{4}{4-2w}$

$4: \quad b + \frac{3b}{1-w} \gtrless \frac{4}{1-w} \Rightarrow b = \frac{4}{4-w}$

$5: \quad 4b \gtrless \frac{3}{1-w} \Rightarrow b = \frac{3}{4-4w}$

$6: \quad 3b + \frac{b}{1-w} \gtrless \frac{3}{1-w} \Rightarrow b = \frac{3}{4-3w}$

$7: \quad 2b + \frac{2b}{1-w} \gtrless \frac{3}{1-w} \Rightarrow b = \frac{3}{4-2w}$

$8: \quad 4b \gtrless \frac{2}{1-w} \Rightarrow b = \frac{2}{4-4w}$

$9: \quad 3b + \frac{b}{1-w} \gtrless \frac{2}{1-w} \Rightarrow b = \frac{2}{4-3w}$

$10: \quad 3b \gtrless \frac{4}{1-w} \Rightarrow b = \frac{4}{3-3w}$

$11: \quad 2b + \frac{b}{1-w} \gtrless \frac{4}{1-w} \Rightarrow b = \frac{4}{3-2w}$

$12: \quad b + \frac{2b}{1-w} \gtrless \frac{4}{1-w} \Rightarrow b = \frac{4}{3-w}$

$13: \quad 2b + \frac{b}{1-w} \gtrless \frac{3}{1-w} \Rightarrow b = \frac{3}{3-2w}$

$14: \quad b + \frac{2b}{1-w} \gtrless \frac{3}{1-w} \Rightarrow b = \frac{3}{3-w}$

$15: \quad 3b \gtrless \frac{2}{1-w} \Rightarrow b = \frac{2}{3-3w}$

$16: \quad 2b + \frac{b}{1-w} \gtrless \frac{2}{1-w} \Rightarrow b = \frac{2}{3-2w}$

$17: \quad 2b \gtrless \frac{3}{1-w} \Rightarrow b = \frac{3}{2-2w}$

$18: \quad b + \frac{b}{1-w} \gtrless \frac{3}{1-w} \Rightarrow b = \frac{3}{2-w}$

$19: \quad \frac{2b}{1-w} \gtrless \frac{3}{1-w} \Rightarrow b = \frac{3}{2}$

$20: \quad \frac{3b}{1-w} \gtrless \frac{4}{1-w} \Rightarrow b = \frac{4}{3}$

References

Abramson, G., Kuperman, M., 2001. Small world effect in an epidemiological model. Phys. Rev. Lett. 86 (13), 2909–2912.

Axelrod, R., 1984. The Evolution of Cooperation. Basic Books, New York.

Axelrod, R., Dion, D., 1988. The further evolution of cooperation. Science 242, 1385–1390.

Axelrod, R., Hamilton, W.D., 1981. The evolution of cooperation. Science 211, 1390–1396.

Balzter, H., Braun, P.W., Kohler, W., 1998. Cellular automata models for vegetation dynamics. Ecol. Model. 107, 113–125.

Berec, L., 2002. Techniques of spatially explicit individual-based models: construction, simulation, and mean-field analysis. Ecol. Model. 150, 55–81.

Brauchli, K., Killingback, T., Doebeli, M., 1999. Evolution of cooperation in spatially structured populations. J. Theor. Biol. 200, 405–417.

Doebeli, M., Hauert, C., 2005. Models of cooperation based on the Prisoner's Dilemma and the snowdrift game. Ecol. Lett. 8, 748–766.

Frank, S.A., 1998. Foundations of Social Evolution. Princeton University Press, Princeton, NJ.

Grafen, A., 2007. An inclusive fitness analysis of altruism on a cyclical network. J. Evol. Biol. 20, 2278–2283.

Hauert, C., 2001. Fundamental clusters in spatial 2×2 games. Proc. R. Soc. Lond. B 268, 761–769.

Hauert, C., Doebeli, M., 2004. Spatial structure often inhibits the evolution of cooperation in the snowdrift game. Nature 428, 643–646.

Hauert, C., Szabo, G., 2005. Game theory and physics. Am. J. Phys. 73, 405–414.

Hofbauer, J., Sigmund, K., 1998. Evolutionary game and population dynamic. Cambridge University Press, Cambridge, UK.

Hofbauer, J., Sigmund, K., 2003. Evolutionary game dynamics. Bull. Am. Math. Soc. 40, 479–519.

Hofbauer, J., Schuster, P., Sigmund, K., 1979. A note on evolutionarily stable strategies and game dynamics. J. Theor. Biol. 81, 609–612.

Huberman, B.A., Glance, N.S., 1993. Evolutionary games and computer simulations. Proc. Natl. Acad. Sci. U.S.A. 90, 7716–7718.

Hui, C., Zhang, F., Han, X., Li, Z., 2005. Cooperation evolution and self-regulation dynamics in metapopulation: stage-equilibrium hypothesis. Ecol. Model. 184, 397–412.

Ifti, M., Killingback, T., Doebeli, M., 2004. Effects of neighbourhood size and connectivity on the spatial continuous prisoners dilemma. J. Theor. Biol. 231, 97–106.

Killingback, T., Doebeli, M., 1996. Spatial evolutionary game theory: Hawks and Doves revisited. Proc. R. Soc. Lond. B 263, 1135–1144.

Killingback, T., Doebeli, M., 1998. Self-organized criticality in spatial evolutionary game theory. J. Theor. Biol. 191, 335–340.

Killingback, T., Doebeli, M., Knowlton, N., 1999. Variable investment, the continuous Prisoner's Dilemma, and the origin of cooperation. Proc. R. Soc. Lond. B 266, 1723–1728.

Lehmann, L., Keller, L., Sumpter, D., 2007. The evolution of helping and harming on graphs: the return of the inclusive fitness effect. J. Evol. Biol. 20, 2284–2295.

Lieberman, E., Hauert, C., Nowak, M.A., 2005. Evolutionary dynamics on graphs. Nature 433, 312–316.

Lindgren, K., Nordahl, M., 1994. Evolutionary dynamics of spatial games. Physica D 75, 292–309.

Masuda, N., Aihara, K., 2003. Spatial Prisoner's Dilemma optimally played in small-world networks. Phys. Lett. A 313, 55–61.

Maynard Smith, J., 1982. Evolution and the Theory of Games. Cambridge University Press, Cambridge.

Maynard Smith, J., Price, G., 1973. The logic of animal conflict. Nature 246, 15–18.

Nakamaru, M., Matsuda, H., Iwasa, Y., 1997. The evolution of cooperation in a lattice-structured population. J. Theor. Biol. 184, 65–81.

Nowak, M.A., 2006. Five rules of the evolution of cooperation. Science 314, 1560–1563.

Nowak, M.A., May, R.M., 1992. Evolutionary games and spatial chaos. Nature 246, 15–18.

Nowak, M.A., May, R.M., 1993. The spatial dilemmas of evolution. Int. J. Bifurcat. Chaos 3, 35–78.

Nowak, M.A., Sigmund, K., 1992. Tit for tat in heterogeneous populations. Nature 355, 250–252.

Nowak, M.A., Sigmund, K., 1993. A strategy of win-stay, lose-shift that outperforms tit for tat in the Prisoner's Dilemma game. Nature 364, 56–58.

Nowak, M.A., Sigmund, K., 1994. The alternating Prisoner's Dilemma. J. Theor. Biol. 168, 219–226.

Nowak, M.A., Sigmund, K., 2000. Games on grids. In: Dieckmann, U., Law, R., Metz, J.A. (Eds.), The Geometry of Ecological Interactions: Simplifying Spatial Complexity. Cambridge University Press, Cambridge, pp. 135–150.

Nowak, M.A., Sigmund, K., 2004. Evolutionary dynamics of biological games. Science 303, 793–799.

Nowak, M.A., Bonhoeffer, S., May, R.M., 1994. Spatial games and the maintenance of cooperation. Proc. Natl. Acad. Sci. U.S.A. 91, 4877–4881.

Ohtsuki, H., Nowak, M.A., 2006. Evolutionary games on cycles. Proc. R. Soc. Lond. B 273, 2249–2256.

Ohtsuki, H., Hauert, C., Lieberman, E., Nowak, M.A., 2006. A simple rule for the evolution of cooperation on graphs and social networks. Nature 44, 502–505.

Ruxton, G.D., Saravia, L.A., 1998. The need for biological realism in the updating of cellular automata models. Ecol. Model. 107, 105–112.

Santos, F.C., Pacheco, J.M., Lenaerts, T., 2006a. Evolutionary dynamics of social dilemmas in structured heterogeneous populations. Proc. Natl. Acad. Sci. U.S.A. 103, 3490–3494.

Santos, F.C., Pacheco, J.M., Lenaerts, T., 2006b. Cooperation prevails when individuals adjust their social ties. PLoS Comput. Biol. 2, 1284–1291.

Santos, F.C., Rodrigues, J.F., Pacheco, J.M., 2006c. Graph topology plays a determinant role in the evolution of cooperation. Proc. R. Soc. Lond. B 273, 51–55.

Schweitzer, F., Behera, L., Muhlenbein, H., 2002. Evolution of cooperation in a spatial Prisoner's Dilemma. Adv. Complex Syst. 5, 269–299.

Sober, E., Wilson, D.S., 1998. Unto Others: the Evolution and Psychology of Unselfish Behavior. Harvard University Press, Cambridge, MA.

Szabo, G., Hauert, C., 2002. Phase transitions and volunteering in spatial public goods games. Phys. Rev. Lett. 89, 118101–118105.

Szabo, G., Toke, C., 1998. Evolutionary prisoners dilemma game on a square lattice. Phys. Rev. E 58, 69–73.

Taylor, P.D., Jonker, L.B., 1978. Evolutionarily stable strategies and game dynamics. Math. Biosci. 40, 145–156.

Taylor, P.D., Day, T., Wild, G., 2007. Evolution of cooperation in a finite homogeneous graph. Nature 447, 469–472.

Trivers, R.L., 1971. The evolution of reciprocal altruism. Q. Rev. Biol. 46, 35–57.

Weibull, J.W., 1995. Evolutionary Game Theory. MIT Press, Cambridge, MA.

Xiao, S., Chen, S.Y., Wang, G., 2007. Does the ESS height of plant population still exist with the inclusion of spatial-structure?—An individual-based model research. Ecol. Model. 204, 213–218.

Zeeman, E.C., 1980. Population dynamics from game theory. In: Nitecki, A., Robinson, C. (Eds.), Proceedings of an International Conference on Global Theory of Dynamical Systems, vol. 819, Lecture Notes in Mathematics. Springer, Berlin.

Zhang, F., Li, Z.Z., Hui, C., 2006. Spatiotemporal dynamics and distribution patterns of cyclic competition in metapopulation. Ecol. Model. 193, 721–735.