## Emerging spatiotemporal patterns in cyclic predator-prey systems with habitats

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Three-species cyclic predator-prey systems are known to establish spiral waves that allow species to coexist. In this study, we analyze a structured heterogeneous system which gives one species an advantage to escape predation in an area that we refer to as a habitat and study the effect on species coexistence and emerging spatiotemporal patterns. Counterintuitively, the predator of the advantaged species emerges as dominant species with the highest average density inside the habitat. The species given the advantage in the form of an escape rate has the lowest average density until some threshold value for the escape rate is exceeded, after which the density of the species with the advantage overtakes that of its prey. Numerical analysis of the spatial density of each species as well as of the spatial two-point correlation function for both inside and outside the habitats allow a detailed quantitative discussion. Our analysis is extended to a six-species game that exhibits spontaneous spiral waves, which displays similar but more complicated results.

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# I. INTRODUCTION

Systems far from equilibrium are often characterized by the spontaneous formation of spatiotemporal patterns [1,2]. These patterns are found at every lengthscale, from the very large (galaxy superclusters [3] and the Sloan Great Wall [4]) to the very small (developmental biology [5] and bacterial colonies [6,7]). Due to their omnipresence, the formation and persistence of patterns is of central importance for statistical physicists interested in nonequilibrium systems. In this context, a special place is taken by population dynamics models, due to the fact that the stability and longevity of ecological structures [8–14] has an intimate relationship with persisting space-time patterns. Although the study of population dynamics models is driven by the desire to better understand ecosystems, biodiversity, and species extinction, these and related models also show up in contexts like biochemical reactions [15], lasers [16], economy [17], epidemiology [18], genetics [19], and social systems [20].

The spontaneous formation of spiral waves, generated for example in a three-species system with cyclic interactions [21], has been shown to favor biodiversity and enhance the stability of an ecosystem. These spirals can be broken up through high mobility rates, which triggers extinction events and the loss of biodiversity [22–26]. Very rich space-time patterns, some in the form of spirals involving numerous species, result from complicated cyclic interaction schemes with more than three species [27-57]. Most of these studies assume spatially homogeneous systems where the rates are species independent and the same throughout the system. As a result, vital aspects of real-world ecologies, such as changing environments, species fitness, and evolutionary changes, are not taken into account. Consequently, these oversimplifications strongly restrict the lessons that can be learned from these setups when it comes to the stability of spatiotemporal patterns and the ensuing persistence of species coexistence and biodiversity.

In this paper we investigate the transient and steady-state properties of modified three-species (the May-Leonard model [21]) and six-species systems [40] that yield in the standard setup of a homogeneous environment a stable ecosystem due to the persistence of spiral patterns. We consider a structured heterogeneous environment where regions with species-independent interactions alternate with regions where one of the species has an enhanced probability to escape its predators. Regions that provide this advantage are viewed as the species' habitats. The same setup was used in Ref. [57] to study extinction probabilities in small heterogeneous systems. In the present study we focus on systems so large that no extinction events happen during our numerical simulations. This allows us to investigate resulting complex space-time patterns, with a focus on how the boundary between the different region types influences the long-time behavior in the different regions. An interesting, and rather counterintuitive, finding is that the enhanced escape probability provided to one species turns out to be most beneficial to one of its predators. This is independent of the escape probability, even so the details regarding the ranking of the species (as measured through the local average population density) depend on the specific value of that probability. As part of our quantitative analysis we also compute locally averaged two-point correlation functions and determine related correlation lengths. Investigation of early time behavior after preparation of the system in a disordered initial state provides insides into how the long-time ("steady-state") properties come to be.

The paper is organized in the following way. In the next section we discuss how we set up our spatially inhomogeneous system for a three- and a six-species case that show spiral waves in a homogeneous environment. We also introduce the quantities we use for our analysis. In Sec. III we have a close look at the three-species system, which is followed by a similar discussion for the six-species model in Sec. IV. We discuss our findings in Sec. V.



FIG. 1. Snapshots of the homogeneous systems with (left) three and (right) six species characterized by the emergence of spirals. In the notation discussed in the main text, these are the (3,1) and (6,4) systems. The linear size of the systems is L = 1000 and the snapshots have been taken at t = 10000 when starting from a fully disordered initial state.

### **II. MODEL AND QUANTITIES**

We consider in the following nonconserved cyclic threespecies [21,24–26] and six-species [40,49,51] models that display the spontaneous formation of spirals where every spiral arm is occupied by one species. In cyclic games the notation (n, r) [40] is sometimes used where n is the number of species and r is the number of prey that each species attacks, i.e., species i attacks species i + 1, ..., i + r (modulo n). In this notation our two games are the (3,1) and (6,4) games. Often, these interaction schemes are put on a homogeneous lattice with at most one individual on each lattice site. Mobility is allowed in the form of diffusion, i.e., jumping to neighboring empty sites, and/or of exchanges of individuals sitting on neighboring lattice sites. All these possibilities can be cast in the following set of chemical reactions involving neighboring sites:

$$s_i + s_j \xrightarrow{\beta} s_i + \emptyset,$$
 (1)

$$s_i + \emptyset \xrightarrow{\beta} s_i + s_i,$$
 (2)

$$s_i + s_j \xrightarrow{1-\beta} s_j + s_i,$$
 (3)

$$s_i + \emptyset \xrightarrow{1-\beta} \emptyset + s_i, \tag{4}$$

where  $s_i$  is an individual of species *i*, *j* is a prey of species *i* and  $\emptyset$  designates an unoccupied lattice site. For every time step, on average, every site is selected once to undergo an interaction which could be predation (1), reproduction (2), swapping (3), or diffusion (4). We choose to have the same rate  $\beta$  for predation and reproduction events, whereas swapping and diffusion, two manifestations of the species' mobility, take place with rate  $1 - \beta$ . In our implementation we select randomly a site and then select randomly one of the four neighboring sites with the same probability. If species *i* and *j* are preying on each other, as it may happen for the (6,4) game, then the individual occupying the site that is selected first is considered to be the predator.

The traditional setup just described has been the focus of a range of studies, especially for the (3,1) model which is better known as the May-Leonard model. We show in Fig. 1 for each model a typical snapshot on a square lattice with linear extent L = 1000 and with  $\beta = 0.75$ , the value used in the following. As already mentioned, the interaction scheme yields rotating spirals where each spiral arm is formed by individuals of one species, with the subsequent spiral arm being formed by the sole species that is not a prey of the species that forms the previous spiral arm.

The focus of the present study is to gain a better understanding of the impact spatial heterogeneity has on species coexistence and spatial pattern formation. For this we overlay our square system with a  $4 \times 4$  checkerboard (so that each of the 16 squares is composed of  $L/4 \times L/4$  sites) formed by two types of environments: habitats, where an advantage is given to one species (species 1) in the form of a nonzero probability to escape attacks from its predator(s), and neutral regions, where the different rates are species independent. This is realized by changing inside the habitat the reaction (1) to

$$s_i + s_1 \xrightarrow{\beta - \alpha} s_i + \emptyset,$$

where for the (3,1) game i = 3, whereas for the (6,4) game i can be 6, 5, 4, or 3. For  $\alpha = 0$  we recover the homogeneous system, whereas for  $\alpha = \beta$  a member of species 1 will always escape when attacked inside its habitat.

Small systems with cyclic interaction schemes on a checkerboard of habitats and neutral regions were simulated in Ref. [57] with the aim of investigating species extinction in heterogeneous systems. The main finding of that study, which was restricted to small values  $\alpha < 0.2$ , has been that with increasing  $\alpha$  the system transitions from stable coexistence to unstable coexistence. Here we consider systems of sizes so large that species extinction is not observed in our simulations. We also focus systematically on large values of  $\alpha$  for which remarkable changes to the space-time patterns take place. As



FIG. 2. Snapshots of the three-species system with habitats, with on the left  $\alpha = 0.60$  and on the right  $\alpha = 0.75$ . The superimposed gridlines show the checkerboard arrangements of the different regions, with the patch in the top left corner being a habitat that provides an advantage to species 1. Species 1 is shown in red, 2 in green, and 3 in blue. The linear size of the systems is L = 1000 and the snapshots have been taken at t = 10000 time steps after starting from a fully disordered initial state.

we will discuss in the following, after an intriguing and very dynamic early time regime, our systems settle into long-lived states characterized by time-independent quantities.

A related setup was considered in Ref. [58] where symmetric and asymmetric May-Leonard systems were connected via diffusive coupling. As a result of this coupling, coexistence is induced in the asymmetric subsystem through the stabilization of spirals.

At the center of our analysis are various species and empty site densities. Starting from an initially disordered state [each lattice site is occupied with the probability 1/(N + 1) by each of the species or is left empty with the same probability 1/(N + 1)], we follow the time evolution of the system through the measurement of ensemble-averaged densities of each species and empty sites both inside and outside of the habitats. With the occupation number  $n^i(x, t)$ , which takes on the value 1 if at time t a member from species i occupies the site x and 0 otherwise, the time-dependent densities averaged over habitats or nonhabitat regions are given by the expressions

and

$$\rho_I^i(t) = \left\langle \frac{1}{N_I} \sum_{x \in I} n^i(x, t) \right\rangle \tag{5}$$

$$\rho_O^i(t) = \left\langle \frac{1}{N_O} \sum_{x \in O} n^i(x, t) \right\rangle,\tag{6}$$

where  $N_I$ , respectively,  $N_O$ , is the number of sites inside respectively outside habitats, whereas  $\langle \cdots \rangle$  indicates an average over an ensemble of independent runs with different realizations of the noise. In the steady state, which is typically reached within a few thousand time steps, with the notorious exception of the limiting case  $\alpha = \beta$  with a much longer relaxation time, we compute the ensemble- and time-averaged species densities  $\rho_s^i(d)$  as a function of the distance *d* from the center of a habitat along a line connecting this center to the center of a neighboring region, i.e., the line crosses the habitat border at d = L/8 (d = 125 when L = 1000). As we will see, the spatial inhomogeneities introduced by the habitats manifest themselves through complicated spatial dependencies of the species densities close to the habitat boundary. For that reason we perform spatial averages in the central region *C* of a habitat or nonhabitat region (a square patch of  $L/10 \times L/10$  sites around the four central sites of a region) where the time-dependent densities are found to be uniform or to change very slowly with position. These locally averaged quantities,  $\rho_{C,I}^i(t)$  and  $\rho_{C,O}^i(t)$ , are given by an expression analog to Eqs. (5) and (6) but with the sums extending to only the central sites. With these densities we can compute various "bulk" space- and time-dependent correlation functions and derive time-dependent correlation lengths.

#### **III. SYSTEMS WITH THREE SPECIES**

Figure 2 provides a first impression of the changes that result from adding to a May-Leonard system habitats where one of the species (species 1 in our study) has an enhanced probability to escape its predator. The snapshot on the left is for  $\alpha = 0.6$ . While in the habitats the cyclic predator-prev relationship is maintained, an uneven distribution of species is observed with species 3 (blue) dominating, whereas species 2 (green) is suppressed. This is an indication of the nonlinear character of the system where a higher probability of escaping a predator may result ultimately in an increase of the number of predators in the habitat. Subtle changes take place close to the habitat boundaries as well as in the regions outside of the habitats, as we will see in the following quantitative investigation. The right panel of Fig. 2 shows the limiting case  $\alpha = \beta = 0.75$  where the predator-prey relationship between species 3 and 1 is replaced by a neutral and symbiotic relationship as species 3 takes advantage of the fact that its new partner is preying on species 2, the predator of species 3. As a result species 2 is practically eliminated inside the



FIG. 3. The steady-state species and empty site densities along a line connecting the center of a habitat with the center of a adjacent region. Simulated are (3,1) games with different values of  $\alpha$  for species 1: (a)  $\alpha = 0.15$ , (b)  $\alpha = 0.45$ , and (c)  $\alpha = 0.75$ . For  $\alpha = 0.15$  and  $\alpha = 0.45$  the steady state is accessed after less than 10 000 time steps, and for  $\alpha = 0.75$  one needs to wait for 30 000 time steps before stationarity is reached. The data shown result from averaging over 1000 independent runs. The vertical dashed line indicates the boundary of the habitat.

habitats, with the exception of close to the boundaries where a more complicated behavior emerges due to exchanges with the outside regions.

In order to develop an understanding of the spatiotemporal behavior emerging in this system, we first discuss the steady state as a function of  $\alpha$  before investigating how the system, initially prepared in a disordered initial state, evolves to this long-lived state (as we do not see during our simulations any changes in the properties of the system once this state is reached, we call this the "steady state" for simplicity, with the understanding that for the models studied here the final configuration is that of fixation where a single species fills the system).

As illustrated in Fig. 3, we find three different scenarios, depending on the value of  $\alpha$ . It is always species 3, the predator of species 1 with the "advantage" within the habitats, that ends up being the dominating species in the habitats. There

exists a critical value  $\alpha_c = 0.40(2)$  of the escape probability at which the preponderance of the species changes: For  $\alpha < \alpha_c$ , species 1 has the lowest density, whereas for  $\alpha > \alpha_c$  it is species 2 that is most suppressed. In the limiting case  $\alpha = \beta$ , shown in Fig. 3(c), the alliance of the neutral species 1 and 3 does not allow species 2 to maintain a sizable presence inside the habitats. The resulting absence of predation events inside the habitats results in the absence of empty sites inside habitats, with the exception of a narrow region close to the boundary where the diffusion of individuals of species 2 into the habitat generates predation events.

Inspection of Fig. 3 reveals a broader transition region on both sides of the habitat boundary where species densities exhibit dramatic changes in order to connect the steady-state densities inside and outside of a habitat. Increasing the value of  $\alpha$  results in increasing deviations from the steady-state densities of the symmetric system. Consequently, changes



FIG. 4. Normalized "bulk" two-point correlation functions for the (3,1) game with  $\alpha = 0.45$  for species 1 inside the habitats. These correlation functions are species dependent inside habitats but species independent outside (magenta dashed line). The shown data, measured once the steady state has been reached (typically after 10 000 time steps), result from both a time average (1000 time steps) and an ensemble average (100 independent runs). The inset shows the steady-state correlation lengths inside and outside (magenta filled circles) of the habitats as a function of  $\alpha$ . The correlation length is defined as the distance at which the normalized two-point correlation function takes on the value 0.1 (indicated by the horizontal black dashed line in the main figure).

inside the transition region are more pronounced for larger  $\alpha$ . Remarkably, the cyclic interaction scheme combined with the nonvanishing probability of escape for individuals of species 1 can result in nonmonotonic changes close to the habitat boundary.

Away from the boundary region, spatial homogeneity allows us to compute in the steady state the spatial correlation

$$C_{I}^{i}(r) = \left\langle \frac{1}{N_{C;I}} \sum_{x \in C} n^{i}(x) n^{i}(x+r) \right\rangle - \left(\rho_{C;I}^{i}\right)^{2}$$
(7)

close to the center of a habitat (the same quantity can of course also be computed inside nonhabitat regions). In Eq. (7) the spatial average is over the central region *C* of the habitat,  $N_{C;I}$  is the number of sites in that region, and  $\rho_{C;I}^i$  is the steady-state density of species *i* in that central region.

Figure 4 shows the normalized correlation functions for the different species inside habitats with  $\alpha = 0.45$  and compares them with the behavior in the region where interactions are species independent (dashed magenta line). Inside the habitat the slower decays as a function of separation indicate the formation of larger correlated regions. Although the correlation function for species 3 decays the slowest, the corresponding functions for the other two species display for this value of  $\alpha$  the same behavior at large distances, but differences are observed for small distances. A correlation length can be

PHYSICAL REVIEW E 105, 054401 (2022)

defined as the distance at which C(r)/C(0) crosses a threshold value  $C_0$  (we choose  $C_0 = 0.1$  in the following). The habitat correlation lengths increase with  $\alpha$  and always exceed the length obtained outside of the habitats, see the inset of Fig. 4. The result for the correlation lengths reinforces the findings of Fig. 3: Although the correlation length for species 3 is the largest for every  $\alpha > 0$ , the curves for species 1 and 2 cross around  $\alpha = 0.45$ , close to the value at which the density of species 1 begins to exceed that of species 2, see Fig. 3. No dependence of the correlation lengths on  $\alpha$  is observed outside of the habitats.

Additional insights emerge from monitoring the time dependence of the different concentrations when starting from a fully disordered state, see Figs. 5 and 6. As already mentioned, it is always species 3, the predator of the advantaged species, that ends up dominating the habitat. While at first glance this seems counterintuitive, it is a direct consequence of the earliest time regime where the short-term advantage of species 1 results in suppression of species 2 followed by a surge of species 3, see the insets in Figs. 5(a) and 5(c). The cyclic interaction scheme then yields oscillations which are damped away on approach to the steady state. For not too large values of  $\alpha$ , the damped oscillations have an exponentially decaying envelop, with the typical time constant  $\tau$  decreasing when  $\alpha$  is increased. For example, for  $\alpha = 0.15$  one finds that  $\tau = 25.4$ , whereas for  $\alpha = 0.30$  one has that  $\tau = 14.7$ . This is accompanied by a slight increase of the oscillation period T, from T = 67 for  $\alpha = 0.15$  to T = 71 for  $\alpha = 0.30$ . It is worth noting that the large population oscillations inside the habitats at early times also induce small oscillations of species densities in the outside region.

In the limiting case  $\alpha = \beta$ , shown in Fig. 6, no oscillatory behavior is observed. Instead, the fact that species 1 can evade any attack from species 3 yields an immediate suppression of its prey, species 2, see inset of Fig. 6. As a result, after only a few time steps species 1 fills almost 80% of the sites inside the habitat. This initial quick change inside the habitats is then followed by a regime of slow decay of the species 1 population and, concomitantly, a slow increase of the species 3 population until the steady state is reached. This slow change is a consequence of individuals of species 2 crossing into the habitat from the outside. Due to the predator-prey relationships with the other species, this provokes a flux of individuals from species 3 away from the boundary, whereas individuals from species 1 are migrating toward and across the boundary.

### **IV. SYSTEMS WITH SIX SPECIES**

The emergence of spiral waves and the subsequent stabilization of species coexistence are not restricted to the three-species system described until now but are also encountered in situations with more complicated interactions. As the snapshot in Fig. 1 shows, spirals in the (6,4) system involve all six species that segregate in separate spiral arms. In order to understand whether lessons learned from the three-species system are applicable to more general situations, we discuss in the following the properties of the (6,4) model on the same checkerboard of habitats, where one species has an enhanced chance to escape unharmed an attack, and outside regions



FIG. 5. Spatially averaged time-dependent empty site and species densities in (3,1) games when starting from a fully disordered initial state. The region used for the average is either inside habitats (left column) or outside habitats (right column). The value of  $\alpha$  is 0.15 in (a) and (b), whereas it is 0.45 in (c) and (d). The predation rate is  $\beta = 0.75$  everywhere. The insets in panels (a) and (c) show the first 100 time steps and illustrate the suppression of species 2 and the resulting surge of species 3 at the very early stages of the temporal evolution of the system. The data result from averaging over 50 runs for a lattice of  $1000 \times 1000$  sites and a  $4 \times 4$  checkerboard structure of habitats and nonhabitat regions.

where all interspecies interactions are the same. The emphasis hereby is to identify commonalities with the three-species case discussed above.

Figure 7 shows typical configurations for large values of  $\alpha$  were the effects coming from the presence of habitats are readily apparent. For the largest possible value  $\alpha = \beta = 0.75$  (right panel), at which a member of species 1 survives all attacks from their predators, we end up deep within a habitat with a neutral coexistence of species 1 and species 6, the only predator species of species 1 that is not at the same time a prey of species 1. Individuals from other species are leaking into habitats from the outside, but due to the combined action of the partnering species 1 and 6, their demise is quick and they are not able to enter deep into a habitat. In the regions outside of the habitats a tendency to form traveling wave like patterns can be observed. For the smaller value  $\alpha = 0.6$  (left panel) the habitats are dominated by three species (species 1, 5, and 6),

which strongly suppresses the remaining species. This snapshot already illustrates that more complicated scenarios show up when considering systems with more than three species that form spiral waves.

For the three cases shown in Fig. 8, the limiting case  $\alpha = \beta = 0.75$  is the simplest and the best aligned with the corresponding three-species system shown in Fig. 3(c). Also for the (6,4) system the fact that species 1 always evades its predators inside a habitat provides a major advantage to the only species not preyed on by species 1. As a result, species 6 has the highest steady-state densities, and all other species are suppressed, with the exception close to the habitat boundary. Also in agreement with the three-species case is the observation that small values of  $\alpha$  are in fact detrimental to species 1, resulting in the lowest steady-state species densities inside habitats, see Fig. 8(a). Due to the complex interaction scheme of the (6,4) system and the resulting nonlinear effects,



FIG. 6. Average time-dependent empty site and species densities in the (3,1) game with  $\alpha = \beta = 0.75$ . The initial state is fully disordered. (a) The time evolution of the densities spatially averaged inside the habitats, with the very first few time steps highlighted in the inset, whereas (b) shows the time evolution of the densities spatially averaged outside of the habitats. The data result from averaging over 50 runs for a lattice of 1000 × 1000 sites and a 4 × 4 checkerboard structure of habitats and nonhabitats.

it is difficult to predict the most and the least successful species for intermediate values of  $\alpha$ , see Fig. 8(c). Some simple statements are still possible (for example, there is a value of  $\alpha$  at which species 2 takes over from species 1 the role of least successful species), but a comprehensive picture is difficult to establish. Finally, we note that for intermediate values of  $\alpha$  the impact of the habitat boundaries is felt for the (6,4) system at rather large distances, and this both inside and outside of the habitats [compare Fig. 3(b) and Fig. 8(b)]. This provides another illustration of the more complex behavior observed when increasing the number of species involved in the formation of spirals.

As for the (3,1) system, the early temporal evolution, shown in Fig. 9, is dominated by oscillations of the species

densities, with the first density maximum being for the advantaged species 1, followed by density maxima for species 6, then 5, and so on. The main differences between the cases shown in Fig. 9 is that species 2 is from the get go strongly suppressed for larger values of  $\alpha$ , due to the initial explosive increase of its predator species 1, 6, 5, and 4. As a result, species 2 never recovers to an extent needed to become at any moment in time the dominating species, see Fig. 9(b). As a result for  $\alpha = 0.45$  the density oscillations die out quickly, whereas for the smaller values of  $\alpha$  they can continue for thousands of time steps. Outside of the habitats, oscillations are also established and species end up with different average concentrations. This is similar to what we discussed previously for the three-species case.



FIG. 7. Snapshots of the six-species system with habitat and escape rates  $\alpha = 0.60$  (left) and  $\alpha = 0.75$  (right). The superimposed gridlines show the checkerboard arrangements of the habitat, with the patch in the top left corner being a habitat that provides an advantage to species 1 (in red). The linear size of the systems is L = 1000 and the snapshots have been taken at t = 10000 when starting from a fully disordered initial state.



FIG. 8. The steady-state species and empty site densities along a line connecting the center of a habitat with the center of a adjacent nonhabit region for (6,4) games with different values of  $\alpha$  for species 1: (a)  $\alpha = 0.15$ , (b)  $\alpha = 0.45$ , and (c)  $\alpha = 0.75$ . For  $\alpha = 0.15$  and  $\alpha = 0.45$  the steady state is accessed after fewer than 10 000 time steps, whereas for  $\alpha = 0.75$  one needs to wait for 30 000 time steps before stationarity is reached. The data shown result from averaging over 10 000 independent runs for  $\alpha = 0.15$  and  $\alpha = 0.45$ , whereas 1000 runs have been used for  $\alpha = 0.75$ . The vertical dashed line indicates the boundary of the habitat.

#### V. DISCUSSION

The study of population dynamics models allows insights into the factors that stabilize an ecology and help maintaining biodiversity. In this context it was found that stable space-time patterns in the form of spiral waves favor species coexistence. Examples can be found in systems with cyclic predator-prey interactions between species, as for example in the seminal May-Leonard model. Changes like enhanced mobility or species-dependent predation rates impede the formation of spirals and result in species extinction and loss of biodiversity.

In our investigation we considered structured spatial heterogeneities in the form of habitats that locally provide one of the species with an advantage. In this spatial setting we perform numerical simulations of two systems with cyclic interactions (one with three species and one with six species) that in the case of species-independent rates display spirals and therefore stable species coexistence. As shown in Ref. [57] for small systems, replacing a spatially homogeneous system with structured spatial heterogeneities results in a transition from stable coexistence to unstable coexistence. Taking a different point of view, it was highlighted in Ref. [58] that diffusively coupling a system with biased predation rates (left alone, this system rapidly yields species extinction) to a system with homogeneous rates stabilizes space-time patterns also in the first system.

For our study we used large systems in order to avoid extinction events during our simulations The observed "steady-state" space-time patterns are complex and result in a hierarchy of different species (from the highest to the lowest species density) which is absent in a spatially homogeneous system. For both the three- and six-species case we observe that the species with an advantage inside the habitats is in fact not the most successful one, and it is always one if its predator species that has the highest species density. Especially for the three-species system, the predator of the species



FIG. 9. Spatially averaged time-dependent empty site and species densities in (6,4) games when starting from a fully disordered initial state. The region used for the average is either inside habitats (left column) or outside habitats (right column). The value of  $\alpha$  is 0.15 in (a) and (b), whereas it is 0.45 in (c) and (d). The predation rate is  $\beta = 0.75$  everywhere. The data result from averaging over 50 runs for a lattice of 1000 × 1000 sites and a 4 × 4 checkerboard structure of habitats and nonhabitat regions.

with the advantage is always the most successful, which is a manifestation of the "law of the weakest" observed previously in models with cyclic interactions [59]. On increasing the escape probability, transitions can be observed that alter the hierarchies of the species.

Our simulations allow us to investigate both the longand the short-time behaviors. Starting from an initially disordered state, the short-time behavior is characterized by violent changes to the species densities. For the small systems, it is these violent changes at early times that result in species extinction [57]. Once this early-time regime has passed, the system settles into damped oscillations, followed by the "steady-state" regime with time-independent species densities. Interestingly, the strong and rapid changes inside the habitats also yield corresponding changes (albeit of a less violent nature) in the outside regions.

Our study highlights the effects introduced by boundaries separating regions characterized by different values of interaction rates (see also Ref. [60] for a discussion of boundary effects in a lattice Lotka-Volterra model). These boundaries induce in their vicinity complex and nonmonotoneous changes of the species densities. In some cases this boundary region is extended, and inside the habitats the species densities are position dependent even far from the boundaries. For the cyclic systems investigated here, the coupling of spatial regions with different predation rates yields many nontrivial effects. It will be worth checking whether also for other interaction schemes boundaries separating regions with different sets of rates have a corresponding impact on the short- and long-time properties of the system.

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