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Basins of attraction for species extinction and coexistence in spatial rock-paper-scissors games

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We study the collective dynamics of mobile species under cyclic competition by breaking the symmetry in the initial populations and examining the basins of the two distinct asymptotic states: extinction and coexistence, the latter maintaining biodiversity. We find a rich dependence of dynamical properties on initial conditions. In particular, for high mobility, only extinction basins exist and they are spirally entangled, but a basin of coexistence emerges when the mobility parameter is decreased through a critical value, whose area increases monotonically as the parameter is further decreased. The structure of extinction basins for high mobility can be predicted by a mean-field theory. These results provide a more comprehensive picture for the fundamental issue of species coexistence than previously achieved.

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Identifying mechanisms that maintain biodiversity is a fundamental problem in science. There has been a growing interest in this interdisciplinary topic [1–5]. Numerous models and experiments have demonstrated that species can coexist through nonhierarchical cyclic competitions. Representative chemical and biological situations where cyclic competitions have been found include competition among carcinogenic microbes [1], mating strategies of side-blotched lizards in California [6], and competition between mutant strains of yeast [7] and coral reef invertebrates [8]. Generic properties of the competition can be characterized by the traditional game of "rock-paper-scissor" in combination with spatial dispersal of static populations. The spatial games can lead to insights into species coexistence that is fundamental to biodiversity. For example, the emergence of self-organized spatial patterns in the coevolution of different species has been found to be crucial to the liability of biodiversity in experimental studies, where local restriction of interactions is more in favor of the formation of coexistence patterns than global interactions [1]. Quite recently, the role of population mobility, a basic parameter in the evolution of realistic ecosystems ranging from bacteria run and tumble to animal migration, has been investigated [4,9–13]. It has been found that mobility can support self-forming spatial patterns such as entangled rotating spiral waves. As an important extension to Ref. [4], it has been shown that breaking the conservation of total population density is key for pattern formation [14]. There have also been works on extinction induced by asymmetric interactions among species [15]. In addition, the size effect of population and the relation between stochastic models and their deterministic counterparts have been explored [16].

In existing works on cyclic dynamics in spatially extended systems, the issue of species coexistence has been addressed with respect to a single initial condition, corresponding to identical initial populations of species [4]. While this choice is convenient for computation and analysis, physically it is difficult to realize. In order to obtain a "global" and more complete understanding of species coexistence, it is necessary to study the system dynamics for all possible initial conditions. Indeed, in nonlinear dynamics, basins of attraction and the boundaries among them are a fundamental issue [17]. The aim of this Rapid Communication is to address the issue of basins of species coexistence and extinction in the framework of cyclic dynamics in spatially extended ecological systems.

To be concrete, we shall consider the paradigmatic setting where three species interact with each other on a square lattice through the "rock-paper-scissor" game [4]. The phase space of the system can be defined by the three population densities, n_r, n_p, and n_s, the ratios of the populations to the total number of lattice sites for the species corresponding to rock, paper, and scissor, respectively. When the initial populations are not identical, we find that there can be situations where species with the least initial population density dominates eventually. In a proper representation (to be described below), depending on the choice of the mobility parameter M, the available phase space is divided either into three regions, corresponding to the basins of the sole survival of one of the three individual species (equivalently, basins of extinction as in each such basin, two species are ultimately extinct), or into four regions, where one additional region, basin of coexistence, appears. In particular, the former situation occurs for relatively large values of M, where only one species can survive finally, regardless of the choice of initial conditions (which one sustains depends on the initial condition). In this case, the three basins are symmetric and spirally entangled around the center point in the phase space where the three population densities are identical. As M is decreased through a critical value M_c, a transition occurs that creates the basin of coexistence around the symmetric point, any initial condition from which generates a final state in which all three species survive and coexist. As M is decreased further, the size of the coexistence basin increases, eventually dominating the phase space. The area of the basin thus provides a quantitative measure of the degree of species coexistence in the system under the cyclic competition dynamics. For high mobility, we are able to obtain analytic prediction for the structures of the extinction basins, which are verified numerically.

We consider the cyclic-competition model with mobile individuals, as proposed in Ref. [4]. Three species populate a square lattice of N sites with periodic boundary conditions. Each site is either occupied or left empty. An individual on a lattice point interacts with four nearest neighbors according to the rock-paper-scissor rule, as follows:

$$RS \xrightarrow{u} R\oslash, \quad SP \xrightarrow{u} S\oslash, \quad PR \xrightarrow{u} P\oslash, \tag{1}$$

$$RS \xrightarrow{s} SR, \quad SP \xrightarrow{s} PS, \quad PR \xrightarrow{s} RP, \tag{2}$$

$$R\oslash \xrightarrow{s} \oslash R, \quad S\oslash \xrightarrow{s} \oslash S, \quad P\oslash \xrightarrow{s} \oslash P, \tag{3}$$

$$R\oslash \xrightarrow{c} RR, \quad S\oslash \xrightarrow{c} SS, \quad P\oslash \xrightarrow{c} PP, \tag{4}$$

where R, S, and P denote individuals from the three species, respectively. Relation (1) describes the cyclic selection, i.e., prey, which occurs at the rate u. Relations (2) and (3) define two types of motions of individuals on the lattice at the rate s, and relation (4) characterizes the reproduction of individuals at the rate c. Following Ref. [4], the rates s, c, and u are normalized so that the occurrence probabilities of motion, reproduction, and prey are $s/(s+c+u)$, $c/(s+c+u)$, and $u/(s+c+u)$, respectively. According to the theory of random walks [18], individual mobility M is defined as $M=s(2N)^{-1}$, to which the number of sites explored by one mobile individual per unit time is proportional. At each time step, a random individual is picked to interact with one of its four nearest neighbors, and the algorithm in [19] is used to determine selection, reproduction, or movement. A generation is defined when every individual in a species has experienced interaction once on average, which is regarded as one time step. Let n_0 be the fraction of empty sites. Initially, n_0 is fixed (e.g., 10%). The three species densities thus satisfy the constraint $n_r+n_p+n_s=1-n_0$, which defines a triangular region in the plane due to the conditions that the sum of the densities is fixed initially. The phase space can thus be represented by a simplex S_2 defined by this triangle [20].

In Ref. [4], the interplay between mobility and coexistence has been investigated but for the symmetrical case where the initial populations of the three competing species are identical. A critical value of mobility $M_c=(4.5\pm0.5)\times10^{-4}$ is identified, where for $M>M_c$, only one species can survive, which is called a uniform state. Coexistence arises for $M<M_c$. In our exploration of the basins of distinct asymptotic dynamical states, we will then choose to vary the parameter M from a value above M_c to zero. In addition, previous works [21,22] established that the mean time T for extinction scales with the system size N as $T\sim N$. In our simulations, the spatially extended ecosystem is represented by a 100×100 square lattice, for which an asymptotic state can be reached in about 10^4 times steps for almost all initial conditions. We use 10^5 time steps in all simulations.

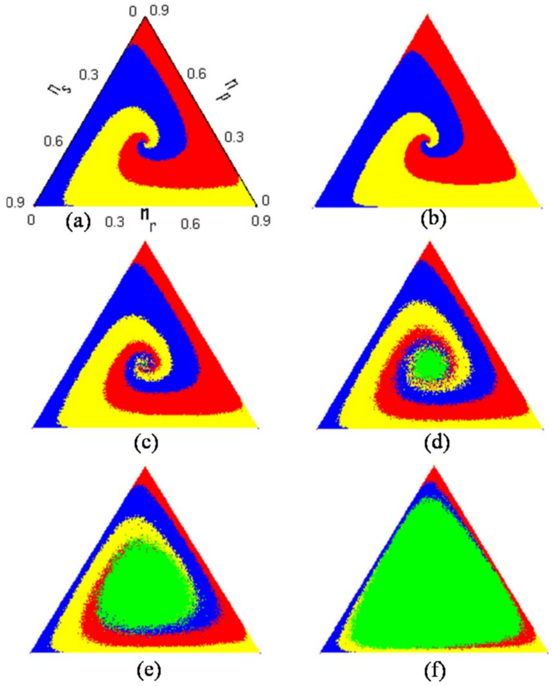

FIG. 1. (Color online) Basins of final states in the triangular representation of the phase space (simplex S_2) for different values of the mobility parameter M for $u=c=1$. The coordinates denote the initial densities of the three species and the color of each point represents the final state obtained from stochastic simulations by using 30 random realizations of the cyclic competition dynamics, under the same initial condition, on a given 100×100 square lattice. For each realization, the simulation consists of 10^5 time steps. (a) For $M=5\times10^{-3}$, the phase space contains three symmetric, extinction basins. There is no coexistence in this case. (b) Theoretically predicted basin structure for $M=5\times10^{-3}$ [cf. (a)]. The center point is green (light gray) in (f). (c) For $M=3\times10^{-4}$, a small coexistence basin with green (light gray) color appears about the center of S_2. (d) For $M=1\times10^{-4}$, the coexistence basin enlarges and the extinction basins shrink. (e) For $M=5\times10^{-5}$, the coexistence basin becomes even larger. (f) For $M=0$, the coexistence basin dominates but the extinction basins are still present around the corners and the edges of S_2.

Figures 1(a)–1(f) present basin structures in the phase space S_2 for different values of the mobility parameter M. The basins reveal the dependence of the final states on the initial population densities. The sum of three species densities is fixed to be 0.9 and the density of empty sites is 0.1 so that the dependence can be represented in S_2. For $M>M_c$, regardless of the choice of the initial population densities, a uniform state is reached in which only one species can survive finally. In this case, the phase space S_2 is divided into three basins, each consisting of initial conditions that lead to a uniform state of one species. The three basins are symmetrical and spirally entangled at the center of S_2, as shown in Fig. 1(a) for $M=5\times10^{-3}>M_c$. Along the boundaries between the basins, the final uniform state is sensitive to small variations in the initial population densities. The center point is actually a Wada point [23] where all three basins meet. This means that, if the initial populations are identical, an arbitrarily small perturbation can lead to a completely different asymptotic state. Which species can survive finally thus depends sensitively on small variations in the initial population densities. As soon as M is decreased through M_c, a new state arises where all three species can coexist. The basin of

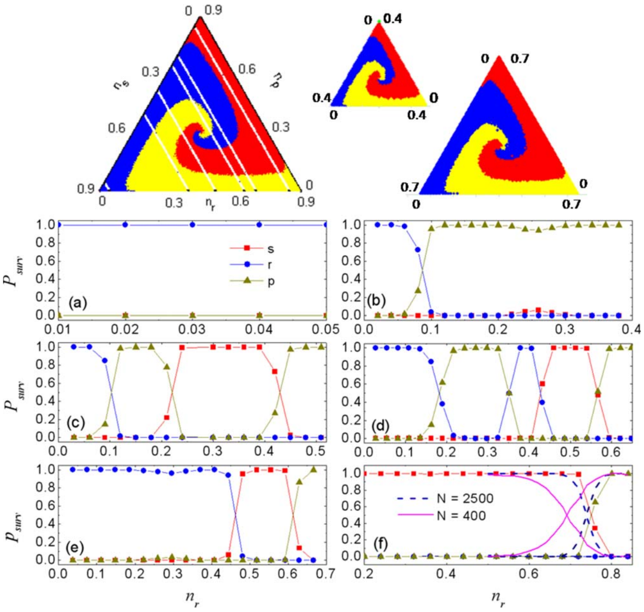

FIG. 2. (Color online) Dependencies of the survival probabilities of s (red square), r (blue circle), and p (orange triangle) on the initial density n_r for different initial values of n_s: (a) 0.85, (b) 0.5, (c) 0.38, (d) 0.25, (e) 0.2, and (f) 0.05, which correspond to the lines in the phase space S_2 from left to right. Along each line, the value of n_s is fixed. In (f), results are shown for two small lattice sizes $N=400$ and $N=2500$. Data points are averages from 5000 random samples. The biggest phase space is obtained by setting the initial density of empty site $n_0=0.1$. The two smaller phase spaces are for $n_0=0.6$ and $n_0=0.3$, respectively. Other parameters are the same as Fig. 1.

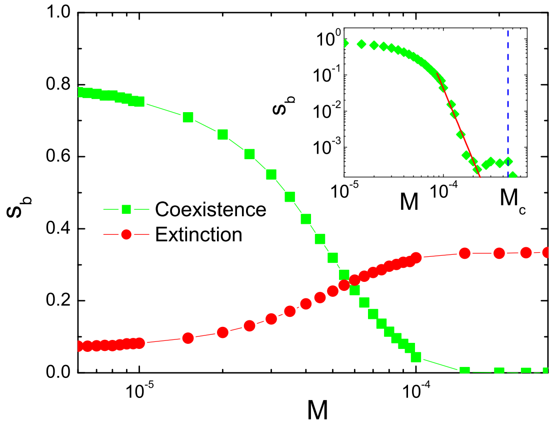

FIG. 3. (Color online) Areas of the coexistence basin and an extinction basin as a function M. The inset shows log-log plot for the area of coexistence basin as a function of M. In the range of small M, the area decreases exponentially as M increases. In the vicinity of M_c ($M>10^{-4}$), the area decreases more slowly than exponential law and can be approximated by algebraic law toward extinction. The slope by the algebraic fitting is about −6.8. M_c is marked by a dashed line. Other parameters are the same as in Fig. 1.

this coexistence state emerges from the center of S_2, as shown in Fig. 1(c) for $M=3\times10^{-4}$. As M is decreased further, the coexistence basin expands, accompanied by the simultaneous shrinking of the three extinction basins, as exemplified in Fig. 1(d) for $M=10^{-4}$. Biodiversity is promoted by inhibiting population mobility, reflected by the augmentation of the area of the coexistence basin, as shown in Figs. 1(e) and 1(f). For $M=0$, the area of the coexistence basin reaches maximum. In this case, for a random choice of the initial densities in S_2, there is a high probability for coexistence. Even then, three extinction basins still exist but they are mainly located near the corners and the edges of S_2. In general, for $M<M_c$, species coexistence can be achieved by decreasing the differences among the initial population densities as the center of the coexistence basin coincides with the center of the phase space. We have also found that the size of lattice does not affect the structure of basins.

To gain further insights, we focus on some typical one-dimensional line in S_2 to examine which species can outperform others based on the survival probability P_{surv}. Representative results are shown in Fig. 2, where we choose some fixed $n_s(0)$ values and adjust the initial densities n_r and n_p. When n_s is large, e.g., $n_s=0.85$ as in Fig. 2(a), r is the sole survivor, regardless of the value of n_p, since the whole line belongs to the basin of a uniform r state. For $n_s=0.5$, the line passes through two basins, as shown in Fig. 2(b). In this case, r survives for small n_r but p survives otherwise. For $n_s=0.5$ (c), 0.38 (d), and 0.25 (e), the line alternates among more basins and every species has at least a region with 100% survival probability. For small value of n_s, e.g., 0.05 (f), only two basins remain. The one-dimensional lines in S_2 thus indicate rich dynamical behavior of survival. The dependence of P_{surv} on the network size is also studied, as shown in Fig. 2(f). We find that the transition in P_{surv} of a species from 1 to 0 is much sharper for larger network size. We thus expect an abrupt transition in P_{surv} when N tends to infinity. We also note that the transition point changes when N increases. However, when N is relatively large, e.g., $N=2500$, the transition point changes a little for larger N, e.g., $N=10^4$, and we find the transition point tends to be the value by theoretical prediction (described later) which is based on the large limit approximation. Hereafter, we investigate the basin structure for different densities n_0 of empty sites, as shown in Fig. 2. We find that n_0 does not change the structures of extinction basins but simply shrinks the area of the simplex S_2.

The degree (or "strength") of species coexistence can be characterized by the size of its basin. Figure 3 shows the area S_b of the coexistence basin (filled squares) as a function of the mobility parameter M. It can be seen that, when M is decreased through M_c, S_b starts to increase from zero monotonically. The size of any one of the extinction basins exhibits the opposite trend. In particular, the area of any extinction basin is small for $M\gtrsim0$ but it approaches the asymptotic value 1/3 for $M>M_c$. In addition, we note that in a recent paper [24], a deterministic rock-paper-scissors game in well-mixed population is studied by relaxing the zero-sum assumption. It is found that in positive-sum game, fixation does not occur in a large central area of the phase space. However, in negative-sum game, fixation is deterministic everywhere with nontrivial dependence on initial conditions. Although the fixation differs much from the concept of species extinction, the role of negative-sum in fixation shows some similarity to the role of high mobility in extinction. This implies that there may be some underlying relationship between relaxation of zero sum and mobility.

For $M > M_c$, the structure of the extinction basins can be predicted analytically. If M is sufficiently high, cyclic dynamics can be described in the mean-field framework [25,26]:

$$\begin{cases} \dot{n}_r = \alpha n_r(1-n_r-n_p-n_s) - \beta n_r n_p \\ \dot{n}_p = \alpha n_p(1-n_r-n_p-n_s) - \beta n_p n_s \\ \dot{n}_s = \alpha n_s(1-n_r-n_p-n_s) - \beta n_s n_r, \end{cases} \tag{5}$$

where $\alpha = c/(s+u+c)$ and $\beta = u/(s+u+c)$. The equilibrium points can be obtained by setting $\dot{n}_r = \dot{n}_p = \dot{n}_s = 0$. Five equilibrium points (n_r, n_p, n_s, n_0) are (i) (1, 0, 0, 0), (ii) (0, 1, 0, 0), (iii) (0, 0, 1, 0), (iv) $(\alpha, \alpha, \alpha, \beta)/(3\alpha+\beta)$, and (v) (0, 0, 0, 0). Note that Eq. (5) cannot yield an absolute, mathematical extinction due to the existence of heteroclinic orbits that approach the corners of the phase space but never reach them [24]. However, the ordinary differential equation (ODE) model can still characterize the basin structures by taking into account the physical meaning of survival that the number of survival species cannot be less than unity due to the discrete nature of individuals. The state of extinction can then be unambiguously determined when the density of any species is less than $1/N$. The species next to the extinction species in the cyclic competition loop is the sole survivor, i.e., the species on which the extinct species prey should be the final survivor. Solutions to Eq. (5) for all possible initial conditions are shown in Fig. 1(b), which agree very well with the results from direct simulation for high mobility [Fig. 1(a)]. We have also examined the influence of our chosen extinction threshold $1/N$ on the basin structure by solving Eq. (5) for different values of N. We find that this choice does not affect the basin structures obtained from theory. It is noteworthy the coordinates of points in the simplex S_2 represent initial configurations. The center point has the Wada property and the three corners are singular points with different final states from the respective basins around them. This means the final state around the corner points are extremely sensitive to perturbations.

In summary, we have addressed the emergence of species coexistence that favors biodiversity in the framework of cyclic competition dynamics. Our approach is to examine all possible initial states to map out the basins for distinct final states of the system as the mobility parameter is changed. This is more systematic than previous approaches that focus on the evolution from a particular initial state, usually the one corresponding to uniform species populations. We have identified two types of basins: one corresponding to coexistence of all three species and another to extinction of two species. For high population mobility, the phase space contains three spirally entangled extinction basins. The basin of coexistence emerges from the center of the phase space when the mobility parameter is decreased through a critical point. The strength of coexistence can be characterized by the area of its basin. Our exploration of the basin structure thus provides a more comprehensive and complete picture concerning the rising and persistence of biodiversity than previously achieved.

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