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A fundamental result in the evolutionary-game paradigm of cyclic competition in spatially extended ecological systems, as represented by the classic Reichenbach-Mobilia-Frey (RMF) model, is that high mobility tends to hamper or even exclude species coexistence. This result was obtained under the hypothesis that individuals move randomly without taking into account the suitability of their local environment. We incorporate local habitat suitability into the RMF model and investigate its effect on coexistence. In particular, we hypothesize the use of "basic instinct" of an individual to determine its movement at any time step. That is, an individual is more likely to move when the local habitat becomes hostile and is no longer favorable for survival and growth. We show that, when such local habitat suitability is taken into account, robust coexistence can emerge even in the high-mobility regime where extinction is certain in the RMF model. A surprising finding is that coexistence is accompanied by the occurrence of substantial empty space in the system. Reexamination of the RMF model confirms the necessity and the important role of empty space in coexistence. Our study implies that adaptation/movements according to local habitat suitability are a fundamental factor to promote species coexistence and, consequently, biodiversity. © *2013 AIP Publishing LLC*. [http://dx.doi.org/10.1063/1.4811298]

A grandly challenging and fundamental problem in ecology is species coexistence. Historically, population models based on nonlinear dynamical-system theory played an important role in elucidating many aspects of the coexistence problem. Such models are, however, macroscopic because they describe the average behavior of many individuals without taking into account the detailed interactions among them. Recent years have witnessed the development of a microscopic approach based on evolutionary-game dynamics, where individuals from the same and/or different species interact following rules of certain types of games. For example, the Reichenbach-Mobilia-Frey (RMF) model, first proposed in 2007, is based on the rock-paper-scissor game to describe the cyclic interactions of three competitive and mobile species in spatially extended ecosystems. Since then the RMF model has become a paradigm in developing microscopic and detailed understanding of the physical and dynamical mechanisms underlying species coexistence. A basic prediction of the RMF model is that extinction is inevitable for highly mobile species. Here, we show that, when the suitability of local habitat is taken into account, coexistence can occur even in the high-mobility regime where extinction is absolute in the RMF paradigm. In particular, we introduce a measure, the habitat suitability index (HSI), to characterize the fitness of each individual's local environment. Actual movements occur only when the local environment becomes unfavorable for survival and growth. For strong habitat suitability, extinction is excluded and coexistence becomes the rule. We find that the dynamical mechanism of such persistent coexistence can be attributed to the emergence of a substantial amount of empty space in the system, which we establish and confirm by revisiting the classic RMF model to reveal the intrinsic interplay between the behavior of the empty sites and coexistence/extinction, and by analyzing the corresponding continuous-space model based on partial differential equations (PDEs). Our work suggests local habitat suitability as a fundamental mechanism to promote coexistence.

I. INTRODUCTION

Understanding the dynamical and physical mechanisms that facilitate or hamper biodiversity is a fundamental issue in interdisciplinary science. Species coexistence is a key to maintaining biodiversity. Traditional approaches to coexistence emphasized niche partitioning, defined broadly to include differentiation in responses to predators and parasites as well as differentiation in resource use,[1] which provides a robust mechanism for coexistence in local communities. Studies revealed another mechanism by which dispersal or mobility can affect species coexistence at landscape scales. An interesting finding was that, without temporal variation, spatial heterogeneity alone does not tend to favor the evolution of dispersal.[2] The importance of chaotic dynamics in promoting coexistence was then recognized[3] and the dynamical origin of the mechanism was subsequently elucidated.[4,5]

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The role of stochastic forcing or noise in promoting coexistence was uncovered.[6] Population models based on evolutionary games were also developed to understand the coexistence of cyclically competing species.[7–12]

The past decade has witnessed the emergence of a powerful theoretical and computational paradigm in nonlinear science/theoretical ecology, namely, evolutionary games, which allows for the first time the species-coexistence problem in spatially extended ecosystems to be addressed quantitatively and microscopically at the individual-interaction level.[13–23] The evolutionary-game approach was mainly motivated by various experiments on the role of non-hierarchical, cyclic competitions in coexistence. Exemplary biophysical systems where such competitions have been observed include coral reef invertebrates,[24] mutant strains of yeast,[25] lizard populations,[26] and carcinogenic microbes.[27] The classical *rock-paper-scissor* game stood out as a paradigm to investigate the evolutionary dynamics driven by cyclic competitions.[15] Of particular importance is the incorporation of a fundamental feature of ecosystems, namely population mobility, into spatial cyclic-competition games. Specifically, in the seminal work by RMF,[13,14] a parameter characterizing species mobility was introduced and a critical mobility was identified below which species can coexist. In the physical space, coexistence is manifested by patterns of entangled traveling spiral waves of population densities. Issues such as noise and correlation,[13,14,16] instability of spatial patterns,[16,18] and conservation law for total density[19] were subsequently addressed. In all these works, a main result was that, when the mobility exceeds a critical value, extinction emerges in general, leading to the loss of coexistence. One intriguing implication of this result is that, about the critical value, the fates of species differing slightly in mobility can be completely different: existence or extinction. Since coexistence is such a ubiquitous phenomenon in nature, it is not unreasonable to conceive that species of relatively large mobility may coexist in certain environment. It is then imperative to search for dynamical mechanisms promoting coexistence even when the species are highly mobile.

Quite recently, three mechanisms have been uncovered, which permit and promote coexistence of highly mobile species: (1) intraspecific competition,[21] (2) virus/infection spreading,[22] and (3) inter-patch migration.[23] For (1), it was found that, counter-intuitively, intraspecific competition can strongly promote 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 coexistence could be induced was found to be independent of the mobility.[21] In mechanism (2), the phenomenon is that intra-species infection can strongly promote coexistence but inter-species spreading is harmful for coexistence.[22] Mechanism (3) is applicable to ecosystems of multiple but distant patches, and the main finding was that long-distance migration of species can trigger and promote coexistence in the form of target wave patterns in the physical space.[23]

In this paper, we report our discovery of a spontaneous type of mechanism promoting coexistence of highly mobile species in a single patchy environment. Since we limit the scale of the ecosystem to a single patch, long-distance migration is irrelevant. By *spontaneity*, we mean that the only interacting dynamics in the system is that due to the intrinsic, cyclic interaction, and there are no additional types of dynamical interactions such as intraspecific competition and infection spreading. Rather, an individual moves according to its *basic instinct*: it hardly moves if the local habitat is favorable for survival, but it is more likely to move if the local habitat becomes hostile. This natural instinct is important for many species including the human race, and may play a fundamental role in evolution and natural selection. To characterize whether a local environment is favorable for habitation, a general HSI was introduced in the literature[28–36] whose value is essentially the carrying capacity of a local area with respect to the habitat resources under optimal conditions (e.g., without any interactions). To extend the characterization to ecosystem governed by cyclic interactions, we introduce a position-dependent, local HSI (to be defined in Sec. II). We find that, in general, when individuals follow their natural instinct to escape from locally hostile environment, coexistence can be significantly enhanced. A surprising finding is that in the high-mobility regime where conventional understanding stipulates species extinction, competitions taking into account habitat suitability can lead to robust coexistence. In particular, for the setting in the classic RMF model[13,14] where coexistence is ruled out when the species mobility exceeds a critical value, we find *persistent coexistence* even in this high-mobility regime.

To search for a plausible explanation for persistent coexistence of highly mobile species, we carry out extensive computations. Strikingly, we find that the underlying physical mechanism can be attributed to the occurrence of substantial *empty space*. In the lattice model, throughout the entire parameter region where mobility is increased from zero, species coexistence is persistently accompanied by the presence of a large number of empty sites that are not occupied by individuals from any species. Intuitively, empty sites are favorable for coexistence because they give a population the necessary "room" to grow and to escape predation. To lend further credence to the importance of empty sites in promoting coexistence, we reexamine the classic RMF model[13,14] where habitat suitability is not included and find an unequivocal correspondence between species coexistence and empty space. Especially, as the mobility exceeds a critical value so that species extinction occurs, the fraction of empty sites simultaneously approaches zero and remain zero beyond the critical point. In fact, in this case, the entire space is dominated by a single species and there is no room even for empty sites. To our knowledge, the state of permanent coexistence in cyclically interacting ecosystems of highly mobile species had not been uncovered prior to our work, and we speculate that adaptation/movements according to local habitat suitability are fundamental to species coexistence and biodiversity. More generally, the exploration leads to the finding that in a spatially extended ecosystem supporting cyclic type of evolutionary-game dynamics, the presence of empty sites is a necessary condition for species coexistence.

In Sec. II, we describe the classic RMF model of cyclic competitions and introduce our modification to include the

measure of habitat suitability. In Sec. III, we present numerical finding of persistent coexistence of highly mobile species and the corresponding evolution of the empty sites. In Sec. IV, we revisit the classic RMF model and establish the distinct correspondence between species coexistence and the presence of empty sites. Further insights into the emergence of empty sites are also provided. In Sec. V, we offer conclusions and discussions.

II. EVOLUTIONARY-GAME MODEL INCORPORATING HABITAT SUITABILITY

May and Leonard first proposed a cyclic-competition model of three species[7] but at the macroscopic level of population dynamics. A microscopic model of cyclically interacting, mobile species in spatially extended systems was introduced by RMF in 2007,[13,14] where the system is represented by a square lattice with periodic boundary conditions. That the system's carrying capacity is finite stipulates that each site can be occupied by an individual from one of the three species or left empty. Interspecific interactions and species reproduction and movements are described by the following set of rules:

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

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

$$AB \xrightarrow{\varepsilon_0} BA, \quad BC \xrightarrow{\varepsilon_0} CB, \quad CA \xrightarrow{\varepsilon_0} AC, \quad (3)$$

where the three populations A, B, and C cyclically dominate each other, and $\varnothing$ represents empty sites. Relation (1) represents interspecific interactions, 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_0, respectively, as shown schematically in Fig. 1. The evolutionary dynamics can be described, as follows. At each time step, a randomly chosen individual interacts with a neighboring individual or moves into one of its nearest neighbors at random. The rates of competition, reproduction, and migration are normalized, which means that, for a pair of individuals at two neighboring sites, the three types of dynamical processes occur at the following probabilities: $\sigma/(\mu + \sigma + \varepsilon_0)$, $\mu/(\mu + \sigma + \varepsilon_0)$, and $\varepsilon_0/(\mu + \sigma + \varepsilon_0)$, respectively. An interaction can actually occur only when the states of both sites meet the requirement for the particular interaction. For instance, if there are no empty sites, then reproduction cannot occur. The individual mobility is proportional to the number of sites explored by one mobile individual per unit time:[37] $M_0 = \varepsilon_0(2N)^{-1}$. In the simulation, an actual time step is defined when, on average, each individual has interacted with others once, i.e., one time step involves N pairwise interactions altogether. Note that, in the RMF model, the migration rate ε_0 is assumed to be the same for all pairwise individuals. As we will discuss below, when the HSI effect is taken into account, the migration rate will depend on the lattice site. In that case, ε_0 serves as a nominal
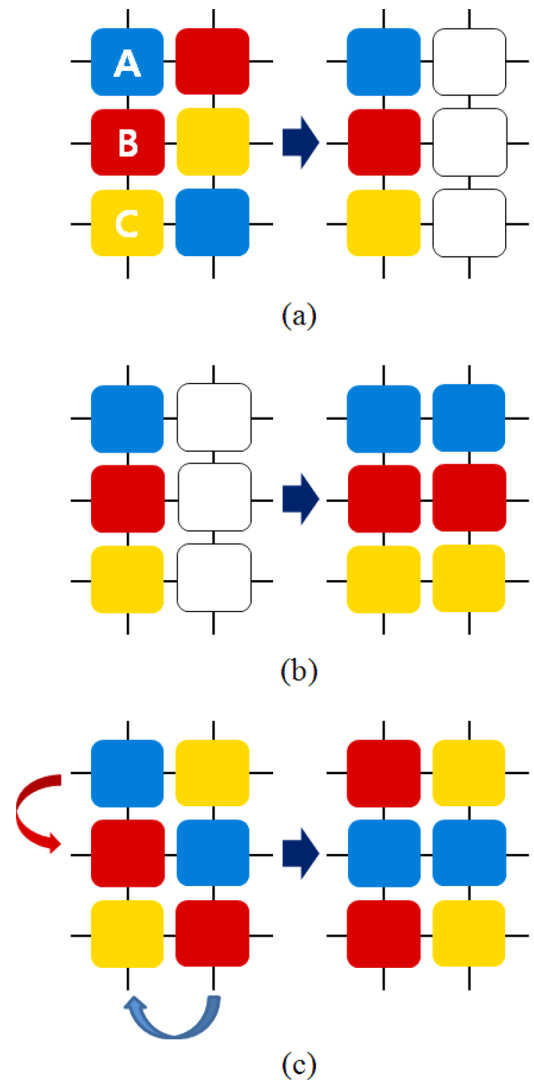

(a)

(b)

(c)

FIG. 1. Schematic illustration of dynamics of three species (A in red, B in blue, and C in yellow) under cyclic interactions. (a) Predation between two different kinds of species in the rock-paper-scissor cycle: A can prey on B, B can invade C, and C in turn out-competes A, leaving behind empty site (white); (b) reproduction which occurs only when empty neighboring sites are available; (c) migration due to the population mobility, such as exchanging positions with neighboring individuals (as denoted, e.g., by the blue arrow $CB \rightarrow BC$) or hopping onto an empty neighbor.

parameter in the definition of the local migration rate, and the mobility M_0 is defined with respect to this nominal migration parameter.

The main motivation to introduce the HSI lies in the intuition that the behavior of a species can be strongly influenced by the habitat condition. In particular, when the habitat has ample resources and no natural predators, species tend not to move. However, when resources are scarce or when a strong predator species begins to invade the habitat to threaten the survival of the species in there, movements are favored. The HSI is a parameter that assumes values between zero and unity, which can in fact be estimated from empirical data[28–36] to study the migration and reproduction behaviors of species,[28,33] at the population level. To define a meaningful HSI microscopically for each individual in the cyclic evolutionary dynamics, we focus on the fitness of the

individual at its particular lattice point. Specifically, for individual i, we define

$$\text{HSI}_i = \frac{-n_{\text{pred}}^i + \beta n_{\text{prey}}^i + w(n_{\text{same}}^i)n_{\text{same}}^i}{K}, \qquad (4)$$

where $w(n_{\text{same}}^i) = -\frac{2}{3}n_{\text{same}}^i + \frac{5}{3}$ is the weight for same individuals, n_{pred} and n_{prey} are the numbers of predators and preys at i's neighboring sites, respectively, β is a parameter characterizing the relative weight of the prey in each individual's neighborhood, and $K = 4$ is the number of neighbors of any site on a square lattice, as shown in Fig. 2. While in the traditional definition, the value of HSI is positive and restricted to the unit interval, our definition allows for both negative and positive values in a broader range, depending on the relative occupancy of an individual's neighboring lattice sites which, together with the parameter β, determines the fitness of the local environment of i. The parameter β is thus effectively a fitness parameter. For example, for $\beta = 1.0$, predators and preys have the same weights so that the HSI assumes equal numbers of positive and negative values. In this case, the individual has equal chances of staying at or moving away from its original site. For $\beta < 1.0$, predators weighs over preys, making the individual's local habitat hostile for staying, so there is a higher probability for the individual to leave its original site. Similarly, for $\beta > 1.0$, the chance of staying is larger. These considerations lead to the following *local* migration rate:

$$\varepsilon_{XY} = \varepsilon_0 \exp(-\alpha \cdot \text{HSI}_{XY}), \qquad (5)$$

where the pairwise habitat suitability HSI_{XY} of a pair of individuals, (X, Y), is defined as the average of the individuals' habitat suitability indices

$$\text{HSI}_{XY} = \frac{\text{HSI}_X + \text{HSI}_Y}{2}, \qquad (6)$$

where ε_0 is the nominal mobility for HSI $= 0$, and α is a parameter characterizing the influence of HSI on mobility. Comparing with the previous models on cyclic competitions, our model considers the fitness of local habitat for individuals by introducing two new parameters: β and α.
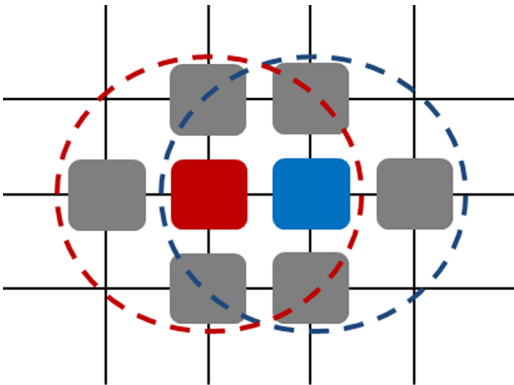

FIG. 2. Incorporation of habitat suitability into the dynamics of cyclic competition: red and blue colors denote a predator and a prey, and their local neighborhood regions for assessing the suitability of their habitats, respectively.

III. NUMERICAL EVIDENCE OF COEXISTENCE OF HIGHLY MOBILE SPECIES

In our numerical simulation, we use square lattices of various sizes, ranging from $N = 40 \times 40$ to $N = 500 \times 500$. Initially individuals from the three species are randomly distributed on the lattice. The boundary conditions are assumed to be periodic. At each time step, a random pair of neighboring sites is chosen, and the likely interaction is one from either predation, reproduction, or exchange, according to the respective probabilities. Whether the interaction can actually occur is determined by the states of both sites. For example, if the pair consists of a predator and a prey, then predation can occur. If there are an individual and an empty site in the pair, then reproduction or movement into the empty site can occur. When both sites are occupied, exchange can occur at a rate determined by the habitat suitability based mobility.

Figures 3(a)–3(t) show twenty representative snapshots of spatial patterns taken in the long-time regime during the evolution of the spatiotemporal dynamical system. In each pattern, the three species are denoted by the colors red, blue, and yellow, respectively. The panels are organized into rows and columns, based on the values of the mobility M_0 and the HSI parameter α. In particular, the four columns (from left to right) are associated with $M_0 = 3 \times 10^{-6}$, 3×10^{-5}, 3×10^{-4}, and 3×10^{-3}, and the five rows (top to bottom) are for $\alpha = 0$ (no HSI effect), $\alpha = 1.0$, $\alpha = 2.0$, $\alpha = 3.0$, and $\alpha = 4.0$, respectively. The value of the parameter β is fixed at $\beta = 2.0$. The behaviors shown in Figs. 3(a)–3(t) are in fact quite typical for other parameter choices.

The main features of Figs. 3(a)–3(t) are the following. For $\alpha = 0.0$ (the top row) so that the HSI effect is absent, we observe the classic phenomenon of extinction of high-mobility species,[13,14] where only one species is present for $M_0 > M_0^c \approx 4.5 \times 10^{-4}$. For relatively small values of α (the second and third rows from the top), we observe qualitatively similar behaviors. The striking phenomenon is, for relatively large values of α (the fourth and fifth rows from the top), coexistence persists even for $M_0 > M_0^c$ where individuals from all three species can be found on the lattice! This phenomenon of habitat suitability promoted coexistence appears to be quite robust, as demonstrated in Fig. 4, where the probability of extinction, P_{ext}, calculated from a large number of initial configurations, is plotted as a function of the mobility M_0 for different values of α. We see that, for relatively small values of α, P_{ext} increases as M_0 is increased and reaches unity for $M_0 \gtrsim M_0^c$. However, for relatively large values of α, although P_{ext} tends to increase with M_0 for $M_0 \gtrsim M_0^c$, it never reaches unity. In fact, it begins to decrease as M_0 is further increased, indicating that, when a proper amount of habitat suitability is taken into account, increasing the mobility can in fact promote coexistence, in contrast to the conventional belief that mobility is detrimental to coexistence.[13,14]

We have also studied the cases where the pairwise habitat suitability is a weighted average of individuals' HSI. For example, we can consider

$$\text{HSI}_{XY} = \frac{\phi \cdot \max\{\text{HSI}_X, \text{HSI}_Y\} + \min\{\text{HSI}_X, \text{HSI}_Y\}}{\phi + 1}, \qquad (7)$$
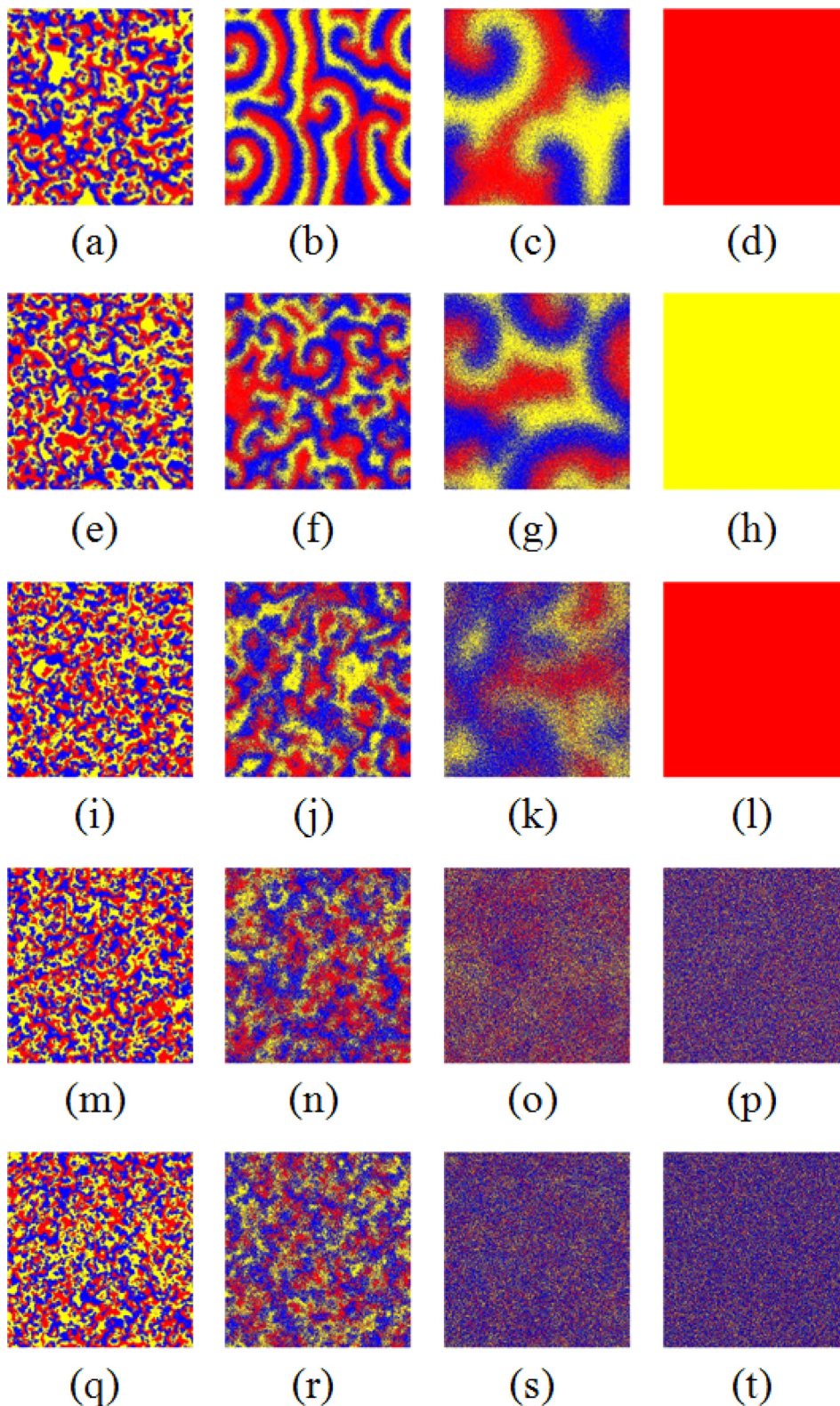
FIG. 3. For a square lattice of size $N = 500 \times 500$, representative snapshots of species distribution on the lattice. Different columns correspond to different values of the mobility: $M_0 = 3 \times 10^{-6}$ for (a), (e), (i), (m), and (q), $M_0 = 3 \times 10^{-5}$ for (b), (f), (j), (n), and (r), $M_0 = 3 \times 10^{-4}$ for (c), (g), (k), (o), and (s), and $M_0 = 3 \times 10^{-3}$ for (d), (h), (l), (p), and (t). Different rows are associated with different values of the HSI parameter α: $\alpha = 0.0$, 1.0, 2.0, 3.0, and 4.0 (top to bottom). The bottom two rows reveal that, for relatively large values of α, coexistence persists even in the large mobility regime.

where the weighting parameter ϕ can be chosen to be the golden mean $\phi \approx 1.618$ or its inverse. Behaviors similar to those in Figs. 3 and 4 have been observed. The common phenomenon is then that incorporation of habitat suitability into the evolutionary-game dynamics can lead to persistent coexistence, regardless of the species mobility.

IV. DYNAMICAL MECHANISM OF PERSISTENT COEXISTENCE: ROLE OF EMPTY SITES

A. Interplay between species coexistence and emergence of empty sites in the presence of HSI effect

Due to the complexity of the game-competition dynamics on lattice, it is difficult to obtain an analytic understanding
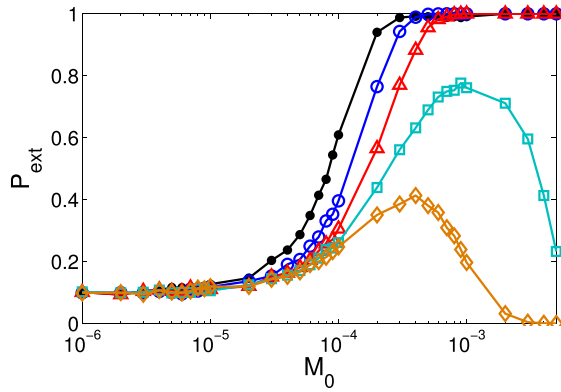
FIG. 4. Extinction probability P_{ext} versus the mobility for different values of the HSI parameter α for systems of size $N = 40 \times 40$. The legends are: $\alpha = 0.0$ (black dots), $\alpha = 1.0$ (blue circles), $\alpha = 2.0$ (red triangles), $\alpha = 3.0$ (light blue squares), and $\alpha = 4.0$ (brown diamonds). The second HSI parameter β is fixed at 2.0. For relatively large values of α, P_{ext} never reaches unity, indicating persistent coexistence, regardless of the mobility.

of the phenomenon of habitat suitability induced persistent coexistence. We are thus led to explore the dynamical mechanism and develop a physical understanding of the phenomenon. An intuitive picture is that the habitat suitability imposes a constraint on species movement. Consider, for example, an individual from one species. When the local environment is favorable for survival and reproduction, movement into a different location is not desirable. When the local environment is hostile, e.g., when there is heavy presence of predators in the individual's neighborhood, there is strong motivation for migration. However, the migration may not actually take place because the individual might have already become a prey before it can move out of the local hostile environment. Thus, habitat suitability induces a kind of asymmetry in species movements, reducing the overall effective mobility. Because of the "slow-down" in species movement, a substantial number of lattice sites will become empty. Our postulate is that *dynamically, persistent coexistence is associated with the emergence of empty sites in the spatially extended system.* Heuristically, the availability of empty space is beneficial for growth and reproduction, making it more likely for species to survive.

To provide support for our postulate, we calculate the time evolution of the densities of the three species and of the empty site. Figures 5(a)–5(d) show, for $\alpha = 1.0$ and $N = 100 \times 100$, time series of the four densities for $M_0 = 3 \times 10^{-6}$, 3×10^{-5}, 3×10^{-4}, and 3×10^{-3}, respectively, where the initial density of empty sites is $\rho_e(0) = 0.1$. We observe that, for relatively small mobility values [panels (a)-(c)] where there is coexistence, $\rho_e(t)$, the density of empty site, approaches asymptotically a constant, non-zero value. However, for $M_0 = 3 \times 10^{-3}$, where coexistence is ruled out, $\rho_e(t)$ approaches zero asymptotically. There is thus strong correlation between coexistence and the asymptotic value of ρ_e in that a non-zero value of ρ_e corresponds to coexistence but a zero value of ρ_e signifies extinction. This observation is reinforced by examining the case of relatively large values of α for which coexistence is persistent, as shown in Figs. 6(a)–6(d) for $\alpha = 4.0$ for the same mobility
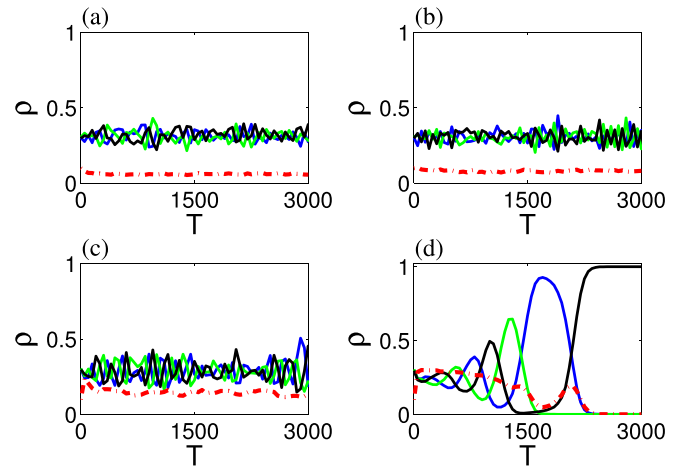

FIG. 5. For $\alpha = 1.0$, time evolution of the densities of the three species (full lines) and the density ρ_e of empty site (red dashed dotted line) for (a) $M_0 = 3 \times 10^{-6}$, (b) $M_0 = 3 \times 10^{-5}$, (c) $M_0 = 3 \times 10^{-4}$, and (d) $M_0 = 3 \times 10^{-3}$. System size is $N = 100 \times 100$. Note that $\rho_e(t)$ approaches a non-zero value for coexistence ((a)-(c)) but $\rho_e \to 0$ for the case of extinction (d). Because of the symmetry among the three species, we simply use three different colors to distinguish them, where the correspondence between one particular color and one particular species can be arbitrary. The same legend applies to all subsequent figures on the density evolution.

values as in Figs. 5(a)–5(d), respectively, where $\rho_e(0) = 0.1$. We observe non-zero asymptotic values of ρ_e for all four cases. The non-zero asymptotic value of ρ_e does not depend on the choice of the initial value of ρ_e, as shown in Figs. 7(a)–7(d) where the initial density of empty sites is set to be zero.

Figures 8(a)–8(d) summarize the behavior of the asymptotic value of $\rho_e(t)$, denoted by $\bar{\rho}_e$, in relation with species coexistence or extinction. In Fig. 8(a), $\bar{\rho}_e$ is plotted versus the HSI parameter α for $M_0 = 3 \times 10^{-5}$. Due to the small mobility, there is coexistence even in the absence of any habitat suitability effect. We observe that $\bar{\rho}_e$ is non-zero in the entire range of variation of α considered. In fact, as α is increased, there is slightly increase in $\bar{\rho}_e$. In Fig. 8(b), the
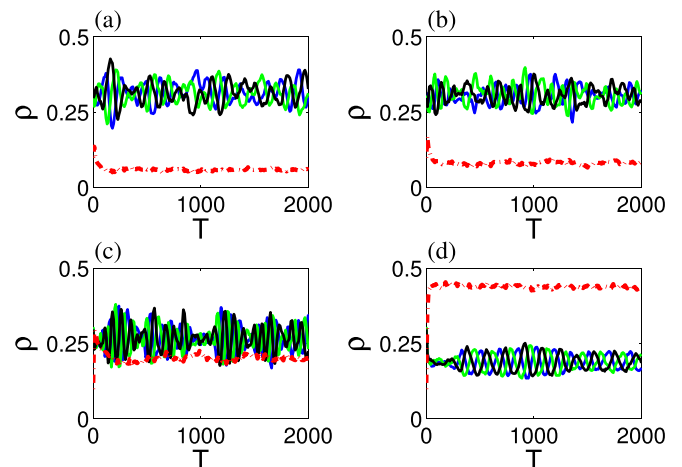

FIG. 6. For $\alpha = 4.0$ and $N = 100 \times 100$, time evolution of the densities of the three species (full lines) and the density ρ_e of empty site (red dashed dotted line) for (a) $M_0 = 3 \times 10^{-6}$, (b) $M_0 = 3 \times 10^{-5}$, (c) $M_0 = 3 \times 10^{-4}$, and (d) $M_0 = 3 \times 10^{-3}$. Initially 10% of the lattice sites are empty: $\rho_e(0) = 0.1$. There is persistent coexistence so that ρ_e never approaches zero.
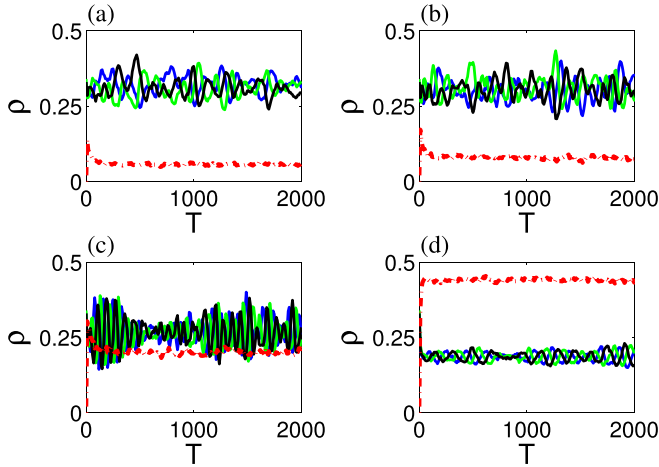
FIG. 7. For $\alpha = 4.0$, $N = 100 \times 100$, and initial zero empty-site density $[\rho_e(0) = 0]$, time evolution of the densities of the three species (full lines) and the density ρ_e of empty site (red dashed dotted line) for (a) $M_0 = 3 \times 10^{-6}$, (b) $M_0 = 3 \times 10^{-5}$, (c) $M_0 = 3 \times 10^{-4}$, and (d) $M_0 = 3 \times 10^{-3}$. Despite $\rho_e(0) = 0$, coexistence is persistent regardless of mobility and $\rho_e(t)$ approaches some non-zero values for all cases.

value of mobility is relatively large: $M_0 = 3 \times 10^{-3}$. In this case, without habitat suitability effect or even when the effect is weak (corresponding to small α values), extinction is inevitable. The value of $\bar{\rho}_e$ is thus zero for small α values but becomes non-zero for relatively large values of α. In Fig. 8(c), $\bar{\rho}_e$ is plotted against $\log_{10} M_0$ for $\alpha = 1.0$. In this case, there is extinction in the large mobility regime, and we observe that $\bar{\rho}_e$ is non-zero initially but becomes zero for $\log_{10} M_0 \gtrsim \log_{10} M_0^c$. Finally, Fig. 8(d) displays the behavior of $\bar{\rho}_e$ versus $\log_{10} M_0$ for $\alpha = 4.0$, where coexistence is persistent. Indeed, we observe that the value of $\bar{\rho}_e$ is never zero across both the small and large mobility regimes. These results suggest strongly a high correlation between coexistence and the emergence of empty sites in the underlying spatiotemporal dynamical system.
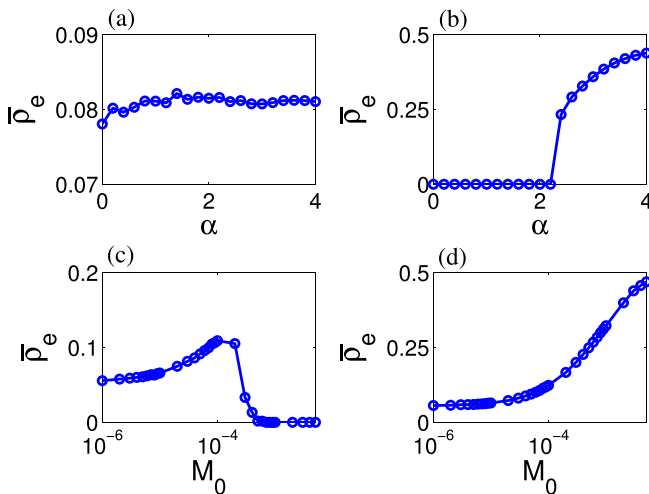

FIG. 8. ((a) and (b)) Asymptotic value of the empty-site density, $\bar{\rho}_e$, versus the HSI parameter α for $M_0 = 3 \times 10^{-5}$ and $M_0 = 3 \times 10^{-3}$, respectively. ((c) and (d)) For $\alpha = 1.0$ and $\alpha = 4.0$, respectively, $\bar{\rho}_e$ versus $\log_{10} M_0$. In all cases, there is a strong correlation between species coexistence and the emergence of substantial number of empty sites. The system size is $N = 100 \times 100$ and the HSI parameter β is set to be 2.0.

B. Evolution of empty sites: Revisiting the classic RMF model

To establish a firm foundation for our postulate regarding the dynamical mechanism of coexistence in terms of empty sites, we revisit the classic RMF model, but from a different perspective. In particular, we shall focus on the emergence and evolution of empty sites in the lattice system. In the absence of HSI effect, the dynamics of the RMF system can be approximately described by PDEs.[13,14]

Consider a two-dimensional square domain and let $a(\mathbf{r}, t)$, $b(\mathbf{r}, t)$, and $c(\mathbf{r}, t)$ be the densities of the three competing species, respectively. The following set of PDEs can be derived to describe the dynamics of the RMF system:[13,14]

$$\frac{\partial a(\mathbf{r}, t)}{\partial t} = M_0 \Delta a(\mathbf{r}, t) + \mu a(\mathbf{r}, t)[1 - \rho(\mathbf{r}, t)] - \sigma a(\mathbf{r}, t)c(\mathbf{r}, t),$$

$$\frac{\partial b(\mathbf{r}, t)}{\partial t} = M_0 \Delta b(\mathbf{r}, t) + \mu b(\mathbf{r}, t)[1 - \rho(\mathbf{r}, t)] - \sigma b(\mathbf{r}, t)a(\mathbf{r}, t),$$

$$\frac{\partial c(\mathbf{r}, t)}{\partial t} = M_0 \Delta c(\mathbf{r}, t) + \mu c(\mathbf{r}, t)[1 - \rho(\mathbf{r}, t)] - \sigma b(\mathbf{r}, t)c(\mathbf{r}, t),$$

$$(8)$$

where $\rho(\mathbf{r}, t) \equiv a(\mathbf{r}, t) + b(\mathbf{r}, t) + c(\mathbf{r}, t)$. The spatially averaged density $\langle a(\mathbf{r}, t) \rangle$ is thus given by

$$\frac{\partial \langle a(\mathbf{r}, t) \rangle}{\partial t} = \frac{1}{L^2} \int_{D=L^2} \frac{\partial a(\mathbf{r}, t)}{\partial t} d\mathbf{r}$$

$$= \frac{1}{L^2} \int_0^L \int_0^L \frac{\partial a(x, y, t)}{\partial t} dx dy,$$

$$= \frac{1}{L^2} \int_0^L \int_0^L M_0 \Delta a(x, y, t) + \mu a(x, y, t)[1 - \rho(x, y, t)]$$

$$- \sigma a(x, y, t)c(x, y, t)dx dy, \qquad (9)$$

where $(x, y) \in D = L \times L$. Similar equations can be written down for $\langle b(\mathbf{r}, t) \rangle$ and $\langle c(\mathbf{r}, t) \rangle$. The evolution of the total species density is thus governed by

$$\frac{\partial \rho(\mathbf{r}, t)}{\partial t} = \frac{\partial \langle a(\mathbf{r}, t) \rangle}{\partial t} + \frac{\partial \langle b(\mathbf{r}, t) \rangle}{\partial t} + \frac{\partial \langle c(\mathbf{r}, t) \rangle}{\partial t}$$

$$= \frac{1}{L^2} \int_D M_0 \Delta(a(\mathbf{r}, t) + b(\mathbf{r}, t) + c(\mathbf{r}, t))$$

$$+ \mu \rho(\mathbf{r}, t)(1 - \rho(\mathbf{r}, t))$$

$$- \sigma[a(\mathbf{r}, t)b(\mathbf{r}, t) + b(\mathbf{r}, t)c(\mathbf{r}, t) + c(\mathbf{r}, t)a(\mathbf{r}, t)]d\mathbf{r}.$$

Neglecting the second-order term $a(\mathbf{r}, t)b(\mathbf{r}, t) + b(\mathbf{r}, t)c(\mathbf{r}, t) + c(\mathbf{r}, t)a(\mathbf{r}, t)$, we obtain

$$\frac{\partial \langle \rho(\mathbf{r}, t) \rangle}{\partial t} \approx \frac{1}{L^2} \int_D M_0 \Delta \rho(\mathbf{r}, t) + \mu \rho(\mathbf{r}, t)(1 - \rho(\mathbf{r}, t))d\mathbf{r}.$$

$$(10)$$

The average density of empty sites is given by $\langle e(\mathbf{r}, t) \rangle = 1 - \langle \rho(\mathbf{r}, t) \rangle$. We thus have

$$\frac{\partial \langle e(\mathbf{r}, t) \rangle}{\partial t} = -\frac{\partial \langle \rho(\mathbf{r}, t) \rangle}{\partial t}, \qquad (11)$$

which can be used to numerically solve the time evolution of the density of empty sites based on the PDE approximation.

Figures 9(a)–9(d) show the representative time evolution of the species densities and also the density of empty sites calculated from the PDE approach, for a number of mobility values. The spatial region is chosen to be the unit square and the initial empty-site density is set to be zero. These results agree, qualitatively, with those from direct lattice simulations. The most relevant feature here is the asymptotic value of $\bar{\rho}_e$, which is non-zero for small-mobility cases where there is coexistence but zero when there is uniform state where two species are extinct. This means that the necessity of empty space for coexistence is already present in the classic RMF model, lending further credence to our explanation that HSI effect causes the dynamics to generate substantial empty space, leading to persistent coexistence even in the high-mobility regime where extinction is certain in the absence of habitat suitability factor.

C. Balance between predation and reproduction/exchange

Figure 8(d) shows that, when the HSI effect is strong so that persistent coexistence occurs, the average density of empty sites actually increases with the mobility. Here, we provide a heuristic analysis of the dynamics of empty sites. In general, empty sites are generated from the interplay between predation and reproduction as well as exchange. Qualitatively, we can write

$$\langle \rho_e \rangle = |\mathrm{P} - C(M_0) \cdot \mathrm{R} \cdot \mathrm{E}|, \qquad (12)$$

where $\mathrm{P} = \sigma/(\sigma + \mu + \varepsilon_0)$, $\mathrm{R} = \mu/(\sigma + \mu + \varepsilon_0)$, and $\mathrm{E} = \varepsilon_0/(\sigma + \mu + \varepsilon_0)$ stand for the average rates of predation, reproduction, and exchange, respectively, and $C(M_0)$ is a constant that depends on mobility. Physically, $C(M_0)$
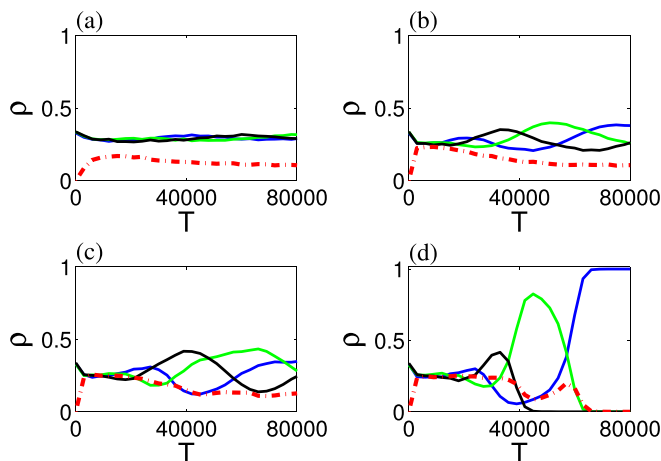
FIG. 10. For a lattice of size $N = 100 \times 100$, the quantity $c(M_0)$ versus mobility M_0 for $\alpha = 0.0$ (black diamonds), $\alpha = 1.0$ (red circles), $\alpha = 2.0$ (blue dots), $\alpha = 3.0$ (brown squares), and $\alpha = 4.0$ (cyan triangles). For cases where extinction occurs at high mobility, $C(M_0) \to 1$ for $M_0 \gtrsim M_0^c$. When persistent coexistence occurs, $C(M_0)$ decreases first but turns around to increase for $M_0 \gtrsim M_0^c$. The green line is the relation $(2 + 2M_0N)/2M_0N$.

measures the balance between predation and reproduction/exchange. For $C(M_0) \gg 1$ or $C(M_0) \ll 1$, reproduction/exchange weights over predation or vice versa, generating empty sites and making coexistence possible. For $C(M_0) \to 1$, predation and reproduction/exchange are balanced, leaving no room for empty space so that extinction emerges. Using $\sigma = \mu = 1$, $\varepsilon = 2M_0N$, the coefficient $C(M_0)$ can be expressed as

$$C(M_0) = \frac{2 + 2M_0N}{2M_0N} - \langle \rho_e \rangle \cdot \frac{(2 + 2M_0N)^2}{2M_0N}, \qquad (13)$$

which is a function of M_0. For high mobility, we have

$$\lim_{M_0 \to \infty} C(M_0) = \lim_{M_0 \to \infty} \left[\frac{2 + 2M_0N}{2M_0N} - \langle \rho_e \rangle \cdot \frac{(2 + 2M_0N)^2}{2M_0N} \right] = 1,$$

with $\langle \rho_e \rangle \to 0$ as $M_0 \to \infty$.[13]

Figure 10 shows the coefficient $c(M_0)$ versus the mobility M_0, where the green line is the relation $(2 + 2M_0N)/2M_0N$. In the absence of HSI effect (black diamond), the behavior of $c(M_0)$ follows the green line and approaches the value 1 for $M_0 > M_0^c$, the extinction regime. When the HSI effect is present, $c(M_0)$ decreases initially with M_0 but near M_0^c, it reverses the decreasing trend and starts to increase with M_0 about $M_0 \gtrsim M_0^c$, due to the counter-balancing effect of the HSI effect in reducing the local effective mobility. As a result, persistent coexistence can emerge in both low- and high-mobility regimes.

V. CONCLUSIONS AND DISCUSSIONS

A fundamental issue in ecology and also in complex dynamical systems is to understand the coexistence of competing species in the same environment. Early models based on population dynamics provided insights into coexistence at the macroscopic level,[7] but such models sometime predict that the state of coexistence is unstable, generating a dilemma as coexistence appears to be a robust phenomenon in

FIG. 9. (a)-(d) For the classic RMF model in the absence of habitat suitability factor, time evolution of the species densities (full lines), and the density of the empty space (red dashed dotted line) from the PDE model for $M_0 = 3 \times 10^{-6}$, $M_0 = 3 \times 10^{-5}$, $M_0 = 3 \times 10^{-4}$, and $M_0 = 3 \times 10^{-3}$, respectively. The spatial region is the unit square in the plane, and the initial density of empty space is set to be zero. Even in this case, there is a unique correspondence between coexistence and substantial empty space in the system asymptotically.
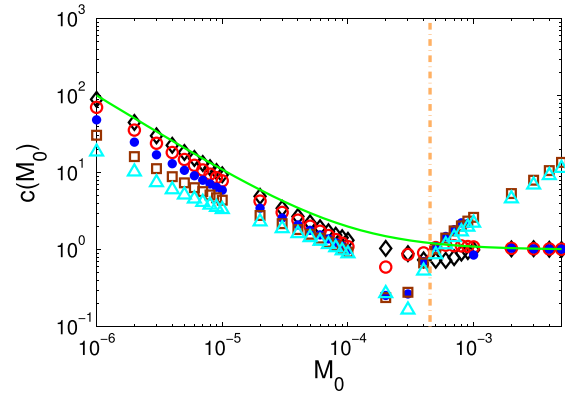
real ecological systems. Recent years have witnessed efforts to resolve this dilemma, most notably through the approach of evolutionary games at a microscopic scale where the interactions are studied at the level of species individuals. In this regard, the celebrated RMF model[13,14] based on the classical rock-paper-scissors game represents a paradigm to address the coexistence of cyclically competing species. A main prediction of the RMF model is that coexistence is not possible when the species are highly mobile. Yes in the real world coexistence is not limited to slow species only.

We have developed a framework to address the question of whether the RMF game model would allow for highly mobile species to coexist, and we have provided computation and analysis, which suggest an affirmative answer. Our key idea is to articulate that species movements depend on the local environment. In particular, for an individual its local habitat suitability represents an important factor in deciding whether it should disperse. By introducing a local habitat suitability index into the RMF model, we have found persistent coexistence in both low and high mobility regimes. This result has two important implications. First, it shows that robust and persistent coexistence can occur in spatially extended dynamical systems, regardless of species mobility, providing a foundation for biodiversity. Second, it further validates the RMF model as a general paradigm to investigate the collective behaviors of complex, spatially extended ecological systems at the microscopic level.

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