Domain expansion and transient scaling regimes in population networks with in-domain cyclic selection

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We investigate a six-species class of May-Leonard models which leads to the formation of networks with two different types of domains (three species each). In these models every species in each domain is in direct competition with all the species in the other domain (bidirectional selection, with a fixed probability \( p \)). On the other hand, the species within each domain compete cyclically (unidirectional selection, with a fixed probability \( p_{PRS} \)), leading to the formation of spiral waves inside the domains. We study the evolution of such networks using stochastic numerical simulations. We show that single species domains may form during the final stages of the collapse of three-species domains and we determine the critical initial radius beyond which single-species spherically symmetric domains are expected to expand as a result of their larger density of individuals compared to that of the outer three-species domain. We further show that a transient scaling regime, with a slower average growth rate of the characteristic length scale \( L \) with time \( t \), takes place before the transition to a standard \( L \propto t^{1/2} \) scaling law (usually associated with curvature driven dynamics), resulting in an extended period of coexistence.

I. INTRODUCTION

There is ample evidence that non-hierarchical interactions between individuals of different species play a crucial role in the development and preservation of biodiversity. Selection, reproduction, and mobility interactions are ubiquitous in nature and constitute a crucial ingredient of most of competition models, many of them inspired in the pioneering work by Lotka and Volterra, and May and Leonard [1–3]. The simplest competition models usually consider three species which cyclically dominate each other, the so-called rock-paper-scissors model [4, 5] (see [6–10] for models with additional interactions). Despite its simplicity, the rock-paper-scissors model [see 11, 12 for recent reviews] has been successful in reproducing crucial dynamical features of some biological systems composed of three species with cyclic selection interactions [4, 13, 14].

In [15, 16], a broad family of spatial stochastic May-Leonard models with an arbitrary number of species has been introduced, thus generalizing the standard rock-paper-scissors model (see also [17, 21]). Some of these models were shown to give rise to complex spatial structures, which may include spiral waves with an arbitrary number of arms [16], domain interfaces (which may themselves develop a non-trivial internal dynamics [22, 24]) and string networks with or without junctions [25, 26]. On the other hand, the scaling laws governing the dynamics of such systems may also be very diverse (see, for example, [16, 23]).

In this paper we consider a particular 6-species subclass of the more general family of May-Leonard models with an arbitrary number of species introduced in [15, 16]. These models naturally lead to the formation of networks with two different types of domains containing individuals from two different partnerships with three species each (see [27, 29] for a discussion of the role of partnerships in the coexistence of biological systems). In this sub-class of models, every species in one domain is able to select any of the species in the other domain (bidirectional selection, with a fixed probability \( p \)). On the other hand, the species within each domain compete cyclically (unidirectional selection, with a fixed probability \( p_{PRS} \)), leading to the formation of spiral waves inside the domain. We shall investigate in detail a particular property of these models associated with the formation of single-species domains during the final stages of the collapse of three-species domains and their subsequent growth if their initial size is above a certain critical radius. The potential impact on the scaling law describing the time evolution of the characteristic length scale of the network will also be investigated.

The outline of this paper is as follows. In Sec. [11] we introduce the class of models investigated in the present paper. The results of a spatial stochastic numerical simulation of the corresponding population dynamics are pre-
Figure 1: Selection rules in our model: bidirectional selection (solid arrows) and cyclic selection (dashed arrows). The selection interaction probability of species \( i \) with species \( i \pm 1 \), and \( i \pm 3 \) is equal to \( p \) (solid arrows). The selection interaction probability of species \( i \) with species \( i + 2 \) is equal to \( p_{PRS} \) (dashed arrows). The cyclic identification \( i = i + 6k \), with \( k \) being an integer, is assumed.

II. MODELS

In this paper we investigate a six species sub-class of the more general family of May-Leonard models with an arbitrary number of species introduced in \[15\] \[16\]. In these models individuals of various species are distributed on a square lattice with \( N \) sites with periodic boundary conditions (see \[30\] \[31\] \[32\] for off-lattice simulations of competition models). Each site may be either empty or occupied by a single individual. The different species are labelled by the number \( i \) (or \( j \)), with \( i, j = 1, \ldots, 6 \), and empty sites shall be denoted by \( \circ \). The number of individuals of the species \( i \) will be denoted by \( I_i \) and the number of empty sites by \( I_\circ \). The possible interactions are: selection

\[
i \ j \rightarrow i \ \circ,
\]

mobility

\[
i \ \circ \rightarrow \ \circ \ \circ,
\]

and reproduction

\[
i \ \circ \rightarrow ii,
\]

where \( \circ \) represents either an individual of any species or an empty space. While the mobility and reproduction interactions occur with probabilities \( m \) and \( r \), respectively (the same for all species), the selection probability may be either \( p \) or \( p_{PRS} \) according to the scheme presented in Fig. 1 (solid black and dashed orange arrows represent the selection interaction probabilities \( p \) and \( p_{PRS} \), respectively): the selection interaction probability of species \( i \) with species \( i \pm 1 \), and \( i \pm 3 \) is equal to \( p \) (solid arrows); the selection interaction probability of species \( i \) with species \( i + 2 \) is equal to \( p_{PRS} \) (dashed arrows). The cyclic identification \( i = i + 6k \), with \( k \) being an integer, is assumed. Except for the labelling of the different species, Fig. 1 is invariant under rotation by an angle of \( 2\pi/6 \) (or equivalently, under the transformation \( i \rightarrow i + k \)), thus leading to a \( \mathbb{Z}_6 \) symmetry.

In our model, at each simulation step, the algorithm randomly selects an occupied site to be the active one, randomly chooses one of its four neighbour sites to be the passive one, and randomly picks an interaction to be executed by the individual at the active position. If the interaction cannot be performed (for example, if the passive is an empty site and a selection interaction is picked), the three steps are repeated until a possible interaction is selected. \( N \) successive interactions are completed in one generation time (our time unit).

III. POPULATION DYNAMICS

In this section we shall consider the results of a spatial stochastic numerical simulation with random initial conditions, where at each site an individual of any of the 6 species or an empty site was selected with a uniform discrete probability of 1/7 at the beginning of the simulation. Figure 2 presents results obtained from a single realization of a 2000\(^2 \) lattice numerical simulation of our model assuming \( p = 0.25 \), \( p_{PRS} = p \), \( m = 0.5 \), \( r = 0.25 \). The upper and lower panels show snapshots of the spatial patterns at various instants of time: \( t_0 = 0 \), \( t_1 = 16000 \), \( t_2 = 37555 \), \( t_3 = 55420 \), \( t_4 = 89870 \), \( t_5 = 97360 \), \( t_6 = 103784 \), \( t_7 = 197600 \), \( t_8 = 211161 \), and \( t_9 = 215000 \).

The central panel shows the fractional number density of the different species

\[ \rho_i = I_i/N, \]

for the entire timespan of the simulation: \( \Delta t = 250000 \). The arrows highlight the instants of time corresponding to the snapshots shown in the lower and upper panels, and the colors follow the scheme depicted in Fig. 1. The video in \[33\] shows the evolution of the spatial patterns for the entire timespan of the simulation.

The snapshot at \( t = t_0 = 0 \) depicts the random initial conditions. After an initial stage, essentially two types of spatial domains appear. This occurs because mutual selection takes place between the groups of species

\{1, 3, 5\}, \quad \{2, 4, 6\}. 
As a result, two partnerships are formed, as shown in the snapshot taken at $t_1$. However, partners do not live peacefully within the domains. On the contrary, they interact with a cyclic selection rule (dashed lines of Fig. 1), creating an in-domain rock-paper-scissors dynamics. Although spiral waves travel across the domains, they do not cross the boundaries due to the mutual selection between the members of distinct partnerships. The dynamics of the interfaces between three-species domains is curvature dominated, as described in detail in [15], with their velocity being roughly proportional to their curvature.

However, Fig. 2 shows that the extinction of one of the species in the final stages of the collapse of three-species domains can lead to the formation of single-species domains, which may then be able to expand. For example, the snapshots taken at $t = t_1$ and $t = t_2$ depict small single-species domains of individuals of species 6 and 2, respectively (note that no single-species domain is present in the snapshot taken at $t = t_3$).

Outside a single-species domain, individuals have to deal with a cyclic selection among partners besides competing with the enemy partnership. As a consequence, individuals from the single-species domain may have the chance of invading the enemy partnership, leading to the expansion of the single-species domains as shown in the snapshots taken at $t = t_4$ and $t = t_5$ (we shall quantify, in the following section, the condition for a spherically symmetric single-species domain to be able to expand). As a single-species domain grows larger, it may reach regions occupied by individuals of their original partnership. When this happens it is immediately invaded by a spiral wave front, as depicted in the snapshot taken at $t = t_6$. The encroaching then causes the disappearance of the single-species domain and, consequently, the decrease of the corresponding fractional density.

In summary, the three main factors affecting the dynamics of the network are: I. the curvature dominated dynamics of interfaces separating domains with three-species enemy partnerships; II. the spiral wave fronts inside the domains and the interference between them, which play a crucial role in the creation of small one-
species domains; III. the growth of one-species domains, if their initial size is large enough for the effect of the difference between the density of individuals in the inner one-species and the outer three-species domains to dominate the effect of the curvature.

For large $t$, the characteristic size of the domains increases and, as a consequence, the rate of formation of single-species domains decreases. However, once they emerge, they have room to expand further on the grid. As shown in the snapshots taken at $t = t_5$, $t = t_6$ and $t = t_8$, these single-species domains can then grow to become with a characteristic size comparable to the one of the three-species domains. The vast territorial invasion of single-species areas for large $t$ leads to an increasingly abrupt variation of the fractional density which is shown in the central panel of Fig. 2.

On the other hand, for small $t$ the average size of the domains is tiny and single-species domains are present throughout the whole lattice. Figure 3 shows the initial stage of the single simulation shown in Fig. 2. As in Fig. 2 the solid lines represent the evolution of the fractional number density of individuals of the different species as a function of time. The snapshots, taken after 1000, 2000, 3000, and 4000 generations, show a fast decrease of the number of single-species domains.

### IV. EXPANSION OF SINGLE-SPECIES DOMAINS

If $p_{PRS} = 0$ then the average number density is the same in all domains and the dynamics is curvature driven [15]. In this case, a circular interface of thickness

$$\delta = R_{out} - R_{in}, \quad (2)$$

has always a tendency to collapse because the average number of selection interactions with the enemy partnership performed, per unit of time, by individuals of the outer domain — proportional to the external radius $R_{out}$ — is larger than those performed by individuals of the inner one — proportional to the internal radius $R_{in}$ (the interface thickness $\delta$ is a function of the parameters $p$, $m$ and $r$). However, if $p_{PRS} > 0$ this is not necessarily the case. One-species domains have a larger number density of individuals than three-species domains because the number density of individuals inside three-species domains is reduced due to in-domain cyclic selection. Here, we shall demonstrate that this effect may more than compensate the impact of the domain curvature, provided that certain conditions are satisfied.

Consider a circular one-species domain surrounded by a three-species one. Let us denote the fractional number density of empty sites away from the borders in three-species domains by

$$\rho_\odot^* = I_\odot^* / N. \quad (3)$$

Note that in one-species domains the corresponding number density of empty sites is equal to zero. If $p_{PRS} > 0$ then $\rho_\odot^* > 0$ (the in-team selection in the outer three-species domain reduces the number of individuals available to compete with individuals of the enemy partnership). In this case, the average number of selection interactions with the enemy partnership performed, per unit of time, by individuals of the inner one-species domain is still proportional to $R_{in}$, but those performed by individuals of the inner one-species domains becomes proportional to $R_{out}(1 - \rho_\odot^*)$. One may then define the critical radius as the value of

$$R = (R_{out} + R_{in}) / 2, \quad (4)$$

for which the average rate of selection interactions with the enemy partnership performed by individuals of the inner one-species and the outer three-species domains are equal, that is

$$R_{in} = R_{out}(1 - \rho_\odot^*). \quad (5)$$

The critical radius is then equal to

$$R_c = \frac{\delta}{2} \left( \frac{2}{\rho_\odot^*} - 1 \right). \quad (6)$$
Figure 4: The probability $P$ that the whole lattice becomes dominated by the species 2 (initially confined to a circular domain of radius $R$) as a function of $R$, assuming that $p = 0.25$, $p_{PRS} = 0.25$, $m = 0.5$, $r = 0.25$. The results for each $R$ are taken from an average over 1000 simulations, considering different initial conditions for the outer domain containing species 1, 3, 5. The critical radius, defined by $P(R_c) = 1/2$ is approximately equal to $R_c = 45$ (grid points). The left and right inset panels show two snapshots of runs with initial radius $R = 30$ and $R = 60$, respectively. The times required for the circle to collapse (left inset panels) or to invade all the territory (right inset panels) are displayed between snapshots.

If $\rho_0^c \ll 1$ then $R_c \propto (\rho_0^c)^{^{-1}}$. If $R > R_c [R_{in} > R_{out}(1-\rho_0^c)]$ the effect of the larger number density of individuals in the inner one-species domain is (on average) the dominant dynamical effect and the circular domain is expected to expand while if $R < R_c [R_{in} < R_{out}(1-\rho_0^c)]$ the dynamics is (on average) curvature dominated and the domain is expected to collapse.

Figure 4 considers the collapse (left inset panels) or expansion (right inset panels) of a single-species domain. It displays the probability $P$ that the whole lattice becomes dominated by the species 2 (initially confined to a circular domain of radius $R$) as a function of $R$, assuming that $p = 0.25$, $p_{PRS} = 0.25$, $m = 0.5$, $r = 0.25$. The results for each $R$ are taken from an average over 1000 simulations, considering different initial conditions for the outer domain containing species 1, 3, 5. The critical radius, defined by $P(R_c) = 1/2$ is approximately equal to $R_c = 45$ (grid points). The left and right inset panels show two snapshots of runs with initial radius $R = 30$ and $R = 60$, respectively. The times required for the circle to collapse (left inset panels) or to invade all the territory (right inset panels) are displayed between snapshots.

Figure 5 shows the value of the critical radius as a function of the fractional number density $\rho_0^c$ of empty sites in the outer domain (left panel) and of $p_{PRS}$ (right panel), assuming that $p = 0.25$, $m = 0.5$, and $r = 0.25$. The best fits represent the power laws $R_c \propto (\rho_0^c)^{\beta_1}$ and $R_c \propto p_{PRS}^{\beta_2}$, with exponents $\beta_1 = -1.16$ and $\beta_2 = -0.98$, respectively.

For $\rho_0^c \ll 1$ gives $R_c \propto (\rho_0^c)^{-1}$ for $\rho_0^c \ll 1$. On the other hand, given that the average number density of empty sites in the outer domain is expected to be roughly proportional to $p_{PRS}$, $\beta_2$ is also expected to be close to $-1$, which is in agreement with our numerical results.

V. SCALING LAWS

Empty sites appear in the simulations both due to the mutual selection interactions between the enemy partnerships {1, 3, 5} and {2, 4, 6}, and as a consequence of in-domain cyclic selection interactions taking place mainly between spiral arms. The density of empty sites associated to the interaction between enemy partnerships is given by

$$\rho_0 = I_0 / N,$$

where $I_0$ is the total number of empty sites generated at the borders of the spatial domains. The characteristic length $L$ of the network may be defined as the ratio between area of the square lattice box and the total interface length $\ell$ ($L = \ell^{-1}$ if both $L$ and $\ell$ are expressed in units of the length of the square box). Given that the interface thickness is essentially fixed in the entire grid, the total interface length $\ell$ is proportional to the total number of empty sites at the borders of the spatial domains $I_0$. Hence $L \propto (I_0)^{-1} \propto (\rho_0^c)^{-1}$. To distinguish the empty sites associated to selection interactions between
the empty partnerships \{1, 3, 5\} and \{2, 4, 6\} from the empty sites associated to in-domain rock-paper-scissors cyclic selection interactions, the four grid sites surrounding each empty site are checked: if individuals of different partnerships are observed, the empty space is assumed to be associated to the corresponding interface separating enemy partnerships. Otherwise, the empty site is assumed to be due to in-team selection interactions.

Figure 6 shows the evolution of the fractional number density \(\tilde{\rho}_e\) of empty sites between the enemy partnership domains as a function of the simulation time (or, equivalently, the number of generations) for a model with \(p = 0.25, m = 0.5, r = 0.25\), and either \(p_{PRS} = 0\) (top panel), \(p_{PRS} = 0.25p\) (middle panel) or \(p_{PRS} = p\) (bottom panel). Both the points and the scaling exponents were obtained from an average over a set of 100 realizations with different initial conditions. The empty sites between spiral arms inside the domains have not been considered in this analysis.

Figure 7 depicts the fractional number density of empty sites between enemy partnership domains as a function of the simulation time (or, equivalently, the number of generations) for a single realization, assuming that \(p = 0.25, m = 0.5, r = 0.25\), and \(p_{PRS} = p\). Both the points and the scaling exponents were obtained from an average over a set of initial conditions. As expected, if \(p_{PRS} = 0\) both scaling exponents are close to \(-0.5\) which is the result expected if the dynamics is curvature dominated. This is indeed the case since for \(p_{PRS} = 0\) the model is equivalent to a two species May-Leonard model having mutual selection with probability \(p\) (see, for example, [24]). However, for \(p_{PRS} = 0.25p\) (middle panel) or \(p_{PRS} = p\) (bottom panel) the two scaling exponents are quite different, the later one being again close to the \(\alpha = -0.5\) regime usually associated to a curvature dominated dynamics. In this case, however, due to the emergence of single-species domains the dynamics is never fully dominated by curvature even in the \(\alpha \sim -0.5\) regime. What the scaling results seem to show is that, in this regime, the average impact of the single-species domains on the evolution of the characteristic length scale \(L\) of the network appears to be small. Figure 7 shows that the \(L \propto t^{1/2}\) regime is preceded by a slower evolution stage where the scaling exponent departs significantly from \(-0.5\), \((\alpha = -0.36\) and \(\alpha = -0.31\), for \(p_{PRS} = 0.25p\) and \(p_{PRS} = p\), respectively). In this phase, the higher \(p_{PRS}\) is the more the scaling exponent deviates from \(-0.5\), which results in an extended period of coexistence. Also note that sharp variations on the evolution \(\tilde{\rho}_e\) associated with the expansion of single-species domains are averaged out in Fig. 6 but are expected to be present in any single realization of our model. Figure 7 also displays the scaling exponents \(\alpha\), defined by \(\tilde{\rho}_e \propto t^\alpha\), associated to two distinct dynamical stages.
VI. CONCLUSIONS

In this paper we investigated the formation and subsequent growth of single-species domains in six-species class of May-Leonard models. These models naturally lead to the formation of networks with two types of domains containing individuals from two different three-species partnerships. On the other hand, the cyclic selection within each partnership is responsible for the spiral waves observed inside each of these two types of domains.

We have shown, using square lattice simulations, that single-species domains may be formed during the final stages of the collapse of three-species domains and expand until they intersect a three-species domain of the same partnership. We have investigated the conditions under which spherical domains are able to grow, using both analytical arguments and numerical simulations, showing that there is a critical initial radius beyond which spherically symmetric domains are expected to expand. We have investigated the corresponding impact on the average time evolution of the characteristic length scale of the networks, identifying two different scaling regimes: a transient scaling regime, with a slower growth rate of the characteristic length scale $L$, takes place before the transition to a standard $L \propto t^{1/2}$ scaling law, resulting in an extended period of coexistence.

It is worth noticing that in previous work two different models, closely related to the one investigated in the present paper, have been investigated. The model considered in ref. [23] is similar to the one studied here, except for the inclusion of a unidirectional selection interaction, rather than a bidirectional one, between species $i$ and $i+1$. This leads to a completely different dynamical behaviour in which the network evolution is never curvature dominated (the evolution does not follow the standard $L \propto t^{1/2}$ scaling law usually associated with a curvature dominated dynamics) — note that the authors of ref. [23] have misidentified their model as being similar to the model V investigated in ref. [15]. Unlike in our model, in the model presented in ref. [23] an individual from the species $i$ is not able to select an individual from the species $i-1$. As a consequence, in that model large-scale coherent fluctuations of the interfaces may arise due to successive spiral wave fronts. This is in sharp contrast with the case studied in the present paper in which spiral waves cannot cross the interfaces between enemy domain partnerships thus leading to much more localized fluctuations of the interfaces. On the other hand, in the model V studied in ref. [15] the bidirectional selection interactions between species $i$ and $i+3$, which are present in the model studied in the present paper, are suppressed.

In this case the impact on the dynamics is less significant (in comparison with that arising in the model considered in ref. [23]). Still, the fact that the species of one partnership do not have selection interactions with all the species of the enemy partnership leads to the development of dynamical structures along the domain interfaces and to the invasion of one-species domains by neutral individuals of the enemy partnership. Hence, although the main effect which is responsible for the expansion of single-species domains (the larger density of individuals in single-species compared to three-species domains) is also present in the models studied in refs. [15] [23], this effect is overshadowed by a more complex dynamics which prevents the growth of single-species domains in those models.

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