

Article

Effect of spatial structure on the evolution of cooperation based on game models

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Abstract

To elucidate the mechanisms for the evolution of cooperation has been a core problem in biology, economics and sociology. Evolutionary game theory has proven to be an efficient approach to investigate the problem by using models based on so-called social dilemmas. Spatial structure is indicated to have an important effect on the evolution of cooperation and has been intensively studied during recent years. From this perspective, we review our studies in evolutionary dynamics based on a repeated game with three strategies, 'always defect' (ALLD), 'tit-for-tat' (TFT), and 'always cooperate' (ALLC). With mathematical analysis and numerical simulations, the results show that cooperation can be promoted in spatially-structured populations. Cooperators prevail against defectors by forming stable clusters, which is called the 'spatial selection'. Meanwhile, lattice structure also inhibits cooperation due to the advantage of being spiteful. Furthermore, simulations demonstrate that a slight enforcement of ALLC can only promote cooperation when there is weak network reciprocity, while the catalyst effect of TFT on cooperation is verified.

Keywords evolutionary game theory; social dilemma; spatial structure; repeated game; enforcement; network reciprocity.

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1 Introduction

The traditional framework of evolutionary dynamics rests on the ideal assumption of infinitely large, well-mixed populations and deterministic dynamics. However, the real population has finite number of individuals and not any of the two meet with the same probability. For instance, the interaction among neighbors is likely than distant ones. Besides, the real spatial configuration always takes on some degree of heterogeneity, which

also causes the randomized interactions of individuals. These realizations lead to the study of spatial structure on the evolutionary ecology, which has been the hotspot of research in recent years.

Cooperation is essential for evolution but may be difficult to achieve within the classic Darwinian framework of evolutionary theory (Zhang, 2015; Zhang and Liu, 2015). Cooperators have to succeed in the struggle for survival with defectors, who by definition have a certain fitness advantage. So the question of how natural selection can lead to cooperation has fascinated evolutionary biologist for a longtime. Evolutionary game theory (Maynard Smith and Price, 1973) has always being used as a standard tool to investigate the problem of cooperation, two most famous metaphors are the Prisoner's Dilemma game (PD) (Rapoport and Chammah, 1965) and the Snowdrift game (SD) which is also known as the Hawk-Dove game, or the Chicken game (Maynard Smith and Price, 1973).

Direct reciprocity (Trivers, 1971) which goes beyond the restriction of kinship was reported as a powerful mechanism for the evolution of cooperation. 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 (Axelrod and Hamilton, 1981). 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 each of the following round. In Axelrod's (1984) seminal computer tournaments, 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). In a well-mixed population, ALLC is dominated by ALLD, which 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).

Network reciprocity has been shown to be an important mechanism for the evolution of cooperation, which is the generalization of spatial reciprocity (Nowak and May, 1992) to evolutionary graph theory (Lieberman et al., 2005; Ohtsuki and Nowak, 2006a, b; Ohtsuki et al., 2006; Szabó and Föth, 2007). They assume that individuals are arranged in a spatial configuration and that interactions between neighboring individuals on this configuration are more likely than between distant individuals. The fitness of individuals is based on interactions with their local neighbors (Nowak and May, 1992, 1993; Lindgren and Nordahl, 1994; Killingback and Doebeli, 1996; Nakamaru et al., 1997; Szabó and Töke, 1998; van Baalen and Rand, 1998; Brauchli et al., 1999; Mitteldorf and Wilson, 2000; Nowak and Sigmund, 2000; Hauert, 2002; Le Galliard et al., 2003; Hauert and Doebeli, 2004; Doebeli and Hauert, 2005; Roca et al., 2009a; Nowak et al., 2010a b; Wu et al., 2010).

Besides the two mechanisms mentioned above, group selection, kin selection, and indirect reciprocity have also been proposed for the evolution of cooperation (for a review, see Nowak, 2006). The most fundamental requirement for the evolution of cooperation is to construct assortative interactions between cooperative individuals (Eshel and Cavalli-Sforza, 1982; Fletcher and Doebeli, 2009), which can guarantee a close relatedness between the actor and recipient, and thus essential for Hamilton rule (Hamilton, 1964). Hamilton rule means that cooperation can be favored by natural selection if the benefit of cooperator, after discounted by the relatedness between players, is larger than the cost.

Our work focuses the attention on systematic and extensively investigations about spatial effect on the evolutionary dynamics of the three strategies, ALLD, TFT, and ALLC. 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 spatially-structured models.

The article is arranged as follows. In section 2, we present the social dilemma games and replicator dynamics of a non-spatial game model. In section 3, different types of spatial game models are presented, where the spatiotemporal dynamics of the three strategies are studied. Section 4 offers a conclusion.

2 Non-spatial Game Models

2.1 Social dilemma game models

Generally, considering a game with two strategies, cooperate or defect, the payoff matrix is denoted as follows,

$$\begin{array}{c|c} & C & D \\ \hline C & R & S \\ D & T & P \end{array} \quad (1)$$

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 .

With $T > R > P > S$ and $2R > T + S$ (Hofbauer and Sigmund, 2003), we have an obvious dilemma, in any round, the strategy D is unbeatable no matter what the opponent does. The four parameters can be reduced to $R = 1$, $T = b$ ($1 < b < 2$), $S = 0$, $P = 0$ (substituting this into Eq.1 gives Eq. 2) for the purpose of analytical simplicity, the only one parameter b characterizes the advantage of defectors against cooperators (Nowak and May, 1992,1993).

$$\begin{array}{c|c} & C & D \\ \hline C & 1 & 0 \\ D & b & 0 \end{array} \quad (2)$$

While for parameters satisfying $T > R > S > P$, it is the so called SD game. Parameterized payoff matrix below is commonly used (Hauert and Doebeli, 2004).

$$\begin{array}{c|c} & C & D \\ \hline C & 1 & 2-b \\ D & b & 0 \end{array} \quad (3)$$

Define ω as the probability that the same two players interact in the following step as well, then $\omega^{n-1}(1 - \omega)$ is the probability that they interact exactly n times ($n = 1, 2, 3, \dots$). The expected number of times that the two players interact is $1/(1 - \omega)$ (Nakamaru et al., 1997). We get the payoff matrix for the three strategies ALLD, TFT, and ALLC as follows,

$$\begin{array}{c|ccc} & ALLD & TFT & ALLC \\ \hline ALLD & P/(1 - \omega) & T + \omega P/(1 - \omega) & T/(1 - \omega) \\ TFT & S + \omega P/(1 - \omega) & R/(1 - \omega) & R/(1 - \omega) \\ ALLC & S/(1 - \omega) & R/(1 - \omega) & R/(1 - \omega) \end{array} \quad (4)$$

Particularly, the parameter setting $R = 1$, $T = b$ ($1 < b < 2$), $S = 0$, $P = 0$ previously preserved in the PD is also used for Eq. 4.

2.2 Replicator equation of non-spatial game model

Traditionally, evolutionary game model always assumes randomly interacting populations; it does not include the effect of spatial structure on population dynamics. 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).

$$\frac{dx_i}{dt} = x_i[(AX)_i - X^T AX], X^T AX = \sum_{j=1}^n x_j (AX)_j \quad i = 1, 2, \dots, n \quad (5)$$

The i_{th} element x_i of x is denoted as the frequency of the strategy i , A is the payoff matrix. Substituting Eq. 4 into Eq. 5, a dynamic system can be obtained. Through the classical equilibrium stability and phase plane analysis, the dynamics was summarized in Table 1, with Fig. 1 illustrating an example.

Table 1 The stability of the equilibria of the replicator dynamics.

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

¹If the parameters chosen satisfy $b(1 - \omega) > 1$, the evolutionary stable state is ALLD. If $b(1 - \omega) < 1$, the evolutionary dynamics is a bistable case depending on the initial state. That is, except ALLD is the evolutionary stable state, the mixed state of TFT and ALLC can also be evolutionary stable for $x_2 > (b - 1)x_3 / (1 - b + b\omega)$ (x_2 and x_3 indicate the frequencies of TFT and ALLC, respectively).

3 Spatial Game Models

3.1 Games on grids

Axelrod (1984) 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. individuals are assumed to distribute on rigid spatial structures as specified by regular lattices. Each individual takes up a single lattice site and engages in pairwise interactions with its local neighbors. The total payoff accumulated in all interactions during one time step is the score of an individual. In the replacement process, each individual changes its strategy according to the score of itself and its neighbors. The lattice is evolved in time by considering successive generations. Each individual has the opportunity to update its strategy according to a concrete updating rule. There are a number of different ways in which such updating procedures can be implemented, which can be deterministic or probabilistic, synchronous or asynchronous. Four updating rules below are often used in simulations.

(1) Best takes over (Nowak and May, 1992). In biological terms, this means that only the most successful neighbor has the opportunity to reproduce and the individual under consideration is replaced by a clonal offspring having the same strategy as its parent. This is a fully deterministic rule.

(2) Proportional update (Nowak et al., 1994). This stochastic updating rule is more realistic, in which one individual adopts the strategy of a neighbor with a probability proportional to the neighbor's score. Describe the probability of the lattice j is taken up by strategy x as follows

$$p(j, x) = \frac{\sum_{i=1}^v s_{ix} A_i^m}{\sum_{i=1}^v A_i^m},$$

where $s_{ix} = 1$ if i is taken up by x , or else, $s_{ix} = 0$. Parameter A_i denotes the total score of individual i by interacting with himself and other local neighbors. Parameter m is the measurement of stochasticity. For $m = 0$, it is neutral evolution; $m = 1$ is called proportional update, note that under this situation, an individual occasionally switches to a strategy that returned a lower score to one of its neighbors than his own strategy has

achieved. $m \rightarrow \infty$ returns to the best takes over rule.

(3) Imitate the better. In analogy to the imitation rule proposed by Weibull (1995) and Schlag (1998), an individual considers the difference between the scores of its neighbors and its own. With a probability proportional to this difference it imitates the neighbor's strategy, provided that the difference is positive, with a probability of zero otherwise.

(4) Stochastic update. In order to emphasize the link between evolutionary game theory and theoretical physics, physicists have revised the imitation probability. Denote the probability of an individual x imitates the neighbor x' as (Szabó and Toke, 1998; Hauert and Szabó, 2005)

$$p(x \leftarrow x') = \frac{1}{1 + \exp[-(A_{x'} - A_x)/k]},$$

where A_x and $A_{x'}$ represent the payoff of x and x' , respectively. The uncertainty in the imitate process (arising from change of payoff or the failure in determining process) is the noise k . This illustrates a good strategy will be easily taken, while it's unlikely to take a bad strategy. When $k \rightarrow \infty$, the payoff has no use (information lost), individuals will take a strategy stochastically.

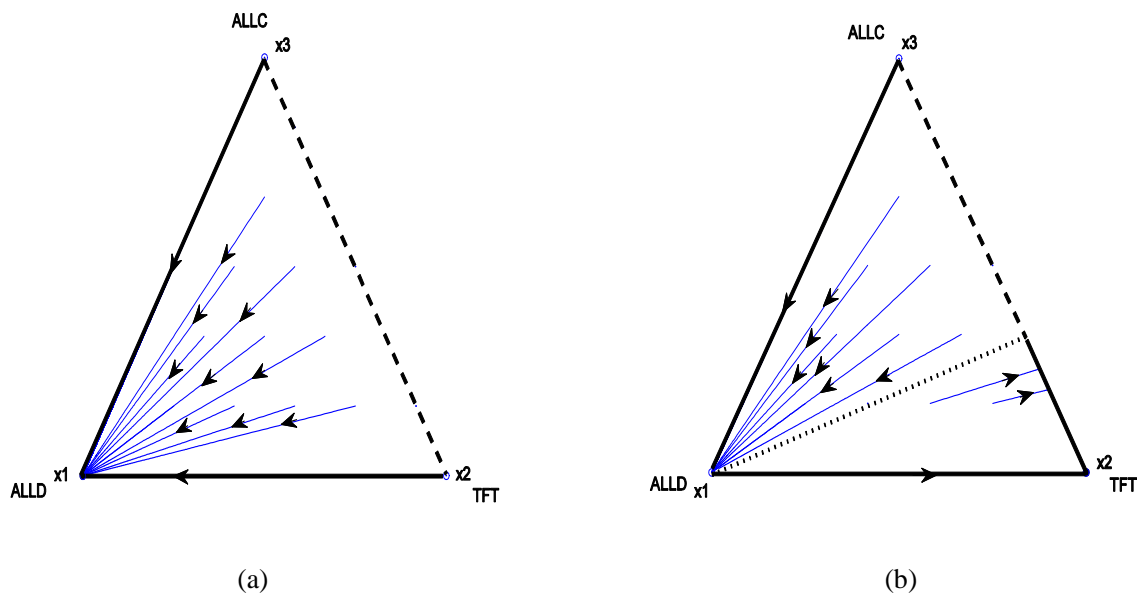


Fig. 1 The replicator dynamics of the three strategies in the completely well-mixed population. Parameters are: (a) $b=9/5$, $\omega=1/3$, and $b > \frac{1}{1-\omega}$; (b) $b=9/5$, $\omega=2/3$, and $b < \frac{1}{1-\omega}$. The lines with arrows are the trajectories, where the arrows indicate the direction 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).

An unambiguous conclusion has been reached from studies of the spatial PD is that spatial structure promotes cooperation (Nowak and May, 1992, 1993; Hubermann and Glance, 1993; Nowak et al., 1994; Killingback et al., 1999). However, in stark contrast to the spatial PD, spatial structure is generally detrimental to cooperation (Hauert and Doebeli, 2004). Moreover, the conclusion that spatial structure is beneficial for cooperation has also been reached for spatial versions of the IPD (Lindgren and Nordahl, 1994; Grim, 1995; Brauchli et al., 1999).

Zhang et al. (2009a) studied the spatiotemporal dynamics of the three strategic players arranged in a two-dimensional spatial lattice by using the best takes over updating rule. Nine representative regions are identified through computer simulations (see Fig. 2). For example, stable coexistence state of the three strategies,

spatiotemporal chaos (Nowak and May, 1992) (take Fig. 3 as an example), stable percolation network, evolutionary kaleidoscope, irregular frozen state (Lindgren and Nordahl, 1994) and so on. The spatial game model gives rise to amazing evolutionary diversity where cooperation could be promoted. Spatial structure is illustrated as the keystone of the evolution of intraspecific diversity.

3.2 Lattice-structured population and approximation method

In the last twenty years, statistical physics have inspired new modelling techniques to ecologists (Dieckmann et al., 2000). Individuality is preserved and space is considered explicitly, either as a continuous arena, or as a network of sites. These models give a deterministic analytical representation of individual-based spatial models. Lattice models as one approach of them are attracting increasing attention from theoretical ecologists for study the relationship between spatially localized interactions and overall population and evolutionary dynamics (Liggett, 1985; Durrett, 1988). Because they are more realistic for many ecological and social phenomena than the classical modelling approaches, such as reaction-diffusion models and patch-structured models (metapopulations, coupled-map lattices, and deme-structured populations), which have various simplifying assumptions that limit their applicability, in particular in evolutionary contexts (Hui and McGeoch, 2007; Lion and van Baalen, 2008).

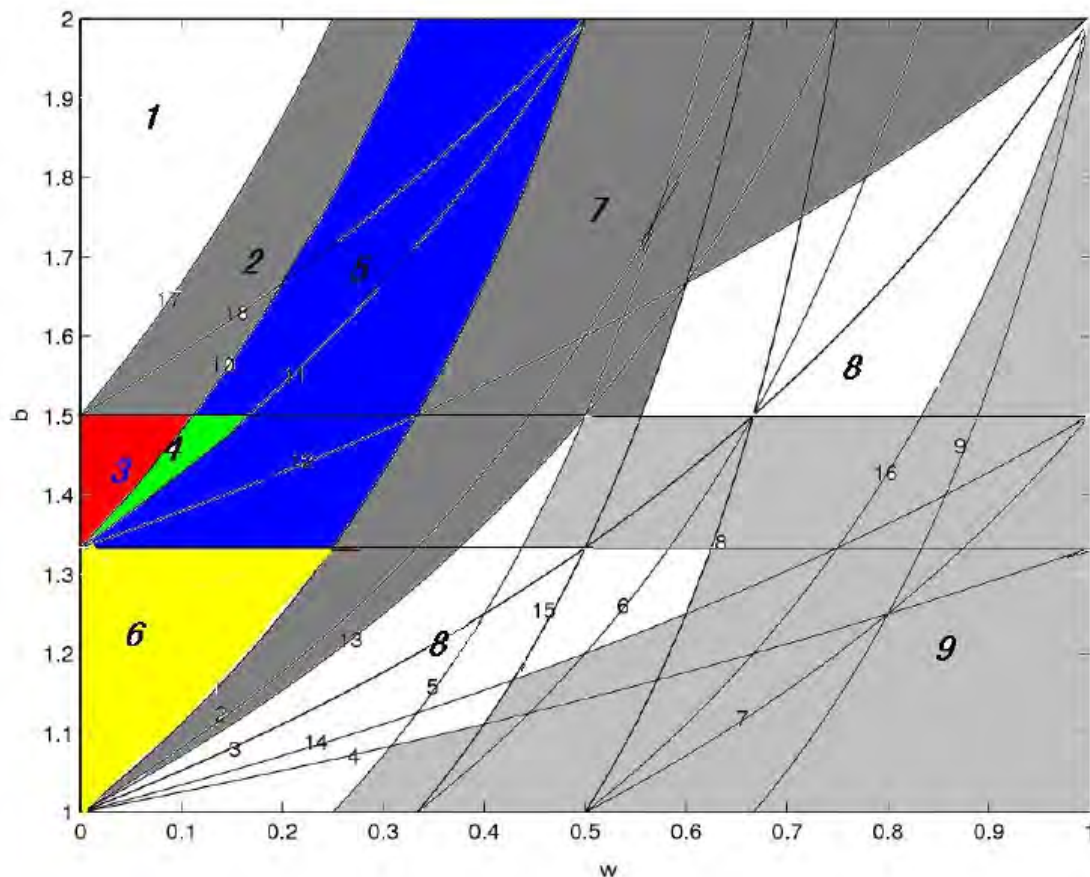
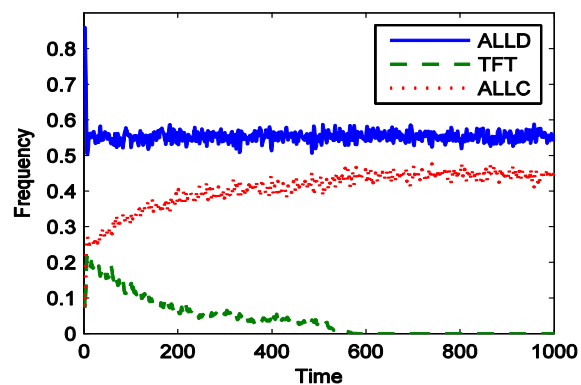
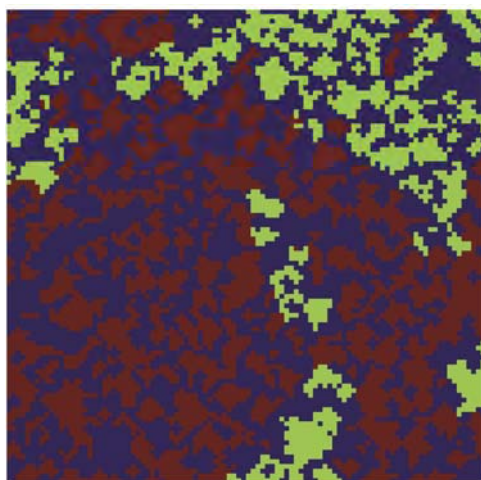


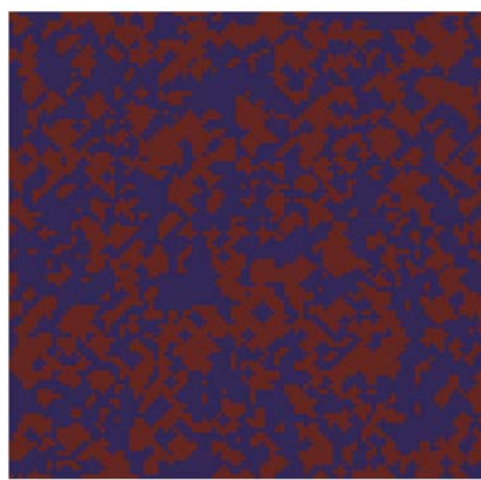
Fig. 2 Based on computer simulations, the parameter areas can be summarized into nine different dynamic regions, each characterized by a distinct temporal dynamics and a corresponding spatial distribution. The horizontal axis is w and the vertical axis is b . All the nine regions are indicated in bold numbers.



(a)



(b)



(c)

Fig. 3 Spatiotemporal dynamics for $b = 1.45$; $\omega = 0.08$ in region 3 (Zhang et al., 2009a). Fig. 3.(a) is the temporal dynamics of frequencies of the three strategies over 1000 generations, Fig. 3.(b) and 3.(c) are the spatial patterns at $G = 100$ and $G = 1000$, respectively.

The most promising approach for understanding the dynamics of lattice models analytically involves the technique of pair approximation (Matsuda et al., 1992; Sato et al., 1994; Satō and Iwasa, 2000). This method devotes to construct a closed dynamical system of overall densities and correlation between nearest neighbors, while neglecting higher order terms. This approach is efficient to gain insight into a model's behavior and avoids the large cost of computation time in direct computer simulations, it often proves very successful in predicting system's behavior even when the mean-field approximation fails dramatically (Harada and Iwasa, 1994; Harada et al., 1995; Kubo et al., 1996; Nakamaru et al., 1997; Iwasa et al., 1998; Dieckmann et al., 2000).

The dynamics of the three strategies on lattice-structured populations was also studied, where the score-dependent viability model (Nakamaru et al., 1997) is used to describe the life history process, and pair approximation is used to mathematical analysis. Simulations show that lattice structure promotes the evolution of cooperation compared with non-spatial populations, which is also confirmed by invasion probability analysis in one dimension. Meanwhile, it also inhibits the evolution of cooperation due to the advantage of being spiteful, which indicates the key role of specific life history assumptions. Mean-field approximation fails to predict the outcome of computer simulations. Pair approximation is accurate in two-dimensional space but fails in one-dimension. Fig. 4 is an example.

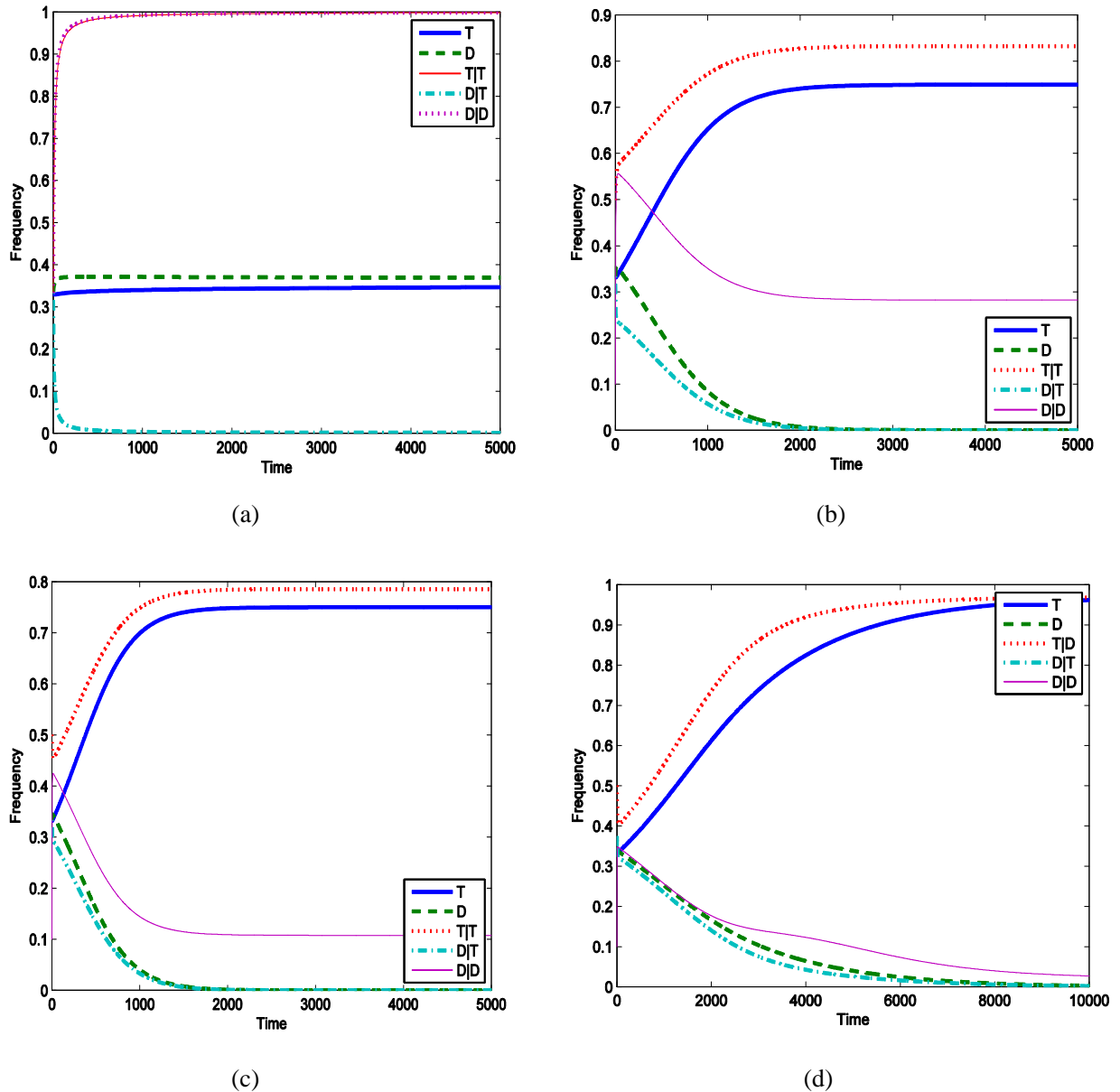


Fig. 4 The dynamics under the pair approximation, parameters values are $b=1.1$, $\omega=0.3$. Fig. 4.(a) is the dynamics in one-dimension, Fig. 4.(b), Fig. 4.(c), and Fig. 4.(d) are the dynamics in two-dimension with neighborhood size are 4, 8, and 25, respectively.

3.3 Evolutionary dynamics on regular graphs

More generally, spatial game belongs to the category of evolutionary graph theory, in which individuals occupy the vertices of a graph, and the edges denote who interacts with whom. A number of different updating mechanisms can be used to determine the evolving state of the graph, specifying how the composition of the population changes under natural selection. A considerable body of researches have been devoted to this subject (Abramson and Kuperman, 2001; Santos and Pacheco, 2005; Antal et al., 2006; Ohtsuki et al., 2006; Ohtsuki and Nowak, 2006a,b; Pacheco et al., 2006; Santos et al., 2006a,b; Ohtsuki and Nowak, 2007; Ohtsuki et al., 2007; Szabó and Fäth, 2007; Taylor et al., 2007; Fu and Wang, 2008; Roca et al., 2009b; Tarnita et al., 2009a,b; Perc and Szolnoki, 2010; Fehel et al., 2011; Allen et al., 2012; Cavaliere et al., 2012). Remarkably,

Ohtsuki et al. (2006) have derived a simple rule as a good approximation for general graphs, which means that natural selection favors cooperation when the benefit of the altruistic act, b , divided by its cost, c , exceeds the average number of neighbors, k (i.e. $b/c > k$ implies cooperation). Particularly, in most studies, the interaction network is assumed to be a regular graph, which is indeed the case if the players are spatially confined.

Ohtsuki and Nowak (2006b) developed a new framework of replicator equation on a regular graph of degree k in the limit of weak selection for large population size:

$$\frac{dx_i}{dt} = x_i[(A + B)x_i - x^T A x], \quad x^T A x = \sum_{j=1}^n x_j (A x)_j, \quad i = 1, 2, \dots, n. \quad (6)$$

Compared with Eq. (1), a new payoff matrix B is added, which describes the local competition of strategies (elements b_{ij} depend on the concrete update rule). Typically, three kinds of update rules of evolutionary dynamics: 'birth-death' (BD), 'death-birth' (DB) and 'imitation' (IM) were introduced. Respectively, the elements of matrix B are defined as

$$b_{ij} = \frac{a_{ii} + a_{ij} - a_{ji} - a_{jj}}{k-2}, \quad (7)$$

$$b_{ij} = \frac{(k+1)a_{ii} + a_{ij} - a_{ji} - (k+1)a_{jj}}{(k+1)(k-2)}, \quad (8)$$

$$b_{ij} = \frac{(k+3)a_{ii} + a_{ij} - a_{ji} - (k+3)a_{jj}}{(k+3)(k-2)}, \quad (9)$$

The evolutionary dynamics of the three strategies on regular graphs are studied. The results show that spatial structure promotes the evolution of cooperation, especially for DB and IM (Zhang et al., 2009b). The mathematical results for stability analysis under the DB updating rule are summarized in Tab. 2, Fig. 5 is an example.

Table 2 The stability of the equilibria and the replicator dynamics for DB updating rule.

b	(0,0)	absorbing state
$\frac{k^2 - 1}{(1 - \omega)(k^2 - k - 1)} < b < 2$	stable	$(\bar{x}_2, 0)$
$\frac{k^2 - 1}{k^2 - 1 - k - \omega} < b < \frac{k^2 - 1}{(1 - \omega)(k^2 - k - 1)}$	unstable	Equilibria between \bar{P}_2 and (1,0)
$\frac{1}{1 - \omega} < b < \frac{k^2 - 1}{k^2 - 1 - k - \omega}$	unstable	$x_2 + x_3 = 1$
$\frac{k^2 - 1}{k^2 - 2} < b < \frac{1}{1 - \omega}$	unstable	Equilibria between \bar{Q}_2 and (1,0)
$1 < b < \frac{k^2 - 1}{k^2 - 2}$	unstable	$x_2 + x_3 = 1$

¹ $\{x_1, x_2, x_3\}$ are the fractions of ALLD, TFT and ALLC, respectively, b is the advantage of defectors over cooperators, ω is the probability that the same two players interact in the following step as well, and k is the degree of the regular graph. $\bar{P}_2 =$

$$\left(\frac{(b-1)(k-2)(k+1) + b(1-\omega) - (k+1)}{b\omega(k-2)(k+1)}, 1 - \frac{(b-1)(k-2)(k+1) + b(1-\omega) - (k+1)}{b\omega(k-2)(k+1)} \right) \text{ and } \bar{Q}_2 = \left(\frac{(k-1)(b-1)}{b\omega(k-2)}, 1 - \frac{(k-1)(b-1)}{b\omega(k-2)} \right).$$

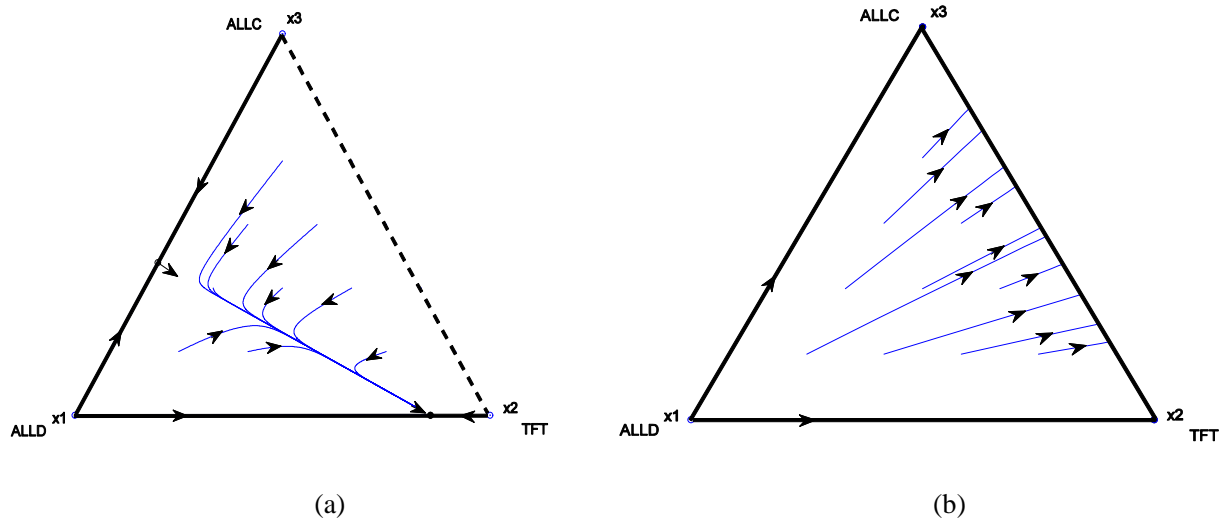


Fig. 5 The replicator dynamics of the three strategies for DB updating on regular graph of degree k . Parameter values: (a) $b=9/5$, $\omega=7/33$, $k=4$, and $b > (k^2 - 1)/((1 - \omega)(k^2 - k - 1))$; (b) $b=29/28$, $\omega=25/29$, $k=4$ and $1 < b < (k^2 - 1)/(k^2 - 2)$. The lines with arrows are 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.

3.4 Evolutionary dynamics on regular graphs with external constraints

External constraint denotes the case where a vacant site on a network adopts a particular strategy with a predefined probability. This behavior can be linked to zealots in social dilemmas and has been shown to change the evolutionary outcome to some extent (e.g. Masuda, 2012; Mobilia, 2012; Liu et al., 2012).

A modified 'death-birth (DB) updating' rule is used for renewing the network (Zhang et al., 2014). In terms of social learning, a randomly chosen individual decides to update his strategy. He is forced to adopt a cooperative strategy with probability p , while with probability $1 - p$, chooses among his neighbor's strategy proportional to their fitness.

Mathematical analyses are conducted via pair approximation and diffusion approximation methods. The results show that the condition for cooperation to be favored on graphs with constraint is $\bar{b}/\bar{c} > k/\bar{A}$ ($\bar{A} = 1 + kp/(1 - p)$), where \bar{b} and \bar{c} represent the altruistic benefit and cost, respectively, k is the average degree of the graph and p is the probability of compulsory cooperation by external enforcement. It illustrates that the external constraint enforced on graph favors the fixation of a cooperative strategy in population. The parameter p has a monotonic effect on k/\bar{A} for a specific k value, hence the larger p , the easier it is for cooperation to be favored. The effect of p is relatively obvious for a large k value, which means external constraint will have a much more pronounced effect on the evolution of cooperation under weak network reciprocity (Ohtsuki and Nowak, 2007).

Furthermore, the evolutionary dynamics of the three strategies under regular graph with external constraints are also studied, by using a similar analysis to the previous one and by referring to the work of Ohtsuki and Nowak (2006b), the dynamics can be described as,

$$\dot{x}_i = \omega_s(1 - p) \frac{(k+1)(k-2)^2}{k(k-1)} x_i (f_i + g_i - \phi) - p x_i + p \delta_{i3}, \quad (10)$$

where $i \in \{1, 2, 3\}$, 1, 2 and 3 represents ALLD, TFT and ALLC, respectively. ω_s is the selection coefficient. $f_i = \sum_j x_j a_{ij}$, $g_i = \sum_j x_j b_{ij}$, $\phi = \sum_i x_i f_i = \sum_{i,j} x_i x_j a_{ij}$, $\delta_{i3} = \begin{cases} 0, & i \neq 3 \\ 1, & i = 3 \end{cases}$, $b_{i,j} = \frac{(k+1)a_{ii} + a_{ij} - a_{ji} - (k+1)a_{jj}}{(k+1)(k-2)}$, $\delta_{i3} = \begin{cases} 0, & i \neq 3 \\ 1, & i = 3 \end{cases}$. (11)

$$b_{i,j} = \frac{(k+1)a_{ii} + a_{ij} - a_{ji} - (k+1)a_{jj}}{(k+1)(k-2)}, \quad \delta_{i3} = \begin{cases} 0, & i \neq 3 \\ 1, & i = 3 \end{cases}. \quad (12)$$

Numerical simulations demonstrate that a slight enforcement of ALLC can only promote cooperation when there is weak network reciprocity (Fig. 6 is an example), while the catalyst effect of TFT on cooperation is verified. In addition, the interesting phenomenon of stable coexistence of the three strategies can be observed. The model can represent evolutionary dynamics on a network structure which is disturbed by a specified external constraint.

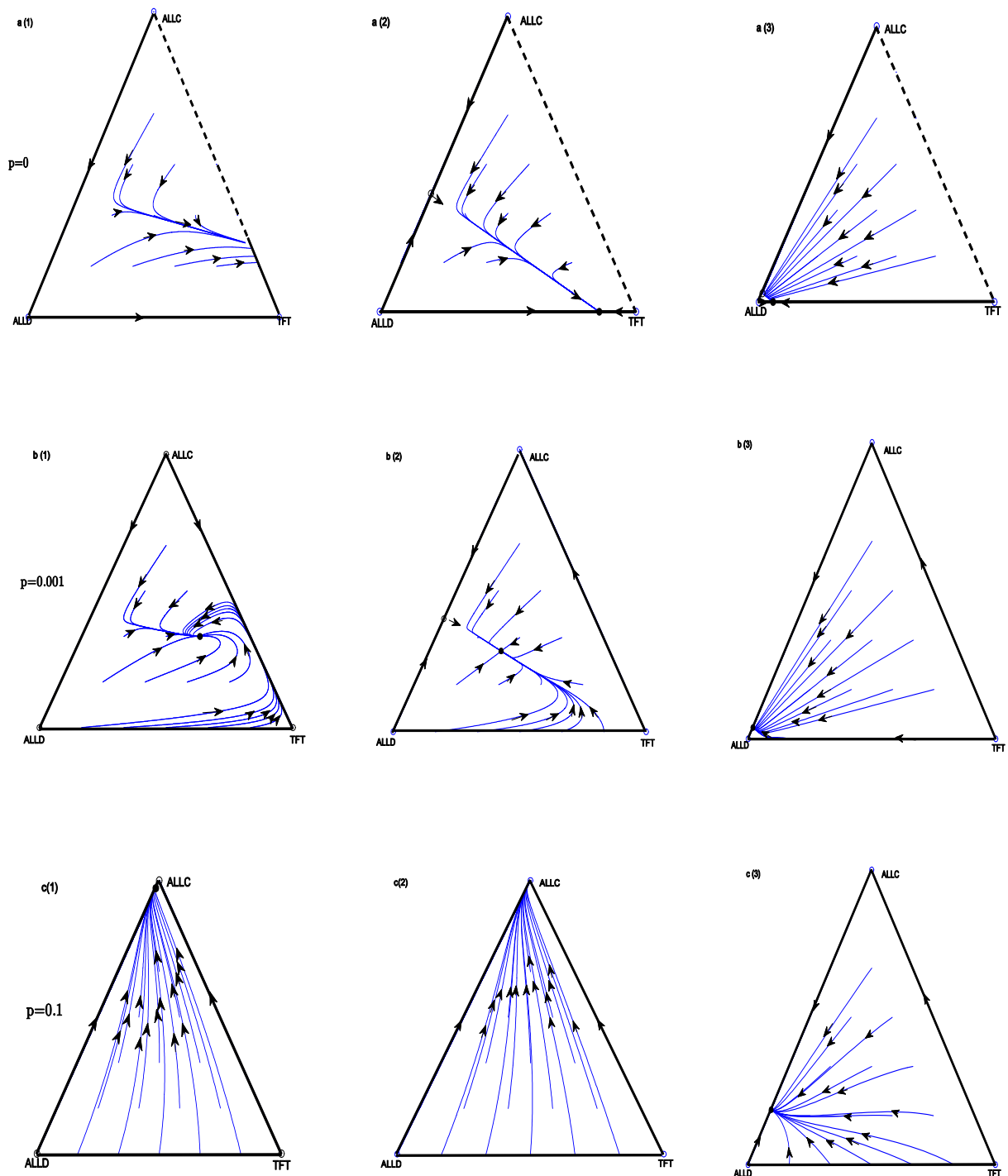


Fig. 6 The evolutionary dynamics of the repeated game by enforcement of ALLC. ω_5 is fixed at 0.1. For Fig.a(1)-c(1), parameters are $b=9/5$; $\omega=1/3$, and $k=4$; For Fig.a(2)-c(2), $b=9/5$; $\omega=7/33$, and $k=4$; For Fig.a(3)-c(3), $b=9/5$; $\omega=7/33$, and $k=40$; From top to bottom of every row, the enforcement strength p are 0, 0.001, and 0.1.

4 Discussion

In this work, I reviewed our works about the spatial game models combining direct reciprocity and spatial reciprocity together to investigate how 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. The results show that evolution of cooperation can be promoted in spatially-structured populations (e.g. rigid grid, lattice structure, regular graphs). Meanwhile, lattice structure also inhibits cooperation due to the advantage of being spiteful. Furthermore, the external enforcement of cooperation on graphs illustrates that it cannot always promote cooperation.

In line with some previous studies, it was observed that the survival of cooperators in spatially-structured populations was based on forming clusters which allowed them to persist despite exploitation by defectors along the cluster boundaries (Doebeli and Hauert, 2005). A detailed analysis by Langer et al. (2008) presented that how a few cooperators invade and expand in a world of defectors. The expansion process takes place once the invasion succeeds. Firstly, cooperators and defectors quickly establish a local equilibrium and then they uniformly expand in space. Simulations show that cooperators typically form a single ever growing cluster interspersed with specks of defectors under hospitable conditions. Whereas under more hostile conditions, cooperators form isolated, compact clusters that minimize exploitation by defectors. More precisely, the impact of geometry of cluster formation to the spatiotemporal dynamics in spatially structured population was revealed (Zhang et al., 2009a). In particular, simulations have shown the coexistence of strategies might be achieved by forming stable spatial domains. Generally, any compact domain formation would be preferable for TFT players, however, ALLD players make them become rare. Domain formation is inevitably changed by competition between these mutual invasion processes of the three types of players, which varies in different parameter regions. For example, TFT and ALLC players can invade the territory of ALLD players along straight boundaries, while ALLD players gain along irregular boundaries for some given interval of b and ω . Visualizing the time dependent configuration, we can observe that the center, size, shape and location of a domain change continuously and a segregated domain may disappear without any trace.

Lattice-structured population has a tendency to make clusters of the same strategy when individuals interact with neighbors repeatedly. However, a negative effect caused by it cannot be neglected. This is due to the spiteful behavior (Gadagkar, 1993) by killing neighbors and replacing them. A player of a lower score is more likely to die and then offers a higher opportunity to colonize the vacant site by a spiteful individual who reduces the player's payoff, which is under the specific life history assumption of the score-dependent viability model. It was demonstrated that pair approximation is accurate to two dimension but failure to one dimension due to the spatial continuity of a two-dimensional lattice (Zhang et al., 2011). Other approximation method such as pair-edge approximation (Ellner et al., 1998) may be needed which deserves further research.

Considering the evolution of cooperation on regular graph, DB updating rule can promote the evolution of cooperation involving the three repeated strategies. Pure cooperation is possible, as well as coexistence of ALLD and TFT (Zhang et al., 2009b). Furthermore, the effect of the presence of constraint makes the dynamics of the system more diverse, depending on the parameter values. In consistent with the work by Liu et al. (2012), external enforcement of cooperation will benefit the evolution of cooperation, as expected. However, the presence of the constraint on ALLC may reduce the frequency of cooperators if the enforcement of ALLC is not too large under strong network reciprocity. Pure cooperation will never evolve unless external constraint of ALLC is strong enough. Moreover, a state of pure cooperation can be reached provided that the compulsory force is put on TFT (Zhang et al., 2014). The result can be interpreted in the context of a social society: some enforcement can lead to an undesired result betraying its original intention (Szabó et al., 2000).

An interesting phenomenon of coexistence of the three strategies (Imhof et al., 2005; Brandt and Sigmund,

2006; Szöllösi and Derényi, 2008; Chatterjee et al., 2012) has also been an attractive research point. Our previous work (Zhang et al., 2009a) has found that there will be a parameter region ($\{(\omega, b) | 3/(2 - 2\omega)\} \cap \{(\omega, b) | 0 < \omega < 1/4, 2/3 < b < 2\}$) characterized by stable coexistence state with large domains of ALLD players in a background of TFT players and ALLC players, the coexistence state can be achieved by forming stable domains in spatial configuration. Moreover, starting from a random spatial pattern in lattice-structured populations, not only can rapid cluster forming process be observed, but also notably that the coexistence of the three strategies for a really long time in one dimensional lattice can be observed (Zhang et al., 2011). Especially, when external constraint is introduced into a dynamic system on regular graph, the coexistence state of the three strategies can appear as a focus or a node which depends on the parameter values (Zhang et al., 2014). This verifies an interpretation for the maintenance of cooperation again, where TFT plays an important role, as reported by Imh of and Nowak (2010). TFT is indicated as a weak catalyst for the emergence of cooperation, while ALLD is a strong catalyst for the emergence of defection.

To understand cooperation among humans is surely an extremely complex topic because diverse factors in social, physiological, emotional are involved. However, van Veelen et al. (2012) have indicated that the essence of conditional strategies under social networks can be summarized in a one sentence recipe of human cooperation: "a strong dose of repetition and a pinch of population structure". Social interaction networks also display community structure, a kind of assortative structure, in which individuals are divided into groups where members within a group are mostly connected to each other (Newman, 2012). How such realistic features of social networks influences the evolution of cooperation will be the research direction in future. The coevolution of game dynamics and network structure has been indicated as one hotspot in recent years (Zimmermann et al., 2005; Fu and Wang, 2008). Furthermore, other complex learning rules could also be taken into account when individuals make decisions. Since the complexity of the game model, a large proportion results are based on numerical simulations, we thus expect much more theoretical and mathematical studies about this area.

Finally, as Lion et al. (2011) indicated, the study of evolution of cooperation in structured populations has the potential to generate insights beyond areas in which it has been traditionally applied, provided that theoreticians and empiricists are willing to adopt a more ecological perspective on the field. Incorporating ecological dynamics in evolutionary games opens up a much wider window for the evolution of cooperation. Mounting studies have documented that ecological and evolutionary dynamics could be commensurate in time and interact in a feedback loop (Schoener, 2011). For example, the evolution of cooperation can be facilitated by ecological factors such as moderate habitat destruction and fragmentation. In return, this behavior evolution can also affect the dynamics and persistence of populations (Hui et al., 2005; Zhang et al., 2005; Zhang et al., 2010). Especially, Zhang et al. (2010) studied the evolution of cooperation on fragmented landscapes and derived a Hamilton rule in the spatial PD, in which the proportion of cooperators among the neighbouring individuals of a cooperator serves the same function as relatedness in kin selection. The results suggest cooperation could be much easier in the density-dependent ecological games than in the classic frequency-dependent selection evolutionary games (Zhang and Hui, 2011). Therefore, future studies are expected to expand along this direction.

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