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Phase transition and selection in a four-species cyclic predator-prey model

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We study a four-species ecological system with cyclic dominance whose individuals are distributed on a square lattice. Randomly chosen individuals migrate to one of the neighboring sites if it is empty or invade this site if occupied by their prey. The cyclic dominance maintains the coexistence of all four species if the concentration of vacant sites is lower than a threshold value. Above the threshold, a symmetry breaking ordering occurs via growing domains containing only two neutral species inside. These two neutral species can protect each other from the external invaders (predators) and extend their common territory. According to our Monte Carlo simulations the observed phase transition seems to be equivalent to those found in spreading models with two equivalent absorbing states although the present model has continuous sets of absorbing states with different portions of the two neutral species. The selection mechanism yielding symmetric phases is related to the domain growth process with wide boundaries where the four species coexist.

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Multispecies ecological models with spatial extension exhibit a large variety of possible stationary states as well as phase transitions when tuning the model parameters. In the original Lotka-Volterra models [1,2] as well as in the generalized versions the spatial distribution of species is neglected (see Refs. [3,4] for reviews). Now we report a phenomenon underlying the role of spatial effects in the biological evolution.

In the simplest spatial version of Lotka-Volterra models (henceforth called predator-prey models) the individuals of competitive species are residing on the sites of a lattice and the system evolution is governed by invasions along the nearest neighbor links. In many cases the species form domains with growing sizes and sooner or later only one species will survive. A significantly different behavior is found if the species dominate cyclically each other, i.e., the corresponding food web is characterized by a directed ring graph [5–7]. Frachebourg and Krapivsky [6] have shown that fixation occurs if the number of species N_s exceeds a threshold value $N_f(d)$ depending on the spatial dimension $d>1$. In this case the species form a frozen domain structure [6]. Conversely $[N_s \leqslant N_f(d)]$, the moving invasion fronts maintain a self-organizing polydomain structure. These patterns are widely studied for $N_s=3$ [5,8,9] because it can provide a stability against some external invaders for the spatial models [10–12]. Sato *et al.* [13] have shown that, if only one of the invasion rates differs from unity for even N_s, then only the species with odd (even) labels survive. Very recently, the species biodiversity was studied by similar models in bacterial [14], phytoplankton [15] systems.

In the above lattice models each site is occupied by an individual of the competitive species. Now we will consider a diluted version of these models on a square lattice for $N_s=4$. That is, the sites may be empty and the individuals are allowed to jump to these empty sites. These elementary events can result in the formation of ‘‘defensive alliances’’ consisting of two neutral species. These two-species mixed states can preserve their territory from external invaders belonging to the remaining two species. Thus, besides the above mentioned four-species state, this model has two sets of ‘‘defensive alliances’’ whose confrontations will determine the final stationary state. When increasing the concentration of vacant sites this system undergoes a phase transition from the symmetric four-species state to one of the symmetric defensive alliances. This transition will be interpreted by considering the average displacement (and velocity) of boundary separating two competitive domains.

Here it is worth mentioning that the one-dimensional version of the above model was already investigated by Frachebourg *et al.* [16] for the absence of vacant sites. It is shown that this system evolves into single-species domains whose average size increases algebraically with time. One can easily see that the introduction of randomly walking vacant sites does not essentially modify the motion of interfaces separating the single-species domains. Thus, a similar domain growth is expected with a rate influenced by the concentration of vacant sites. Henceforth, our analysis will be restricted to the two-dimensional system where the cyclic invasions can maintain a self-organizing pattern [6].

In the present model the site *i* of a square lattice can be empty ($s_i=0$) or single occupied by one of the four species (i.e., $s_i=1$, 2, 3, and 4) dominating cyclically each other (1 beats 2 beats 3 beats 4 beats 1). The time evolution is controlled by subsequent jumps or invasions at randomly chosen nearest neighbor sites *i* and *j*. The individual will jump to the empty site, i.e., the values of s_i and s_j are exchanged ($s_i \leftrightarrow s_j$) if $s_i=0$ and $s_j>0$ or $s_i>0$ and $s_j=0$. Invasion occurs if the predator and prey meet. For example, both the (1,2) and (2,1) pairs transform into the (1,1) pair (the further elementary invasions are given by cyclic permutation of the species labels). Nothing happens if $s_i=s_j$ as well as for neutral pairs, i.e., pairs (1,3), (3,1), (2,4), and (4,2) remain un-

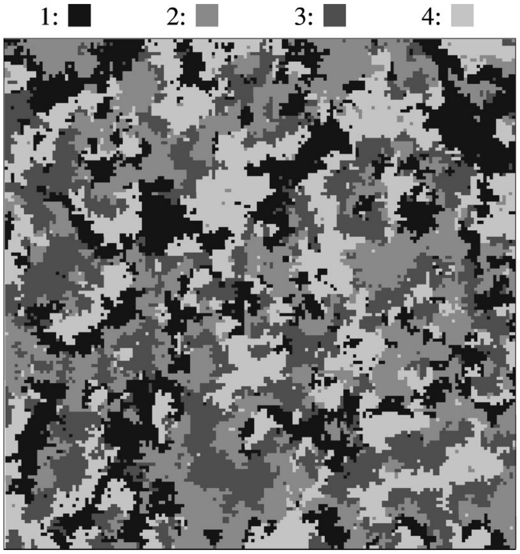

FIG. 1. Spatial distribution of the four species on the square lattice if $\rho_0 = 0$. The grayscale of the four species is indicated above the snaphot.

changed. The system is started from a random initial state. After some transient time the system reaches a stationary state we study.

Notice that the above elementary rules leave the number of vacant sites unchanged and their distribution becomes uncorrelated after a suitable relaxation time. The states containing only one species are considered as absorbing states because the above rule does not create new species. Besides this, the mixed states containing only two neutral species (1+3 or 2+4) are also absorbing states and will be denoted as D_{13} and D_{24}. In these stationary states the ratio of the two species remains constant. In the presence of vacant sites the migration eliminates the spatial correlations. For small sizes this system can easily reach one of these absorbing states and afterwards it stays there forever.

Our Monte Carlo (MC) simulations are performed on a square box with periodic boundary conditions. In order to avoid the above mentioned small size effect the linear size is varied from $L = 400$ to 2000. The systematic simulations are started from a random initial state for different concentration of vacant sites (ρ_0). Within a time unit MCS (Monte Carlo steps per site) each pair has a chance once on the average to modify the state at one of the corresponding sites. During the simulations we have recorded the concentration of species and the pair configuration probabilities on the nearest neighbor sites. Averaging over a suitable sampling time interval we have determined the average species concentrations (ρ_α, $\alpha = 1$, 2, 3, and 4). Furthermore, we have deduced two quantities P_{pp} and P_n describing the probability of finding predator-prey and neutral pairs on two nearest neighbor sites. Evidently, P_{pp} measures the invasion activity that vanishes in the absorbing states.

The visualization of species distribution shows a self-organizing polydomain structure in the absence of vacant sites (for a typical snapshot, see Fig. 1). The species occur cyclically at each site, however, the short range interaction can not synchronize these accidental events. In the pattern evolution one can easily recognize the traveling invasion fronts that play a crucial role in the maintenance of this polydomain structure [5,9]. Similar spatiotemporal patterns can be observed for a low concentration of vacant sites. Henceforth this spatiotemporal pattern is called C state.

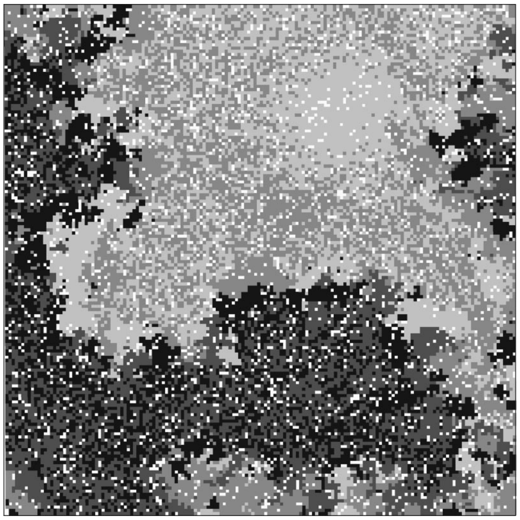

FIG. 2. Typical domain structure at time $t = 3000$ MCS (Monte Carlo steps per site) if initially ($t = 0$) the spatial distribution was random for $\rho_0 = 0.1$. The white boxes refer to empty sites while the grayscale of species is as in Fig. 1.

In the stationary C state $\rho_1 = \rho_2 = \rho_3 = \rho_4 = (1 - \rho_0)/4$ due to the cyclic symmetry. A strikingly different behavior occurs if $\rho_0 > \rho_{cr} = 0.0623(1)$. When using lighter (darker) grayscales for species 1 and 3 (2 and 4) two types of growing domains (namely D_{13} and D_{24}) can be distinguished as shown in Fig. 2. These growing domains are separated by wide regions of C states. The growth process is similar to those observed in systems with two equivalent absorbing states [17–21]. Finally the present system develops into one of the symmetric two-species absorbing states D_{13} or D_{24} where $\rho_1 = \rho_3 = (1 - \rho_0)/2$ and $\rho_2 = \rho_4 = 0$, or $\rho_2 = \rho_4 = (1 - \rho_0)/2$ and $\rho_1 = \rho_3 = 0$. The time of transition toward one of these states depends on ρ_0 and L.

Both species 1 and 3 benefit from their spatially mixed coexistence because they protect each other from the external invasions. For example, species 2 can invade the sites occupied originally by species 3, however, the neighboring species 1 strikes back and eliminates the invaders 2. At the same time, species 3 protects species 1 against species 4. This is the reason why this association is called defensive alliance. Due to the cyclic symmetry species 2 and 4 can form a similar defensive alliance.

The formation of defensive alliances was already observed in some other multispecies ecological model where the cyclic invasion itself has provided the protection mechanism [11,12]. In the present model, however, the protection is due to the mixing of neutral species via the jumps to empty sites.

Figure 3 demonstrates that the probability of neutral pairs (P_n) increases with the concentration of vacant sites in the stationary states. Above the mentioned threshold value (ρ_0

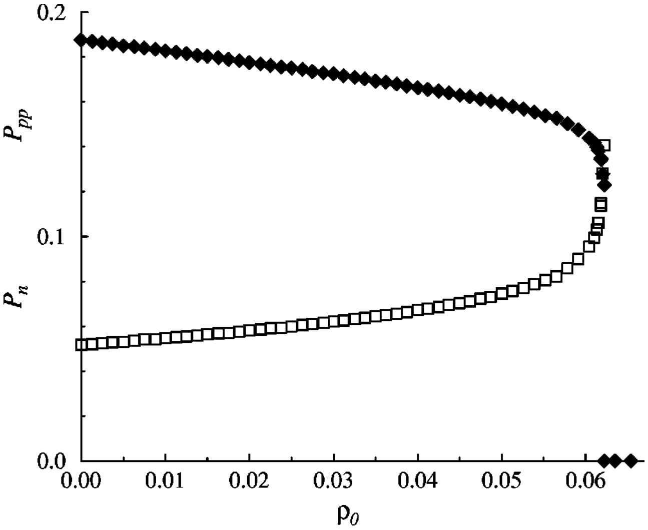

FIG. 3. Monte Carlo results for the probability of finding predator-prey (closed diamonds) and neutral pairs (open squares) on two nearest neighbor sites in the stationary states.

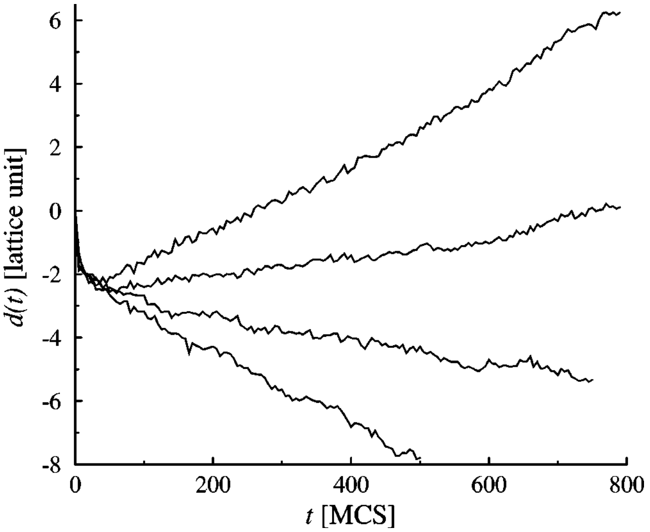

FIG. 4. Average displacement of boundaries between states C and D_{13} as a function of time for $\rho_0 = 0.056$, 0.060, 0.064, and 0.070 (from top to bottom).

$>\rho_{cr}$) this quantity tends to the uncorrelated value $P_n = (1-\rho_0)^2/2$, characteristic of the symmetric defensive alliance state. Simultaneously, the invasion activity (or P_{pp}) decreases and drops suddenly to zero at $\rho_0 = \rho_{cr}$. In the description of this transition the probability of finding predator-prey pairs on two nearest-neighbor sites (P_{pp}) can be considered as an order parameter that becomes zero in the absorbing (homogeneous) D_{13} and D_{24} states. At first glance our results are consistent with a first-order phase transition. A more rigorous analysis of this transition is prevented by the enhanced fluctuations (in all the quantities we studied) and by a critical slowing down inspite of the fact that our simulations were performed on large systems ($L = 2000$) with long relaxation and sampling times ($t_r > 10^4$ MCS and $t_s > 10^5$ MCS) in the close vicinity of the transition point. The corresponding MC data refer to the divergency of the stationary variance of the order parameter (χ as defined in Ref. [22]). Due to the mentioned reasons, the low accuracy of our numerical results does not allow us to derive an adequate exponent (γ).

Similar difficulties (in the characterization of transition) were reported and discussed by Hinrichsen [18], Dornic *et al.* [19], and Lipowski and Droz [21], who considered simpler models exhibiting a phase transition to one of the two equivalent absorbing states. In these models the absorbing states are independent of time; therefore, the authors could use a very efficient method based on the numerical investigation of spreading from a single seed (details are given in Refs. [22,23]). Considering several d-dimensional models with q absorbing states Lipowski and Droz have conjectured that in the $q-d$ phase diagram the case $d=q=2$ is close to or is at the crossing point of lines separating three different types of phase transitions [21]. Unfortunately, we could not utilize the advantage of the mentioned technique because the absorbing states depend on time in the present model.

The universal behavior of the nonequilibrium transitions into absorbing states have extensively been studied for several decades (for a review see Refs. [22,23]). The dynamical systems with two equivalent absorbing states represent a curious universality class (named after the voter model) [17–19,24,25] whose general features are consistent with those described above. Systems with infinitely many absorbing states have also been studied by several authors [25–29]. In light of the previous investigations the main curiosity of the present model is that here there are two equivalent (infinite) sets of absorbing states that coexist during a domain growing process as described above. This coexistence implies a selection mechanism (as described below), resulting in one of the only two symmetric phases (D_{13} and D_{24}) in the final stationary state if $\rho_0 > \rho_{cr}$. Consequently, the general features (symmetries, domain growing, etc.) of the present system are very similar to those characterizing the universality class of the voter model.

To gain a deeper insight into the dynamics of the present model we now study the displacement of interfaces separating the C state and one of the stationary defensive alliances (D_{13} or D_{24}). For the preparation of such an artificial domain structure the whole area (torus) is divided into parallel strips with width of 500 lattice units. The MC simulation is started from a random initial state (as above) for $L = 4000$ and, after a suitable relaxation time t_r, an uncorrelated D_{13} state is created in every second strip. More precisely, species 1 and 3 are substituted randomly for the occupied sites located inside the corresponding strips. First we consider the results obtained for symmetric distribution, i.e., when inside the defensive alliances (D_{13}) $\rho_1 = \rho_3 = (1-\rho_0)/2$. The expansion (or shrinking) of the C domains can be monitored by evaluating the quantity $\Phi(t) = \rho_1(t) - \rho_2(t) + \rho_3(t) - \rho_4(t)$. Notice that Φ vanishes ($\langle\Phi\rangle = 0$) for the state C whereas $\Phi(t) = \pm(1-\rho_0)$ in the absorbing states. The average displacement (measured in lattice unit) of the parallel interfaces are derived straightforwardly from the variation of $\Phi(t)$.

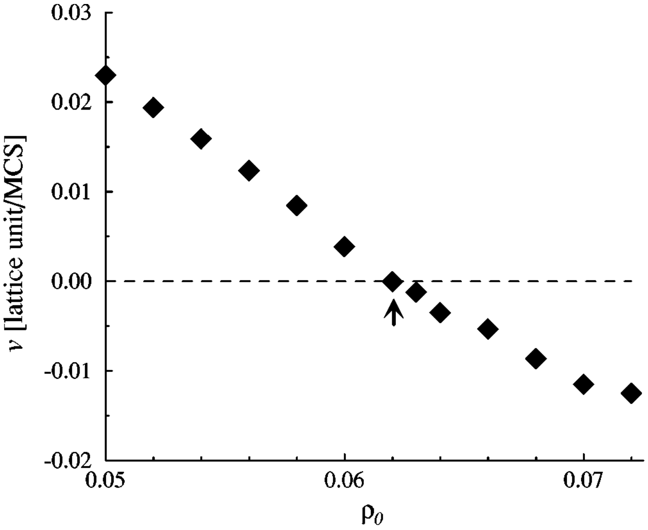

FIG. 5. Average velocity of the invasion front between the states C and D_{13} as a function of the concentration of vacant cites. The arrow indicates the critical point derived from the investigation of the stationary states. The statistical error is comparable to the symbol size.

Figure 4 displays the typical time dependences of the average displacement $d(t)$ of the boundaries separating the C and D_{13} states. The increase of $d(t)$ corresponds to the expansion of C domains. The MC data are obtained by averaging over 20 runs performed for $L=4000$ and $t_r=3000$ MCS if $\rho_0<\rho_{cr}$. Above the critical point ($\rho_0>\rho_{cr}$) we have to use significantly shorter relaxation times ($t_r=200$ MCS) to avoid the difficulties caused by the appearance of the D_{13} and D_{24} nucleons. It is remarkable that at the beginning $d(t)$ decreases suddenly. After a suitable transient time, however, the variation of $d(t)$ becomes linear and the fitted slope can be interpreted as the average velocity v of the invasion front.

Figure 5 clarifies that the C state invades the territories of defensive alliances for low concentration of vacant sites. The average invasion velocity decreases monotonously with ρ_0 and becomes zero at $\rho_0=\rho_{cr}$. In agreement with the expectation, the area of the C domains shrinks for $\rho_0>\rho_{cr}$.

The above simulations were repeated by choosing asymmetric compositions (e.g., $\rho_1>\rho_3$) within the D_{13} state. It is found that the asymmetry influences only the short time behavior. For example, if $\rho_1\gg\rho_3$ then the C state can invade fast ($v\sim 1$) those neighboring patches occupied by only the species 1 in the D_{13} domains. Consequently, in this case one can observe a sudden increase (instead of decrease as plotted in Fig. 4) in $d(t)$. In the subsequent linear region, however, the average velocity v becomes independent of $(\rho_1-\rho_3)$ within the statistical error. The visualization of the species distribution has indicated that the boundary between the C and D_{13} domains fluctuates very intensively. In fact, it is not a well defined boundary because the sites occupied by species 1 and 3 can belong to both phases within a boundary layer. Within this boundary layer the cyclic invasions sustain the equivalence between ρ_1 and ρ_3 on average for long times. This boundary layer can be considered as a symmetric species reservoir that drives an equalization between the different species concentration in the asymmetric D_{13} phase via diffusion.

This scenario is checked by considering the evolution from such an initial state where the parallel strips (created as above) are filled alternately by the symmetric D_{24} and asymmetric D_{13} states. The simulations (for $\rho_0>\rho_{cr}$) have confirmed that the variation of $d(t)$ is similar to a random walk; meanwhile the difference $\rho_1-\rho_3$ tends to zero for long times. This is the reason why we have always found symmetric D_{13} or D_{24} states after the domain coarsening process for sufficiently large system sizes. At the same time this phenomenon can be interpreted as a selection mechanism favorizing the symmetric defensive alliances.

Here it is worth mentioning that the traditional mean-field and pair approximations (for details, see Refs. [22,30]) are capable of reproducing the existence of the above mentioned absorbing states. However, these techniques are not capable of describing the observed phase transition. We think that this failure is due to the very complex mechanisms consisting of many elementary steps within a local cycle.

In summary, our work shows that a slight migration in the lattice predator-prey models may significantly affect the species biodiversity. Dilution and migration are attributes usually found in ecosystems whose description should include these features. The present model exemplifies that the migration of species supports the formation defensive alliances in the multispecies ecological systems. Furthermore, the confrontation between the different associations of species plays crucial role in the selection of the survival population structure. In this case a phase transition occurs when the rate of migration is increased by allowing more and more vacant sites (and jumps) on the lattice.

The above described features are observed for many other systems. Preliminary results indicate clearly that a similar behavior occurs if the mixing is provided by the site exchange for neutral pairs without introducing vacant sites. Furthermore, a quantitatively similar behavior is found for the continuous version of the present model, i.e., when the individuals move freely on a planar surface and they create an offspring if they eat a prey caught within a short distance. In fact, this former finding inspired us to introduce a simpler model for the more rigorous analysis.

We think that the mixing of neutral species can result in other defensive alliances in multispecies systems. For example, two equivalent alliances are expected to emerge in the N_s-species model with a circular food web for even N_s. Evidently, such alliances can occur for more complicated food webs when the species have several preys and predators [11,12]. In these situations the competition between the possible (defensive) alliances will affect the evolution of the ecological system including the food web itself [31,32].

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