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Space promotes the coexistence of species: Effective medium approximation for rock-paper-scissors system

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ABSTRACT

Stochastic cellular automata for rock-paper-scissors games are related to Lotka-Volterra model. Simulations are usually performed by two methods local and global interactions. It is well known that the population dynamics with local interaction is stable, where all species coexist. In contrast, global interaction leads to extinction. So far, theories such as mean-field theory and pair approximation have been presented, but they never explained the stable dynamics in local simulation. In the present article, we apply effective medium approximation (EMA) which has been developed in Physics. The effective medium is determined in a self-consistent way. The EMA theory well predicts the stability of population dynamics. Moreover, it fairly explains the aggregation of each species observed in the stationary state.

1. Introduction

The coexistence of multiple species has been discussed by many authors and the plausible mechanisms have been proposed for the coexistence (Chesson and Warner, 1981; Gauze, 1934; Muko and Iwasa, 2000; Sugden, 2001; Tilman, 1994; Tubay et al., 2013). Recently, cooperative interactions among species, rather than competition, predation, and parasitism, are getting known for promoting biodiversity (Bruno et al., 2003; Tainaka and Hashimoto, 2016). Cooperative, facilitative, or positive interactions are the broad concepts including mutualism and commensalism. Basically, if two different species compete for the identical niches, one will eventually die out because of the competitive exclusion principle (Gauze, 1934). However, cooperative interactions allow two different species to coexist by differentiating the niches (Gatti, 2011). That generated biodiversity becomes the source of further biodiversity (Gatti et al., 2017; Janz et al., 2006; Sugden, 2001). In contrast, it has been said since many years ago that spatial structure is the key to maintain biodiversity.

Among theoretical ecologists, lattice models (stochastic cellular automata) of rock-paper-scissors (RPS) game have been investigated to reveal the role of spatial structures in various fields (Reichenbach et al., 2007; Szabó and Fáth, 2007; Szolnoki et al., 2014; Szolnoki and Perc, 2016; Tainaka, 1993). Especially, the connection to real ecosystems is well known. The cyclic relationship among three species RPS is important in the sense that they are quite useful to maintain biodiversity from plants to animals. One of the best examples is the mating strategies of side-blotched lizards (Sinervo and Lively, 1996). Other examples are marine sessile organisms (Burrows, 1998; Buss, 1980), competition between mutant strains of yeast (Paquin and Adams, 1983), prey-predator system (Tainaka and Fukazawa, 1992), grass-tree system (Durrett and Levin, 1994), three strains of E. coli (Kerr et al., 2002) and fishes in fresh water (Sugiura et al., 2016). These species in cyclic relation can coexist in nature.

For spatial RPS models, simulations are usually carried out by two methods: local and global interactions (Frean and Abraham, 2001; Sato et al., 1994; Tainaka, 1989, 1988). In the former, interaction occurs between neighboring cells, whereas in the latter it occurs between any pair of cells. It is well known that the population dynamics differs depending on simulation methods. Theoretical works firstly showed that the dynamics is unstable for global interaction (Itoh, 1973), while it is stable for local interaction (Tainaka, 1988). Then, this fact was proved by some elegant experiments (Kerr et al., 2006, 2002; Weber et al., 2014). There exists unsolved problem for a long time: no theory explains the stable dynamics in local interaction. So far, two approximation theories are widely recognized: mean-field theory and pair approximation.

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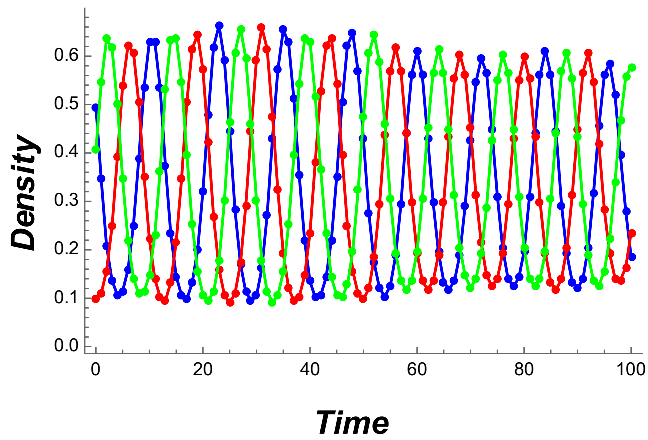

Fig. 1. Simulation results of population dynamics for global interaction. Time dependences of densities are depicted for $L = 100 \times 100$. Initial condition is set to be $(x, y, z) = (0.5, 0.1, 0.4)$. Blue, red and green mean species X, Y and Z, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

However, these theories never predicted the stable dynamics in local simulation (see Appendix A).

In the present paper, we apply effective medium approximation (EMA) which has been developed in Physics (Hori, 1977; Hori and Yonezawa, 1974; Nagatani, 1981a,b). In real nature, EMA corresponds to the state that the distributions of species reach the equilibrium after the longtime period. We explore two types of EMA theories: one-site and two-site EMAs. It is found that both theories well predict the stability of population dynamics: all species can coexist for local interaction.

2. Preliminary

We deal with a RPS system on a square lattice composed of L cells. Each cell is occupied by one of three species: X (rock), Y (scissors) and Z (paper). The interaction between a pair of cells occurs as

$$X + Y \rightarrow X + X \tag{1a}$$

$$Y + Z \rightarrow Y + Y \tag{1b}$$

$$Z + X \rightarrow Z + Z \tag{1c}$$

Simulation method for local interactions is as follows:

1) We choose a pair of adjacent cells randomly.
2) If the chosen cells occupy different species, then reactions (1) take place. For example, if X and Y are chosen, then Y becomes X.
3) Repeat the steps 1) and 2), until the system reaches a stationary state.

Next, the simulation procedure for global interaction is described. Almost all procedures are the same as local interaction, but the step 1) is changed as follows: "we choose two cells randomly and independently".

Simulation results are entirely different depending on simulation method. In the case of global interaction, RPS system is unstable [see Fig. 1]. Two species eventually go extinct. Itoh first proved such an extinction (ruin) (Itoh, 1973). His proof is very simple. Let $x(t)$, $y(t)$ and $z(t)$ be the population densities of X, Y and Z at time t, respectively. Here, the total density is unity: $x(t) + y(t) + z(t) = 1$. He showed that the expectation value of $P(t)$ always decreased, where $P(t)$ is the triple product defined by $x(t)y(t)z(t)$. The decreasing rate of $P(t)$ was proportional to L^{-1}. Here L is the total cell number. His proof has the following meanings. When $L$is finite, the system evolve to the extinction (ruin). In contrast, if $L \rightarrow \infty$, the product $x(t)y(t)z(t)$ becomes the constant in motion. In this case, mean-field theory (Lotka-Volterra equation) holds, so that the dynamics is neutrally stable (see Appendix A).

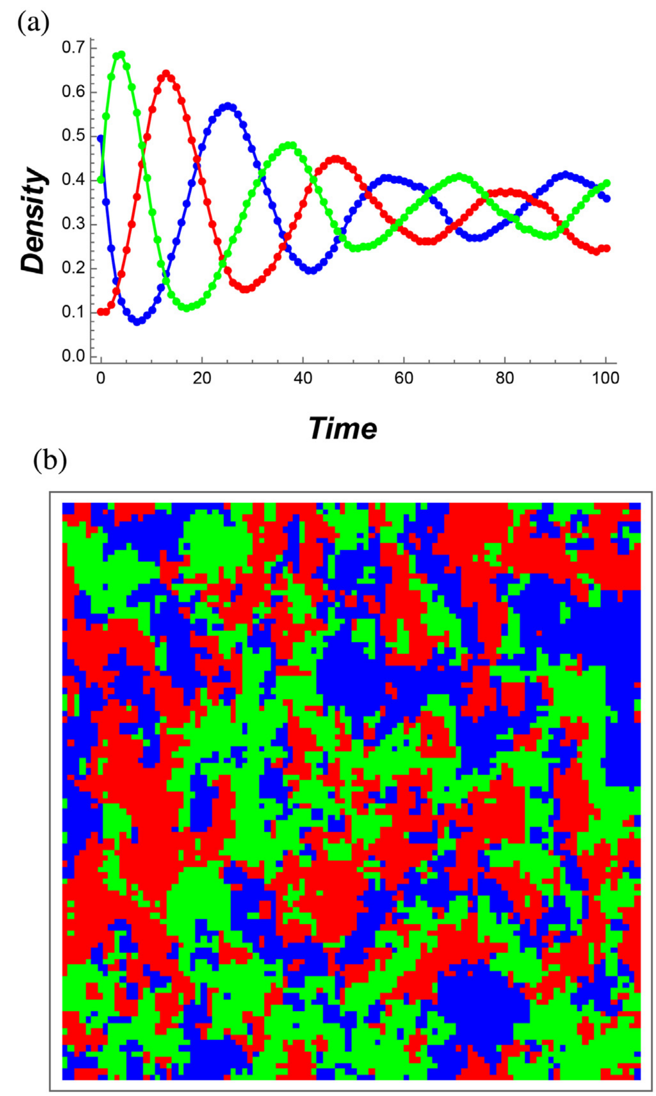

Fig. 2. Simulation results of for local interaction. (a) Same as Fig. 1 but for local interaction. (b) Typical spatial pattern in stationary states. Three colors mean the same species as in Fig. 1.

When the interaction occurs locally, the dynamics becomes stable. Tainaka first showed the stable dynamics as illustrated in Fig. 2 (Tainaka, 1989, 1988). When L is finite, an undamped oscillation (stochastic limit cycle) is observed (Itoh and Tainaka, 1994). The amplitude of oscillation was found to proportional to L^{-1}. Namely, if $L \rightarrow \infty$, the dynamics becomes asymptotically stable; all species eventually have the same density ($x = y = z = 1/3$).

3. Theory

3.1. Basic equations

Time dependences for densities can be represented by

$$dx/dt = aP_{XY} - cP_{ZX} \tag{2a}$$

$$dy/dt = bP_{YZ} - aP_{XY} \tag{2b}$$