

Basins of coexistence and extinction in spatially extended ecosystems of cyclically competing species

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Microscopic models based on evolutionary games on spatially extended scales have recently been developed to address the fundamental issue of species coexistence. In this pursuit almost all existing works focus on the relevant dynamical behaviors originated from a single but physically reasonable initial condition. To gain comprehensive and global insights into the dynamics of coexistence, here we explore the basins of coexistence and extinction and investigate how they evolve as a basic parameter of the system is varied. Our model is cyclic competitions among three species as described by the classical rock-paper-scissors game, and we consider both discrete lattice and continuous space, incorporating species mobility and intraspecific competitions. Our results reveal that, for all cases considered, a basin of coexistence always emerges and persists in a substantial part of the parameter space, indicating that coexistence is a robust phenomenon. Factors such as intraspecific competition can, in fact, promote coexistence by facilitating the emergence of the coexistence basin. In addition, we find that the extinction basins can exhibit quite complex structures in terms of the convergence time toward the final state for different initial conditions. We have also developed models based on partial differential equations, which yield basin structures that are in good agreement with those from microscopic stochastic simulations. To understand the origin and emergence of the observed complicated basin structures is challenging at the present due to the extremely high dimensional nature of the underlying dynamical system.

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Species coexistence is essential to biodiversity, and it is a fundamental issue in ecological science. Ecosystems consisting of three species subject to cyclic competitions have become a paradigm to address the coexistence problem. Early works based on population models provided useful insights into the dynamics of coexistence at a macroscopic level, but these models often tended to predict that coexistence is structurally unstable. To resolve this dilemma, microscopic models based on stochastic interactions at the individual level have been introduced. In this regard, the classical game of rock-paper-scissors (RPS) has been used to mimic cyclic competitions at the microscopic level of interactions. In fact, the past several years have witnessed a growing interest in this direction, addressing the role of factors in the coexistence such as species mobility, virus spreading, intraspecific competitions, etc. Inspired by these works, here we address the species coexistence problem in the framework of RPS competitions on spatially extended ecosystems from a global standpoint, i.e., we are interested in how the basins of coexistence and extinction depend on factors such as the species mobility, the interaction range, and the rate of intraspecific competition. An obstacle that needs to be overcome is to find a suitable representation of the phase space to compute

the basin structure in a meaningful way, as the underlying dynamical system is spatiotemporal and extremely high dimensional. We find the simplex representation S_2 in the three-dimensional space of population densities effective. We then use two characterizing methods, namely, final state and the inverse of the convergence time toward the final state, to map out the structures of the coexistence and extinction basins by using direct simulations of the microscopic interaction model. In particular, calculating the final states can reveal the boundaries among the coexistence and extinction basins, whereas the points within a basin are indistinguishable. The basins depicted by the convergence time to reach the final state provide additional information about the intrinsic difference inside each extinction basin. The coexistence basin can emerge at the central area of S_2 surrounded by three rotationally entangled extinction basins. The convergence time within each extinction basin increases universally along the spiral toward the center point. The area of the coexistence basin in the phase space measures the robustness of species coexistence and the convergence time within the extinction basins quantifies the degree of extinction. To provide credence for the validity of the basin structures, we derive theoretical models based on partial differential equations, which yield results that agree well with those from microscopic models. Our results provide

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insights into the species coexistence problem at a global level.

I. INTRODUCTION

Species diversity is ubiquitous in nature. Uncovering the factors that support biodiversity is a fundamental problem in interdisciplinary science. Essential to biodiversity is species coexistence, a problem that has been investigated experimentally, computationally, and theoretically.¹⁻⁹ In this regard, empirical observations from experimental studies suggested nonhierarchical, cyclic competitions among species as an important mechanism for species coexistence, the essential features of which can be captured by the childhood game “rock-paper-scissors” (RPS).¹⁰ In a RPS game, three strategies form a cyclic loop and any strategy can defeat the one next to it in the loop. Indeed, cyclic competitions of the RPS nature have been found in different contexts in ecosystems and in laboratory experiments as well. Typical examples include colicinogenic microbes’ competition,¹¹ mating strategies of side-blotched lizards in California,¹² and competition among mutant strains of yeast¹³ and coral reef invertebrates.¹⁴ In computational and theoretical exploration of species coexistence, the RPS game has been a paradigm,¹⁵ where it was found that the incorporation of spatial structure is absolutely necessary to model the competition dynamics in real ecosystems.^{15,16} This is due to the fact that, for well-mixed populations under global interactions, macroscopic population models based on ordinary differential equations (ODEs) predicted that species coexistence is unstable in the RPS game.¹ That is, stochastic effects and small external perturbation can typically destroy species coexistence, in contrast to empirical observations. Computational studies have shown that, when a spatial structure is introduced into the RPS game, species coexistence can become stable and robust, which is consistent with experimental observations.¹⁶⁻¹⁸ For example, in both simulations and *E. coli* experiments,¹⁶ it was found that local interactions and dispersal enable coexistence of all three species in the RPS game, while coexistence is lost when the ecological processes take place over large scale so that the spatial structure is effectively averaged out. Notice that two features appear in the RPS game model when spatial structures are taken into account: (1) the underlying dynamics becomes spatiotemporal as the RPS competitions now occur in space and (2) the model becomes *microscopic* as competitions must now be treated at the level of species individuals, in contrast to the macroscopic population models described by ODEs.

Spatially extended RPS game models thus provide a powerful, microscopic paradigm to address various fundamental issues associated with species coexistence in realistic ecosystems. For example, when competitions are deemed to occur on space, the issue of species mobility becomes important.^{19,20} Indeed, mobile behaviors ranging from bacteria run to animal migration play an important role in species coexistence. In the work of Reichenbach *et al.*,^{19,20} a critical mobility value has been identified, below which species stably coexist in the form of moving spiral waves on spatially extended scales, whereas above the critical mobility, the

wavelength of the spiral waves exceeds the size of the underlying spatial structure, resulting in extinction of two species with only one surviving species.^{19,20} The formation of moving spiral waves induced by stochastic interactions at a microscopic level is a surprising finding, since these waves arise mostly in models based on partial differential equations (PDEs). This finding has stimulated a series of subsequent works. For example, in Refs. 21 and 22, instability of the spatial patterns and the effect of noise were investigated. In Ref. 23, it was found that breaking the conservation law was crucial for the formation of spiral waves. In Ref. 24, a zero-one behavior was revealed in that the weakest species has the highest survival probability. The effect of zero-sum and non-zero sum in the payoff matrix in the RPS game was investigated in Refs. 25 and 26, respectively. It was reported in Ref. 27 that intraspecific epidemic spreading can promote species coexistence, whereas interspecies epidemic spreading tends to suppress species coexistence. In Ref. 28, it was reported that intraspecific competition can effectively promote biodiversity. The RPS game has also been extended to more than three species in Ref. 29 and to spatial small-world networks in the presence of shortcuts.^{30,31} In a fairly recent work,³² entropy production has been used to characterize nonequilibrium behavior in the RPS game.

In a recent Rapid Communication,³³ we proposed to explore the concept of attraction basin in spatially extended RPS game dynamics. This was motivated by the consideration that basin structure provides a more comprehensive characterization of the nonequilibrium dynamics in the RPS game. In contrast to most previous works where computations and analysis were carried out with respect to a single initial configuration with identical species densities, basin structure obtained from all possible initial densities of species can yield a “global” picture of the coexistence dynamics. In Ref. 26, the authors studied the fixation probability in the deterministic RPS game, which depends on the initial densities of three species, with respect to both zero-sum and non-zero sum assumptions in finite populations. A graphical representation analogous to the method in Ref. 33 was exploited to characterize the fixation probability. This issue, however, is somewhat different from species coexistence in mobile populations. In nonlinear dynamics, the basins of attraction and the boundaries among different basins are a fundamental problem.³⁴ The purpose of this paper is to provide a more extensive treatment of the problem of basins in spatially extended RPS game models of mobile species. In particular, we propose a different method to explore basins by resorting to the convergence time for different initial configurations. This time not only can distinguish the boundaries among extinction and coexistence basins but also reveal the intrinsic difference within each extinction basin. Such a difference cannot be detected using the final state characterization method.³³ Going beyond the model in Ref. 33 that treated mobile populations under cyclic competition on lattice, here we consider two additional types of model extension: (i) mobile populations with intraspecific competitions and (ii) populations dispersing on a continuous geographical space with adjustable interaction ranges. Results of basins are obtained from both microscopic, stochastic simulations and

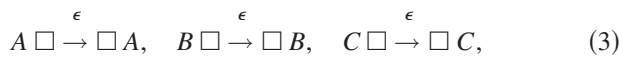
models based on PDEs, and a good agreement between the two types of results is demonstrated with respect to the structures of the coexistence and extinction basins. We note that the area of the coexistence basin in the phase space provides a meaningful measure of biodiversity, which is unable to be quantified when identical initial densities are used, as in most previous works. In all cases considered in this paper, the extinction basins show a universal rotational structure toward the central point in the phase space. The investigation of basins leads to *quantitative* insights into the evolutionary dynamics in spatial RPS game under various conditions.

In Sec. II, we describe the spatial RPS model of mobile individuals and two methods for computing attraction basins. In Secs. III and IV, we apply the basin characterizations to RPS games under intraspecific competitions on lattice and games on continuous geographical space, respectively. Conclusions are presented in Sec. V.

II. BASINS OF THE COEXISTENCE AND EXTINCTION

A. Model of RPS games in spatially extended ecosystems

The cyclic competition model with mobile individuals was originally proposed in Ref. 3 and 19, where each site of a square lattice with periodic boundary condition can be occupied by an individual from one of the three species or left empty so that the system has a finite carrying capacity. Interactions and dispersing behaviors among neighboring sites are described by the following set of rules:



where A , B , and C denote the three cyclically competing species, \emptyset represents empty sites, and \square denotes any species or empty sites. Relation (1) denotes the cyclic competitions, i.e., one species preys on a less-predominant species in the cycle (e.g., A can kill B , B outcompetes C , C in turn outcompetes A , leaving behind empty sites). Relations (2) represent reproduction of an individual at a neighboring empty site at rate μ . Relation (3) defines migration by position exchange between two neighboring individuals or between one individual and one of its neighboring empty sites. Migration occurs at rate ϵ . To be concrete, at each time step, a randomly chosen individual interacts with or moves to one of its nearest neighbors at random. For the pair of neighboring sites, cyclic competition, reproduction, and migration occur at the probabilities $\sigma/(\mu+\sigma+\epsilon)$, $\mu/(\mu+\sigma+\epsilon)$, and $\epsilon/(\mu+\sigma+\epsilon)$, respectively, so the rates of competition, reproduction, and migration are normalized. Whether an interaction can successfully occur is determined by the states of both sites. For example, if reproduction is chosen but there are no empty sites, the reaction fails. According to the theory of random walk,³⁵ individual mobility M is defined as $M = \epsilon(2N)^{-1}$, to which the number of sites explored by one

mobile individual per unit time is proportional. An actual time step is defined when each individual has interacted with others once on average. In other words, in one actual time unit, N pairwise interactions will have occurred.

In Ref. 33, we introduced the concept of attraction basin in the RPS game. Let n_0 be the fraction of empty site. For example, we can fix n_0 to be 10% of the N lattice sites. Since the initial densities of the three species satisfy $n_a+n_b+n_c = 1-n_0$, all possible combinations of n_a , n_b , and n_c define a triangular region. The phase space at time $T=0$ can thus be represented by the simplex S_2 defined by this triangle. There are four possible final states, corresponding to three extinction states, each converging to one of the three single species, and a coexistence state. In the phase space S_2 , the coordinates of a point denote a combination of the initial densities of the three species, and we can use four different colors to represent the final states. The basins can thus be defined by regions in S_2 , within which initial densities converge to the same final state. Alternatively, the basins can be characterized by the convergence time t_c for each point in S_2 . Note that different initial states in the same basin cannot be distinguished by the final state, but their convergence times t_c can be quite different. For computational convenience, we use the quantity $1/t_c$ to distinguish different points in S_2 .

In Ref. 19, a critical mobility $M_c = (4.5 \pm 0.5) \times 10^{-4}$ was derived for identical initial densities of three subpopulations. For $M < M_c$, species can stably coexist, while for $M > M_c$ only one species can survive finally and coexistence is lost. We investigate basins of coexistence and extinction in the two regions separated by M_c by varying M . Numerical simulations are implemented for a large time T that scales with the system size N . To make an unbiased comparison with previous works, we assume equal reaction probabilities for reproduction and competition rates, i.e., $\mu = \sigma = 1$. The mobility M is thus the only control parameter of the system. In our simulations, square lattices of 100×100 sites are used and the simulation time is chosen to be $T=5000$ to ensure that the final state can be reached from any initial point in S_2 .

B. Basin structure from microscopic simulations

Figures 1(a)–1(e) show the basin structures in S_2 for different values of M for both regimes of $M < M_c$ and $M > M_c$. The basins for all values of M exhibit rotational symmetry around the center point of S_2 . For $M < M_c$, e.g., (a) $M = 5 \times 10^{-5}$, (b) $M = 1 \times 10^{-4}$, and (c) $M = 3 \times 10^{-4}$, there exists a coexistence basin at the central area of S_2 and three extinction basins are rotationally entangled around the coexistence basin. As M is increased, the coexistence basin shrinks toward the center point together with the expansion of the three extinction basins. This indicates that population mobility tends to inhibit coexistence for $M < M_c$, as the area of the coexistence basin decreases by increasing M . In previous works that focused on identical initial densities of species (corresponding to the a single point in S_2 , its center), the effect of mobility on the coexistence cannot be revealed in this parameter region where species can always coexist. The basins thus provide a global picture of the coexistence problem. At the boundaries among different basins, the final state

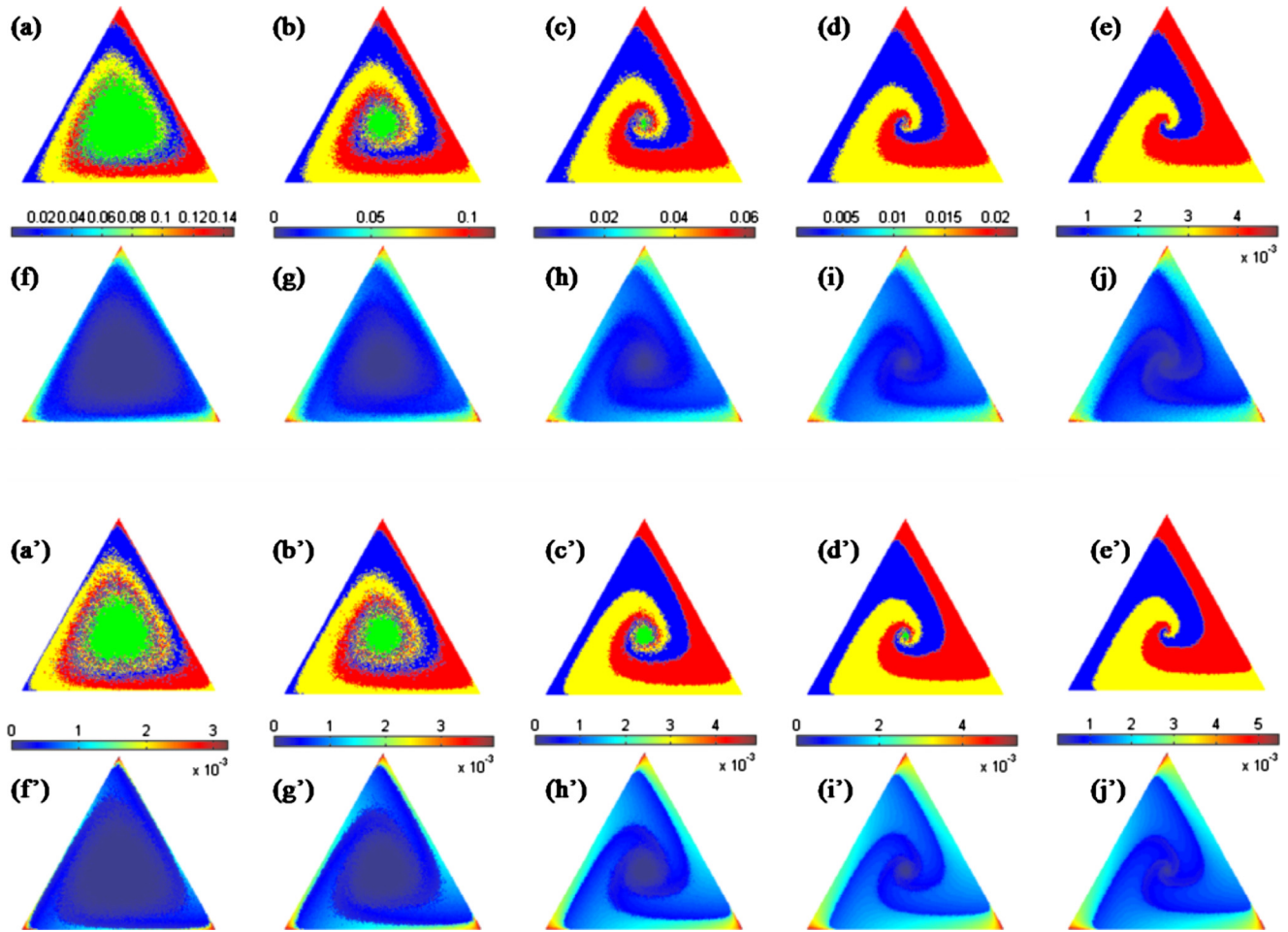


FIG. 1. (Color online) Basin structures of mobile individuals with cyclic competition on lattice for different values of mobility by using the characterizations of final state and convergence time. Panels (a)–(e) are the basins obtained by using the final state for $M=5 \times 10^{-5}$, 1×10^{-4} , 3×10^{-4} , 1×10^{-3} , and 5×10^{-3} , respectively. Panels (f)–(j) are the basins obtained by using the convergence time. The mobility values in (f)–(j) are the same as those in (a)–(e), respectively. Panels (a')–(j') are the basins obtained by the PDEs under the same set of mobility values as in (a)–(j). The final state is represented by one of the four colors at each point from stochastic simulations using 30 random realizations of the cyclic competition dynamics, under the same initial condition, on a given 100×100 square lattice. In (a)–(e) and (a')–(e'), blue (dark-gray), yellow (white), and red (gray) at three sides denote the three single-species states composed of species A , B , and C , respectively. Green (light-gray) at the center denotes the coexistence of species in the steady state. For each realization, the simulation consists of $5000 \times N$ time steps. We have checked that $5000 \times N$ time steps are sufficient long for the system reaching a steady state.

depends sensitively on the initial state and small initial perturbations can drive the system to an entire different final state. As soon as M exceeds the critical value M_c , coexistence basin vanishes, as exemplified by Fig. 1(d) for $M=1 \times 10^{-3}$. We see that, in this case, the phase space S_2 is shared exclusively by three extinction basins. The center point is where all three basins meet. At this point, the final convergence state is hard to be predicted due to the presence of stochastic effect and the sensitivity of final state to small variations in the initial densities. Further increase of M , e.g., (e) $M=5 \times 10^{-3}$ leads to the same structure of extinction basins as shown in Fig. 1(d) for $M=1 \times 10^{-3}$. We can expect the same basin structures for very large values of M , which correspond to the well-mixed and globally interacting case without the restriction of lattice links. Our finding is thus consistent with the known result that global interactions can exclude the coexistence in the RPS game.

Basin structures obtained by using the inverse $1/t_c$ of convergence time in the phase space S_2 are shown in Figs. 1(f)–1(j), corresponding to panels (a)–(e), 1(f)–1(j), respectively. We

see that $1/t_c$ offers a detailed characterization of the different states within each extinction basin, where $1/t_c$ decreases along the rotational structure of the basin toward the central area. An interesting behavior is that the boundaries of basins can be identified solely based on t_c in the sense that there is sharp transition in $1/t_c$ from one extinction basin to another when crossing the boundary. For the coexistence basin, since species can always coexist, t_c in the basin tends to ∞ and $1/t_c$ equals zero, so all points appear identical in the coexistence basin. The boundary between the coexistence and extinction basins is thus unequivocal since t_c in the extinction basins are always finite.

C. Basin structure from PDE model

The PDEs can be derived by a continuous approximation for the three reactions among geographically neighboring individuals. Let $n_a(\mathbf{r}, t)$, $n_b(\mathbf{r}, t)$, and $n_c(\mathbf{r}, t)$ be the densities of populations A , B , and C at time t and site $\mathbf{r}=(r_1, r_2)$ in the two-dimensional space, respectively. Neighbors are located

at $\mathbf{r} \pm \delta r \cdot \mathbf{e}_i$, where $\{\mathbf{e}_i\}$ ($i=1,2$) are the base vectors of the two-dimensional lattice. We have, for the average value of an arbitrary population $a(\mathbf{r}, t)$, the following evolutionary equation:

$$\begin{aligned} \partial_t n_a(\mathbf{r}, t) = & \frac{1}{z} \sum_{\pm, i=1}^2 \{2\epsilon [n_a(\mathbf{r} \pm \delta r \cdot \mathbf{e}_i, t) - n_a(\mathbf{r}, t)] \\ & + \mu n_a(\mathbf{r} \pm \delta r \cdot \mathbf{e}_i, t) [1 - n_a(\mathbf{r}, t) - n_b(\mathbf{r}, t) \\ & - n_c(\mathbf{r}, t)] - \sigma n_c(\mathbf{r} \pm \delta r \cdot \mathbf{e}_i, t) n_a(\mathbf{r}, t)\}, \end{aligned} \quad (4)$$

where z is the number of nearest neighbors of each lattice site. On the right-hand side of the equation, the first term denotes the exchange process, where the neighbors moving into a site and the individual at this site moving out to its neighbors will induce an increase and a decrease in $n_a(\mathbf{r})$, respectively. The second term describes the increase in $n_a(\mathbf{r})$ due to reproduction, and the third term characterizes the decrease in $n_a(\mathbf{r})$ due to competition. We set the length of the lattice to unity and, hence, the distance between two nearest neighbors is $\delta r = 1/\sqrt{N}$. For $N \rightarrow \infty$ and lattice size fixed to 1, $\delta r \rightarrow 0$. Thus, \mathbf{r} can be treated as a continuous variable. Using Taylor expansion to the second order, we have

$$\begin{aligned} n_a(\mathbf{r} \pm \delta r \cdot \mathbf{e}_i, t) = & n_a(\mathbf{r}, t) \pm \delta r \partial_i n_a(\mathbf{r}, t) + \frac{1}{2} \delta r^2 \partial_i^2 n_a(\mathbf{r}, t) \\ & + O(\delta r^3). \end{aligned}$$

The first term on the right-hand side of Eq. (4) becomes

$$\frac{2\epsilon}{z} \sum_{\pm, i=1}^2 [n_a(\mathbf{r} \pm \delta r \cdot \mathbf{e}_i, t) - n_a(\mathbf{r}, t)] = \frac{\epsilon}{2} \delta r^2 \partial_i^2 n_a(\mathbf{r}, t).$$

By rescaling the exchange rate ϵ with the system size N and the fixed (diffusion) constant M according to

$$\epsilon = 2MN, \quad (5)$$

we have

$$\frac{\epsilon}{2} \delta r^2 = M. \quad (6)$$

For other terms in Eq. (4), only the zeroth-order contributions to $n_a(\mathbf{r}, t)$ in the expansion of $n_a(\mathbf{r} \pm \delta r \cdot \mathbf{e}_i, t)$ are important in the large system-size or the $\delta r \rightarrow 0$ limit. These considerations lead to the following set of PDEs:

$$\begin{aligned} \partial_t n_a = & M \nabla^2 n_a + \mu n_a (1 - \rho) - \sigma n_c n_a, \\ \partial_t n_b = & M \nabla^2 n_b + \mu n_b (1 - \rho) - \sigma n_a n_b, \\ \partial_t n_c = & M \nabla^2 n_c + \mu n_c (1 - \rho) - \sigma n_b n_c, \end{aligned} \quad (7)$$

where $\rho = n_a(\mathbf{r}, t) + n_b(\mathbf{r}, t) + n_c(\mathbf{r}, t)$ is the local species density and $1 - \rho$ denotes the density of empty sites. Basin structures in the PDE model can be obtained by numerically solving the equations for random initial species densities. Specifically, for an arbitrary density, at $t=0$, for any given site only one quantity of $n_a(r_x, r_y)$, $n_b(r_x, r_y)$, and $n_c(r_x, r_y)$ is equal to 1 and the other two are 0, the probability of which is determined by the initial densities of n_a , n_b , and n_c altogether. For the PDEs, extinction is defined when the density of any species is less than $1/N$. The species preyed by the

extinction species is the exclusive survivor. The definition takes into account the physical meaning of survival in that the number of survival species cannot be less than 1.

The results of basins from the PDE model are shown in Figs. 1(a')–1(j'), which correspond to the stochastic simulation results in Figs. 1(a)–1(j), respectively. We see that the results from the PDE model are in good agreement with simulations in terms of both the basin structures and the areas of the coexistence and extinction basins for different values of the individual mobility. The stochastic fluctuations in the basins obtained from the PDE model are a result of the initial randomness of species densities [$n_a(r_x, r_y)$, $n_b(r_x, r_y)$, and $n_c(r_x, r_y)$] used in the numerical solution of the PDEs.

Our exploration of basin structures in terms of the final convergence state, the inverse of the survival time, and the PDE model thus provides a more complete picture concerning the emergence and loss of biodiversity in the spatial RPS game in the presence of individual mobility.

III. BASINS OF SPATIAL RPS DYNAMICS UNDER INTRASPECIFIC COMPETITION

In nature, intraspecific competitions are quite common.^{36–39} Individuals within the same species do compete for essential life-sustaining resources such as food, water, light, opposite sex, etc. Intraspecific competitions can have a significant impact on species diversity in both predator-prey-like interaction and cyclic competition systems. Intraspecific competition is also quite common in various food chains. Here we explore the basin structure in the presence of intraspecific competitions, which can be incorporated in the game model in Sec. II as follows:



where \emptyset represents empty sites. Due to the competition of two neighboring individuals in the same species, one individual will die at random and leave its site empty at rate p . Intraspecific competition occurs with the probability $p/(p + \mu + \sigma + \epsilon)$ and the rates of interspecies competition, reproduction, and motion are normalized by $p + \mu + \sigma + \epsilon$ as well. We set the summation of intraspecific competition, interspecific competition, and reproduction rates to be 2, i.e., $p + \sigma + \mu = 2$ so that the dependence on the mobility probability ϵ is the same as compared to models in Sec. II.

Using the continuous approximation, we can derive a PDE model from the four types of reactions for the spatiotemporal dynamics of RPS game under intraspecific competition.²⁸ The model is given by

$$\begin{aligned} \partial_t n_a = & M \nabla^2 n_a + \mu n_a (1 - \rho) - \sigma n_c n_a - (p/2) n_a n_a, \\ \partial_t n_b = & M \nabla^2 n_b + \mu n_b (1 - \rho) - \sigma n_a n_b - (p/2) n_b n_b, \\ \partial_t n_c = & M \nabla^2 n_c + \mu n_c (1 - \rho) - \sigma n_b n_c - (p/2) n_c n_c. \end{aligned} \quad (9)$$

Numerical solution of the PDEs yields two dynamical regions in the parameter space, as shown in Fig. 2, where region I corresponds to coexistence and region II to extinction. In each region, we select two groups of parameter combinations (M, p) to explore the basin structures. The chosen

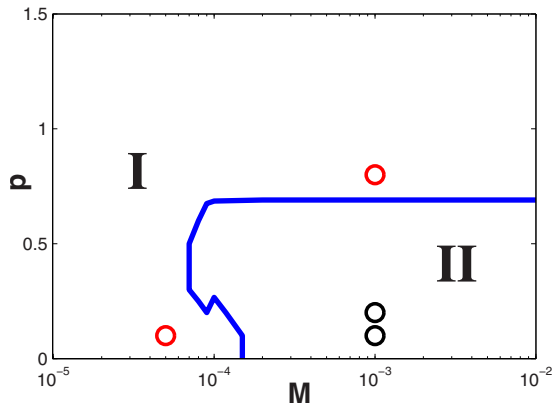


FIG. 2. (Color online) Dependence of extinction probability on the intraspecific competition rate p and mobility M , where regions I and II denote coexistence and extinction, respectively. Simulation results are obtained by averaging over 50 random initial configurations on a lattice of size of 100×100 . The boundary between regions I and II is obtained by PDE model equation (9). We select four sets of parameter combinations to explore the basin structures, as indicated by the four open circles.

points are marked in Fig. 2. Results from direct stochastic simulations are shown in Fig. 3. For the two points in the extinction region [(a) and (c)], we observe three entangled extinction basins that meet at the center of the phase space

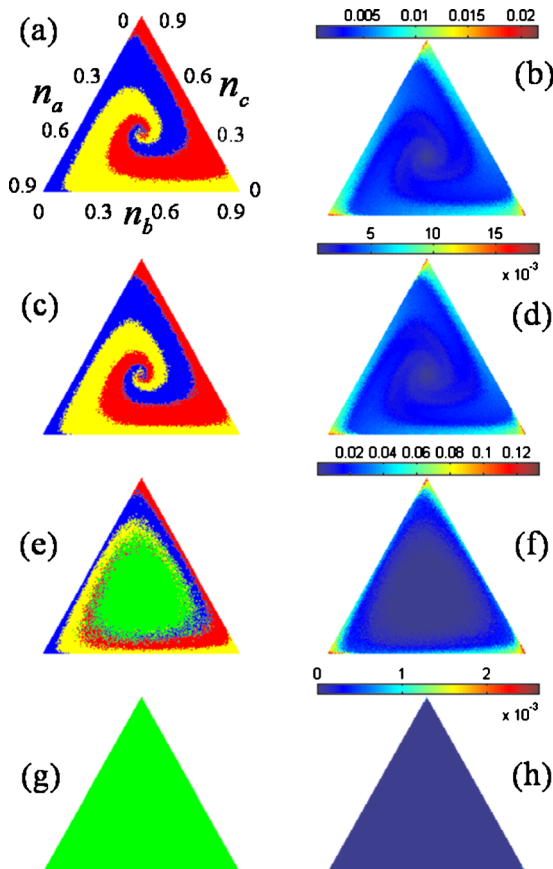


FIG. 3. (Color online) Basins of mobile individuals under interspecies and intraspecific competitions on lattices for [(a) and (b)] $M=1 \times 10^{-3}$ and $p=0.1$, [(c) and (d)] $M=1 \times 10^{-3}$ and $p=0.2$, [(e) and (f)] $M=5 \times 10^{-5}$ and $p=0.1$, and [(g) and (h)] $M=1 \times 10^{-3}$ and $p=0.8$. Panels (a), (c), (e), and (g) are obtained by the final state criterion, and panels (b), (d), (f), and (h) are calculated according to the convergence time. Other simulation parameters are the same as for Fig. 2.

S_2 , which is similar to the basins in the absence of intraspecific competition in Sec. II. In this region, intraspecific competition is not sufficient to induce coexistence. In contrast, in the coexistence region [(e) and (g)], a large area of the coexistence basin dominates the central area of S_2 . In particular, for strong intraspecific competition (large value of p), the phase space S_2 is almost exclusively a coexistence basin and the extinction basins almost vanish [Fig. 3(g)]. Such a domination of the coexistence basin is general for large values of p , indicating that coexistence is strongly promoted by intraspecific competitions. The inverse of the convergence time $1/t_c$ identifies the boundaries among different extinction basins and between the extinction and the coexistence basin. Within each extinction basin, $1/t_c$ decreases along the rotational direction of the basins toward the central area, which is similar to the situation without intraspecific competition. Another feature is that the rising of the coexistence basin when p exceeds the critical value 0.7 is quite sharp. That is, for $p < 0.7$ in the extinction region, the coexistence basin does not exist. For $p > 0.7$, a vast area of the coexistence basin arises and dominates the phase space S_2 associated with the loss of the extinction basins. In this regard, the phase transition from extinction to coexistence at the critical value $p=0.7$ is of the first order.

IV. BASINS OF RPS DYNAMICS ON CONTINUOUS SPACE

Most existing models based on stochastic interactions assume discrete lattices as the underlying spatial structure, on which cyclic competition, reproduction, and movement occur among neighboring sites. In such a case, the underlying geographical space is discrete. In realistic ecosystems, the intrinsic geographical space can be continuous. In this section, we study RPS dynamics with individuals dispersing on a continuous space, which allows the effect of nonlocal interactions on species coexistence to be studied in terms of the basin structures. In our model, we assume that individuals of the three species are randomly dispersed on a square cell of linear size $L=1$ under periodic boundary conditions. A competition occurs only if the geographical distance between two cyclic individuals is less than the interaction radius R , as schematically illustrated in Fig. 4. At each simulation step, an individual is randomly selected. For example, in Fig. 4(a), an individual belonging to species A is chosen. After this, within the interaction range, the A individual randomly kills an individual belonging to B which is next to A in the cyclic competition loop. At the same time, the A individual reproduces itself at the position of the B individual. If the A individual cannot find any B individual within the range, no interaction occurs. The rate of killing is σ . Note that the absolute value of the rate σ only affects the evolution speed of the system but does not influence the convergence toward the final state. The radius R of interaction range is thus the sole physical parameter in the model.

We calculate the basins in the simplex S_2 by using different initial densities of three species. Because of the absence of empty sites in the continuous space, the range of S_2 is unity. Basin structures for different values of R obtained from stochastic simulations are shown in Fig. 5. In particular,

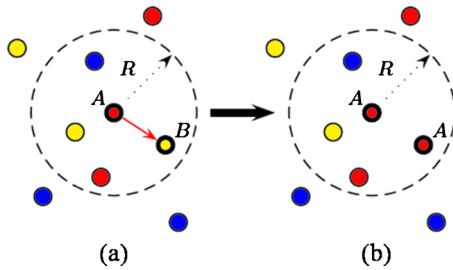


FIG. 4. (Color online) Schematic illustration of continuous-space model. Three subpopulations, A, B, and C represented by red, yellow, and blue, respectively, dominate each other in a cyclic manner. (a) An individual belonging to A randomly selects an individual B within its selection range R , where B is next to A in the cyclic competing loop. (b) The A individual kills the B individual and at the same time replicates itself. If within the interaction range, an individual cannot find any inferior individual, nothing happens.

we observe that the area of the coexistence basin is a *non-monotonic* function of R . When R is increased to 0.045, coexistence is lost, as shown in Fig. 5(a), and there is an entangled and disordered region in the central area where small deviations in the initial densities can lead to completely different final extinction states. This behavior is distinct from those in the lattice models treated in Secs. II and III. Except the central region, three extinction basins exhibit a rotational symmetry around the central point, similar to the behavior in the lattice models. As R reaches 0.07 [Fig. 5(c)], a small

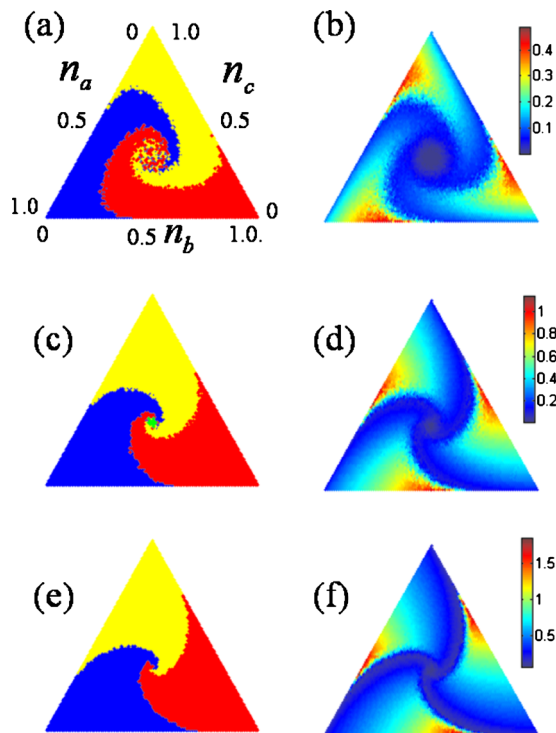


FIG. 5. (Color online) Basins of cyclically competing subpopulations on continuous geographical space for [(a) and (b)] interaction radius $R=0.045$, [(c) and (d)] $R=0.07$, and [(e) and (f)] $R=0.1$. Panels (a), (c), and (e) are obtained according to the final-state criterion while panels (b), (d), and (f) are calculated according to the convergence-time criterion. The number of individuals is fixed at 3000 and the size of the square cell is 1×1 . Each point in the phase space is obtained by 100 different realizations. The initial positions of individuals in the geographical space are random.

coexistence basin re-emerges at the center and the degree of rotation of the three extinction basins is reduced as compared to that in Fig. 5(a). This behavior is contrary to the existing result from lattice models in the literature that local interactions promote the coexistence while it is lost at larger interaction scale. For larger interaction range, e.g., $R=0.1$ [Fig. 5(e)], coexistence basin vanishes again and the rotational degree of extinction basins is reduced further. We have examined that for R larger than 0.1, the phase space S_2 is shared exclusively by three extinction basins. The phase-space structures obtained by the convergence-time t_c in Figs. 5(b), 5(d), and 5(f) are consistent with those from the final state criterion. In particular, the characteristics of the behavior of t_c in each extinction basin are qualitatively similar for discrete-lattice and continuous-space models. While the basin structures exhibit some small difference for small [Figs. 5(a)] and large [Figs. 5(e)] values of R , extinction is the exclusive outcome in these cases.

V. CONCLUSION

In conclusion, we have studied basins of species coexistence and extinction in three spatial RPS game models: (1) mobile species on lattice, (2) mobile species on lattice under intraspecific competition, and (3) mobile species on continuous space. Two criteria are used to characterize the basin structures in the phase space S_2 : the final state and the convergence time. We have found that for all three models, three extinction basins spirally entangle around the center point in S_2 . About the center, a coexistence basin can emerge, depending on the parameters of the underlying spatiotemporal dynamical system. The boundaries among basins can be distinguished by the final convergence state and the fine structure within each single basin can be resolved by the convergence time, which exhibits a general behavior in that it increases along the spiral of the basin toward the central area, signifying a dependence of the degree of extinction (within the same basin) on initial configurations. There is a sharp transition in the convergence time at the boundary between two extinction basins, so the boundary can also be identified by this time. In the coexistence basin, the convergence time tends to infinity, separating the coexistence from extinction basins in a straightforward manner.

For each model, a set of PDEs can be derived to capture the basic features of the spatiotemporal evolutionary dynamics, and we find that the PDEs can generate basin structures that are consistent with those from microscopic stochastic simulations. While our computational efforts establish a plausible picture for the basin structures associated with the evolutionary dynamics of cyclically competing species on spatially extended scales and thereby provide deeper insights into the species coexistence problem, the dynamical origin of the emergence of the basin structure revealed in this paper is not understood at the present. Further efforts in this direction are required.

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