

Role of intraspecific competition in the coexistence of mobile populations in spatially extended ecosystems

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Evolutionary-game based models of nonhierarchical, cyclically competing populations have become paradigmatic for addressing the fundamental problem of species coexistence in spatially extended ecosystems. We study the role of intraspecific competition in the coexistence and find that the competition can strongly promote the coexistence for high individual mobility in the sense that stable coexistence can arise in parameter regime where extinction would occur without the competition. The critical value of the competition rate beyond which the coexistence is induced is found to be independent of the mobility. We derive a theoretical model based on nonlinear partial differential equations to predict the critical competition rate and the boundaries between the coexistence and extinction regions in a relevant parameter space. We also investigate pattern formation and well-mixed spatiotemporal population dynamics to gain further insights into our findings.

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Identifying mechanisms that maintain or jeopardize biodiversity is a fundamental problem in ecological and nonlinear science. There has been a growing interest in this interdisciplinary topic. Numerous models and experiments have demonstrated that species can coexist through nonhierarchical cyclic competitions, and generic properties of the competition can be characterized by the traditional game of “rock-paper-scissor” in combination with spatial dispersal of static populations. Our work extends this pursuit by studying the role of intraspecific competition in coexistence. We find that species coexistence can be favored in the two previously known situations where extinction is certain in the absence of this type of competition: (1) locally interacting species with high mobility and (2) globally interacting or well-mixed species. In particular, in both cases, when a parameter characterizing the degree of intraspecific competition, the intraspecific competition probability, exceeds a critical value, stable coexistence can occur in a wide parameter range. While it has been known in the ecological literature through the study of macroscopic population models that intraspecific competition can promote coexistence, our model provides a confirmation of this result but at a microscopic level. We have also developed a theoretical framework based on nonlinear partial differential equations, which is capable of producing results that are in good agreement with direct simulations. We note that intraspecific competitions are also common in other disciplines (e.g., social interactions) and we expect our results

to provide insights into the dilemma of competition and cooperation widely observed in social, economical, and political systems.

I. INTRODUCTION

Coexistence is fundamental to biodiversity in ecosystems composed of large numbers of interacting species. Understanding the factors that promote or jeopardize the coexistence of competing species is a central issue in contemporary ecology and biological physics.^{1–10} In the past decades, predator-prey models associated with habitat patches have been investigated intensively and extensively through deterministic equations with respect to coexistence.^{11–15} Besides, as a generalized version of the predator-prey models, food-web models have been investigated for their dynamical stabilities.^{16–18} Recently nonhierarchical, cyclic interactions have been observed in different biological systems as an important underlying mechanism for species coexistence, which can be modeled by evolutionary games such as the “rock-paper-scissor” game.^{6,19–22} The cyclic relationships have been observed in a number of contexts in natural systems and experiments such as colicinogenic microbes’s competition,²³ mating strategies of side-blotched lizards in California,²⁴ and competition among mutant strains of yeast²⁵ and coral reef invertebrates.²⁶ To model these real systems, it is necessary to consider spatial distributions^{6,23,27} of populations under the cyclic dynamics, leading to quantitative insights into species coexistence. For example, previous theoretical models^{28,29} predict that local interaction and dispersal are sufficient to ensure the coexist

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ence of all three species under the cyclic relationship, whereas the coexistence is lost when ecological processes occur over larger scales. These predictions have indeed been verified in both *in vitro*³⁰ and *in vivo*³¹ experiments.

Quite recently, in the seminal work of Reichenback et al.,^{32,33} population mobility, as an important feature of ecosystems, has been incorporated into spatial cyclic dynamics to better model individual activities ranging from bacteria run to animal migration. It has been discovered that mobility can support moving spiral waves and the wavelength can increase with a parameter characterizing the mobility. When the mobility parameter exceeds a critical threshold, spiral waves can outgrow the size of the supporting spatial structure, preventing species from coexisting. Thus, in general, the coexistence can occur only when the mobility is sufficiently weak. Although spiral waves have been known in ecosystem models such as those for prebiotic evolution processes,^{4,5} it is still surprising that spiral waves can arise in rock-paper-scissors games with *stochastic* interactions. In particular, individual mobility, as a common feature in ecosystems, can naturally lead to species coexistence in the form of spiral-wave patterns and extinction occurs only for high mobility. Identifying additional factors that promote or hamper species coexistence in the paradigm of cyclic dynamics has been an active area of research.

In nature, intraspecific competitions are quite common.^{34–37} Individuals in the same species do compete for essential life-sustaining resources such as food, water, light, opposite sex, etc. Intraspecific competition can be expected to have significant impact on biodiversity associated with cyclic competitions among species. For example, for side-blotched lizards in California, those with the same strategy also compete for mating opportunity. Intraspecific competition is also common in variety of food chains.^{34–37} In deterministic models, this competition mechanism has been found to be essential for species coexistence.^{1,38,39} To our knowledge, the role of intraspecific competition in the coexistence of spatially dispersed populations under cyclic competitions remains to be an unaddressed issue, and the purpose of this paper is to address it. Our main finding is that, when individuals locally interact, in the high-mobility regime, intraspecific competition can strongly promote coexistence. In particular, for high mobility, when the rate of intraspecific competition exceeds a critical value that does not depend on the mobility, the coexistence is stable, whereas in the absence of the competition, the coexistence is unlikely. We derive a theoretical model based on nonlinear partial differential equations (PDEs) to predict the boundary between the coexistence and extinction regions in a relevant parameter space, as well as the critical competition rate. Typical spatial patterns under the influence of intraspecific competition for different mobilities are also investigated, both from direct numerical simulation of game dynamics and from the theoretical PDE model, to yield more insights into the role of intraspecific competition in coexistence. For global interaction, we also find that species coexistence can be facilitated by intraspecific competition. It is noteworthy that for both local interactions with high individual mobility and global interactions, the observation of species coexistence as pro-

moted by intraspecific competition is consistent with the findings from studies of the Lotka–Volterra system.^{40–42}

In Sec. II, we describe our rock-paper-scissors game based model for studying cyclic interactions among three mobile species, incorporating intraspecific competitions. In Sec. III, we present results from direct game simulations, derive a set of nonlinear PDEs for the underlying dynamical process, and compare the predictions of the PDEs with the direct numerical results. Conclusions are presented in Sec. IV.

II. THE MODEL

We use the rock-paper-scissors game to model the cyclic interactions among three mobile species with intraspecific competition. Species populate a square lattice with periodic boundary conditions. Each site is either occupied by one individual or empty so that the system has a finite carrying capacity. Interactions occur among nearest neighboring individuals, as follows:

$$AB \xrightarrow{\sigma} A \emptyset, \quad BC \xrightarrow{\sigma} B \emptyset, \quad CA \xrightarrow{\sigma} C \emptyset, \quad (1)$$

$$A \emptyset \xrightarrow{\mu} AA, \quad B \emptyset \xrightarrow{\mu} BB, \quad C \emptyset \xrightarrow{\mu} CC, \quad (2)$$

$$A \square \xrightarrow{\epsilon} \square A, \quad B \square \xrightarrow{\epsilon} \square B, \quad C \square \xrightarrow{\epsilon} \square C, \quad (3)$$

$$AA \xrightarrow{p} A \emptyset, \quad BB \xrightarrow{p} B \emptyset, \quad CC \xrightarrow{p} C \emptyset, \quad (4)$$

where three populations A , B , and C cyclically dominate each other, \emptyset represents empty sites and \square denotes any species or empty sites. Relation (1) represents interspecific competitions, i.e., one species preys on a less-predominant species in the cycle and leaves the invaded site empty, which occurs at the rate σ . Relations (2) and (3) define reproduction and migration that occur at the rates μ and ϵ , respectively. The three types of interactions are based on the model in Ref. 32. Relation (4) models intraspecific competitions as a natural mechanism incorporated into the game. 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 . A more detailed illustration of four relations on square lattice can be seen in Fig. 1. To be concrete, at each simulation step, a randomly chosen individual interacts with one of its nearest neighbors at random. For the pair of selected nodes, intraspecific competition, interspecific competition, reproduction, and exchange occur with probabilities $p/(p+\mu+\sigma+\epsilon)$, $\sigma/(p+\mu+\sigma+\epsilon)$, $\mu/(p+\mu+\sigma+\epsilon)$, and $\epsilon/(p+\mu+\sigma+\epsilon)$, respectively. After a random pair of nearest-neighboring sites is selected, a chosen type of interaction (intraspecific competition, interspecific competition, reproduction or exchange) is performed, if the interaction is allowed. For example, if reproduction is chosen but there are no empty sites, the reaction fails. We carry out simulations for a typical waiting time T until extinction occurs for the high-mobility regime and use the same time for all regimes of mobility considered in this paper. In the literature,^{32,33} it has been established that this time is proportional to the sys-

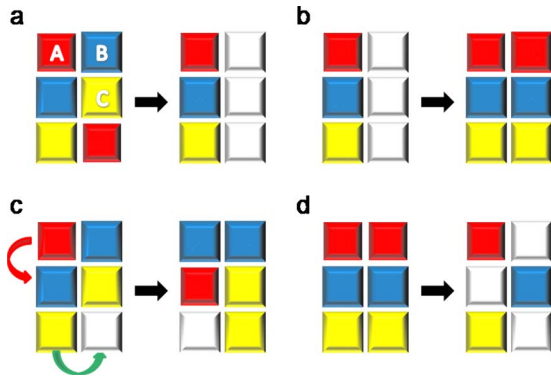


FIG. 1. (Color online) Schematic illustration of the specific types of interactions among three species A in red (dark), B in blue (grey), and C in yellow (light grey). For example, interspecific competition (a) happens only between different kinds of species, i.e., A can kill B, B can invade C, and C in turn outcompetes A, leaving behind empty sites (white). Reproduction (b) is only allowed when empty neighboring sites are available. Migration (c) happens due to the population mobility, such as exchanging positions with neighboring individuals (as denoted by red arrow, $AB \rightarrow BA$) or hopping onto an empty neighbor (as denoted by green arrow, $C\emptyset \rightarrow \emptyset C$, where \emptyset represents the empty site). Intraspecific competition (d) occurs between individuals from the same kind of species and leaves behind one site empty randomly, such as $AA \rightarrow A\emptyset$ or $\emptyset A$.

tem size N . To make an unbiased comparison with previous works,^{32,33} we assume equal reaction probabilities for reproduction and interspecific competition, i.e., $\mu = \sigma$, and 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 the literature.^{32,33}

III. SIMULATION AND THEORETICAL ANALYSIS

We focus on two situations reported recently^{30,32} where extinction is certain in the absence of intraspecific competition: (1) locally interacting species with mobility and (2) globally interacting or well-mixed species.

A. Locally interacted species with mobility

For the scenario that every individual interacts with any one of the four nearest neighbors on a square lattice with equal probability, the theory of random walks gives that the mobility or diffusion constant M is the typical area explored by one mobile individual per unit time, i.e., $M = \epsilon(2N)^{-1}$. For a 100×100 lattice, without intraspecific competition, the critical value $M_c = (4.5 \pm 0.5) \times 10^{-4}$ has been identified in Ref. 32. For $M < M_c$, the coexistence of three species is guaranteed; while for $M > M_c$ two species become extinct, leaving behind a uniform state with only one species. Reference 32 states that, when the mobility M is low ($M < M_c$), the interacting populations exhibit an entanglement of spiral-wave patterns, which characterize the endless interspecific competition, as shown in Fig. 2(a). With the increase in mobility M , the spiral waves become larger and larger. Once M goes above the threshold M_c , the spiral-wave patterns outgrow the system size, causing the loss of coexistence.

Typical snapshots of spatial patterns for different values of intraspecific competition rate p for small M in the regime

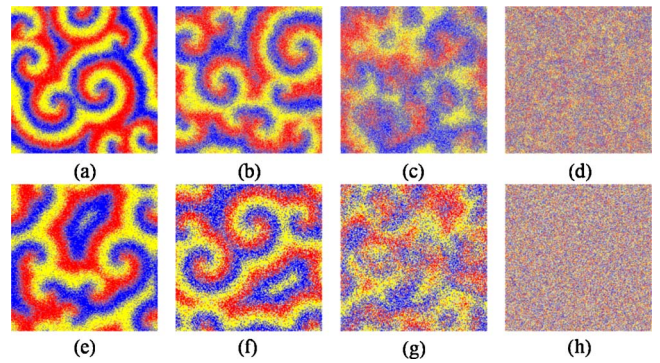


FIG. 2. (Color online) Typical snapshots of spatial patterns for different intraspecific competition rate p under same mobility $M = 6 \times 10^{-5} < M_c$: $p=0$ for (a) and (e), $p=0.3$ for (b) and (f), $p=0.6$ for (c) and (g), and $p=1.6$ for (d) and (h). The upper four panels are from direct game simulations and the lower ones are from our PDE model. Each color represents one of the species and gray represents empty sites. System size is $N = 500 \times 500$. The color in the theoretical patterns at each spatial site is determined by the densities of three populations, i.e., if the density of a population is larger than the others, the color of the site will be set to the color of the population with a higher probability.

of $M < M_c$ are shown in Fig. 2. Snapshot (a) is obtained for $p=0$, which exhibits representative moving spiral waves, as reported in Ref. 32. For small values of p , say $p=0.3$, as shown in (b), spiral waves are somewhat blurred with more empty sites, resulting from death induced by intraspecific competition. When the value of p is increased to 0.6, as shown in (c), patterns become more fuzzy and no clear spiral waves can be identified. For larger values of p , for example, $p=1.6$, species together with empty sites tend to be well mixed. Time series of population densities associated with these patterns demonstrate that the three species coexist with small fluctuations in their densities around the respective average values. The four bottom panels in Fig. 2 correspond to theoretical predictions from PDEs (to be described later). These observations suggest that, for small mobility, intraspecific competition does not jeopardize biodiversity but merely perturbs the spatial pattern. In the regime of $M > M_c$, for $p=0$, the patterns outgrow the system size, causing the loss of coexistence as exhibited in Fig. 3(a) by simulations and Fig. 3(b) by theory. However, in the presence of intraspecific competition [Figs. 3(c) and 3(d)], species can coexist and tend to be well mixed. We observe that well-mixed patterns appear to be the only pattern in the original extinction regime $M > M_c$. It is noteworthy that the simulations are carried out on lattices of relatively large size, e.g., $N = 100 \times 100$ so as to suppress any stochastic fluctuations. Our computa-

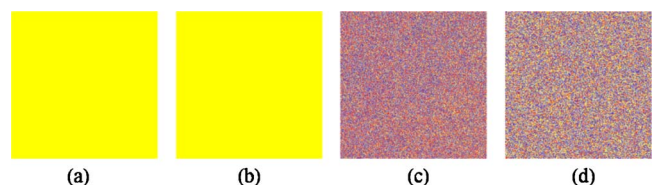


FIG. 3. (Color online) Typical snapshots of spatial patterns for different p under the same mobility $M = 6 \times 10^{-3} > M_c$: $p=0$ for (a) and (b) and $p=1.0$ for (c) and (d). (a) and (c) are from computer simulation and (b) and (d) are from theoretical analysis. System size is $N = 500 \times 500$.

tions reveal that for sizes of this order of magnitude, the survival and extinction behaviors are stable from independent realizations.

The simulation patterns can be predicted by deriving a set of PDEs.³² The new ingredient here is the incorporation of intraspecific competition in the PDE model. Let us denote $n_a(\mathbf{r}, t)$, $n_b(\mathbf{r}, t)$, and $n_c(\mathbf{r}, t)$ as 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 $\{\mathbf{e}_i\}$ is the basis of the two-dimensional lattice. Then we can obtain the following evolutionary equation for the average value of an arbitrary population $a(\mathbf{r}, t)$:

$$\begin{aligned} \partial_t n_a(\mathbf{r}, t) = & \frac{1}{z} \sum_{\pm, i=1}^2 \left\{ 2\epsilon [n_a(\mathbf{r} \pm \delta r \cdot \mathbf{e}_i, t) - n_a(\mathbf{r}, t)] \right. \\ & + \mu n_a(\mathbf{r} \pm \delta r \cdot \mathbf{e}_i, t) \\ & \times [1 - n_a(\mathbf{r}, t) - n_b(\mathbf{r}, t) - n_c(\mathbf{r}, t)] \\ & - \sigma n_c(\mathbf{r} \pm \delta r \cdot \mathbf{e}_i, t) n_a(\mathbf{r}, t) \\ & \left. - \frac{p}{2} n_a(\mathbf{r} \pm \delta r \cdot \mathbf{e}_i, t) n_a(\mathbf{r}, t) \right\}, \end{aligned} \quad (5)$$

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 increase and decrease in $n_a(\mathbf{r})$. The second term describes the increase in $n_a(\mathbf{r})$ due to reproduction, and the third and fourth terms characterize the decrease

in $n_a(\mathbf{r})$ due to interspecific and intraspecific competition, respectively. The coefficient $p/2$ in the last term comes from the fact that intraspecific competition induces a death in a pair of individuals at random with rate p .

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 the lattice size fixed to 1, $\delta r \rightarrow 0$. Thus, \mathbf{r} can be treated as a continuous variable together with the expansion,

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

Using this expansion, up to the second order, the first term in the right-hand side of the Eq. (5) 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 system size N and a fixed (diffusion) constant M according to

$$\epsilon = 2MN, \quad (6)$$

we can get that

$$\frac{\epsilon}{2} \delta r^2 = M, \quad (7)$$

where $\delta r=1/\sqrt{N}$. For other terms in Eq. (5), 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:

$$\begin{cases} \partial_t n_a(\mathbf{r}, t) = M \Delta n_a(\mathbf{r}, t) + \mu n_a(\mathbf{r}, t) (1 - \rho(\mathbf{r}, t)) - \sigma n_c(\mathbf{r}, t) n_a(\mathbf{r}, t) - \frac{p}{2} n_a(\mathbf{r}, t) n_a(\mathbf{r}, t) \\ \partial_t n_b(\mathbf{r}, t) = M \Delta n_b(\mathbf{r}, t) + \mu n_b(\mathbf{r}, t) (1 - \rho(\mathbf{r}, t)) - \sigma n_a(\mathbf{r}, t) n_b(\mathbf{r}, t) - \frac{p}{2} n_b(\mathbf{r}, t) n_b(\mathbf{r}, t) \\ \partial_t n_c(\mathbf{r}, t) = M \Delta n_c(\mathbf{r}, t) + \mu n_c(\mathbf{r}, t) (1 - \rho(\mathbf{r}, t)) - \sigma n_b(\mathbf{r}, t) n_c(\mathbf{r}, t) - \frac{p}{2} n_c(\mathbf{r}, t) n_c(\mathbf{r}, t), \end{cases} \quad (8)$$

where $\rho(\mathbf{r}, t)=n_a(\mathbf{r}, t)+n_b(\mathbf{r}, t)+n_c(\mathbf{r}, t)$ is the local species density and $1-\rho$ denotes the density of empty sites. Theoretical patterns are obtained by numerically solving Eq. (8) from random initial configurations, which agree well with patterns from direct game simulations as shown in Figs. 2 and 3.

To obtain a general understanding of the combined effect of intraspecific competition and mobility on species coexistence, we examine the dependence of species coexistence and uniformity on both the intraspecific competition rate p and mobility M by calculating the probability of extinction P_{ext} . A contour plot is displayed in Fig. 4. The blue solid curve represents the theoretical prediction for the boundary between the coexistence and extinction regions by numerically

solving Eq. (8). In the contour plot, two distinct regions can be distinguished: (I) coexistence region and (II) extinction region. An interesting finding is that in high mobility region, species can coexist when p exceeds a critical value p_c , regardless of the mobility rate M . The same value of p_c has been successfully predicted by theory. This region is in sharp contrast to that in the absence of intraspecific competition in that species coexistence is now promoted in this region. We note that the theoretical prediction of the boundary for intermediate values of M exhibits some difference as compared to direct simulations. The disagreement is due to stochastic effect in simulations that are difficult to be accounted for in the theoretical framework of nonlinear PDEs. In particular, in this regime of M values, the wavelength of spirals ap-

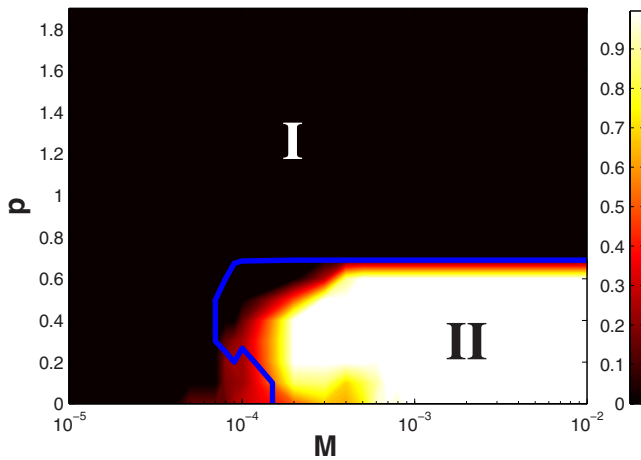


FIG. 4. (Color online) Dependence of extinction probability P_{ext} on the intraspecific competition rate p and mobility M . Blue solid line denotes the critical value $p_c(M)$ from theoretical analysis, i.e., the theoretical boundary of the black area. Both simulation and theoretical results are obtained by averaging over 50 random initial configurations on a lattice of size 100×100 . Four distinct phases are identified (see text for their meanings).

proaches the system size and the evolution of the system is more sensitive to stochastic effects than in other regimes of M . The theoretical model is thus incapable of accurately assessing the boundary in the parameter space for intermediate values of M .

B. Globally interacted species without mobility

We have also considered well-mixed individuals with global interaction. In this case, individuals can be regarded as being placed on a fully connected network. Since there is no mobility, we can set the exchange rate to be $\epsilon=0$. Without loss of generality, we still set $\sigma=\mu$ and $p+\sigma+\mu=2$. In the absence of intraspecific competition, the coexistence is unstable and extinction can occur.^{30,32} However, when p exceeds the same critical value $p_c \approx 0.7$, the probability of ex-

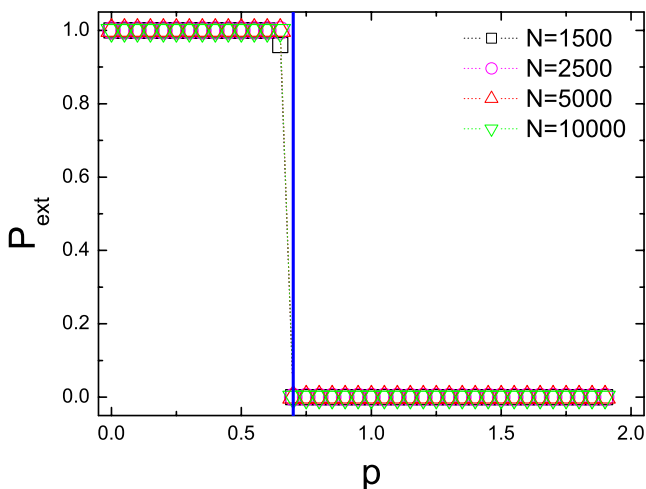


FIG. 5. (Color online) Extinction probability P_{ext} as a function of intraspecific competition rate p for fully connected networks of different sizes. Data points are direct simulation results, averaged over 100 random initial configurations. The solid blue line indicates the phase transition position from theoretical analysis.

tingtion P_{ext} abruptly decreases from 1 to nearly zero, regardless of the system size, as shown in Fig. 5. Removing the diffusion terms, our theory in Eq. (8) predicts that $p_c=0.7$, which agrees well with simulation results, demonstrating that the critical intraspecific competition rate is universal for both local and global interactions.

IV. CONCLUSION

In summary, we have studied the role of intraspecific competition in the coexistence in the framework of spatially mobile populations under cyclic competitions. For high mobility, when the rate of intraspecific competition exceeds a critical value, the likelihood of species coexistence can be considerably enhanced as compared with that in the absence of the competition. The boundary between these regions and the critical competition rate have been successfully predicted by a theoretical PDE model. We have also explored the organization of spatial population patterns. Overall, our results demonstrate that the effect of intraspecific competition can be quite complicated in mobile populations with stochastic interactions as compared with that in the underlying deterministic system. Our study may have direct implications for experimental research on biodiversity. For instance, in the experiment on colicinogenic *E. coli*,^{30,31} nutrients in Petri dish can be reduced to motivate competition within species. Experimental support for the effects of competition within species can then be possible. A limitation of the current game on lattices is the restriction of local interaction to individuals on neighboring sites. In reality, long-range interactions are possible. Cyclic game model incorporating both short- and long-range interactions can be studied in the framework of structured game or in continuous space.

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- ¹R. M. May, *Stability and Complexity in Model Ecosystems* (Princeton University Press, Princeton, N.J., 1973).
- ²R. M. May, *Science* **186**, 645 (1974).
- ³R. M. May and W. J. Leonard, *SIAM J. Appl. Math.* **29**, 243 (1975).
- ⁴M. C. Boerlijst and P. Hogeweg, *Physica D* **48**, 17 (1991); **88**, 29 (1995).
- ⁵M. C. Boerlijst and P. Hogeweg, *J. Theor. Biol.* **176**, 199 (1995).
- ⁶G. Szabó and G. Fath, *Phys. Rep.* **446**, 97 (2007).
- ⁷G. Szabó, Attila Szolnoki, and I. Borsos, *Phys. Rev. E* **77**, 041919 (2008).
- ⁸L.-L. Jiang, T. Zhou, M. Perc, X. Huang, and B.-H. Wang, *New J. Phys.* **11**, 103001 (2009).
- ⁹M. Perc and A. Szolnoki, *New J. Phys.* **9**, 267 (2007).
- ¹⁰M. Perc, A. Szolnoki, and G. Szabó, *Phys. Rev. E* **75**, 052102 (2007).
- ¹¹P. M. Hassell, H. N. Comins, and R. M. May, *Nature (London)* **353**, 255 (1991).
- ¹²S. A. Levin, *Am. Nat.* **108**, 207 (1974).
- ¹³B. Blasius, A. Huppert, and L. Stone, *Nature (London)* **399**, 354 (1999).
- ¹⁴A. A. King and A. Hastings, *Theor. Popul. Biol.* **64**, 431 (2003).
- ¹⁵Y.-C. Lai and Y.-R. Liu, *Phys. Rev. Lett.* **94**, 038102 (2005).
- ¹⁶N. Rooney, K. McCann, G. Gellner, and J. C. Moore, *Nature (London)* **442**, 265 (2006).
- ¹⁷A.-M. Neutel, J. A. P. Heesterbeek, J. van de Koppel, G. Hoenderboom, A. Vos, C. Kaldeway, F. Berendse, and P. C. de Ruiter, *Nature (London)* **449**, 599 (2007).

- ¹⁸T. Gross, L. Rudolf, S. A. Levin, and U. Dieckmann, *Science* **325**, 747 (2009).
- ¹⁹J. Hofbauer and K. Sigmund, *Evolutionary Games and Population Dynamics* (Cambridge University Press, Cambridge, 1998).
- ²⁰G. Szabó, A. Szolnoki, and R. Izsák, *J. Phys. A* **37**, 2599 (2004).
- ²¹J. C. Claussen and A. Traulsen, *Phys. Rev. Lett.* **100**, 058104 (2008).
- ²²M. Perc and A. Szolnoki, *BioSystems* **99**, 109 (2010).
- ²³T. L. Czárán, R. F. Hoekstra, and L. Pagie, *Proc. Natl. Acad. Sci. U.S.A.* **99**, 786 (2002).
- ²⁴B. Sinervo and C. M. Lively, *Nature (London)* **380**, 240 (1996).
- ²⁵C. E. Paquin and J. Adams, *Nature (London)* **306**, 368 (1983).
- ²⁶J. B. C. Jackson and L. Buss, *Proc. Natl. Acad. Sci. U.S.A.* **72**, 5160 (1975).
- ²⁷R. Durrett and S. Levin, *Theor Popul. Biol.* **46**, 363 (1994); *J. Theor. Biol.* **185**, 165 (1997); *Theor Popul. Biol.* **53**, 30 (1998).
- ²⁸L. A. Dugatkin, *Cooperation Among Animals* (Oxford University Press, Oxford, 1997).
- ²⁹E. Fehr and U. Fischbacher, *Nature (London)* **425**, 785 (2003).
- ³⁰B. Kerr, M. A. Riley, M. W. Feldman, and B. J. M. Bohannan, *Nature (London)* **418**, 171 (2002).
- ³¹B. C. Kirkup and M. A. Riley, *Nature (London)* **428**, 412 (2004).
- ³²T. Reichenbach, M. Mobilia, and E. Frey, *Nature (London)* **448**, 1046 (2007); *Phys. Rev. Lett.* **99**, 238105 (2007); *J. Theor. Biol.* **254**, 368 (2008).
- ³³T. Reichenbach and E. Frey, *Phys. Rev. Lett.* **101**, 058102 (2008).
- ³⁴L. Van Valen, *J. Theor. Biol.* **44**, 19 (1974).
- ³⁵B. J. Rathcke, *Ecology* **57**, 76 (1976).
- ³⁶M. D. Bertness, *Ecology* **70**, 257 (1989).
- ³⁷Y. Yom-Tov, S. Yom-Tov, and H. Moller, *J. Biogeography* **26**, 947 (1999).
- ³⁸J. M. Chase, P. A. Abrams, J. P. Grover, S. Diehl, P. Chesson, R. D. Holt, S. A. Richards, R. M. Nisbet, and T. J. Case, *Ecol. Lett.* **5**, 302 (2002).
- ³⁹P. Chesson and J. J. Kuang, *Nature (London)* **456**, 235 (2008).
- ⁴⁰R. Levins, *Am. Nat.* **114**, 765 (1979).
- ⁴¹R. MacArthur, *Theor Popul. Biol.* **1**, 1 (1970).
- ⁴²P. Chesson, *Theor Popul. Biol.* **37**, 26 (1990).