

Interfaces with internal structures in generalized rock-paper-scissors models

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In this work we investigate the development of stable dynamical structures along interfaces separating domains belonging to enemy partnerships in the context of cyclic predator-prey models with an even number of species $N \geq 8$. We use both stochastic and field theory simulations in one and two spatial dimensions, as well as analytical arguments, to describe the association at the interfaces of mutually neutral individuals belonging to enemy partnerships and to probe their role in the development of the dynamical structures at the interfaces. We identify an interesting behavior associated with the symmetric or asymmetric evolution of the interface profiles depending on whether $N/2$ is odd or even, respectively. We also show that the macroscopic evolution of the interface network is not very sensitive to the internal structure of the interfaces. Although this work focuses on cyclic predator-prey models with an even number of species, we argue that the results are expected to be quite generic in the context of spatial stochastic May-Leonard models.

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I. INTRODUCTION

The development of diversity in nature results in multi-scale dynamics associated with cooperation, mobility, and competition between a large number of species in many different scenarios (see, e.g., Refs. [1–4]). The development of macroscopic complexity seems to arise very naturally even in the case of very simple cyclic predator-prey models with a low number of species, as in the case of the classic rock-paper-scissors (RPS) game [5–9]. The RPS model describes the evolution of three species in cyclic interaction, and if the population mobility is small enough, the spatial RPS model has been shown to allow for the stable coexistence of the three species with the formation of complex patterns [6–9]. See also Refs. [10–13,13–25] for other investigations of direct interest to the current work.

The basic interactions behind the RPS model are motion, reproduction, and predation, but generalizations incorporating new interactions and further species have also been proposed in the literature [13,14,17–21,26]. We learned from these investigations that the increase in the number of species generally leads to the development of more complex dynamical patterns. In particular, in [19,20] it has been shown that the spatial structure and dynamics of population networks are extremely dependent both on the predator-prey interaction rules (leading in many cases to the development of partnerships between individuals of different species) and on the number of competing species. These studies inspired Roman *et al.* [21] to investigate similar models, focusing on the interplay between competition and partnership in spatial environments occupied by a large number of species. They worked to quantify coarsening behavior and pattern formation, noting the presence of partnerships among distinct species following the maxim that “the enemy of my enemy is my friend.” Another interesting effect may appear in predator-prey models defined in three spatial dimensions: the generation of string networks, as recently investigated in [22].

Here, we study the development of peaceful associations between individuals belonging to enemy partnerships and its effect on the development of dynamical structures along the interfaces separating competing domains. We extend previous work by Szabó *et al.* [13] which also noted the development of dynamical structures at the interfaces. Their model, however, did not include the presence of empty sites, which is an essential ingredient for the development of the associations studied in the present paper. Other investigations on the dynamics of interfaces in a biological framework were developed in [18] and [21] in the case of cyclic predator-prey models with four and six species, respectively.

This paper is organized as follows. In Sec. II we investigate the development of dynamical structures along interfaces separating enemy partnerships in cyclic predator-prey models using two-dimensional stochastic network simulations. In Sec. III the results of the previous section are confirmed using mean field theory simulations. In Sec. IV we investigate in more detail the stability of the dynamical structures at the interfaces, using a combination of one-dimensional mean field theory simulations and analytical arguments. In Sec. V we focus on the macroscopic evolution of interface networks and determine whether or not it can be affected by the presence of dynamical structures along the interfaces. Finally, we conclude in Sec. VI.

II. STOCHASTIC NETWORK SIMULATIONS

We start by considering a family of spatial stochastic May-Leonard models. In this family, individuals of N species and some empty sites (E) are initially distributed on a square lattice with \mathcal{N} sites. The different species are labeled by $i, j = 1, \dots, N$, with the cyclic identification $i = i + kN$, where k is an integer. The number of individuals of species i (I_i) and the number of empty sites (I_E) obey the relation $I_E + \sum_{i=1}^N I_i = \mathcal{N}$. The possible interactions are classified as motion, reproduction, and predation, represented by

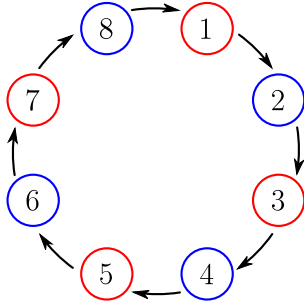


FIG. 1. (Color online) Illustration of the cyclic predator-prey rule in the case with eight species.

$i \ominus \rightarrow \ominus i$, $i \otimes \rightarrow ii$, and $i(i+1) \rightarrow i \otimes$, respectively, where \otimes represents an empty site and \ominus represents an arbitrary individual (of any of the N species) or an empty site. For simplicity, we shall assume that motion (m), predation (p), and reproduction (r) interaction probabilities are the same for all species. A random individual (active) is selected to interact with one of its four nearest neighbors (passive) at each time step. The unit of time $\Delta t = 1$ is defined as the time necessary for \mathcal{N} interactions to occur (one generation time).

Let us start by focusing on models with an even number of species N , following a cyclic predator-prey rule. Unlike the odd N case, which gives rise to spiral patterns, even N models produce interface networks without junctions, separating domains with two different partnerships (see, for example, [19,20], and references therein). In these models each individual chases and is hunted by only one different species. The predator-prey interactions are illustrated in Fig. 1 in the case of a model with eight species.

In this paper we present the results of a large number of network simulations assuming periodic boundary conditions. At the initial time, the number density, $n_i = I_i/\mathcal{N}$, is assumed to be the same for all species, while the number density of empty sites is set to zero, that is, $n_E = I_E/\mathcal{N} = 0$. All the stochastic simulations presented in this work have been obtained with $m = 0.50$, $r = 0.25$, and $p = 0.5$, and the snapshots were taken after 5000 generations. However, we verified that the same qualitative results also hold for other choices of the parameters m , r , and p .

Soon after the simulations start, individuals separate into two partnerships. The maxim “the enemy of my enemy is my friend” plays a role as species of a given partnership peacefully share common regions of space, with the battles with the enemy partnership taking place at the domain boundaries. The competition between individuals of different partnerships creates empty sites along the interfaces separating the various domains.

Let us first consider the $N = 4$ model, where mutually neutral species aggregate in two partnerships, $\{1,3\}$ and $\{2,4\}$, as shown in the top left panel of Fig. 2. Note that the distribution of individuals of the two species that aggregate in each partnership is statistically homogeneous inside the respective domain. Although a nonzero mobility gives rise to intrusions of individuals into enemy domains, the invasion is rapidly put to an end by individuals of the competing domains. For example, individuals of species 1 can predate individuals of species 2, reproduce, and then cross the interface into the enemy domain.

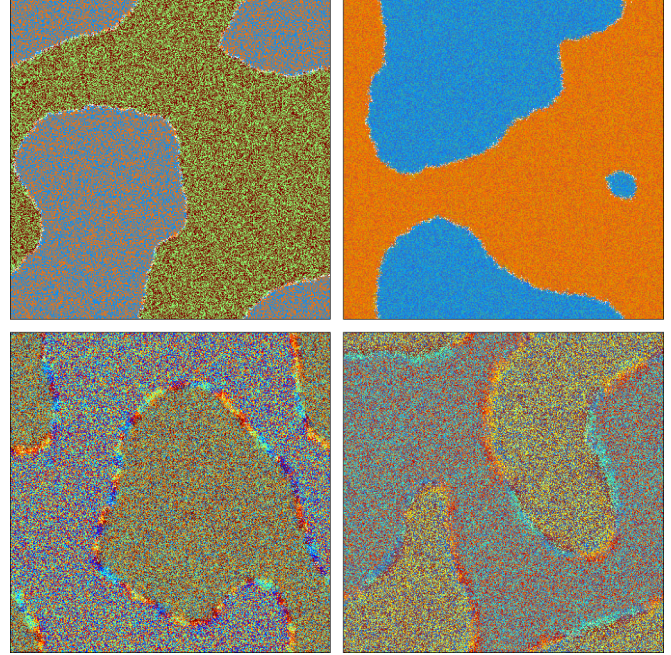


FIG. 2. (Color online) The 512^2 stochastic network simulations of models with $N = 4$ (top left), $N = 6$ (top right), $N = 8$ (bottom left), and $N = 10$ (bottom right). The snapshots were taken after 5000 generations.

They may keep going until they find individuals of species 4, that are ready to defend the territory by killing the invaders. The width of the interface depends on the mobility probability of the species; that is, the higher the mobility is, the farther the individuals can invade the enemy territory before being caught, and consequently, the thicker the interface will be.

We now focus on the $N = 6$ model. There are two partnerships, $\{1,3,5\}$ and $\{2,4,6\}$, each occupying separate spatial regions on the lattice. However, species i does not interact with species $i+3$, which belongs to the competing partnership. This implies that whenever individuals of species i , present at the battlefront, find individuals of species $i+3$, they can peacefully share common spatial regions even though they are in a conflict zone and belong to competing partnerships. However, the top right panel in Fig. 2 shows that this is not a stable situation. The frequent attacks of predators from both sides of the interfaces do not allow for long lasting peaceful interactions at the interfaces. Hence, in this case the peaceful associations between species of competing partnerships do not give rise to stable dynamical structures at the interfaces. The top right panel of Fig. 2 shows a snapshot of a simulation of the $N = 6$ model. As in the $N = 4$ model, the distribution of the species belonging to a given partnership is statistically homogeneous inside the domains, while the individuals fighting at the boundaries give rise to a statistically homogeneous distribution of empty sites along the interfaces.

In the $N = 8$ model the partnerships $\{1,3,5,7\}$ and $\{2,4,6,8\}$ are formed. In this case there is a larger number of possible peaceful interactions at the interfaces, which leads to the development of stable dynamical structures along the interfaces, as shown in the snapshot in the bottom left panel of Fig. 2. The mixing of colors is always changing (in space and

time) as a result of the constant development and destruction at the interfaces of the structures made of mutually neutral individuals belonging to competing partnerships.

In general, an individual of an arbitrary species i can peacefully coexist at the interfaces with species $i \pm k$ belonging to the enemy partnership, where k is an odd integer such that $3 \leq k \leq N - 5$. In other words, the number of species belonging to the enemy partnership with which species i can peacefully coexist is $(N - 4)/2$. Therefore the larger N is, the more complex the behavior of the dynamical structures formed at the interfaces will be.

This can be seen in the snapshot obtained for $N = 10$ in the bottom left panel of Fig. 2. The larger number of peaceful associations between individuals of species belonging to enemy partnerships ($\{1,3,5,7,9\}$ and $\{2,4,6,8,10\}$) compared to the $N = 8$ case results in more complex interface profiles, which we will investigate in more detail in the forthcoming sections.

III. MEAN FIELD THEORY SIMULATIONS

Let us now investigate cyclic predator-prey models using mean field theory simulations. Consider $N + 1$ scalar fields $(\phi_0, \phi_1, \phi_2, \dots, \phi_N)$ representing the fraction of space around a given point occupied by empty sites (ϕ_0) and by individuals of the species i (ϕ_i), satisfying the constraint $\phi_0 + \phi_1 + \dots + \phi_N = 1$. The mean field equations of motion,

$$\dot{\phi}_0 = D\nabla^2 \phi_0 - r\phi_0 \sum_{i=1}^N \phi_i + p \sum_{i=1}^N \phi_i \phi_{i+1}, \quad (1)$$

$$\dot{\phi}_i = D\nabla^2 \phi_i + r\phi_0 \phi_i - p\phi_i \phi_{i-1}, \quad (2)$$

describe the average dynamics of the models studied in the previous section. In the above equations, a dot stands for the time derivative, ∇^2 is the Laplacian, and D is the diffusion rate.

We performed a set of two-dimensional mean field theory simulations starting with initial conditions satisfying $\phi_i = 1$ if $i = j$ and $\phi_i = 0$ if $i \neq j$, where a species j was randomly selected with uniform probability at every grid point (ϕ_0 was initially set to zero at every grid point). Snapshots of two-dimensional 512^2 numerical mean field simulations (using $D = 0.5$, $r = 0.25$, and $p = 0.5$) taken after 5000 generations for $N = 4, 6, 8$, and 10 are shown in Fig. 3. The results provided by the mean field simulations are consistent with those obtained from the stochastic network simulations discussed in the previous section. While for $N = 4$ and $N = 6$ (top left and right panels, respectively) no stable dynamical structures develop along the interfaces, it is clear that they do form in the $N = 8$ and $N = 10$ cases (bottom left and right panels, respectively). As expected, the field theory simulations also show that for $N = 10$ the internal structures are more complex than in the $N = 8$ case.

IV. STABILITY OF THE DYNAMICAL STRUCTURES AT THE INTERFACES

In order to better resolve the evolution of the dynamical structures at the interfaces, we perform one-dimensional mean

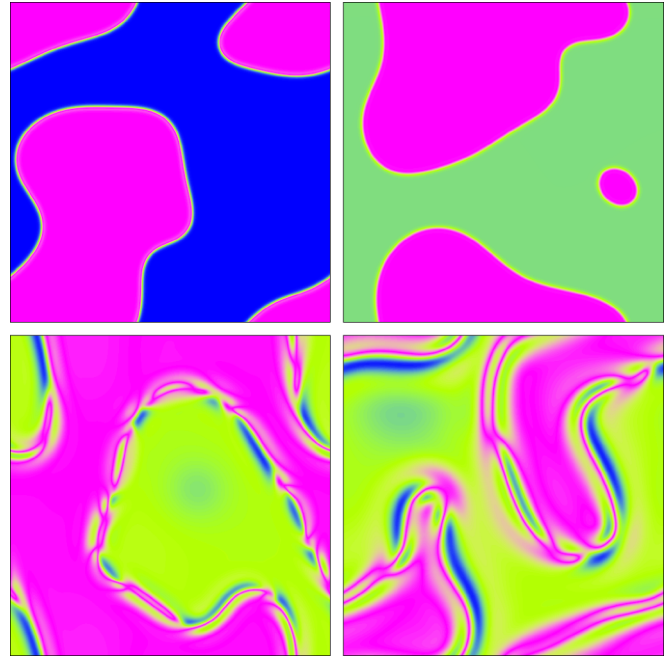


FIG. 3. (Color online) The 512^2 mean field theory simulations of models with $N = 4$ (top left), $N = 6$ (top right), $N = 8$ (bottom left), and $N = 10$ (bottom right). The snapshots were taken after 5000 generations.

field theory simulations for the models described above. Here, we set initial conditions, where the left (right) domains of the grid are homogeneously populated with $\phi_i = 2/N$, for odd (even) i [with $\phi_i = 0$ for even (odd) i and $\phi_0 = 0$], respectively. At the interface, the site located at the position $\mathcal{N}/2$ was initially populated with $\phi_1 = 1$ (and $\phi_0 = \phi_i = 0$ for all $i \neq 1$), while the site located at the position $\mathcal{N}/2 + 1$ was populated with $\phi_2 = 1$ (and $\phi_0 = \phi_i = 0$ for all $i \neq 2$). We verified that our main results are not strongly dependent on the particular choice of initial conditions at the interface. In these simulations we consider $r = 0.25$ and $p = 0.5$, as before. Given that the thickness of the interfaces is proportional to $D^{1/2}$, here we choose a larger value of D ($D = 250$) in order to better resolve the dynamics of the interfaces.

We start investigating the model with $N = 4$, even though it does not support stable dynamical structures at the interfaces. Figure 4 shows the time evolution of ϕ_0 (solid black line) and ϕ_i (colored lines) at the interface for the model with four species. We observe no prominent dynamical structures in this case, with the values of ϕ_i and ϕ_0 rapidly approaching their constant asymptotic values.

A slightly different behavior can be observed for $N = 6$, as we show in Fig. 5. For $N = 6$ there are three couples of mutually neutral individuals belonging to enemy partnerships ($\{1,4\}, \{2,5\}, \{3,6\}$). This is responsible for the transient dynamical structures appearing in Fig. 5, which nevertheless are rapidly damped. Similar to the $N = 4$ case, at late times the values of ϕ_i and ϕ_0 approach their constant asymptotic values, and no prominent dynamical structures survive at the interface.

On the other hand, Fig. 6 shows that for $N = 8$ stable dynamical structures develop at the interface. It is possible to observe in Fig. 6 the periodic process of creation and

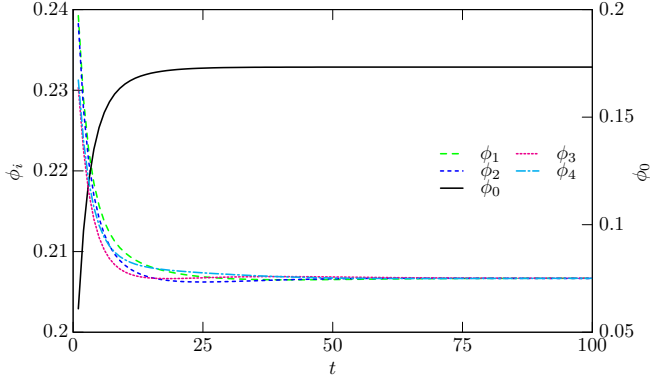


FIG. 4. (Color online) Time evolution of ϕ_0 (solid black line) and ϕ_i (colored lines) at the interface for the model with four species. No prominent dynamical structures are formed at the interfaces in this case.

annihilation of couples of mutually neutral individuals belonging to enemy partnerships. The values of ϕ_i change in time, evolving to become periodic, with constant amplitude, leading to stable dynamical structures at the interface. In this model there are eight possible couples of mutually neutral individuals belonging to enemy partnerships ($i, i \pm 3$). These pairs are continuously created and destroyed, resulting in a specific sequence of minimums and maximums ($\{ \dots, 1, 4, 7, 2, 5, 8, 3, 6, 1, \dots \}$) in Fig. 6. Note that, in general, there is always one dominant species belonging to one of the partnerships which is associated with an asymmetric evolution of the interface profile.

Finally, Fig. 7 shows the time evolution of ϕ_0 and ϕ_i for the model with ten species. In this model there are 15 possible pairs of mutually neutral species belonging to enemy partnerships, ($i, i \pm 3$) and ($i, i \pm 5$) (each species can form a couple with three different species from the enemy partnership). This is responsible for the double sequence of minimums and maximums ($\{ \dots; (1,6); (8,3); (5,10); (2,7); (4,9); \dots \}$) observed in Fig. 7. In this case there is never a dominant partnership, which is responsible for a symmetric evolution of the interface profile. This happens whenever $N/2$ is odd since in the case

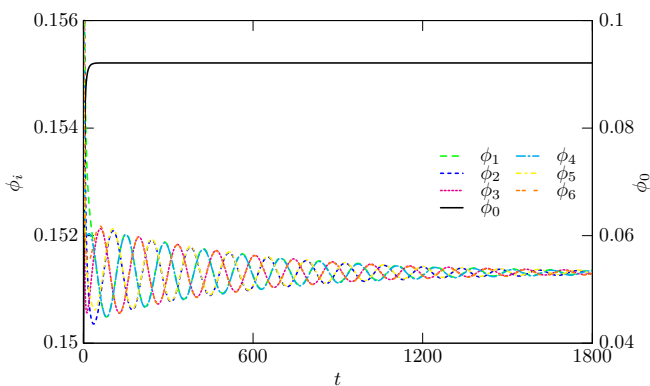


FIG. 5. (Color online) Time evolution of ϕ_0 (solid black line) and ϕ_i (colored lines) at the interface for the model with six species. Transient dynamical structures are formed at the interfaces, but they are rapidly damped.

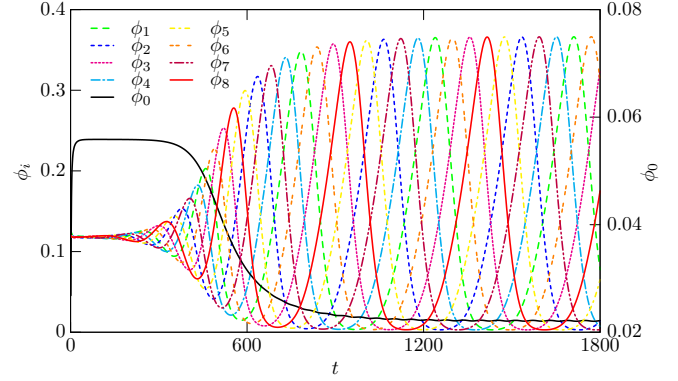


FIG. 6. (Color online) Time evolution of ϕ_0 (solid black line) and ϕ_i (colored lines) at the interface for the model with eight species. The oscillation amplitudes of ϕ_i increase until they reach a constant value, indicating the stability of the dynamical structures at the interface.

for $N \neq 2$, species i and $i + N/2$ are mutually neutral and belong to enemy partnerships. For both $N = 8$ and $N = 10$ the values of ϕ_i oscillate periodically, ensuring stability of the dynamical structures formed at the interface. Note also that the oscillatory behavior of ϕ_0 is much more pronounced for $N = 10$ than for $N = 8$.

Figure 8 shows the evolution of the interface profiles $\phi_0(x)$ for different values of the time t . They show a symmetric or asymmetric evolution, depending on whether $N/2$ is odd [second ($N = 10$) and fourth ($N = 14$) panels] or even [first ($N = 8$) and third ($N = 12$) panels], respectively, thus confirming the behavior discussed above. The movies in Refs. [27,28] illustrate the dynamical behavior of the different species at the interface for $N = 8$ [asymmetric evolution of $\phi_0(x)$] and $N = 10$ [symmetric evolution of $\phi_0(x)$].

V. MACROSCOPIC BEHAVIOR OF INTERFACE NETWORKS

Let us now focus on the macroscopic evolution of the interface networks in order to determine whether or not the

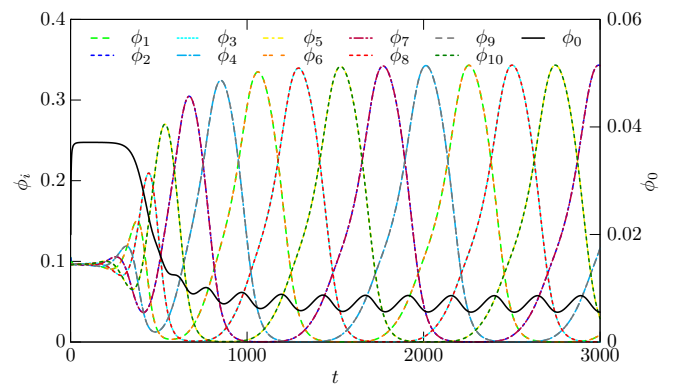


FIG. 7. (Color online) Time evolution of ϕ_0 (solid black line) and ϕ_i (colored lines) for the model with ten species. Similar to the $N = 8$ case, the results indicate the stability of the dynamical structures at the interface. However, the oscillatory behavior of ϕ_0 is much more pronounced for $N = 10$ than for $N = 8$.

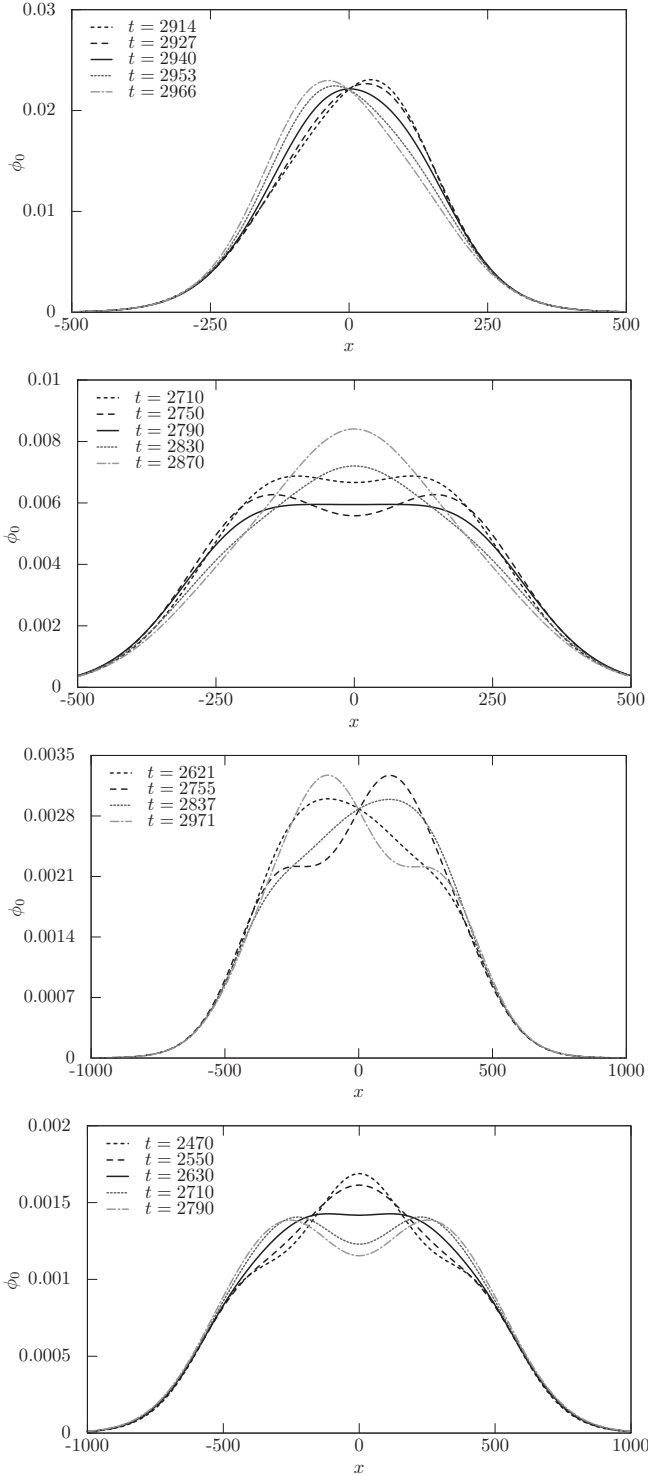


FIG. 8. Interface profiles $\phi_0(x)$ for different values of the time t , showing a symmetric or asymmetric evolution, depending on whether $N/2$ is odd [second ($N = 10$) and fourth ($N = 14$) panels] or even [first ($N = 8$) and third ($N = 12$) panels], respectively.

presence of stable dynamical structures along the interfaces might leave an imprint on the macroscopic dynamics of the network. The characteristic length of the network can be defined as $L \equiv A/L_T$, where A is the (constant) area of the simulation box (proportional to the total number of sites of

the grid \mathcal{N}) and L_T is the total length of the interfaces. Taking into account that the average width and profile of the interfaces remains fixed throughout the simulations, the number of empty sites per unit length is approximately constant, and consequently, L_T is roughly proportional to the total number of empty sites I_E . This implies that the length scale L is inversely proportional to the number of empty sites, that is,

$$L \propto 1/I_E, \quad (3)$$

which follows from [19,20].

The average evolution of $L \propto I_E^{-1}$ with time t was calculated by carrying out sets of 25 distinct two-dimensional stochastic network and mean field theory simulations with distinct random initial conditions. We found that the scaling law $L \propto t^\lambda$ describes well the late time evolution of the interface networks investigated in the present paper.

The top panel of Fig. 9 shows the results for the evolution of the characteristic scale L with time t obtained with stochastic network simulations for different values of N . We found that $\lambda = 0.49 \pm 0.03$, $\lambda = 0.46 \pm 0.04$, $\lambda = 0.46 \pm 0.03$, and $\lambda = 0.51 \pm 0.04$ for $N = 4, 6, 8$, and 10 , respectively. In Fig. 9, the bottom panel shows analogous results, using mean field theory simulations. The results of the stochastic and mean field network simulations agree well, indicating that the evolution of the characteristic scale L of the network is not significantly

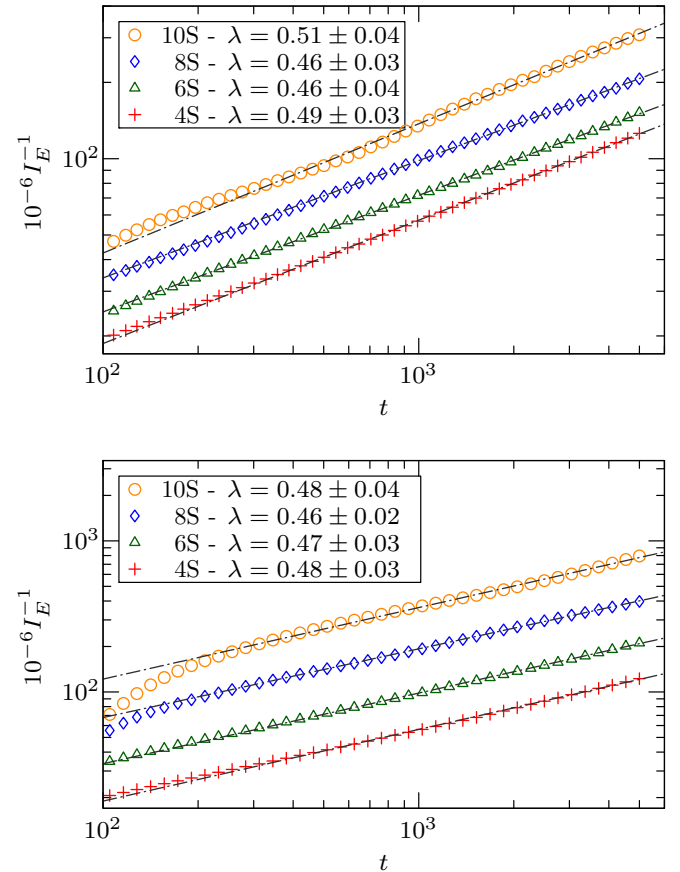


FIG. 9. (Color online) Late time behavior of the length scale L , computed from ensembles of twenty 1024^2 (top) stochastic network and (bottom) mean field theory simulations, for models with $N = 4, 6, 8$, and 10 species.

affected by the presence of dynamical structures along the interfaces. In all the cases we find a result consistent with the scaling coefficient expected in the case of curvature driven dynamics ($\lambda = 1/2$).

VI. ENDING COMMENTS

In this work we described the development of dynamical structures along the interfaces separating domains belonging to enemy partnerships. This was done in the context of cyclic predator-prey models with an even number of species, which naturally leads to the partition of the N species into two distinct partnerships. We have shown that as the number of species N increases, the number of peaceful associations at the interfaces of mutually neutral individuals also increases, inducing the generation of stable dynamical structures at the interfaces whose complexity also increases with N . This behavior was confirmed using both stochastic and field theory simulations in one and two spatial dimensions. We have also shown that the evolution of the interface profiles can be symmetric or asymmetric depending on whether $N/2$ is odd or even, respectively. We have illustrated this behavior in several figures throughout the paper as well as in the movies in Refs. [27,28]. Finally, we have shown that the internal structure details at the interfaces do not appear to produce any significant changes with respect to the standard macroscopic dynamical evolution of curvature driven interface networks, with the scaling exponent λ being consistent with the standard value $\lambda = 1/2$ in all cases studied in this paper.

The dynamics of boundary layers is also discussed in detail in [13]. However, their numerical results are significantly different from ours since in their model no empty site is created when prey is hunted. The authors stressed the formation of constellations of species in the boundary layers between the alliances. However, these patterns arise for a narrow range of

mobility rate, and the species organize themselves such that predators and prey compose adjacent domains. In contrast, in our model the structures are generated at the interfaces for any choice of the diffusion parameter, and they are formed by pairs of mutually neutral species.

Although the present work focused on cyclic predator-prey models with an even number of species, many of the results are expected to be quite generic in the context of spatial stochastic May-Leonard models. Once we consider more general classes of models, the presence of structures at the interfaces is no longer restricted to models with even N . In fact, if one considers a model with N species where the predation [$i (i + \alpha) \rightarrow i \otimes$] probabilities p are nonzero for $\alpha = 1, \dots, n - 1$ (and zero for other values of α), the species separate themselves in n alliances of N/n species. In this case the domains are separated by interfaces with stable dynamical structures if $N/n \geq 4$. For example, for $N = 12$ if the species are separated in two or three alliances, stable dynamical structures may develop at the interfaces. Although many of these models lead to more complex network patterns with Y-type and higher order junctions [19,20], the dynamics of the structures at the interfaces is essentially analogous to that studied in the present paper in the context of simpler models. The generalization of the analysis to models whose food webs are more complex and involve less mutually neutral pairs as in [18–20,23–26] is left for future work.

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