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A swarm intelligence sustains biodiversity

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Multi-layered model for rock-paper-scissors game: A swarm intelligence sustains biodiversity

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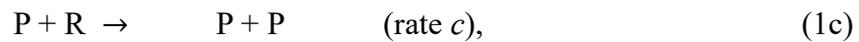
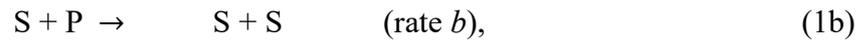
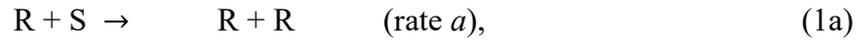
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Abstract

Much literature exists for rock-paper-scissors (RPS) game. It is well known in a single habitat that spatial models are more stable than well-mixed population. However, the mechanism of spatial stabilization has been unclear. In the present article, we study multilayer model of RPS game in a patchy environment; respective patches are set as lattices. The predation probability of one of three species is assumed to be reduced as a parameter. Simulations on two-layer system reveal the opposite result to those on a single-habitat system. Namely, the well-mixed population becomes stable. In contrast, extinction occurs by random migration in spatially-explicit model, when the reduced predation probability is below a certain critical value. The extinction in spatial model is found to be caused by the collapse of a kind of swarm intelligence (SI). In RPS system, large swarms of each species are automatically protected from its predator. Such a self-organized protection is one of the simplest examples of SI. We also discuss some serious problems for random migration.

1. Introduction

Rock-paper-scissors (RPS) game has increased interest in various fields (Bazeia et al., 2021; Abu-Akel et al., 2020; Li et al., 2020; Dyson et al., 2020; Epstein and Hadany, 2019; Ryan et al., 2020; Douglas and Das, 2019; . Kabir and Tanimoto, 2020). The game has long been studied in relation to biodiversity (Itoh, 1973; Tainaka, 1988; Reichenbach et al., 2007; Szabó and Fátth, 2007; Avelino et al., 2012a; 2012b; Liao et al., 2019; Nagatani, 2019; Park et al., 2020). Concrete example of RPS relations are males of lizard (Sinervo and Lively, 1996), strains of micro-organism (Kerr et al., 2002), marine organisms (Buss, 1980) and plant systems (Lankau and Strauss, 2007). A food chain in small ecosystem, called "microcosms" (Beyers and Odum, 1993), also represents a kind of RPS game; e.g. the system composed of producer, consumer and decomposers. The producer utilizes decomposers, but it is eaten by the consumer; when the consumer dies, they become nutrition for decomposers. We consider RPS game as follows (Frachebourg et al., 1996; Reichenbach and Mobilia, 2007; Claussen and Traulsen, 2008; Szolnoki et al. 2014; Szolnoki and Perc, 2016):



where R, P and S respectively mean the agent of rock, paper and scissors. The parameters a , b , and c denote the victory (predation) rates of R, S and P, respectively. Reaction (1a) represents R beats S. Similarly, P beats R, but it is beaten by S.

In one-population system, two typical methods have been proposed: well-mixed and spatially-explicit models. Itoh (1973) has presented a well-mixed population of RPS game; individuals (agents) of three species (R, S, P) randomly interact. Species changed according to reaction (1). On the other hand, in the spatially explicit model, agents locate on a lattice; the

interaction occurs between adjacent cells (Tainaka, 1988; Bramson and Griffeath. 1989). Although all species cannot survive in well-mixed population, they stably survive in spatially-explicit model with local interaction. Such a difference in dynamics has been experimentally verified by the use of *E. coli* (Kerr et al. 2002). However, the mechanism why spatial pattern formation stabilizes the biodiversity has long been unclear. The aim of the present article is to show the spatial mechanism of biodiversity.

We apply agent-based model (Sato et al., 1994; Szolnoki and Szabó, 2004; Szabo et al., 2007; Tubay and Yoshimura, 2013; Hódsági and Szabo, 2015; Wang et al., 2015; Szolnoki and Perc, 2017; Szolnoki et al., 2020) to a multi-patch system. Habitats of biospecies usually locate in spatially separated patches (Levin, 1974; Hanski et al., 1996). The dynamics in such patchy environment have been studied by metapopulation and network models (Allesina and Levine, 2011; Kivelä et al., 2014; Szczesny et al., 2014; Barabási, M. Pósfai, 2016). Some authors have applied RPS game to metapopulation model (Czárán, R. F Hoekstra, 2003; Nagatani et al., 2018a; Voit and Meyer-Ortmanns, 2019; Nagatani and Ichinose, 2020). A distinct point of the present paper is to set a lattice as a patch. There are several merits to use lattices. i) Spatially-explicit model. Inside respective patches, the simulation with local interaction can be carried out. ii) Finite capacity of patch. The migration of an individual (agent) is only allowed to move into an empty cell in the destination patch. iii) Non-random migration. An animal moves with avoiding danger, and may have some strategy for migration.

2. Preliminary: Results in One-Patch System

Results of Well-Mixed Population

First, we describe the results for well-mixed population. Itoh mathematically proved the instability (extinction) in well-mixed population (Itoh, 1973). When the total population size (C) of three species (R, S, P) is infinite ($C \rightarrow \infty$), the dynamics are well described by mean-field theory (MFT):

$$\frac{d\rho_R(t)}{dt} = a\rho_R(t)\rho_S(t) - c\rho_P(t)\rho_R(t) \quad (2a)$$

$$\frac{d\rho_P(t)}{dt} = c\rho_P(t)\rho_R(t) - b\rho_S(t)\rho_P(t) \quad (2b)$$

$$\frac{d\rho_S(t)}{dt} = b\rho_S(t)\rho_P(t) - a\rho_R(t)\rho_S(t) \quad (2c)$$

where $\rho_\alpha(t)$ is the population size (density) of species α ($\alpha = R, P, S$). The population sizes of three species oscillate periodically as shown in Fig. 1(a). A pair of species behave like prey and predator for classical Lotka-Volterra equation (Hofbauer and Sigmund, 1998). Since the dynamics has no asymptotic stability, three species cannot survive under slight disturbances. When C takes a finite value, two species eventually go extinct [see Fig. 1(b)]. Only one species survives at the final equilibrium.

Results of Spatially Explicit Model

Next, we describe the results for spatial (lattice) model with local interaction. The stability on a lattice becomes opposite to that for well-mixed population (Tainaka, 1988; 1989; Bramson and Griffeath, 1989; Kerr et al., 2002). In spatial model (local interaction), three species stably coexist. Note the extinction occurs in small (e.g., $C = 10 \times 10$) systems. In Fig. 2(a), the population dynamics is displayed for $C=200 \times 200$. When C is infinitely large ($C \rightarrow \infty$), the dynamics asymptotically stable. For a finite value of C ($C \gg 1$), undamped oscillations are observed at the final attractor (Itoh and Tainaka, 1994). Each species forms different sizes of swarms (clusters), but spatial

structure chaotically oscillates; the square of vibration amplitude is inversely proportional to C [see Fig. 2(b)]. The reason why all species survive in spatially-explicit model has been discussed. Tainaka and Itoh have explained the stabilization in lattice model by counting both creation and annihilation speeds of vortex (spiral) (Tainaka, 1989; Itoh and Tainaka, 1994). Nagatani et al. (2017) have proved the coexistence of species by applying "effective medium approximation" (Choy, 2016). However, it is still unclear what kind of spatial structure stabilizes the lattice system. As we will describe later, the biodiversity is sustained by a kind of "swarm intelligence" (Beni and Wang, 1989; Kaveh and Talatahari, 2010; Waibel et al., 2011; Santos et al. 2020). Each species can avoid extinction by a spatial pattern formation.

3. Method

Simulation method is a combination of migration and RPS game. First, migration method is described. We prepare n lattices (layers); the layer i contains C_i cells ($i = 1 \dots n$). Each cell is either empty (O) or agent of species α ($\alpha = R, P, S$). The agent migrates from layer i to j by rate m_{ji} ($i \neq j$). In Fig. 3, the migration of agent α from patch 1 to 2 is displayed, where (a) conventional migration and (b) the present migration. In Fig. 3 (a), the size (capacity) of patch has been ignored, and the well-mixed population has been assumed inside respective patches. In contrast, in the present paper, we regard lattices (layers) as patches. An agent of species α can migrate, only when there are empty cells in the destination layer. After the migration, both occupied and empty cells are exchanged. Namely, the cell α in layer 1 changes to the empty cell, while the empty cell in layer 2 changes to cell α . Note that the capacity (C_i) of layer i takes a constant value.

Next, we describe the method of RPS game which is played inside respective layers. In the present paper, we fix $b = c = 1$, and change the value of predation rate (a) of species R ($0 <$

$a \leq 1$). Simulation is carried out by either local or global interaction. In the former the reactions (1a)-(1c) occur between adjacent cells, whereas in the latter they occur between any pair of cells. The results of global interaction agree with those for well-mixed population. Throughout simulations, the total density (ρ_T) of agents in all patches is unchanged.

In the case of well-mixed population, the dynamics can be described by mean-field theory (MFT). Let $\rho_{\alpha,i}(t)$ be the density of species α in patch i at time t . Namely, the density means (cell number of species α in patch i)/ C_T , where C_T is the total cell number in the whole system: $C_T = \sum_i C_i$. We also define N_i and $\rho_i(t)$ be the ratio of capacity and the total density of agents in layer i , respectively: $N_i = C_i/C_T$ and $\rho_i(t) = \sum_{\alpha} \rho_{\alpha,i}(t)$. For convenience, we assume the migration rates are unchanged for any pair of i and j ($m_{ji} = m$). When the population size in each patch is sufficiently large ($C_i \rightarrow \infty$), the dynamics are well described by MFT.

$$\begin{aligned} \frac{d\rho_{R,i}(t)}{dt} = & [a\rho_{R,i}(t)\rho_{S,i}(t) - c\rho_{P,i}(t)\rho_{R,i}(t)]/N_i \\ & + m[\rho_{R,j}(t)E_i(t)/N_i - \rho_{R,i}(t)E_j(t)/N_j] \end{aligned} \quad (3a)$$

$$\begin{aligned} \frac{d\rho_{P,i}(t)}{dt} = & [c\rho_{P,i}(t)\rho_{R,i}(t) - b\rho_{S,i}(t)\rho_{P,i}(t)]/N_i \\ & + m[\rho_{P,j}(t)E_i(t)/N_i - \rho_{P,i}(t)E_j(t)/N_j] \end{aligned} \quad (3b)$$

$$\begin{aligned} \frac{d\rho_{S,i}(t)}{dt} = & [b\rho_{S,i}(t)\rho_{P,i}(t) - a\rho_{R,i}(t)\rho_{S,i}(t)]/N_i \\ & + m[\rho_{S,j}(t)E_i(t)/N_i - \rho_{S,i}(t)E_j(t)/N_j] \end{aligned} \quad (3c)$$

where $E_i(t)$ is the density of empty cells in layer i : $E_i(t) = N_i - \rho_i(t)$. In equation (3), the first and second terms on the right-hand sides denote the RPS reaction and migration, respectively. It is emphasized that the migration terms differ from those in conventional metapopulation model: the migration terms in equation (3) are represented by nonlinear functions of densities ("nonlinear migration") (Yokoi et al., 2019; 2020). From equation (3), we can obtain nonzero values of equilibrium densities ($\rho_{R,i}^*, \rho_{P,i}^*, \rho_{S,i}^*$).

Putting all time derivatives to be zero, we can get

$$\rho_{R,i}^* = \rho_i b / (a + b + c), \quad \rho_{P,i}^* = \rho_i a / (a + b + c), \quad \rho_{S,i}^* = \rho_i c / (a + b + c) \quad (4)$$

When $b = c = 1$, we have

$$\rho_{R,i}^* = \rho_{S,i}^* = \rho_i / (2 + a), \quad \rho_{P,i}^* = a \rho_i / (2 + a). \quad (5)$$

4. Results

4-1. Results for Well-Mixed Population

We report the population dynamics for global interaction (well-mixed population). Hereafter we assume the system contains two patches ($n = 2$). It is found that the stabilities in one- and two-patch systems are just opposite. Although all species cannot survive in a single population, they stably survive in two-patch system. As shown in Fig. 4 (a), the dynamics becomes asymptotically stable; no extinction occurs for $C_i > > 1$ and $C_1 \neq C_2$. When the migration rate (m) increases, the system rapidly reaches equilibrium. Note the case of $C_1 = C_2$ is exceptional: the extinctions of two species occur for a finite value of C_i .

In the case of traditional (linear) migration, the dynamics in two-layer system is never stable (Nagatani, et al., 2018a), because the densities of each species become immediately the same in both layers. In contrast, we assume patch capacities are finite; an agent moves into an empty cell. When both patches have different capacities, the densities in both layers are not equal. It may suppress the oscillation of densities.

In Fig. 4 (b), the equilibrium densities are depicted against the predation rate (a). The simulation results (plots) for global interaction well agree with the prediction of MFT (curves). With the decrease of a , the densities of paper (P) in both layers are decreased; in contrast, the densities of R and S are increased. This is paradoxical, because R should be the weakest for $a < 1$ ($b = c = 1$). Such a paradox is very popular in RPS systems (Tainaka, 1993; Frean and Abraham, 2001; Nagatani et al., 2018b; Avelino et al., 2019;

2021).

4-2. Results for Spatially Explicit Model

Simulations for local interaction exhibit that the stability is also opposite between one- and two-lattice systems. The population dynamics tends to be unstable in double-layer case. Fig. 5 displays the population dynamics for $a = 1$ and $a = 0.4$, respectively ($m = 1$ and $b = c = 1$). All species survive for $a = 1$, while the extinction occurs for $a = 0.4$. In the latter case, species P first goes extinct, and only R survives finally. This is also paradoxical: only the weakest species (R) survives. As parameter a decreases or m increases, the vibration of each density becomes large. Since the amplitude of vibration becomes too large, the extinction of species occurs. In Fig. 6 (a), the steady-state densities are depicted against the predation rate (a) of species R, where the dotted line represents the critical condition ($a = a_c$). Phase transition occurs between survival ($a_c < a$) and extinct ($a_c < a$) phases. The critical value a_c can be estimated by "finite-size stability analysis" (Sakisaka et al., 2008). We prepare five pairs of square lattices under the condition of $L_2 = L_1/2$ ($N_1 = 0.8$). For respective two-layer systems, we obtain the waiting time (τ) to extinction. In Fig. 6 (b), $\log(\tau)$ is plotted against $\log(L_1)$. The threshold between survival and extinction phases for $C_i \rightarrow \infty$ can be estimated in the power law case ($a_c \approx 0.57$).

Critical behaviors elucidate the mechanism of destabilization. In Fig. 7 (a), the population dynamics near extinction are displayed ($a = 0.59$). We observe larger oscillations, compared to the case of $a = 1$ [see Fig. 5 (a)]. The mechanism of large oscillation can be understood by spatial patterns. Figs. 7 (b) and (c) represent poor- and rich-density cases of P, respectively. We compare stable spatial pattern [Fig. 2 (b)] and spatial pattern near extinction [Fig. 7 (b)]. In the former (one-layer case), we find a kind of swarm intelligence (SI) (Beni and Wang, 1989; Santos et al. 2020). In Fig. 2 (b), large swarms are automatically protected from predators. For example, we pay attention to a

large blue swarm. One or few cells enclosed in the swarm are usually green which is weaker than surrounding species. Namely, predators (red cells) have been excluded inside the blue swarm. In contrast, in two-layer case [Fig. 7 (b) or (c)], SI is broken in the spatial patterns: not only green but also red cells are enclosed inside a large blue swam. Since a predator (red cell) invades near the center of large blue swarm, the population size of predator rapidly increases; conversely, the blue swarm rapidly collapses. Thus, the large oscillation and instability are caused by the collapse of SI. Moreover, Fig. 7 (b) can explain the paradox: since species P strongly forms clusters, it effectively disappears on lattices. If P disappears, then R beats S. Hence, R prevails in both lattices (paradox).

5. Conclusions

Spatial pattern dynamics is known to be stable in a single population. To date, the mechanism of stabilization has been unknown. The present work elucidates the mechanism of biodiversity. In two-layer model, we fix $m = 1$. This value of migration rate may be small, since each species forms clusters. If the migration rate is extremely high ($m \gg 1$), the spatially-explicit model should become the same as the well-mixed population. Even though the migration rate is low, the random migration has a significant impact. When $a \leq a_c$ ($a_c \approx 0.57$), species go extinct for $m = 1$. The extinction caused by the fact that a predator can invade near the center of large prey swarm. Realistically, however, such a lucky migration is infeasible (Greig and Pruett-Jones, 2010; Holmern et al., 2016). In multi-layers model, we can perform various simulations of non-random migrations. Simulations for more realistic migration reveal that all species survive, because the migration never causes the collapse of SI. For instance, we carry out simulation in the case that an agent migrates into (or next to) a flock of the same species. In this case, no extinction occurs, because the SI structure remains mostly. Hence, the two-layer system is considered to be stable for both local and global interactions. The method of the present article may be applicable more generally, such as off-lattice

populations (Bazeia, et al., 2021; Oliveira and Szolnoki, 2021) and public goods game with punishment (Szolnoki and Perc, 2013; 2017).

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Figure captions

Fig. 1. Results of well-mixed population in a single habitat ($a = b = c = 1$) (Itoh, 1973). (a) $C \rightarrow \infty$, (b) $C=10^4$. Initially ($t = 0$), the population sizes of (R, P, S) are set as (0.56, 0.08, 0.08). The colors blue, red and green denote rock (R), paper (P) and scissors (S), respectively. The population dynamics is not stable in a single habitat.

Fig. 2. Results of RPS population on a single lattice ($a = b = c = 1$) (Tainaka, 1988; Bramson and Griffeth, 1989). The RSP game is played between adjacent cells ($C=200 \times 200$). (a) population dynamics, (b) spatial pattern in stationary state ($t = 200$). The dynamics is usually stable on a single lattice.

Fig. 3. Schematic illustration of two types of migrations. (a) Conventional migration, (b) Migration between two layers. We only display the case that an agent (individual) of species α migrates from patch 1 to 2 (see blue arrows). In (a), agents freely move. However, in (b), agents are possible to move into the empty cells in layer 2. After the migration, both empty and occupied cells are exchanged.

Fig. 4. Results of two-layer system for global interaction (well-mixed population).

(a) Population dynamics for global interaction ($\rho_T=0.8$, $a = b = c = 1$, $C_2/C_1 = 1/4$). The upper three curves represent patch 1 and the lower three curves represent patch 2. At time $t = 100$, migration starts between both patches. (b) Equilibrium densities are depicted against the predation rate (a) of species R ($t = 10^4$). Plots and curves represent the results of simulation and theory, respectively. The colors blue, red and green denote rock (R), paper (P) and scissors (S), in order. Both densities of R and S are overlapped. Hence, the population dynamics for well-mixed population becomes stable.

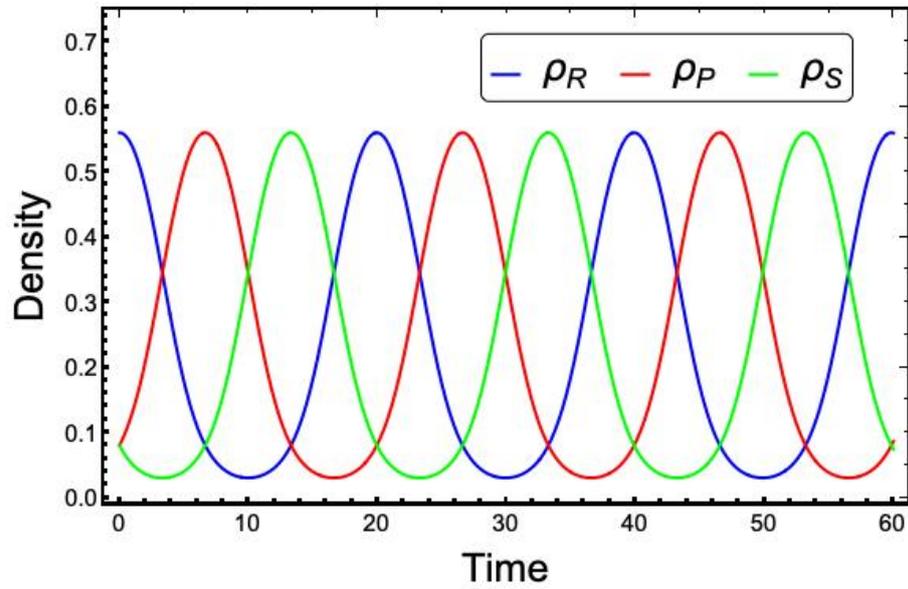
Fig. 5. Population dynamics of local interaction in two-layer system ($m = 1$). The system sizes of two lattices are set as $C_1 = 200 \times 200$ for patch 1 and $C_2 = 100 \times 100$ for patch 2. (a) $a = 1$, (b) $a = 0.4$. We only show the results in layer 1, because both layers 1 and 2 have the similar behaviors. On two-lattice system, three species cannot coexist for $a = 0.4$.

Fig. 6. Phase diagram for local interaction in two-layer system. (a) Steady-state densities are plotted against a . The vertical dotted line means the phase-transition point ($a_c \approx 0.57$) which is obtained by finite-size stability analysis (FSSA) [48]. (b) The result of FSSA. The waiting time (τ) to extinction are plotted against lattice size (L_1) for various values of a ($N_1 = 0.8$, $m = 1$, $\rho_T = 0.9$). We use $L_1 \times L_1$ for layer 1 and $L_2 \times L_2$ for layer 2, where $L_2 = L_1 / 2$ ($L_1 = 40, 80, 120, 160, 200$). Fitting curves are $\tau = \exp[1.3554L^{0.408}]$ for $a = 0.59$, $\tau = 0.138L^{2.085}$ for $a = 0.57$, $\tau = 0.234(\ln L)^{5.39}$ for $a = 0.54$ and $\tau = 0.921(\ln L)^{4.10}$ for $a = 0.50$. The critical point can be estimated in the power law case (see solid black line: $a_c \approx 0.57$).

Fig. 7. Dynamical behaviors near critical point ($a = 0.59$, $m = 1$). (a) Population dynamics of undamped oscillation. Both (b) and (c) represent spatial pattern in patch 1 at the final attractor; (b) $t = 1080$ and (c) $t = 1090$. The large oscillation is caused by the collapse of swarm intelligence.

Fig. 1

(a)



(b)

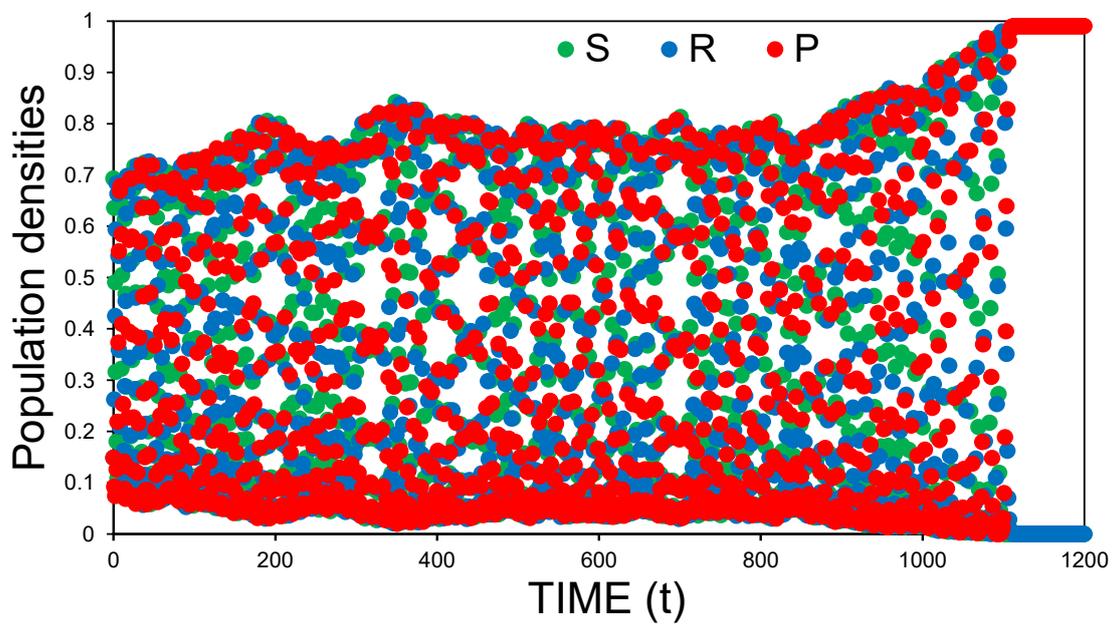
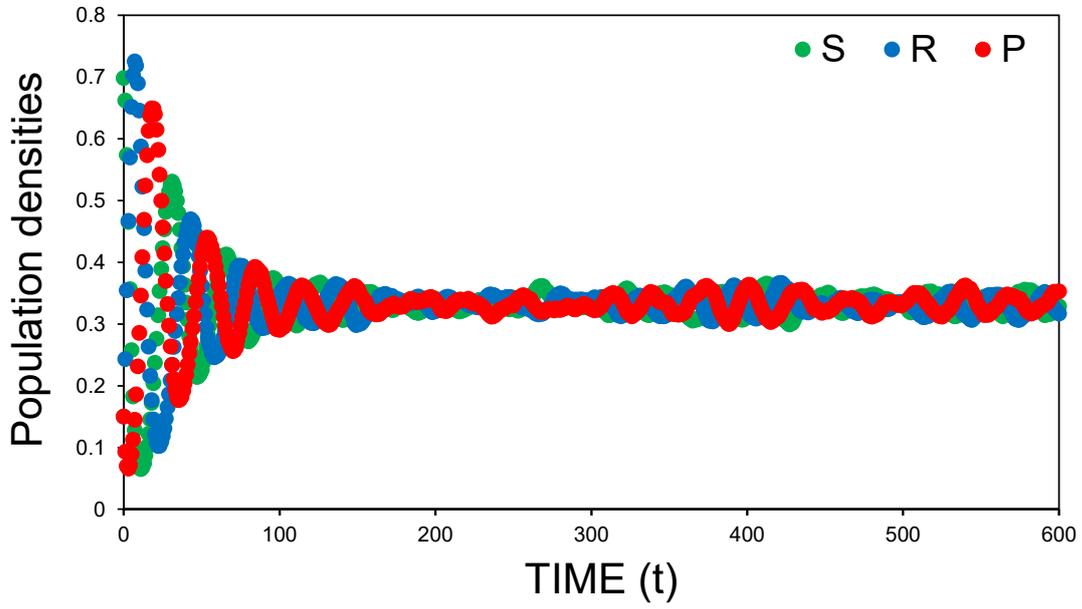


Fig. 2

(a)



(b)

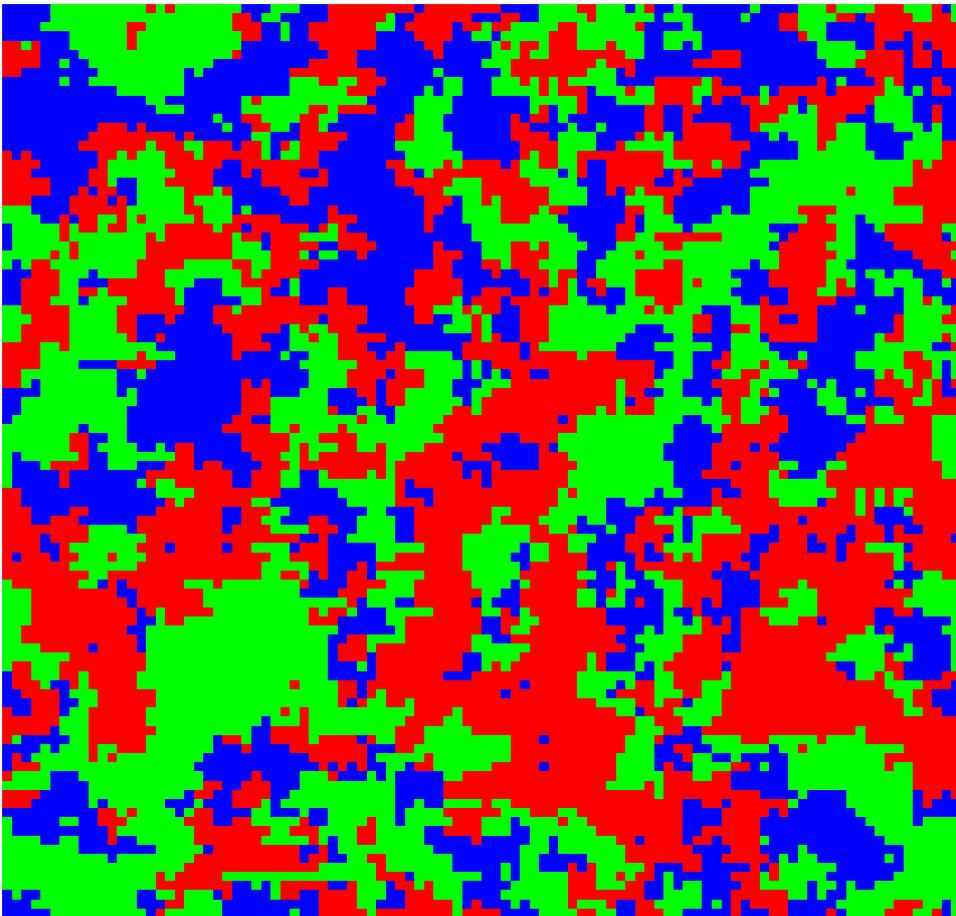
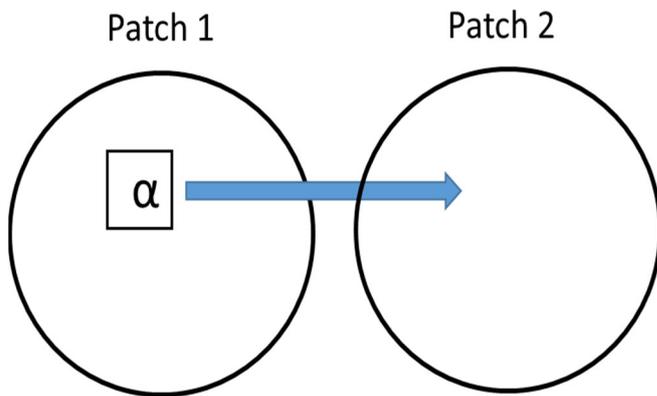


Fig. 3

(a)



(b)

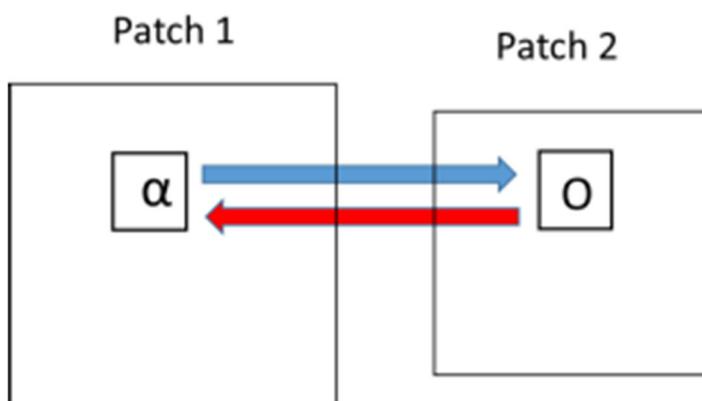
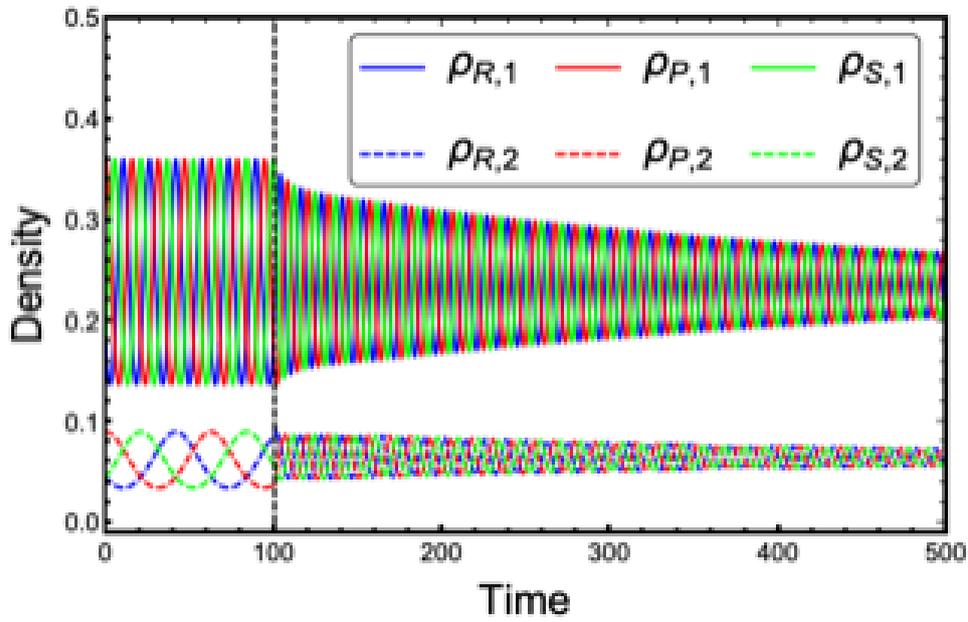


Fig. 4

(a)



(b)

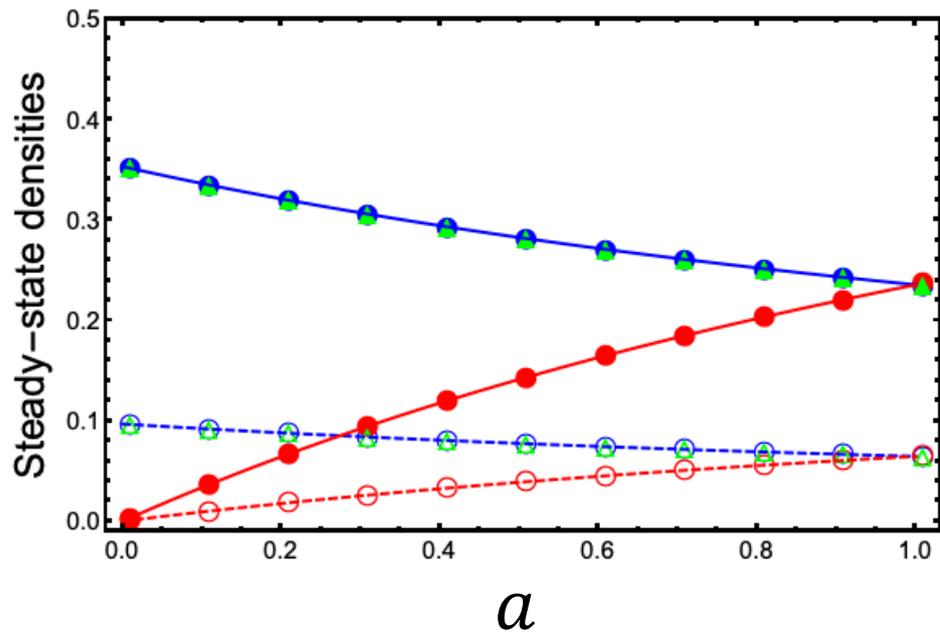
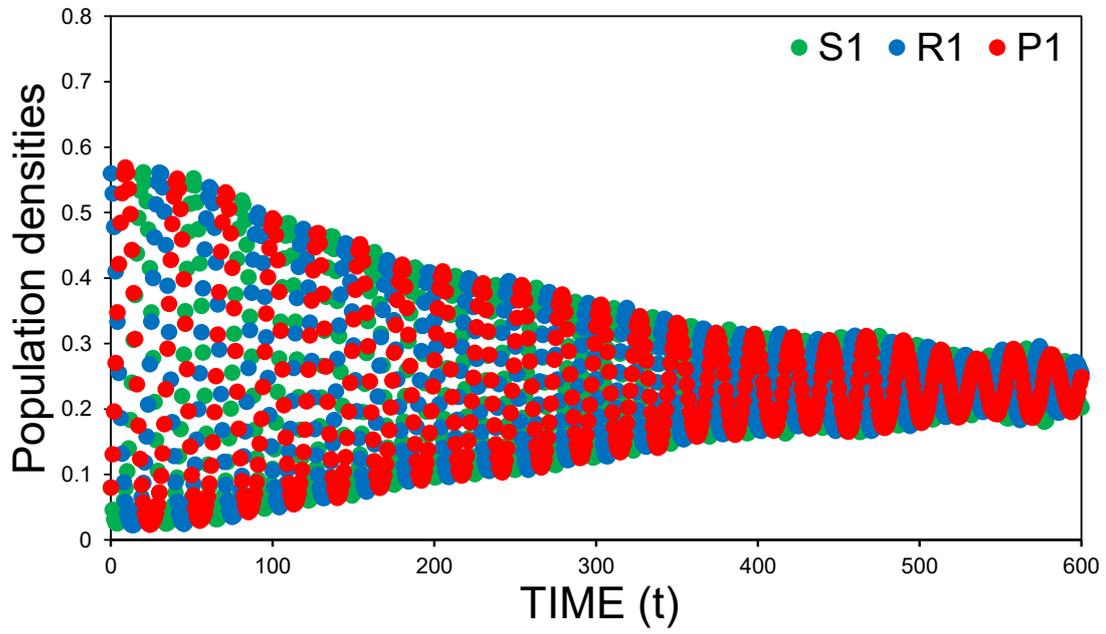


Fig. 5

(a)



(b)

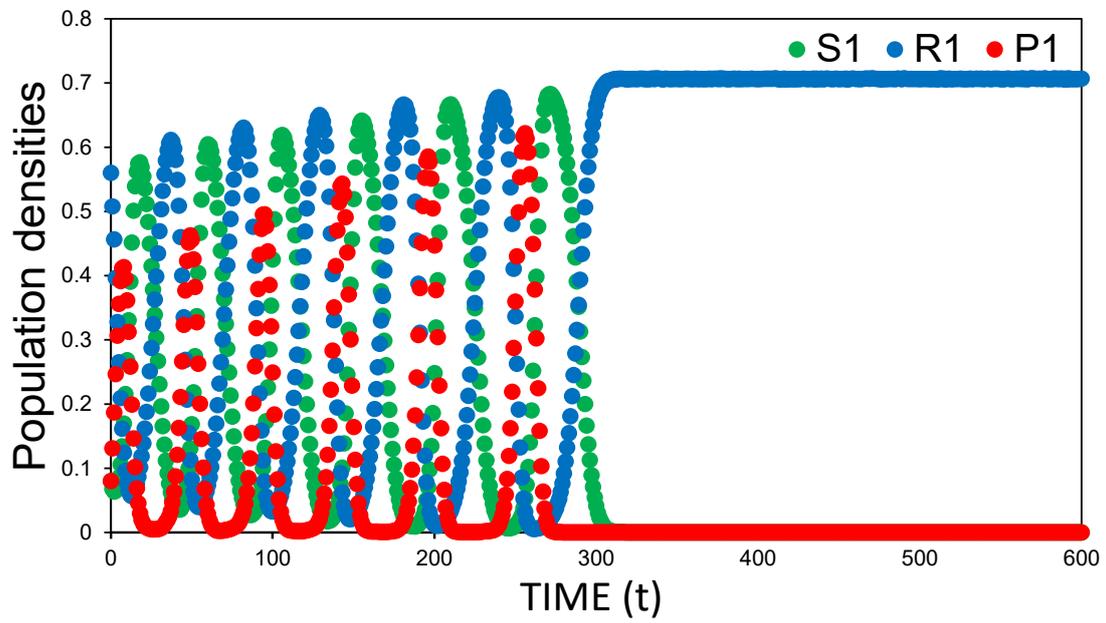
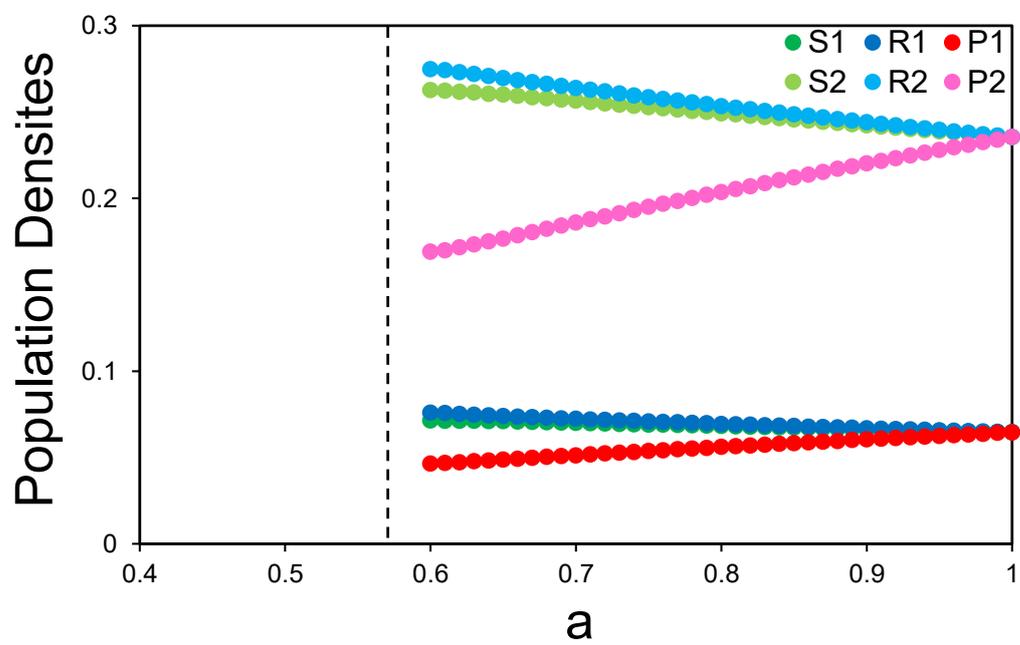


Fig. 6

(a)



(b)

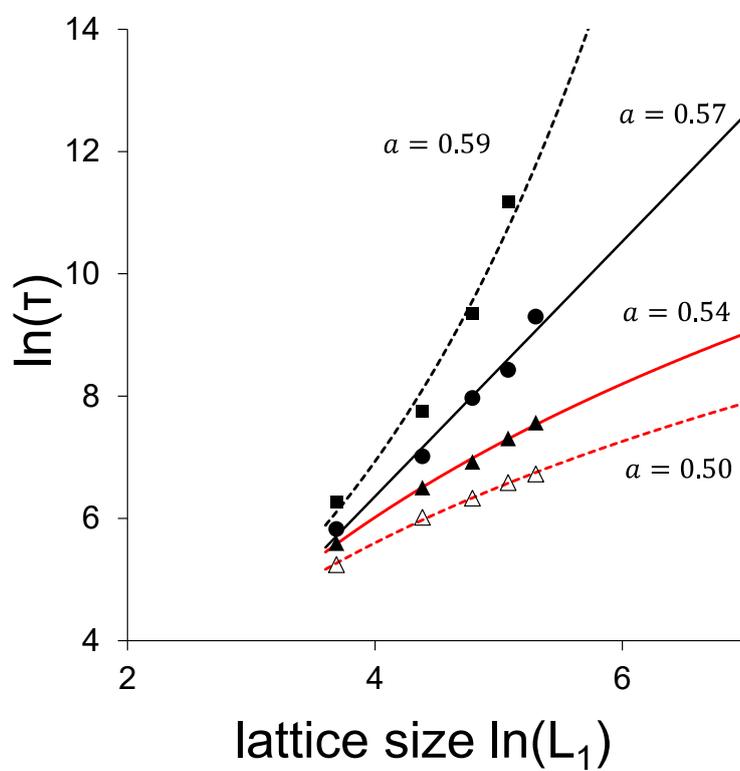
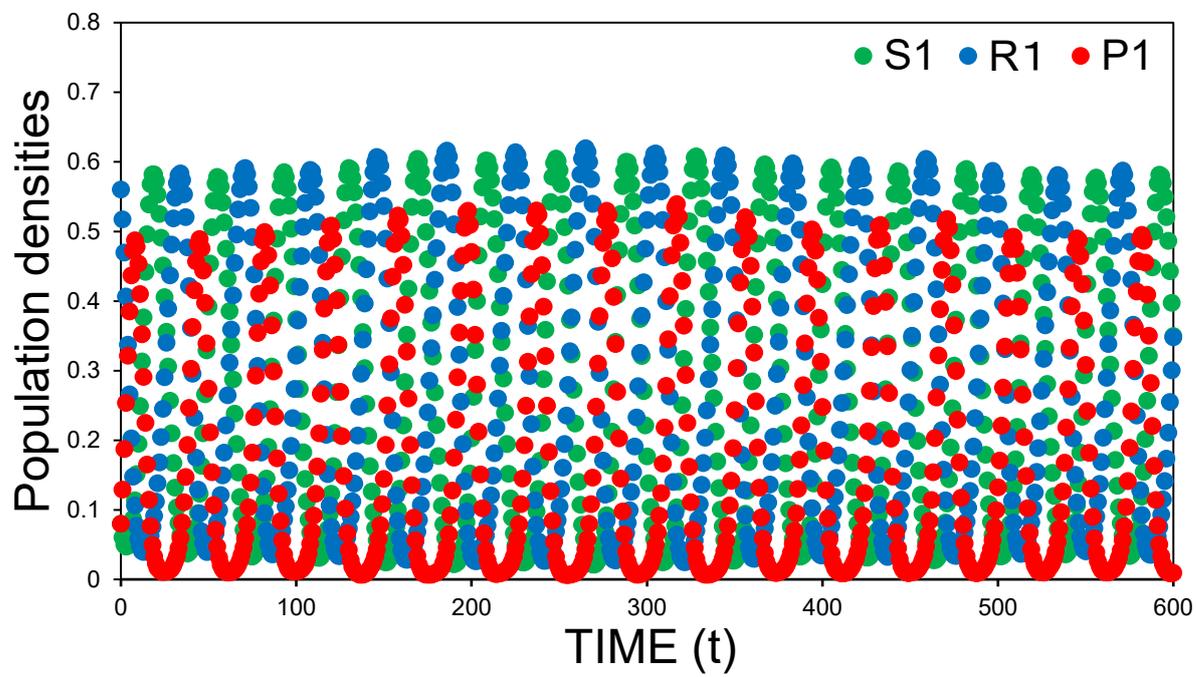
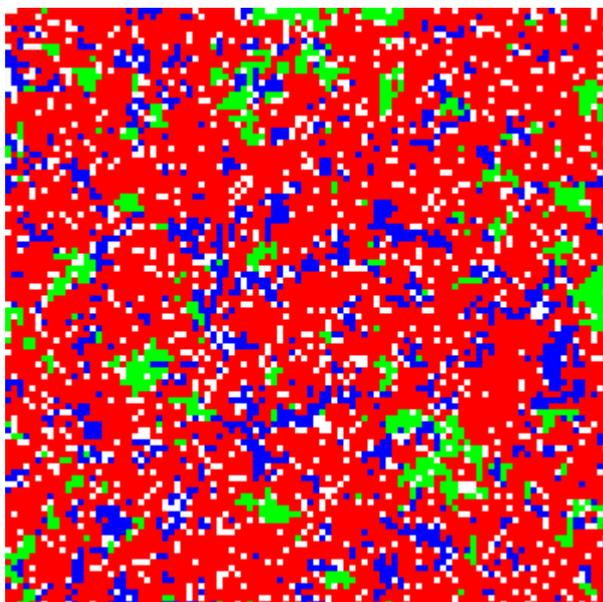


Fig. 7

(a)



(b)



(c)

