



The ambivalent effect of lattice structure on a spatial game

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ARTICLE INFO

Article history:

Received 30 November 2009

Received in revised form 27 October 2010

Available online 6 December 2010

Keywords:

Lattice-structured populations

Spiteful

Mean-field approximation

Pair approximation

ABSTRACT

The evolution of cooperation is studied in lattice-structured populations, in which each individual who adopts one of the following strategies 'always defect' (ALLD), 'tit-for-tat' (TFT), and 'always cooperate' (ALLC) plays the repeated Prisoner's Dilemma game with its neighbors according to an asynchronous update rule. Computer simulations are applied to analyse the dynamics depending on major parameters. Mathematical analyses based on invasion probability analysis, mean-field approximation, as well as pair approximation are also used. We find that the lattice structure promotes the evolution of cooperation compared with a non-spatial population, this 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 dimensions but fails in one dimension.

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1. Introduction

Lattice models (variously called interacting particle systems) as one of the statistical physics approaches are attracting increasing attention from theoretical ecologists for study the relationship between spatially localized interactions and overall population or evolutionary dynamics [1–4]. This is because they are more realistic for many ecological and social phenomena than the classical modeling approaches, such as reaction–diffusion models and patch-structured models (meta-populations, coupled-map lattices, and deme-structured populations), which have various simplifying assumptions that limit their applicability, in particular in evolutionary contexts [5]. Correspondingly, Matsuda et al. [6] developed a method to construct a closed dynamical system of overall densities and correlation between nearest neighbors, by adopting pair approximation for lattice structured population dynamics. This approach solves the difficulty in gaining 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 the system's behavior even when the mean-field approximation fails dramatically [7–12].

Cooperation is essential for evolution but may be difficult to achieve within the classic Darwinian framework of evolutionary theory. In the past two decades, a major goal of theoretical biology is to explain the fascinating problem of evolution by elucidating biological meaningful mechanisms [13]. Particularly, explorations based on Prisoner's Dilemma game (PD) [14–16] thrived in resolving the dilemma of cooperation [17] (and reference therein). In the two players PD game, players can adopt two strategies, cooperate or defect. If both cooperate, they get a payoff of magnitude R , if both defect they

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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 game's biggest 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, two group parameters were used. One is, $R = 1$, $T = b$ ($1 < b < 2$), $S = 0$, $P = 0$ [28,30]; the other is, $R = 3$, $T = 5$, $S = 0$, $P = 1$ [19].

get P . If one player defects while the other cooperates, the defector gets the game's biggest payoff T , while the cooperator gets S . Now, with $T > R > P > S$, and $2R > T + S$ we have an obvious dilemma, in any one round, the strategy defect is unbeatable, regardless of what the opponent does. Thus, individuals that play defect will always be favored by natural selection, even though the average payoff in a population of defectors is less than in a population of cooperators [18].

The attempt to resolve the dilemma goes back to a seminal paper by Trivers [15], where a new notion of reciprocal altruism was introduced, and repeated game models were always used as basis [16,19–23]. This is one type of solutions to the dilemma. The most famous strategy of repeated PD 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 [19], TFT was proven as the only successful strategy against a range of other strategies, such as the two extreme unconditional strategies, 'always cooperate' (ALLC, which is an alternative best reply to TFT, and both strategies fare equally well against each other) and 'always defect' (ALLD).

The second solution to the dilemma are models that introduce some kind of spatial structure [24–26], so that within a population all interactions are local, i.e. individuals play against their nearest neighbors and not against random opponents or against all other individuals of the population [17,18,27]. Nowak and May [28] 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. Actually, there are plenty of spatial evolutionary game models and we cannot list and review all of them. At the same time, we know there is a fundamental oscillation between cooperation and defection in the repeated PD. ALLD can be replaced by TFT, which loses to 'generous tit for tat' (GTFT, which cooperates after a co-player's cooperation, but also cooperates with a certain probability after a defection), which is undermined via neutral drift by ALLC, which invites invasion by ALLD, resembling cycles of war and peace [29]. Thus, it stimulates us to consider, what will the dynamics be for these strategies without G-TFT, whether or not they will form the interesting cyclic relationship 'rock–paper–scissors' (R–P–S) under some certain mechanism? Specifically, how the dynamics be when the three strategies ALLD, TFT, ALLC are introduced to a spatially-structured lattice model?

Based on the repeated PD game, we begin with the spatial model and computer simulations will be performed. Particularly, we will focus on two major parameters b (the advantage for defectors) and w (the same two players interact in the following step as well). Meanwhile, mathematical analysis of invasion success probability, mean-field approximation and pair approximation will be used in investigations. 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 lattice-structured model.

2. The repeated PD model

Each player adopts one of the strategies, ALLD, TFT and ALLC. Let w be the probability that the same two players interact in the following step as well, a payoff matrix is obtained as shown in Table 1.

Four parameters of the PD can be reduced for the purpose of analytical simplicity. Particularly, they are $R = 1$, $T = b$ ($1 < b < 2$), $S = 0$, $P = 0$, where only one parameter b characterizes the advantage of defectors against cooperators retains [28,30,31]. This parameter setting preserves the essentials of the PD, and is widely accepted as its simplicity and generality. Meanwhile, the second set of payoff values $R = 3$, $T = 5$, $S = 0$, $P = 1$ [19] will be used for comparative illustrations.

3. The spatial game model, methods and results

3.1. The model

Three types of players are arranged on spatial lattices, an asynchronous update rule which is the 'score-dependent viability' model [11] was used. That is, one randomly selected individual "plays the game" with its immediate z neighbors in a sufficiently short time interval, the mortality of a player is determined by its total score, which is the sum of the scores obtained by interacting with the z neighbors. After the death of an individual, the empty lattice site is filled immediately by a copy of a neighbor randomly chosen among z possible sites. On average, every site is examined once in each round, and so to the next round of the game.

Let B_{X,n_1,n_2} be the score of a X (where $X \in \{D, T, C\}$, D, T, C are the simplifications of ALLD, TFT, ALLC respectively) player if it is surrounded by $n_1 T$ neighbors, $n_2 C$ neighbors and $z - (n_1 + n_2)D$ neighbors. The instantaneous mortality of X is $M_{X,n_1,n_2} = \exp(-\alpha \times B_{X,n_1,n_2})$. Specifically, we choose $\alpha = 0.2(1 - w)$ [11].

3.2. Computer simulations

Computer simulations were carried on one-dimensional lattices with sizes of 500 and 600, and two-dimensional lattices with a size of 100×100 . The initial sites were filled independently either by D, T or C with equal probability, and the periodic boundary condition was used to remove the effect of edges. Fig. 1 illustrates the final outcome of the simulations for different parameters w and b . Although both are in one-dimension, Fig. 1(a) and (b) represent an obvious difference. There is a state where some runs end up with TFT and other runs end up with ALLD for certain parameters in Fig. 1(a), which is caused by stochasticity due to the finiteness of the lattice size [11]. This demographic stochasticity operates independently among individuals, it leads to average out in large populations and has a greater impact on small populations. Compared to Fig. 1(c), the result that two-dimensional spatial structure is much more profitable for promoting the evolution of cooperation than one dimension can be got. Figs. 2 and 3 show specific examples of spatiotemporal dynamics. Starting from a random spatial pattern, not only can a rapid cluster forming process be observed, but also notably that the coexistence of the three strategies for a really long time in a one dimensional lattice can be observed (see Fig. 3(a)). Why? As we know, the evolutionary fate is mainly influenced by the boundary at two adjacent clusters in the spatial setting. In one dimension, the space will be segregated into some countable different regions once clusters have formed, there is extremely little chance of choosing a neighbor who has a different strategy from your own, so the dynamic change is tiny in one time step because of these limited borders. Therefore, the transient time for the outcome where the fixation of one strategy is very large, which is different from that in two dimensions where its topological structure is characterized as a spatial continuity. In addition, there are more individuals sited on the border of a cluster, so each individual probably has different types of neighbors, which makes it easy to change strategy, thus much shorter generations for the dynamic change can be observed in two dimensions. This implies that the transient time largely depends on lattice topologies. Next, we will apply analytical calculations to verify the results of computer simulations.

3.3. Mathematical analyses in one-dimensional lattice

Let ρ_T be the total fraction of T in the whole lattice, called the global density of T , and ρ_D be the global density of D . The time changes of ρ_T, ρ_D are given by,

$$\begin{aligned} \frac{d\rho_T}{dt} = & -M_{T,1,0}[DTT] - M_{T,1,1}[TTC] - 2M_{T,0,1}[DTC] - M_{T,0,2}[CTC] \\ & - M_{T,0,0}[DTD] + M_{D,1,0}[TDD] + M_{D,1,1}[TDC] + M_{D,2,0}[TDT] \\ & + M_{C,1,0}[TCD] + M_{C,1,1}[TCC] + M_{C,2,0}[TCT] \end{aligned} \quad (1a)$$

$$\begin{aligned} \frac{d\rho_D}{dt} = & -M_{D,1,0}[TDD] - M_{D,0,1}[DDC] - 2M_{D,1,1}[TDC] - M_{D,2,0}[TDT] \\ & - M_{D,0,2}[CDC] + M_{T,0,1}[CTD] + M_{T,1,0}[TTD] + M_{T,0,0}[DTD] \\ & + M_{C,0,1}[CCD] + M_{C,1,0}[TCD] + M_{C,0,0}[DCD] \end{aligned} \quad (1b)$$

where, every term in the square brace represents the density of the triplet. Using only global densities to express the frequency of a triplet is not enough, a conditional probability for a site to be a ($a = T, C, D$) if it is chosen next to a a is necessary, which is expressed as $q_{a|a}$ and called the conditional density or local density of a sites [6,7]. In a similar way, $q_{a|bc}$ ($a, b, c \in \{T, C, D\}$) indicate a conditional density of a higher order, which means the probability that a is in the neighborhood of b whose neighbor is c . Using these notations, for instance, the density of triplet DTT is $\rho_T q_{T|T} q_{D|TT}$. The frequencies of the various triplets in Eqs. (1a) and (1b) can be rewritten as,

$$\begin{aligned} \frac{d\rho_T}{dt} = & -M_{T,1,0}\rho_T q_{T|T} q_{D|TT} - M_{T,1,1}\rho_T q_{C|T} q_{T|TC} - 2M_{T,0,1}\rho_T q_{C|T} q_{D|TC} - M_{T,0,2}\rho_T q_{C|T} q_{C|TC} \\ & - M_{T,0,0}\rho_T q_{D|T} q_{D|TD} + M_{D,1,0}\rho_D q_{D|D} q_{T|DD} + M_{D,1,1}\rho_D q_{C|D} q_{T|DC} + M_{D,2,0}\rho_D q_{T|D} q_{T|DT} \\ & + M_{C,1,0}\rho_C q_{D|C} q_{T|CD} + M_{C,1,1}\rho_C q_{C|C} q_{T|CC} + M_{C,2,0}\rho_C q_{T|C} q_{T|CT} \end{aligned} \quad (2a)$$

$$\begin{aligned} \frac{d\rho_D}{dt} = & -M_{D,1,0}\rho_D q_{D|D} q_{D|DD} - M_{D,0,1}\rho_D q_{C|D} q_{D|DC} - 2M_{D,1,1}\rho_D q_{C|D} q_{T|DC} - M_{D,2,0}\rho_D q_{T|D} q_{T|DT} \\ & - M_{D,0,2}\rho_D q_{C|D} q_{C|DC} + M_{T,0,1}\rho_T q_{D|T} q_{C|TD} + M_{T,1,0}\rho_T q_{D|T} q_{T|TD} + M_{T,0,0}\rho_T q_{D|T} q_{D|TD} \\ & + M_{C,0,1}\rho_C q_{D|C} q_{C|CD} + M_{C,1,0}\rho_C q_{D|C} q_{T|CD} + M_{C,0,0}\rho_C q_{D|C} q_{D|CD}. \end{aligned} \quad (2b)$$

3.3.1. Mean-field approximation

Mean-field approximation assumes a random spatial configuration all the time. The conditional density is the same as the global density under this assumption, i.e. $q_{T|ab} = q_{T|c} = \rho_T$ ($a, b, c \in \{T, C, D\}$), e.g. the density of triplet DTT is simply

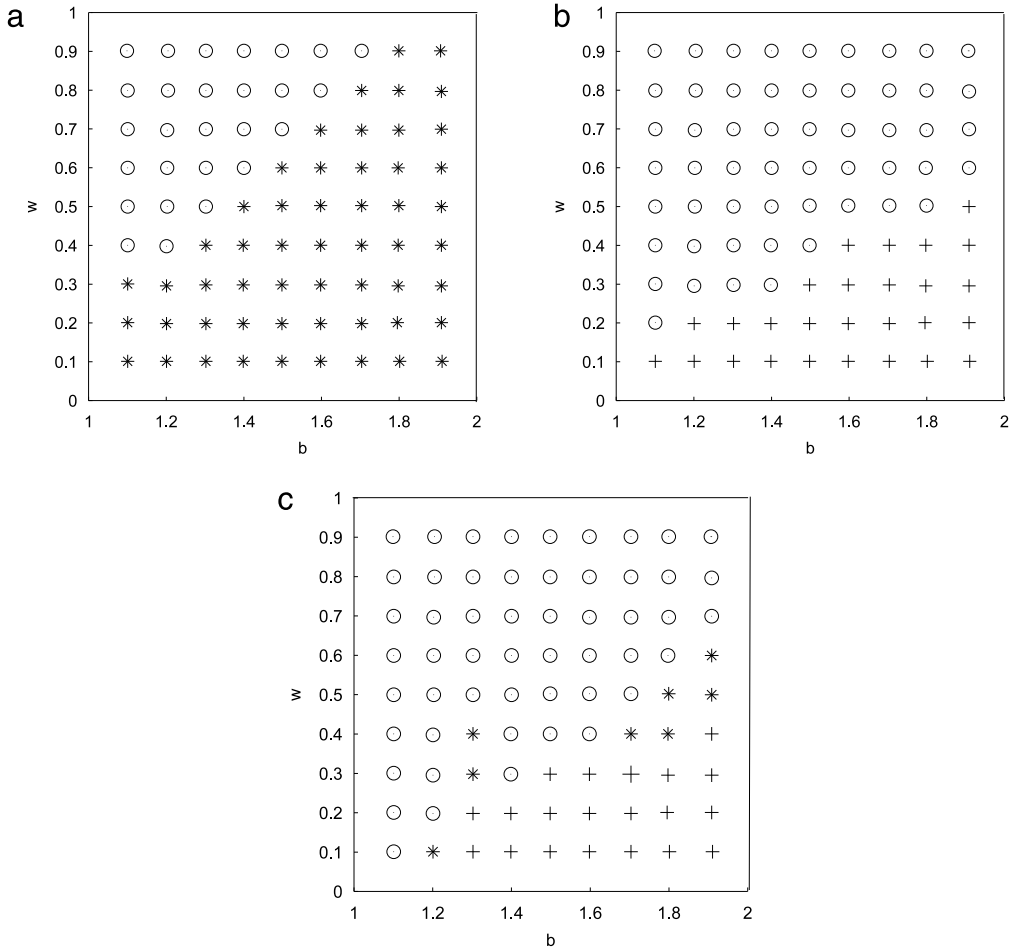


Fig. 1. Fig. 1(a) is the results of the computer simulations on a one dimensional lattice with size of 500. The horizontal axis is the parameter b and the vertical axis is w . Open circles indicate the parameters for which all the runs converged to the TFT state, whilst stars indicate the parameters for which some runs end up with the TFT state and other runs end up with ALLD. Fig. 1(b) is the results of the computer simulations on a one dimensional lattice with size of 600. + indicates the parameters for which all the runs converged to the ALLD state. Fig. 1(C) is the results of the computer simulations on a two dimensional lattice with a size of 100×100 . The meaning of the marks is the same as Fig. 1(a) and (b).

$\rho_T^2 \rho_D$. To adopt these simplifications as well as $\rho_C = 1 - \rho_D - \rho_T$, the dynamics of global densities given by Eqs. (2a) and (2b) become,

$$\begin{aligned} \frac{d\rho_T}{dt} = & \rho_T[-M_{T,1,0}\rho_T\rho_D - M_{T,1,1}\rho_T(1 - \rho_D - \rho_T) - 2M_{T,0,1}\rho_D(1 - \rho_D - \rho_T) - M_{T,0,2}(1 - \rho_D - \rho_T)^2 \\ & - M_{T,0,0}\rho_D^2 + M_{D,1,0}\rho_D^2 + M_{D,1,1}\rho_D(1 - \rho_D - \rho_T) + M_{D,2,0}\rho_D\rho_T + M_{C,1,0}\rho_D(1 - \rho_D - \rho_T) \\ & + M_{C,1,1}(1 - \rho_D - \rho_T)^2 + M_{C,2,0}\rho_T(1 - \rho_D - \rho_T)] \end{aligned} \tag{3a}$$

$$\begin{aligned} \frac{d\rho_D}{dt} = & \rho_D[-M_{D,1,0}\rho_D\rho_T - M_{D,0,1}\rho_D(1 - \rho_D - \rho_T) - 2M_{D,1,1}\rho_T(1 - \rho_D - \rho_T) - M_{D,0,2}(1 - \rho_D - \rho_T)^2 \\ & - M_{D,2,0}\rho_T^2 + M_{T,0,1}\rho_T(1 - \rho_D - \rho_T) + M_{T,1,0}\rho_T^2 + M_{T,0,0}\rho_T\rho_D + M_{C,0,1}(1 - \rho_D - \rho_T)^2 \\ & + M_{C,1,0}\rho_T(1 - \rho_D - \rho_T) + M_{C,0,0}\rho_D(1 - \rho_D - \rho_T)]. \end{aligned} \tag{3b}$$

Denote (x_1, x_2, x_3) as a point in three-dimensional space, (x_1, x_2, x_3) are the frequency of T, D, C respectively. Obviously, the system has four equilibria: $(0, 1, 0), (1, 0, 0), (0, (M_{D,0,2} - M_{C,0,1}) / (M_{D,0,2} - M_{C,0,1} + M_{C,0,0} - M_{D,0,1}), (M_{C,0,0} - M_{D,0,1}) / (M_{D,0,2} - M_{C,0,1} + M_{C,0,0} - M_{D,0,1})), ((M_{T,0,2} - M_{C,1,1}) / (M_{T,0,2} - M_{C,1,1} + M_{C,2,0} - M_{T,1,1}), 0, (M_{C,2,0} - M_{T,1,1}) / (M_{T,0,2} - M_{C,1,1} + M_{C,2,0} - M_{T,1,1}))$. Meanwhile, $(x_0, 0, 1 - x_0)$ ($0 < x_0 < 1$) is also a fixed set. In addition, there may be an intermediate equilibrium with $0 < x_1 < 1, 0 < x_2 < 1, 0 < x_1 + x_2 < 1$, which can be obtained by using the computer software mathematica, but the mathematical expression is very messy so that just printing it would require many pages. And any insight cannot be derived from these equations on the behavior of the system.

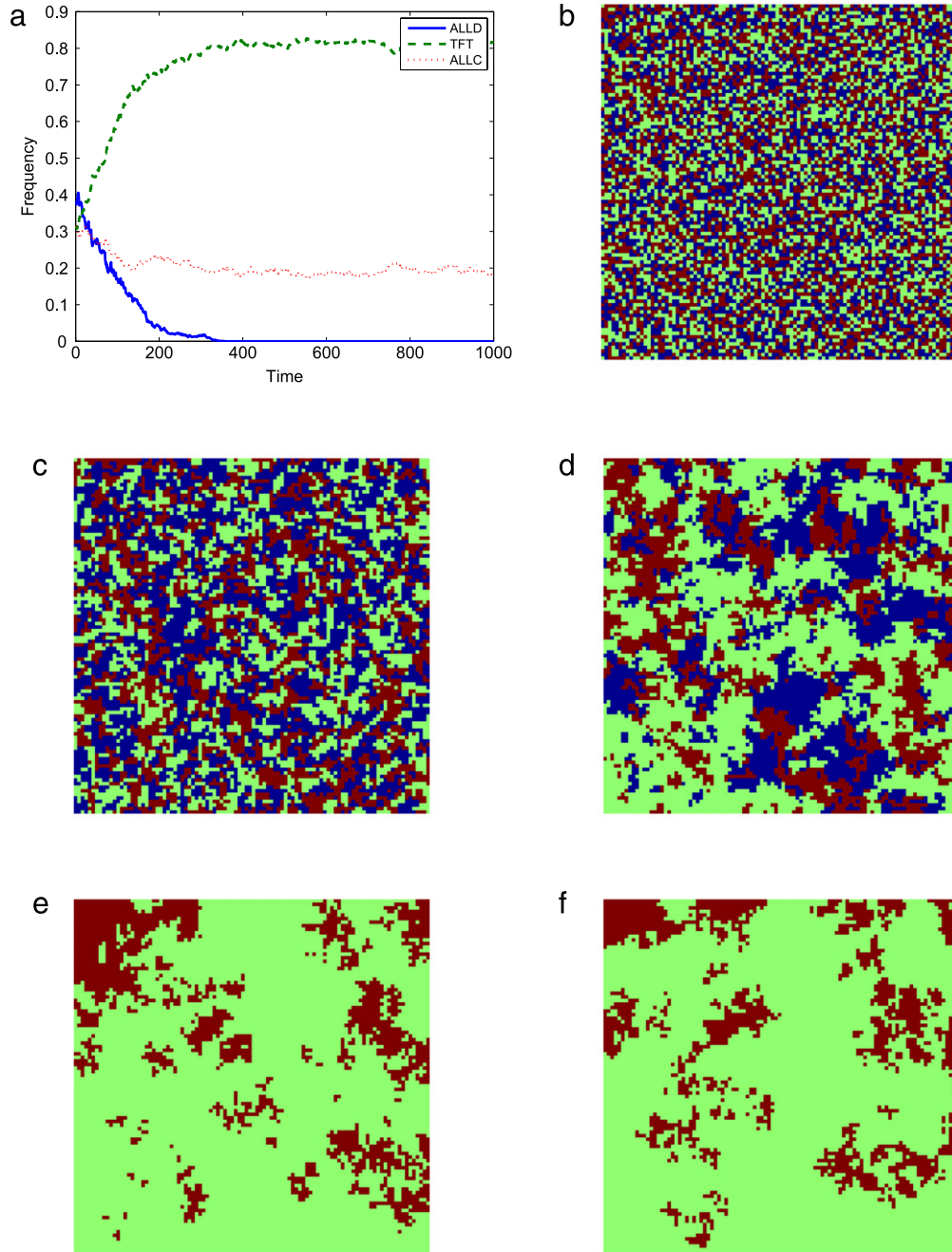


Fig. 2. The dynamics of the three strategies on a two dimensional lattice with size of 100×100 , parameters are, $b = 1.1$, $w = 0.3$. Fig. 2(a) is the frequency of the three strategies over 1000 generations. Fig. 2(b) is the initial spatial configuration. The color coding is as follows, blue is an ALLD, green is a TFT, and red is an ALLC (For interpretation of the references to color in these figure legend, the reader is referred to the web version of the article). Fig. 2(c)–(f) are the spatial distributions at 5, 50, 800, 1000 generations, respectively.

With the first set of payoff values in the Table 1, these equilibria above are $(0, 1, 0)$, $(1, 0, 0)$, $(0, 1/(1 + b), b/(1 + b))$, $(0, 0, 1)$. By applying dynamic system analysis to investigate the stability of these equilibria by Jacobian matrix of the Eqs. (3a) and (3b), we know that $(0, 1, 0)$ is the only globally stable point if $0 \leq w \leq w_a$ (a specific w_a depends on b), which means D is the unique evolutionary stable strategy when w is relatively small. In contrast, both $(x_0, 0, 1 - x_0)$ ($0 < x_0 < 1$) and $(0, 1, 0)$ are locally stable if $w_a < w < 1$, the system is bistable and the evolutionary end point depends on the initial frequency, which means the state mixed with T and C is also evolutionary stable when w is larger than w_a . Let b vary from 1.1 to 1.9, the corresponding w_a which induces a bistable state changes from 0.57 to 0.75. This is a distinct difference compared with computer simulation results in Fig. 1. See Fig. 4 as an example in simplex for a couple of w and b .

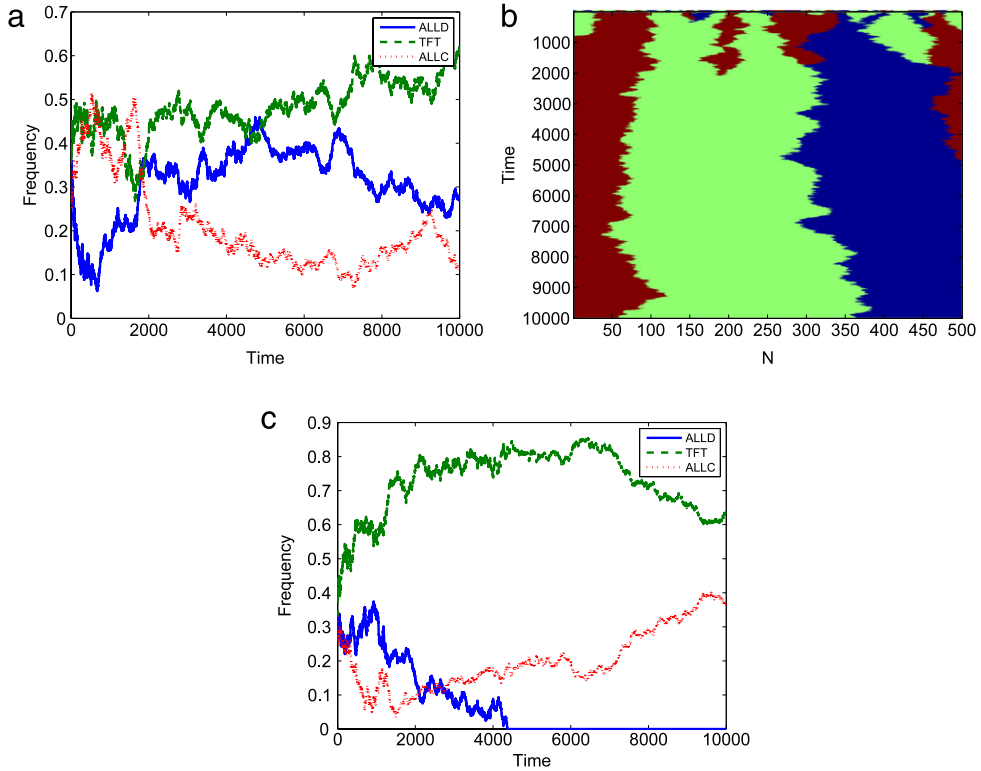


Fig. 3. The dynamics of the three strategies on a one dimensional lattice of size 500, parameter values are the same as in Fig. 2. Fig. 3(a) is the frequency of the three strategies over 10,000 generations. Fig. 3(b) is the spatial temporal distributions over 10,000 generations. The color coding has the same meaning as in Fig. 2. Fig. 3(c) is the dynamics of the three strategies on one dimensional lattice of size 600, parameters are identical to Fig. 2.

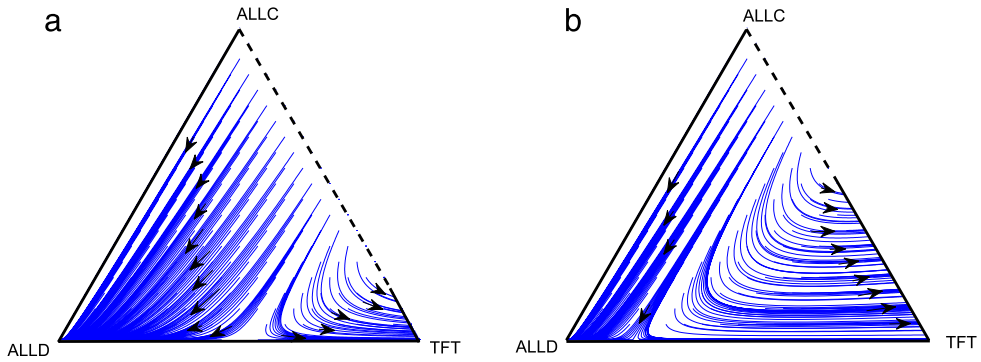


Fig. 4. The dynamics under mean-field approximation, parameters are, $b = 1.1, w = 0.7$. Fig. 4(a) is the dynamics in one-dimension, Fig. 4(b) is the dynamics in two-dimension, the neighborhood size is 4. The lines with arrows are the trajectories, where the arrows indicate the direction of the trajectories. The solid lines without arrows are stable fixed sets, while the dashed lines are unstable manifold.

3.3.2. Pair approximation

Denote ρ_{TT} as the doublet density, i.e. the probability that a randomly chosen pair of nearest neighbors are both T . The local density of T is the ratio of the doublet density to the average (single) density, $q_{T|T} = \rho_{TT} / \rho_T$. We have

$$\frac{dq_{T|T}}{dt} = \frac{1}{\rho_T} \frac{d\rho_{TT}}{dt} - \frac{q_{T|T}}{\rho_T} \frac{d\rho_T}{dt}, \tag{4}$$

which implies that the computation of doublet density is necessary for local density. The global densities of doublet densities in one dimension are derived as follows,

$$\begin{aligned} \frac{d\rho_{TT}}{dt} = & -M_{T,1,0}\rho_T q_{D|T} q_{T|TD} - M_{T,1,1}\rho_T q_{C|T} q_{T|TC} + M_{D,1,0}\rho_D q_{T|D} q_{D|DT} + M_{D,1,1}\rho_D q_{T|D} q_{D|DT} \\ & + 2M_{D,2,0}\rho_D q_{T|D} q_{T|DT} + M_{C,1,0}\rho_C q_{T|C} q_{D|CT} + M_{C,1,1}\rho_C q_{T|C} q_{C|CT} + 2M_{C,2,0}\rho_C q_{T|C} q_{T|CT} \end{aligned} \tag{5a}$$

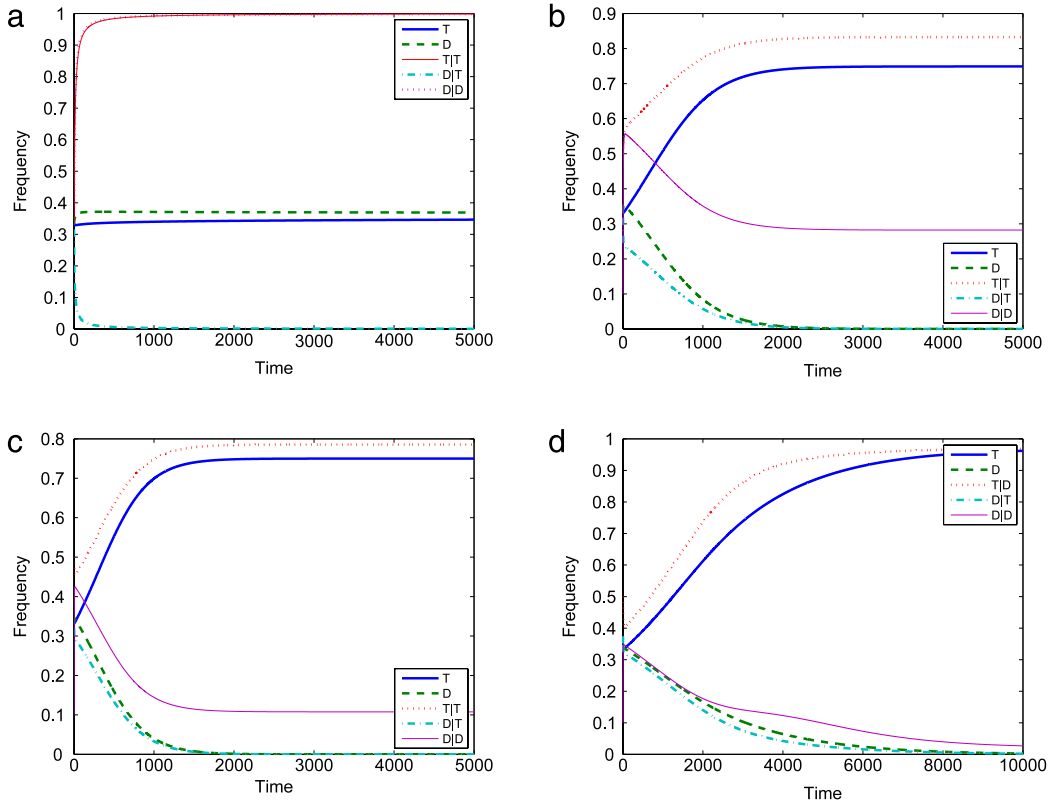


Fig. 5. The dynamics under pair approximation, parameters values are the same as in Fig. 2. Fig. 5(a) is the dynamics in one-dimension, Fig. 5(b)–(d) are the dynamics in two-dimension with neighborhood size of 4, 8, and 25, respectively.

$$\begin{aligned} \frac{d\rho_{DD}}{dt} = & -M_{D,1,0}\rho_Dq_{T|D}q_{D|DT} - M_{D,0,1}\rho_Dq_{C|D}q_{D|DC} + M_{T,1,0}\rho_Tq_{T|T}q_{D|TT} + M_{T,0,1}\rho_Tq_{C|T}q_{D|TC} \\ & + 2M_{T,0,0}\rho_Tq_{D|T}q_{D|TD} + M_{C,0,1}\rho_Cq_{C|C}q_{D|CC} + M_{C,1,0}\rho_Cq_{T|C}q_{D|CT} + 2M_{C,0,0}\rho_Cq_{D|C}q_{D|CD} \end{aligned} \quad (5b)$$

$$\begin{aligned} \frac{d\rho_{DT}}{dt} = & -2M_{D,1,0}\rho_Dq_{T|D}q_{C|DT} - 2M_{D,2,0}\rho_Dq_{T|D}q_{T|DT} - 2M_{T,0,1}\rho_Tq_{C|T}q_{D|TC} \\ & - 2M_{T,0,0}\rho_Tq_{D|T}q_{D|TD} + 2M_{C,1,0}\rho_Cq_{D|C}q_{T|CD}. \end{aligned} \quad (5c)$$

In order to construct a closed dynamical system, we introduce an approximation method for neglecting the correlation of state beyond the nearest neighbor pairs

$$q_{a|bc} = q_{a|b} \quad (a, b, c \in \{T, C, D\}), \quad (6)$$

which is called pair approximation, or doublet decoupling approximation [6,8]. It is also noticeable that $\rho_{TD} = \rho_{DT}$. In addition, other relations, coming from the definition of conditional probabilities can also be derived, such as,

$$\rho_C = 1 - (\rho_T + \rho_D) \quad (7a)$$

$$\rho_{C|T} = 1 - (\rho_{T|T} + \rho_{D|T}). \quad (7b)$$

There are twelve global and local density variables after applying Eq. (6) to system (5), select $\rho_T, \rho_D, q_{T|T}, q_{D|T}, q_{D|D}$ as five independent variables, the other seven variables can be fully expressed by them because of the relationship of conditional probability exemplified in Eqs. (7a) and (7b). Resorting to the method of nonlinear analysis, we find that all the points satisfying $q_{T|T} = 1$ or $q_{D|D} = 1$ are equilibria irrespective of the initial configuration. This is consistent with simulations which showed that the individuals with the same strategy are inclined to form clusters for a short transition period. Fig. 5(a) gives an example.

3.3.3. Invasion success probability

In one dimension, the probability of successful invasion by a single player to a population occupied by other kinds of players can be calculated using the technique of birth-and-death processes [32]. Detailed analysis for probability of each kind to survive and ultimately dominate the population are given in Appendix.

The critical values for several parameters based on the first set of payoff values in Table 1 can be calculated. when $b = 1.1$, w_T, w_C, w_D are 0.1316, 0.2904, 0.1800 respectively; for $b = 1.5$, they are 0.4793, 1.0332, 0.6363 respectively; while $b = 1.9$, the values are 0.6764, 1.4298, 0.8750 respectively. Compared with it, computer simulations show a much wider range of w for T to be evolutionary stable, especially for $b = 1.9$. What is the reason? It is caused by the assumption of uniform distribution of the strategies, but computer simulations showed that same strategies are inclined to form clusters which are beneficial for cooperators, as Axelander [33] reported that assortative interaction facilitates the evolution of cooperative strategy.

For the second set of payoff values, $w_T = 0.6267, w_C = -3.4258, w_D = 1.0419$. So T can invade in case $w > 0.6267$, D can invade for any given value of w ($0 \leq w < 1$) but C cannot invade. And yet, we have known that the critical value is 0.6 for a T can invade under the situation without C [11]. The result is instinctive, D is always advantageous to C which is neutral with T , D makes itself prosperous by exploiting C , so the existence of C facilitates the invasion of D . Accordingly, the critical value for invasion of T in our model is larger than the case that there are only T and D . The same reason also holds for the wider range of a single D can invade.

3.4. Mathematical analyses in two-dimensional lattice

The model will also be examined on two-dimensional square lattices, the number of nearest neighbors with whom a single player interacts is $z = 4$ (Neumann neighborhood). Similar to Eqs. (1a)–(1b), (5a)–(5b) but with a little intricacy, the time change of global densities in two-dimensional lattices can be expressed as,

$$\begin{aligned} \frac{d\rho_T}{dt} = & - \sum_{n_1=0}^{z-1} \sum_{n_2=0}^{z-n_1} \binom{z}{n_1} \binom{z-n_1}{n_2} M_{T,n_1,n_2} [\text{density of } T, n_1, n_2] \frac{z-n_1}{z} \\ & + \sum_{n_1=1}^z \sum_{n_2=0}^{z-n_1} \binom{z}{n_1} \binom{z-n_1}{n_2} M_{D,n_1,n_2} [\text{density of } D, n_1, n_2] \frac{n_1}{z} \\ & + \sum_{n_1=1}^z \sum_{n_2=0}^{z-n_1} \binom{z}{n_1} \binom{z-n_1}{n_2} M_{C,n_1,n_2} [\text{density of } C, n_1, n_2] \frac{n_1}{z} \end{aligned} \tag{8a}$$

$$\begin{aligned} \frac{d\rho_{TT}}{dt} = & - \sum_{n_1=1}^{z-1} \sum_{n_2=0}^{z-n_1} \binom{z}{n_1} \binom{z-n_1}{n_2} M_{T,n_1,n_2} [\text{density of } T, n_1, n_2] \frac{z-n_1}{z} \times n_1 \\ & + \sum_{n_1=1}^z \sum_{n_2=0}^{z-n_1} \binom{z}{n_1} \binom{z-n_1}{n_2} M_{D,n_1,n_2} [\text{density of } D, n_1, n_2] \frac{n_1}{z} \times n_1 \\ & + \sum_{n_1=1}^z \sum_{n_2=0}^{z-n_1} \binom{z}{n_1} \binom{z-n_1}{n_2} M_{C,n_1,n_2} [\text{density of } C, n_1, n_2] \frac{n_1}{z} \times n_1 \end{aligned} \tag{8b}$$

$$\begin{aligned} \frac{d\rho_{DT}}{dt} = & - \sum_{n_1=0}^z \sum_{n_2=0}^{z-n_1} \binom{z}{n_1} \binom{z-n_1}{n_2} M_{D,n_1,n_2} [\text{density of } D, n_1, n_2] \times \left\{ \frac{n_2}{z} \times n_1 + \frac{n_1}{z} \times [n_1 - (z - n_1 - n_2)] \right\} \\ & + \sum_{n_1=0}^z \sum_{n_2=0}^{z-n_1} \binom{z}{n_1} \binom{z-n_1}{n_2} M_{C,n_1,n_2} [\text{density of } C, n_1, n_2] \\ & \times \left\{ \frac{n_1}{z} \times (z - n_1 - n_2) + \frac{(z - n_1 - n_2)}{z} \times n_1 \right\} \\ & - \sum_{n_1=0}^z \sum_{n_2=0}^{z-n_1} \binom{z}{n_1} \binom{z-n_1}{n_2} M_{T,n_1,n_2} [\text{density of } T, n_1, n_2] \\ & \times \left\{ \frac{n_2}{z} \times [z - (n_1 + n_2)] + \frac{z - n_1 - n_2}{z} \times (z - n_1 - n_2 - n_1) \right\} \end{aligned} \tag{8c}$$

$$\begin{aligned} \frac{d\rho_D}{dt} = & - \sum_{n_1=0}^z \sum_{n_2=0}^{z-n_1} \binom{z}{n_1} \binom{z-n_1}{n_2} M_{D,n_1,n_2} [\text{density of } D, n_1, n_2] \frac{n_1 + n_2}{z} \\ & + \sum_{n_1=0}^{z-1} \sum_{n_2=0}^{z-1-n_1} \binom{z}{n_1} \binom{z-n_1}{n_2} M_{T,n_1,n_2} [\text{density of } T, n_1, n_2] \frac{z - (n_1 + n_2)}{z} \\ & + \sum_{n_1=0}^{z-1} \sum_{n_2=0}^{z-1-n_1} \binom{z}{n_1} \binom{z-n_1}{n_2} M_{C,n_1,n_2} [\text{density of } C, n_1, n_2] \frac{z - (n_1 + n_2)}{z} \end{aligned} \tag{8d}$$

$$\begin{aligned}
 \frac{d\rho_{DD}}{dt} = & - \sum_{n_1=0}^{z-1} \sum_{n_2=0}^{z-1-n_1} \binom{z}{n_1} \binom{z-n_1}{n_2} M_{D,n_1,n_2} [\text{density of } D, n_1, n_2] \frac{n_1+n_2}{z} \times (z-n_1-n_2) \\
 & + \sum_{n_1=0}^{z-1} \sum_{n_2=0}^{z-1-n_1} \binom{z}{n_1} \binom{z-n_1}{n_2} M_{T,n_1,n_2} [\text{density of } T, n_1, n_2] \frac{z-(n_1+n_2)}{z} \times (z-n_1-n_2) \\
 & + \sum_{n_1=0}^{z-1} \sum_{n_2=0}^{z-1-n_1} \binom{z}{n_1} \binom{z-n_1}{n_2} M_{C,n_1,n_2} [\text{density of } C, n_1, n_2] \frac{z-(n_1+n_2)}{z} \times (z-n_1-n_2) \tag{8e}
 \end{aligned}$$

where, $\{T, n_1, n_2\}$ indicates a T surrounded by n_1T, n_2C and $z - n_1 - n_2D$. It can be expressed as [density of T, n_1, n_2] $\approx \rho_T q_{T|T}^{n_1} q_{C|T}^{n_2} q_{D|T}^{z-n_1-n_2}$ with pair approximation.

The autonomous system which only consists of two global variables ρ_T and ρ_D can be analysed by adopting mean-field approximation, trends of trajectories are found to be similar to one dimension, except the differences in critical values. When b varies from 1.1 to 1.9, the corresponding w_a which induces bistable state changes from 0.35 to 0.63.

Consider pair-approximation, it can be easily got that individuals with the same strategy form clusters within a short time period, i.e., the local probability of the strategies $q_{T|T}, q_{C|C}$ and $q_{D|D}$ increases rapidly. Moreover, the time needed to approach a stable state is much shorter compared with the situation in one dimension. This result is very consistent with computer simulations. Fig. 5(b)–(d) give an example.

4. Discussion and conclusions

Our research confirms the conclusion that the lattice model prompts the evolution of cooperation [11,19,28,34–36]. We find that the problem of invasion and establishment of the cooperative strategy in a population dominated by a noncooperative one can be resolved in a lattice structured populations. Cooperative behaviors become more likely to spread as the probability of iteration w increases. Moreover, the smaller the advantage of defectors b , the easier it is for TFT to be an ESS (evolutionary stable state). Meanwhile, lattice-structured populations are also found to inhibit the evolution of cooperation because of spiteful behavior.

First, we will focus our interest on the differences between non-spatial and spatial game models. Obviously, spatial structure benefits the evolution of cooperation. In a complete well-mixed population, starting from a population with equal frequencies of the three strategies, the state where cooperation is evolutionary stable requires $1 > w > 2(b-1)/b$ [36], but the range of w becomes much wider with spatial structure, no matter what the dimension is. A lattice-structured population has a tendency to make clusters of the same strategy when individuals interact with neighbors repeatedly. Moreover, cooperators can survive by forming stable clusters which defend exploitation by defectors.

Simultaneously, a negative effect caused by the lattice structure for the evolution of cooperation cannot be neglected, although its influence is relatively weak compared to a positive effect because the ultimate outcome still shows promotion. It is due to the spiteful behavior [37,38] by killing neighbors and then replacing them. A player of a lower score is more likely to die and then offer 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 [11]. Take the work of Zhang et al. [39] as a reference for this point. The $b-w$ parameter region indicated by + (ALLD is ESS) in Fig. 1(c) just roughly corresponds to regions 1–6 which always characterizes a coexistence state with ALLD in their work, which implies this stochastic update rule is weaker than the deterministic rule for the promotion of cooperation in lattice, which is due to spiteful behavior.

Furthermore, the effect of patch connectivity (the neighborhood's size) studied in two dimensions also supports the view above. Simulations show that the higher the patch connectivity, the more time is required for the extinction of ALLD (see Fig. 5(c) and (d) as examples). Unlike with a neighborhood size of 4, neighbors can be potential competitors for a vacancy to reproduce when their common neighbor died, because a neighbor's neighbor can also be a neighbor, which gives an advantage of spiteful behavior to reduce the payoffs of the opponents.

Next, we will give comparisons about the three kinds of mathematical approaches.

The mean-field approximation fails to explain the results of computer simulations no matter what the dimension is, especially notable in one-dimension. And now, a puzzling problem confronts us. The spread of TFT is much more difficult under mean-field dynamics than in the completely well-mixed dynamics, although both approximations assume perfectly randomized spatial configuration. The condition for an increase of TFT is $(b-1)/b < w < 1$ for the first case [39], but the range of w becomes narrower for the second. This is still owing to the possibility of an advantage of spiteful behavior, which can be explained by considering two population processes. There is no difference in these two methods in the interaction process until the death of a player before filling the vacant site. However, the situation absolutely changes in the replacement process. For the completely well-mixed assumption, individuals will be relocated on the lattice according to the new fraction derived from the interaction process; replacement will happen after that. Yet, a randomization procedure for spatial configuration happens after replacement for another one. Any behavior to reduce the score of its neighbors enhances the mortality of neighbors, and can be advantageous to it who enjoys a higher opportunity to reproduce in the vacant sites produced due to death of the neighbor. This makes the mean-field approximation more profitable for a spiteful behavior.

Pair-approximation fails to explain the results of computer simulations in one dimension. In particular, we observed the coexistence of the three strategies independent of parameter values, and the global density will be fixed at its current value once the local density approaches 1 in Fig. 5(a), although simulation shows that the coexistence state is sustained for a long period before one strategy dominates. However, in two dimensions, a synchronous change between local and global densities can be observed, and pair-approximation is always quite accurate. These differences also arise due to the spatial continuity of a two-dimensional lattice which has been explained in Section 3.2. In contrast, strategy distribution tends to be separated in one dimension, pair approximation can be inaccurate for this situation and a different approximation, such as pair-edge approximation may be needed [40]. This deserves further research.

Invasion probability analysis in one dimension is powerful to estimate the probability that one behavior individual can invade a population composed by the other. The simplified assumption of uniform distribution at initial state is convenient to construct the model. However, it is more realistic to consider the aggregation degree of the same strategy at the initial configuration, which should be taken into account in future.

Finally, the results show that invasion of ALLD will be facilitated in the case where ALLC are introduced to the populations composed of ALLD and TFT. Moreover, coexistence between cooperators and defectors cannot be observed, which has been explained as a result of the 'spiteful' behavior to some extent. However, it is well known that Nowak and May [28] observed the perpetual coexistence of cooperative and defective players for a particular set of parameters. There is also coexistence with ALLD in the work of Zhang et al. [39]. Actually, it has been reported that cooperators and defectors are more difficult to coexist with stochastic state-transition than suggested by deterministic models [35]. Hence, the key role of specific interacting rules in the evolutionary process is undoubted. Differences in the assumption may cause qualitative discrepancies in the models' behavior to evolve. E.g., a fertility model is much more favorable for the spread of TFT than the corresponding viability model [35]. In fact, there are many variants about construction of the model, which merits further theoretical as well as empirical investigations in the future.

Acknowledgements

We are grateful to the editor and three anonymous reviewers for their helpful comments. We thank Dr. Feng Zhang to useful comments on earlier version of the manuscript. We also thank Dr. Jan Engelstädter, for his kind help with the English of this manuscript. This work was supported by the National Natural Science Foundation of China (No. 30700100, No. 30970478, No. 30970491). M.G. also acknowledges the support from National Natural Science Foundation of China (No. 31000197) and Knowledge Innovation Project of The Chinese Academy of Sciences (No. KZCX2-EW-QN209).

Appendix

A continuous sequence of T is called a 'cluster', and the number of T is the 'cluster size', so do as C or D . Let $Q_n(t)$ be the probability that a cluster containing nT in time t goes extinct eventually. Let $\lambda_n \Delta t$ be the transition probability in a short time interval of Δt from the cluster containing nT to a cluster with $(n + 1)T$, and $\mu_n \Delta t$ be the transition probability from nT to $(n - 1)T$. Thus we have the basic equation of a Random-Walk as,

$$Q_n = Q_n(1 - \lambda_n \Delta t - \mu_n \Delta t) + Q_{n+1} \lambda_n \Delta t + Q_{n-1} \mu_n \Delta t. \quad (\text{A.1})$$

First, we consider the case in which the cluster will not go extinct once it reaches a sufficiently large size $k + 1$, later we make k infinitely large. Then the boundary conditions are,

$$Q_n = 0 \quad (n \geq k - 1) \quad (\text{A.2a})$$

$$Q_0 = 1. \quad (\text{A.2b})$$

From the definition of the processes, the transition occurs when a site at the boundary between a run of T -sites and a run of D -sites dies and is subsequently replaced by its neighbor. Assuming the spatial configuration is uniformly clumped, the transition rates λ_n and μ_n can be rewritten as follows,

$$\lambda_n = \begin{cases} 0, & n = 0 \\ (M_{D,1,0} + M_{D,1,1} + M_{C,1,0} + M_{C,1,1})/4, & n = 1, 2, 3, \dots \end{cases} \quad (\text{A.3a})$$

where $n = 0$ is an absorbing point

$$\mu_n = \begin{cases} (2M_{T,0,1} + M_{T,0,0} + M_{T,0,2})/4, & n = 1 \\ (M_{T,1,0} + M_{T,1,1})/2, & n = 2, 3, 4, \dots \end{cases} \quad (\text{A.3b})$$

In following, we put $\lambda = (M_{D,1,0} + M_{D,1,1} + M_{C,1,0} + M_{C,1,1})/4$, $\mu = (M_{T,1,0} + M_{T,1,1})/2$, $\mu' = (2M_{T,0,1} + M_{T,0,0} + M_{T,0,2})/4$. Using Eqs. (A.2a), (A.2b), (A.3a) and (A.3b), Eq. (A.1) can be rewritten as,

$$Q_n = Q_n(1 - \lambda \Delta t - \mu \Delta t) + Q_{n+1} \lambda \Delta t + Q_{n-1} \mu \Delta t \quad (2 \leq n \leq k) \quad (\text{A.4a})$$

$$Q_1 = Q_1(1 - \lambda \Delta t - \mu' \Delta t) + Q_2 \lambda \Delta t + Q_0 \mu' \Delta t. \quad (\text{A.4b})$$

From Eqs. (A.2a) and (A.4a) we have

$$Q_{n+1} = Q_1 + \sum_{k=1}^n \left(\frac{\mu}{\lambda}\right)^{k-1} (Q_2 - Q_1). \tag{A.5}$$

From Eqs. (A.2b) and (A.4b) we have

$$Q_2 = \frac{-\mu'}{\lambda} + \frac{\lambda + \mu'}{\lambda} Q_1. \tag{A.6}$$

From Eqs. (A.2a), (A.5) and (A.6), Q_1 is derived as,

$$Q_1 = \frac{\mu' \left(1 - \left(\frac{\mu}{\lambda}\right)^k\right)}{\lambda - \mu + \mu' \left(1 - \left(\frac{\mu}{\lambda}\right)^k\right)} \quad \text{if } \lambda \neq \mu \tag{A.7a}$$

$$Q_1 = \frac{\mu'k}{\lambda + \mu'k} \quad \text{if } \lambda = \mu. \tag{A.7b}$$

$\lambda = \mu$ occurs when $w = w_T$.

From Eqs. (A.7a) and (A.7b), when $k \rightarrow \infty$, Q_1 converges to the following values,

$$Q_1 \rightarrow \frac{\mu'}{\lambda + \mu' - \mu} \quad \text{if } \lambda > \mu \ (w > w_T), \tag{A.8a}$$

$$Q_1 \rightarrow 1 \quad \text{if } \lambda \leq \mu \ (w \leq w_T). \tag{A.8b}$$

From Eqs. (A.8a) and (A.8b), we can derive the ultimate extinction probability Q_1 for a single T to go extinct. Then we can obtain the invasion success probability by a single T , $Q_T = 1 - Q_1$. In a similar way, the probability R_n , that a colony consisting of nC goes extinct is also derived as follows,

$$\lambda_n = \begin{cases} 0, & n = 0 \\ (M_{D,0,1} + M_{D,1,1} + M_{T,0,1} + M_{T,1,1})/4, & n = 1, 2, 3, \dots, \end{cases} \tag{A.9a}$$

$$\mu_n = \begin{cases} (2M_{C,1,0} + M_{C,0,0} + M_{C,2,0})/4, & n = 1 \\ (M_{C,0,1} + M_{C,1,1})/2, & n = 2, 3, 4, \dots, \end{cases} \tag{A.9b}$$

where $\lambda = (M_{D,0,1} + M_{D,1,1} + M_{T,0,1} + M_{T,1,1})/4$, $\mu = (M_{C,0,1} + M_{C,1,1})/2$, $\mu' = (2M_{C,1,0} + M_{C,0,0} + M_{C,2,0})/4$. We have recurrence formulae as,

$$R_n = R_n(1 - \lambda \Delta t - \mu \Delta t) + R_{n+1} \lambda \Delta t + R_{n-1} \mu \Delta t \quad (2 \leq n \leq k) \tag{A.10a}$$

$$R_1 = R_1(1 - \lambda \Delta t - \mu' \Delta t) + R_2 \lambda \Delta t + R_0 \mu' \Delta t. \tag{A.10b}$$

Then, when $k \rightarrow \infty$

$$R_1 \rightarrow \frac{\mu'}{\lambda + \mu' - \mu} \quad \text{if } \lambda > \mu \ (w \leq w_C), \tag{A.11a}$$

$$R_1 \rightarrow 1 \quad \text{if } \lambda \leq \mu \ (w > w_C). \tag{A.11b}$$

Using the same procedure, the probability, P_1 , that a colony consisting of one D goes extinct is also derived, when $k \rightarrow \infty$

$$P_1 \rightarrow \frac{\mu'}{\lambda + \mu' - \mu} \quad \text{if } \lambda > \mu \ (w \leq w_D), \tag{A.12a}$$

$$P_1 \rightarrow 1 \quad \text{if } \lambda \leq \mu \ (w > w_D), \tag{A.12b}$$

where,

$$\lambda_n = \begin{cases} 0, & n = 0 \\ (M_{T,1,0} + M_{T,0,1} + M_{C,1,0} + M_{C,0,1})/4, & n = 1, 2, 3, \dots, \end{cases} \tag{A.13a}$$

$$\mu_n = \begin{cases} (2M_{D,1,1} + M_{D,2,0} + M_{D,0,2})/4, & n = 1 \\ (M_{D,1,0} + M_{D,0,1})/2, & n = 2, 3, 4, \dots \end{cases} \tag{A.13b}$$

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