Segregation process and phase transition in cyclic predator-prey models with even number of species

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We study a spatial cyclic predator-prey model with an even number of species (for \( n = 4, 6, 8 \)) that allows the formation of two defective alliances consisting of the even and odd label species. The species are distributed on the sites of a square lattice. The evolution of spatial distribution is governed by iteration of two elementary processes on neighboring sites chosen randomly: if the sites are occupied by a predator-prey pair then the predator invades the prey’s site; otherwise the species exchange their site with a probability \( X \). For low \( X \) values a self-organizing pattern is maintained by cyclic invasions. If \( X \) exceeds a threshold value then two types of domains grow up that formed by the odd and even label species, respectively. Monte Carlo simulations indicate the blocking of this segregation process within a range of \( X \) for \( n = 8 \).

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Interesting phenomena in the cyclic predator-prey systems initiated a progressive research in the last decades. In the simplest case the system has three species dominating cyclically each other, that is, \( S_1 \) beats \( S_2 \) beats \( S_3 \) beats \( S_1 \). Cyclic dominance occurs in many systems including biological models \([1, 2, 3, 4]\) and evolutionary games \([5, 6]\). It is well known that such a cyclic dominance can sustain all of the three species in a well-mixed community \([7, 8]\). In the spatial version of this system the individuals stay on the sites of a lattice \([9]\) and the cyclic invasions maintain a self-organizing pattern in the spatial distribution of species. Nowadays, this system is frequently referred to as an evolutionary spatial Rock-Scissors-Paper game (for a review see \([10]\)).

Within the framework of mean-field approximation (assuming well-mixed population) the species densities can be either stationary or oscillatory (for the latter case both the sum and product of species densities are conserved quantities \([8, 11]\)). Furthermore, these systems exhibit unusual response to the variation of invasion rates or to any external support \([12, 13]\). For finite population the system evolves into one of the homogeneous state via a Moran process \([14, 15]\). On the other hand, when the species are distributed on a lattice the cyclic invasions yield a self-organizing pattern \([1, 16]\) providing stability against some types of external invaders \([17, 18]\) if the spatial dimension is larger than one \((d > 1)\). For the one-dimensional lattice the dynamical rule results in growing domains and super-domains \([9, 19, 20]\). On the Bethe lattice one can observe limit cycle behavior (for a degree of \( z = 3 \) or \( 4 \)) and the oscillation grows until the system reaches one of the homogeneous states if \( z \geq 6 \) \([21, 22]\). More complicated behavior is reported on some types of directed graphs \([23]\).

Starting from the simplest model there are many ways for the generalization of the evolutionary Rock-Scissors-Paper game. A straightforward possibility is to increase the number \( n \) of species (states) so that the cyclic invasion remains valid, i.e., \( S_1 \) invades \( S_2 \) invades \( S_3 \) etc. and finally \( S_n \) invades \( S_1 \). In the one-dimensional lattice domain growth can be observed until \( n \leq 5 \), otherwise the spatial distribution tends towards a frozen domain structure where the species staying in neighboring domains cannot invade each other (shortly, they are neutral). Similar fixation process was reported for both the two- and three-dimensional lattices if \( n \) exceeds a critical value dependent on \( d \) \([24]\). Further relevant observation is related to the parity of \( n \) affecting some features (e.g., the sensitivity to the inhomogeneous invasion rates) in the system \([11, 25]\).

Consequences of supplementary microscopic processes are also investigated. For example, one can introduce mutation, extinction, and empty sites to which the neighboring species can jump, allowing spatial mixing \([26, 27]\). Now our efforts will be concentrated on a lattice Lotka-Volterra system with an even number \( n \) of species dominating cyclically each other while the stochastic local mixing is described by a site exchange mechanism between neutral pairs. The simplest model where such a process can be introduced is the four-species version that exhibits a phase transition when increasing the strength of mixing \([26, 28]\). More precisely, for low rate of mixing one can observe a self-organizing pattern resembling the sample of evolutionary Rock-Scissors-Paper game. On the contrary, if the strength of mixing exceeds a threshold value then phase segregation occurs, i.e., the well-mixed odd end even label species form growing domains and finally one of these states dominates the whole finite system. Our primary interest was to investigate how the critical value of mixing decreases when increasing the number of species. During this study, however, an unexpected intermediate phase was found for \( n = 8 \) and 10 as will be reported below.

We consider a lattice Lotka-Volterra model on a square lattice where each site \( x \) is occupied by a single individual belonging to one of the \( n \) species \((n \) is even), that is, the distribution of species can be described by the site variables \( s_x = 1, \ldots, n \) referring to the label of species. The time evolution of the species distribution is determined by invasions between the site \( x \) (chosen at random) and one of the (randomly chosen) neighboring sites \( y \) if the sites are occupied by a predator-prey pair, i.e., the \((s_y, s_x)\) and [also the \((s_y, s_x)\)] pair transforms into \((s_x, s_x)\) if the species \( s_x \) is the predator of \( s_y \). The predator-prey relation is defined by a cyclic food web and the invasion rates between any predator-prey pair are equivalent and chosen to be unity. Besides it, if the species \( s_x \) and \( s_y \) are neutral then the species may exchange their site.
with a probability $X$ characterizing the strength of mixing. Obviously, nothing happens if $s_x = s_y$. During the time unit (called Monte Carlo step, shortly MCS) the above elementary process is repeated once on average for each site.

For the Monte Carlo (MC) simulations the system is started from a random initial state (providing equivalent (average) number of individuals for the species) on a square lattice (consisting of $N = L \times L$ sites) with periodic boundary conditions. When repeating the above defined elementary step (invasion or local mixing) for sufficiently large size the system evolves into a stationary state that can be described by the average density $\rho_i$ of species $i$ (satisfying the condition $\sum_i \rho_i = 1$) and by the pair configuration probabilities $p_2(i, j)$ of finding species $i$ and $j$ on two neighboring sites. In the limit $N \to \infty$ each species density remains constant, that is $\rho_i(t) = 1/n$. Whereas the ordering processes can be well quantified by considering the time-dependence of pair configuration probabilities. Due to the symmetries we will distinguish two basic quantities. The predator-prey pair probability is given as

$$p_{pp}(t) = \sum_{i=1}^{n} [p_2(i, i+1) + p_2(i+1, i)]$$

(1)

where the time-dependence of $p_2(i, j)$ is not denoted and $i+1$ means 1 for $i = n$. The other analogous quantity is the neutral pair probability that can be expressed as

$$p_n(t) = \sum_{i=1}^{n} \sum_{k=2}^{n-2} p_2(i, i+k)$$

(2)

where $i + k$ is cyclically reduced to the range 1 to $n$. For the MC simulations these quantities are determined by averaging over a suitable sampling interval.

For small size (e.g., $L < 10$) the system quickly develops into one of the states in which several species and simultaneously the predator-prey invasions are missing, thus the composition remains constant. The average fixation (transient) time increases fast with the linear size $L$. For sufficiently large size, however, most of the latter phases can also be observed locally within small patches and the evolution of spatial distribution is affected by the competition between these phases [28].

First we briefly recall the MC results obtained for $n = 4$ [29]. According to the simulations all the four species are sustained by the cyclic invasions if $X < X_c(4) = 0.02662(2)$. Within this region of $X$ the value of $p_n$ increases monotonously with $X$ meanwhile an opposite trend occurs in $p_{pp}$ as demonstrated in Fig. 1. At the critical value of $X$ a sudden change occurs in both quantities because, through a domain growing process, the finite system evolves into a state where either the odd or the even labelled species form a well-mixed phase, that is, $p_1(\infty) = p_3(\infty) = 1/2$ and $p_2(\infty) = p_4(\infty) = 0$ or $p_1(\infty) = p_3(\infty) = 0$ and $p_2(\infty) = p_4(\infty) = 1/2$. In both phases $p_{pp}(\infty) = 0$ and $p_n(\infty) = 1/2$ (if $X > X_c(4)$).

To support our previous MC results we have also performed generalized mean-field approximations at different levels. In the case of the four-species version of this model, all the configuration probabilities on $2 \times 1$, $2 \times 2$, and $3 \times 3$-site clusters have been evaluated (for details of the method see [10]).

Evidently, the traditional mean-field approach (one-site approximation) cannot take into account the effect of mixing. At the levels of $2 \times 1$- and $2 \times 2$-site cluster approximation this method is not capable to describe the transition observed by MC simulations although the solution of many well-mixed phases exists. The more accurate $3 \times 3$-site approximation predicts a phase transition at $X = X_c(3S)(4) = 0.1285(5)$. The large deviation from the MC results indicates the importance of consecutive elementary steps yielding important correlations in the spatial distribution.

For sufficiently strong mixing the phase segregation process seems to be a robust phenomenon as it is observed for other dynamical rules [10,26,27]. It turned out that the well-mixed phases of the odd (as well as even) label species can be considered as a defensive alliance because within this spatial association the species guard each other against the external invaders. For example, if species 1 is attacked by an individual of species 4 then one of the neighboring species 3 strikes back within a short time. Due to the cyclic symmetry species 1 guards species 3 against species 2 and similar mechanism protects the well mixed spatial association of the even label species.

One can easily check that the above concept of defensive alliances remains valid for any even number of species. Namely, within the well-mixed phase of the odd label species the species protect each other against the invasion of even label species and vice versa. Thus for larger $n$ one can expect a similar phase transition from the cyclic self-organizing pattern to the phase segregation phenomenon if we increase the value of $X$. MC simulations confirm this expectation for $n = 6$ as illustrated in Fig. 2. The predator-prey probability ($p_{pp}$) drops suddenly to zero at $X = X_c(6) = 0.00654(2)$. The generalized mean-field analysis of this system is not per-
formed for \( n \geq 6 \) because the numerical solution becomes time-consuming due to the large number of configurations at a sufficiently accurate level (e.g., \( n^6 \) configurations exist on a \( 3 \times 3 \) cluster).

![FIG. 2: The non-vanishing predator-prey pair probabilities vs. \( X \) in the stationary states for \( n = 4 \) (triangles), 6 (squares), and 8 (circles).](image)

Notice that many possible solutions emerge if \( n \) is increased. For example, the well-mixed phases of the mutually neutral species (e.g., \( 1+3+6 \) for \( n = 8 \)) with arbitrary composition are stationary states. All these states can occur in the MC simulations for small sizes \((L \leq 10)\) and can also be reproduced by the generalized mean-field methods. Indeed, the solutions of the subsystems (several species are missing) are solutions for the whole system too. Despite of the large number of possible solutions, the visualization of spatial distributions in the MC simulation indicates the presence of only the above mentioned relevant phases for sufficiently long times.

Surprisingly, for the eight-species system three types of phases (behaviors) can be distinguished as illustrated in Fig. 3. These MC data are obtained for \( L = 400 \) or 600. For these sizes the domain growing process ends within a few million MCS and one of the four-species defensive alliances (consisting of only the odd or even label species) prevails the whole system in the final state if \( X > X_{c2}(8) \approx 0.0042(5) \). The self-organizing spatio-temporal pattern can be maintained by the cyclic invasions until \( X < X_{c1}(8) \approx 0.00285(3) \). As a consequence, the MC simulations reveal the appearance of an intermediate phase within a region of \( X_{c1}(8) < X < X_{c2}(8) \) where the domain growing process stops (or becomes extremely slow).

To illustrate the formation of defensive alliance in the intermediate region \((X_{c1} < X < X_{c2})\) the odd and even label species are denoted by light and dark colors in Fig. 3. The snapshot for \( t = 400000 \) MCS shows clearly that the territories of defensive alliances are separated by a boundary layer where the cyclic invasions govern the time evolution. Similar patterns (with a thickness dependent on \( X \)) can be observed during the domain growing process for \( X > X_{c2}(8) \). We have to emphasize that these boundary layers play crucial role in the formation of final pattern. Namely, these layers serve as a symmetric species reservoir for both defensive alliances and help the equalization of their composition via diffusion.

As mentioned above the domain growing process can be investigated quantitatively by recording the probability of predator-prey pairs because such a constellation occurs exclusively within the boundary layers. One can think that the inverse of \( p_{pp} \) is proportional to the average linear size of domains of defensive alliances.

Figure 4 shows some typical behaviors when considering the time-dependence of \( p_{pp} \) for such a system size where \( L \) is significantly larger than the average domain size at the end of simulation (here at \( t = 10^6 \) MCS). In order to suppress the short-time fluctuations, the numerical data of \( p_{pp}(t) \) are averaged over a time interval with a typical width of \( t_w \approx \min(t/20, 1000 \) MCS). The upper curve \((X = 0.0025)\) in Fig. 4 illustrates that the frequency of invasions reaches a high stationary value \((p_{pp} \approx 0.11)\) characterizing the cyclic self-organizing pattern if \( X < X_{c1}(8) \). The lowest curve \((X = 0.008)\) indicates a typical domain growing process when the asymptotic behavior \((p_{pp} \sim t^{-1/2})\) becomes similar to phase ordering process with non-conserved dynamics [29]. From the plotted MC data at \( X = 0.005 \) and 0.008 one can suggest similar asymptotic behavior. Data for \( X = 0.003 \), however, indicates that the domain growth is stopped and the process itself is resembling the segregation of a water-oil mixture in the presence of surfactant [30, 31]. Notice that in this spatio-temporal pattern all the eight species remain alive, thus the spontaneous formation of this inhomogeneous pattern ex-
process is observed if the system size exceeds a threshold value dependent on $X$. According to our MC simulations this system evolves into a pattern (for $n \geq 6$) where the domains of defensive alliances are separated by boundary layers having a different structure. This phenomenon raises further questions about the role of boundary layers in these types of complex systems.

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