

Competing associations in bacterial warfare with two toxins

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Abstract

Simple combinations of common competitive mechanisms can easily result in cyclic competitive dominance relationships between species. The topological features of such competitive networks allow for complex spatial coexistence patterns. We investigate self-organization and coexistence in a lattice model, describing the spatial population dynamics of competing bacterial strains. With increasing diffusion rate the community of the nine possible toxicity/resistance types undergoes two phase transitions. Below a critical level of diffusion, the system exhibits expanding domains of three different defensive alliances, each consisting of three cyclically dominant species. Due to the neutral relationship between these alliances and the finite system size effect, ultimately only one of them remains. At large diffusion rates the system admits three coexisting domains, each containing mutually neutral species. Because of the cyclical dominance between these domains, a long term stable coexistence of all species is ensured. In the third phase at intermediate diffusion the spatial structure becomes even more complicated with domains of mutually neutral species persisting along the borders of defensive alliances. The study reveals that cyclic competitive relationships may produce a large variety of complex coexistence patterns, exhibiting common features of natural ecosystems, like hierarchical organization, phase transitions and sudden, large-scale fluctuations. © 2007 Elsevier Ltd. All rights reserved.

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1. Introduction

Considering cyclic patterns of population interactions is still uncommon, although the few existent theoretical studies on such systems emphasize the important role they might play in the maintenance of biodiversity (Durrett and Levin, 1998; Gilpin, 1975; May and Leonard, 1975; Hofbauer and Sigmund, 1998; Czárán et al., 2002). Substantial field evidence for the existence of real cyclic interaction topologies have accumulated in the past few decades, many of which come from studies of ecological succession, biomass flow in food webs and competition. For example, it is long known that in certain plant communities the successional states of the vegetation may follow one another in a cyclic order, cf. Watt (1947). In food webs, material flows from primary producers to top predators, while decomposers merge distant parts of the

food web, by making the material available again for primary producers in the form of mineral resources. This, however, is not a homogeneous cycle regarding the nature of the population interactions, because decomposers are in a different (commensal) ecological relation to the rest of the species in the food web which play a predatory type of game among themselves.

Our focus in this study is on competitive dominance networks. These seem to exhibit both hierarchical and cyclic topological features, depending on how general our concept of competition is. According to the resource competition theory of Tilman (1982), the competitive ability of species depends on the particular resource under consideration. Considering one resource, if species *A* is dominant over *B* and species *B* is dominant over *C* then species *C* cannot be dominant over *A*. Due to the presence of trade-offs between different traits, none of the species can be dominant for all resources, therefore an overall dominance network is not feasible. By the inclusion of direct interactions between species the competitive relationships

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might be even more intricate, allowing for cyclic dominance networks. The best known classical examples of cyclic competition are three-species competitive (overgrowth) cycles which seem to be rather frequent in marine (benthic) communities (Buss and Jackson, 1979; Russ, 1982; Buss, 1990; Johnson and Seinen, 2002).

The relevance of cyclic interactions in maintaining competitive coexistence is even more conspicuous in microbial communities, however. Recent research on bacteriocins (Chao and Levin, 1981; Durrett and Levin, 1997; Iwasa et al., 1998; Pagie and Hogeweg, 1999; Nakamaru and Iwasa, 2000; Czárán et al., 2002; Kerr et al., 2002) suggests that competitive cycles are in fact the rule rather than the exception in communities of microorganisms.

Bacteriocins are toxins produced by bacteria against other species of bacteria or often even against conspecific strains, used as “chemical weapons” to eliminate competitors from the common habitat. The toxins are small peptides with diverse points of attack and mechanisms of killing—some inhibit the buildup of the cell wall, others bilge the cell membrane, yet others stop or impair DNA replication, to mention just a few of the many possibilities. The genetic background of bacteriocin production and resistance is also rather colorful, but there are two features in common for almost all known bacteriocin systems: the corresponding genes reside on extrachromosomal DNA, i.e., on plasmids, and they are organized in operon-like structures. The same bacterium may carry many different plasmids, each harboring a different bacteriocin operon.

Even a single species may exist in three different genotypes with respect to the production of, and its resistance to, a single bacteriocin: one is sensitive to the toxin (*S*), the other is resistant to it (*R*), and the third one is a killer (*K*) which is both resistant and a toxin producer. Since both resistance and toxin production carries a certain metabolic cost which lowers fitness, the three strains can be ordered in terms of metabolic efficiency as $S > R > K$. That is, the sensitive has no extra metabolic cost, the resistant pays that of producing the resistance factor, and the killer carries the metabolic burden of synthesizing both the toxin and the resistance factor. Thus, based on metabolic efficiency alone, i.e., in terms of resource competition, *S* should be dominant over both *R* and *K*, and *R* would be superior to *K*. This line of resource-competitive hierarchy is bent to form a cycle by the interference-competitive dominance of *K* over *S* due to toxic killing. In other words, *S*, *R* and *K* play the Rock-Scissors-Paper game which is known to be stable in a spatial setting: in a lattice model implementation of the game the three strains maintain coexistence in a spatially dynamic pattern (Tainaka, 1988; Kerr et al., 2002; Czárán et al., 2002; Kirkup and Riley, 2004).

In any traditional analysis of the spatial Rock-Scissors-Paper game identical invasion rates are assumed (for a survey see the reviews by Tainaka, 2001; Szabó and Fátih, 2007). Detailed investigations have proven later that the

introduction of different invasion rates does not modify the basic conclusions significantly. Namely, the self-organized patterns remain similar while the average frequencies of the strains depend on the ratios of invasion rates (Tainaka, 1993; Durrett and Levin, 1997). Boerlijst and Hogeweg (1991) have shown that the corresponding patterns provide stability against some types of external invaders. The unusual response to external effects is discussed by Tainaka (1993) and Frean and Abraham (2001). The main results in lattice systems remain qualitatively unaffected if we assume mutations from *S* to *K*, from *K* to *R*, and from *R* to *S* (mutations in the opposite directions are ineffective, because the mutant is immediately outcompeted by the resident type, cf. Szabó and Czárán (2001b)).

By considering more than a single bacteriocin operon the maximum number of different strains becomes the corresponding power of three (the number of repetitive variations of *S*, *K* and *R* types for each operon). Previous work (Czárán et al., 2002) has demonstrated that in an evolving many-toxin lattice system the final quasi-stationary state is characterized by a high number of resistance genes and a low number of toxin genes present within the population. This so-called “hyperimmunity” state has a very dynamical structure both in space and in terms of the actual toxin and immunity alleles present at different times. Due to the astronomical number of potentially different strains there is little hope in any attempt to discover the regularities of the competitive interactions within such an evolving, spatial multi-toxin system. Therefore later we reduced the number of toxins to two and examined the corresponding nine-strain system in detail (Szabó and Czárán, 2001b). Surprisingly, it has proven to admit a critical phase transition along the uniform mutation rate as its critical parameter. Above the critical rate of mutation the system maintains all the nine strains in a spatially dynamic, fine-grained pattern, whereas below the critical value it nurses three indefinitely expanding domains, each of which consists of three strains playing the Rock-Scissors-Paper game among themselves. The strains within a domain form “defensive alliances” in the sense that all invasion attempts by any single strain from among the remaining six is doomed: the invader is extinguished by one of the members of the three-strain alliance. In practice the simulations ended with one of the three domains having taken over, and each domain had the same chance of becoming the winner. This outcome is the result of neutral drift due to the finite size of the system.

Since subcritical rates of mutation typically resulted in unlimited domain expansion, i.e., in homogeneous three-species patches of ever increasing size, one might think that the spatial constraints on the system (namely, the strictly localized nature of competitive interactions) must play a key role in the dynamics of the community. Mutations can obviously perturb spatial structure, but in fact any mechanism confounding the emergent self-organized patchy structures might also be expected to change the dynamics of species frequencies. A very simple way of

disturbing the spatial structure of a community is allowing for site swaps between neighbors. This mimics diffusive movement on the lattice scale—and this is what we have included in the present version of the model. Besides the random initial pattern of the strains within the lattice, diffusion is another source of spatial randomness in community structure formation.

Therefore we consider a two-toxin bacterial competition model without mutations but with short range diffusion. We wish to understand the role of cyclic competitive dominance networks and spatial constraints in ecological coexistence by investigating this simple model system. First we discuss some topological features of the competitive network, then review some features of the corresponding spatially homogeneous (mean-field) model, and finally we investigate the dynamics of its spatial counterpart in detail.

2. The competitive network

Assuming two bacteriocin operons present in a bacterium population the topology of the competitive interactions among the nine different strains is illustrated in Fig. 1. The labels KK , KS , KR , SK , SS , SR , RK , RS and RR correspond to the different genotypes with regard to bacteriocin production and resistance. For notational convenience these types will be denoted by

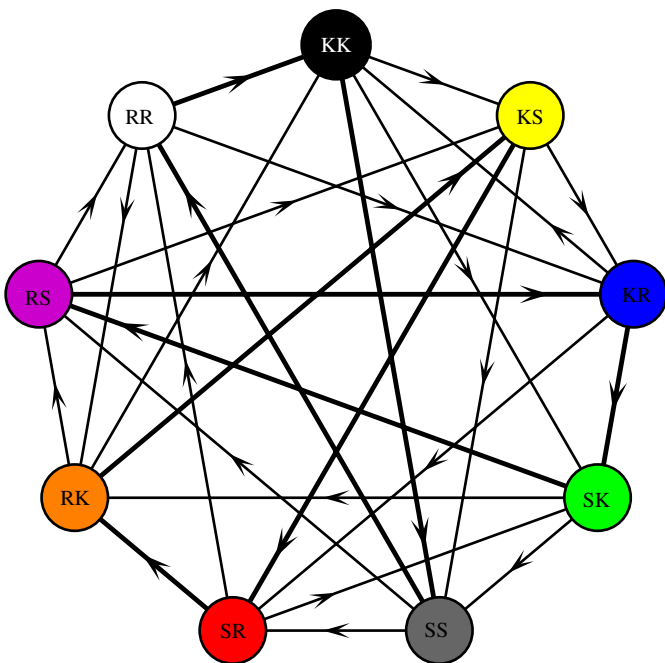


Fig. 1. The competitive relations of the nine species. Each species is characterized by its toxin and resistance factor producing capabilities, regarding two toxins. S , R and K stand for sensitive, resistant and killer, respectively. Arrows point at the competitively inferior species. Thick lines connect cyclic defensive alliances playing an important role in the dynamics of the community—these are the edges along which the competitively superior species wins on both accounts against the inferior one.

numbers ranging from 0 to 8, respectively, in the equations. We shall call these genotypes “strains” or “species” in the sequel, but one has to keep in mind that these “species” need not be genetically distant in the biological sense: they are definitely different in terms of the two bacteriocin systems, but may (or may not) be genetically identical otherwise. Since we assume neither mutations nor recombinations in this model it is safe to assume that the nine genotypes are distinct species. However, apart from their different positions in the competitive network (i.e., their competitive relations to the other species) the nine strains are assumed to be phenotypically equivalent.

These nine species occupy the surface of a solid medium at a fixed total density. The densities of competitively superior populations can increase at the expense of the densities of inferior ones by competitive displacement. For sake of simplicity, we assume that all invasion rates are equivalent (and set to be 1 on a suitable time scale). This means that once competitive interaction takes place between two strains, the dominant certainly defeats the inferior. Some features of this system are common for both homogeneous (non-spatial) and spatially organized settings—we shall discuss them briefly in turn.

In the absence of mutations the system admits many stationary solutions, each corresponding to certain subsets of the interaction graph. It is obvious that all the homogeneous states (with just one of the species present) remain unchanged whenever reached. These stationary states, however, are not stable because they can be invaded by competitively superior species. There exist nine two-species stationary states with two neutral strains at arbitrary proportions; one example for such a neutral pair is $(KK + RS)_m$. The system admits three different three-species states as well, each composed of three mutually neutral species at arbitrary portions, for which $(KK + SR + RS)_m$ is an example. These neutrally coupled two- and three-species stationary states are also unstable against external invasions. Most important for our present study: the competition network contains nine cyclic three-species subsystems playing the Rock-Scissors-Paper game among themselves, i.e., the species of these subsystems form an intransitive competition cycle: A beats B beats C beats A . Three of these subsystems are favored by selection because their members protect each other against external invaders (Szabó and Czárán, 2001a, b). Note that these defensive alliances are such that the winner dominates the loser on both bacteriocin operons, which amounts to the seemingly paradoxical statement that the most desperate enemies are the most efficient allies. We shall return to this paradoxical feature later.

3. Mean-field model and theory

The traditional mean-field model of this system cannot account for the effects of spatially constrained mixing (X). Yet, the mean-field analysis might confirm the existence of most of the possible solutions and indicates the important

dynamical role that some species combinations like defensive alliances play in the dynamics of the system.

Given linear interactions, the equations of motion for the mean-field approximation to the simulated system take the following form:

$$\frac{d\rho_i}{dt} = \rho_i \sum_{j=0}^8 A_{ij} \rho_j \quad \text{for } i = 0, \dots, 8, \quad (1)$$

where ρ_i stands for the density of species i and \mathbf{A} is the adjacency matrix of the competition network (see Fig. 1). That is,

$$\mathbf{A} = \begin{pmatrix} 0 & 1 & -1 & 1 & 1 & 0 & -1 & 0 & -1 \\ -1 & 0 & 1 & 0 & 1 & 1 & -1 & -1 & 0 \\ 1 & -1 & 0 & 1 & 0 & 1 & 0 & -1 & -1 \\ -1 & 0 & -1 & 0 & 1 & -1 & 1 & 1 & 0 \\ -1 & -1 & 0 & -1 & 0 & 1 & 0 & 1 & 1 \\ 0 & -1 & -1 & 1 & -1 & 0 & 1 & 0 & 1 \\ 1 & 1 & 0 & -1 & 0 & -1 & 0 & 1 & -1 \\ 0 & 1 & 1 & -1 & -1 & 0 & -1 & 0 & 1 \\ 1 & 0 & 1 & 0 & -1 & -1 & 1 & -1 & 0 \end{pmatrix}. \quad (2)$$

These equations have a lot of trivial solutions—we have mentioned some of these in the previous section. For example, a possible single-species solution is: $\rho_0 = 1$ and $\rho_1 = \dots = \rho_8 = 0$. A two-species solution is $\rho_0 = 1 - \varepsilon$, $\rho_5 = \varepsilon$ ($0 < \varepsilon < 1$) and $\rho_i = 0$ for all other species.

If the system is initiated with a random species composition then chaotic oscillations of species densities ensue as shown in Fig. 2. This oscillating behavior satisfies several constraints due to the symmetries of \mathbf{A} . One can easily check that both the sum and the product of species

densities are conserved quantities, i.e.,

$$\sum_{j=0}^8 \rho_j = 1 \quad (3)$$

expressing normalization and

$$\prod_{j=0}^8 \rho_j = C_0 = \text{constant}. \quad (4)$$

The first conservation law comes from the antisymmetry of \mathbf{A} , i.e., $A_{ij} = -A_{ji}$. The second constraint, (4), comes from the fact that the sum of the matrix elements in each column is zero, that is $\sum_{i=0}^8 A_{ij} = 0$. Moreover, the product of the species densities within each cyclic defensive alliance remains constant:

$$\rho_0 \rho_4 \rho_8 = C_1 = \text{constant}, \quad (5)$$

$$\rho_1 \rho_5 \rho_6 = C_2 = \text{constant}, \quad (6)$$

$$\rho_2 \rho_3 \rho_7 = C_3 = \text{constant}, \quad (7)$$

because $A_{0i} - A_{4i} + A_{8i} = 0$ for arbitrary i , etc.

The latter constraints prevent any species from going extinct in the mean-field system. Note that this system has many other cyclic three-species subsets (e.g., $(KK + KS + KR)_c$) for which similar constraints do not apply in general, except with all the rest of the species missing.

Considering those subsets which consist of the species of two cyclic defensive alliances further conserved quantities can be derived. For example, within the subsystem $(KS + KR + SK + SR + RK + RS)$ (for which $\rho_0 = \rho_4 = \rho_8 = 0$) the non-vanishing species densities satisfy additional conservation laws:

$$\rho_1 \rho_3 = C_{13} = \text{constant}, \quad (8)$$

$$\rho_2 \rho_6 = C_{26} = \text{constant}, \quad (9)$$

$$\rho_5 \rho_7 = C_{57} = \text{constant}. \quad (10)$$

Interestingly, these conservation laws apply for those neutral pairs whose well-mixed phase is also considered as a defensive alliance in the corresponding six-species subsystem (Szabó, 2005).

Except for Eq. (3) all the above conservation laws are broken in the spatial system, which exhibits more complex behavior than the mean-field approximation.

4. The spatial model

The spatial model is similar to that used in Szabó and Czárán (2001b), except for the lack of mutations and the inclusion of diffusion. We consider a $N = L \times L$ square lattice of sites with periodic boundary conditions. Each site $x \in N$ is described by a site variable $s_x = 0, \dots, 8$ expressing that it is occupied by a single individual belonging to one of the nine bacterial species. The dynamics of the population is driven by local interactions; competitive replacements and diffusion events between neighboring

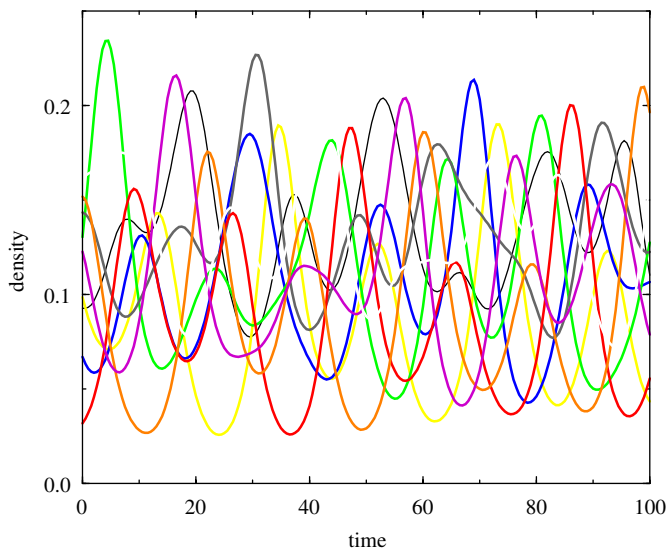


Fig. 2. Typical chaotic oscillations of species densities in the mean-field model if the system is started from a random initial composition.

sites. Since competitive interactions produce identical sites, site swaps due to diffusion are visible only between competitively neutral, yet different pairs of sites. Accordingly, the state of the lattice is updated by repeating the following elementary steps. First we choose two nearest neighbor sites x and y at random. Nothing happens when $s_x = s_y$. If s_x is competitively superior to s_y then the (s_x, s_y) pair transforms into (s_x, s_x) . In the opposite case, (s_x, s_y) transforms into (s_y, s_y) . If s_x and s_y is a neutral pair then the (s_x, s_y) pair changes to (s_y, s_x) with probability X . One Monte Carlo step (MCS) means repeating this elementary step N times, hence it will be used as a lattice size independent temporal unit in the sequel.

5. Results of the spatial model

Simulations were performed at different linear lattice sizes (L). On small lattices ($L \approx 10$) the random initial state typically develops into a homogeneous state or the mixture of two or three (mutually) neutral species. For larger lattice sizes ($L \approx 100$) self-organizing patterns driven by cyclic invasions develop, which enables the coexistence of several species. To obtain and study more complex patterns we have to choose L to be significantly larger than any characteristic length of the system (e.g., the typical linear size of domains or super-domains) in the final stationary state. For the quantitative analysis of these states we have recorded the average densities of the species ρ_i ($i = 0, 1, \dots, 8$) and the probabilities p_c and p_n of finding competing or neutral pairs on two neighboring sites. To quantify the magnitude of fluctuations we have also determined the variable

$$\chi = \frac{N}{9} \sum_{j=0}^8 \langle [\rho_j - \langle \rho_j \rangle]^2 \rangle, \quad (11)$$

where $\langle \dots \rangle$ is the time average for a sufficiently long time window of sampling.

Surprisingly, the Monte Carlo results suggest three phases and two phase transitions along the X parameter of the model (see Fig. 3) as indicated by changes in p_c and p_n . These curves indicate two critical values of diffusion; the break points in p_n and p_c at $X_{c1} = 0.0560(5)$ and $X_{c2} = 0.0720(5)$ are the positions of the two phase transitions. Notice that within the second and the third phase the value of p_n increases monotonously with X .

The first phase, corresponding to low migration probabilities, was already discussed in detail in Szabó and Czárán (2001b). Simulations started from an uncorrelated initial distribution of the species at $X = 0$ produce growing domains of the three cyclic defensive alliances $[(KK + SS + RR)_c, (KS + SR + RK)_c$ and $(KR + SK + RS)_c]$ as illustrated in Fig. 4. The average linear size of domains increases with \sqrt{t} . Since the lattice size is finite in any simulation, the final stationary state of the system will be dominated by one of the three cyclic defensive alliances. Which of the alliances takes over finally is a matter of

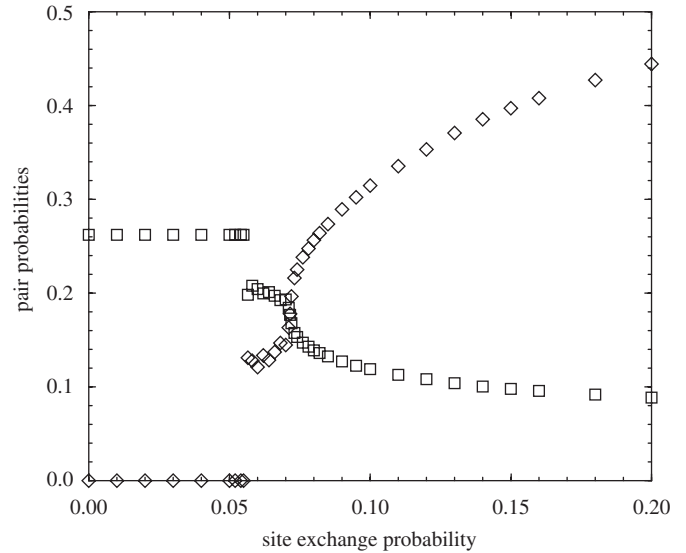


Fig. 3. Monte Carlo results for the competing and neutral pair probabilities p_c (open squares) and p_n (open diamonds) as a function of the site exchange probability X . Changes in these pair probabilities indicate two phase transitions at $X_{c1} = 0.0560(5)$ and $X_{c2} = 0.0720(5)$. Cyclic defensive alliances dominate the stage at high p_c values below X_{c1} , while neutral coalitions are stable at high p_n values above X_{c2} . In the second phase between X_{c1} and X_{c2} both types of species associations are present in a dynamical pattern.

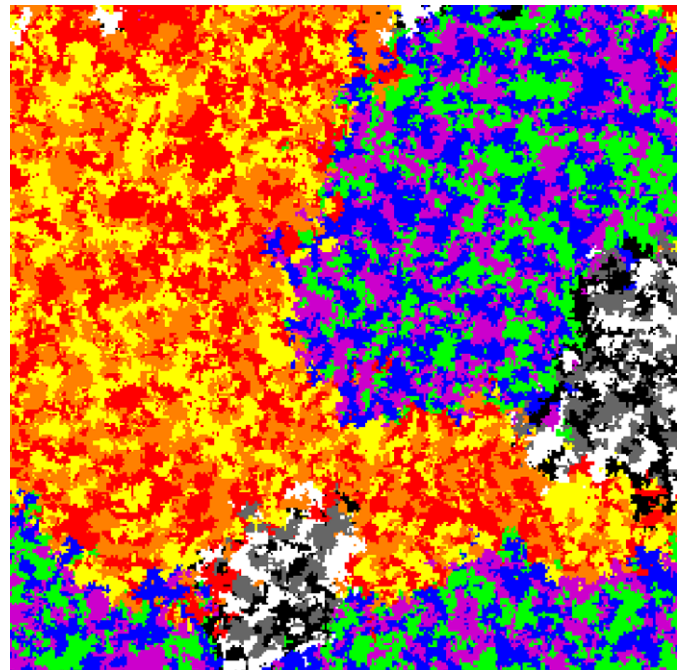


Fig. 4. Typical spatial distribution of species within a 300×300 box after 1500 MCS for $X = 0$. The system exhibits growing domains of the three cyclic defensive alliances $(KK + SS + RR)_c$, $(KS + SR + RK)_c$ and $(KR + SK + RS)_c$. The initial state was a random pattern of the nine species. Species colors are defined in Fig. 1.

(equal) chance. The takeover is also indicated by the vanish of the relative frequency of neutral pairs p_n . Fig. 3 shows that this behavior is found at $X < X_{c1} = 0.0560(5)$.

Notice that the site-swapping process does not affect the formation of spatial distributions within the bulk of the defensive alliances. This is the reason why the domain-expansion process is hardly affected by the actual value of X if $X < X_{c1}$. In the opposite case ($X > X_{c1}$) mixed phases of neutral species occur, and some of them can invade the territories of the cyclic defensive alliances. We have checked the invasion dynamics along the straight-line boundaries separating a cyclic defensive alliance from a well-mixed phase of two or three neutral species. We found that the cyclic defensive alliance occupies the neighboring territory with an average invasion velocity proportional to $X_{c1} - X$ if $X < X_{c1}$. Conversely, the territory of a cyclic defensive alliance can be invaded by several well-mixed (symmetric) phase of two neutral species with an average velocity proportional to $X - X_{c1}$. For example, the territory of the $(KK + SS + RR)_c$ alliance could be occupied by the associations $(KK + RS)_m$, $(KK + SR)_m$, $(SS + KR)_m$, etc., which are invadable themselves too.

As a result, significantly different behavior is found for large values of X as demonstrated by a snapshot in Fig. 5. In this case one can observe the formation of three domains $[(KK + SR + RS)_m, (KS + SK + RR)_m$ and $(KR + SS + RK)_m]$, each containing three mutually neutral species. For these associations we can distinguish two types of external invaders. The first type finds two competitively inferior species, and only the third member of the association is capable to strike back. For the second type of invaders the situation is reversed: they face two competitively superior and only one inferior species when

attacking the association. Surprisingly, the first (and second) type of invading species belong to the same neutral triplet. Consequently, the association $(KK + SR + RS)_m$ is dominant over $(KS + SK + RR)_m$ defeating $(KR + SS + RK)_m$, which dominates over $(KK + SR + RS)_m$ in turn. Shortly, the cyclic dominance between the three well-mixed neutral triplets maintains a self-organizing pattern analogous to those observed for the spatial Rock-Scissors-Paper game.

When displaying the temporal changes of species distribution one can easily observe the corresponding movement of invasion fronts. Both the typical domain size and the average thickness of boundary layers depend on the intensity of mixing (X). In this self-organizing pattern the average densities of species are the same, $\rho_i = \frac{1}{3}$ for all i .

The second phase between X_{c1} and X_{c2} resembles both the first and the third phase in many respects, but the quantities p_c or p_m , and the quantitative analysis of fluctuations also indicate striking differences between them. Fig. 6 shows a snapshot of the second phase, illustrating the appearance of all possible three-species cyclic defensive alliances and two-species neutral domains as well as the cyclic invasions among the latter.

Besides, one can also observe the well-mixed states of two neutral species. In fact, a previous analysis of the six-species subsystems (Szabó, 2005) has justified the appearance of this state for $X > 0.0595(5)$. This means, for example, that at the boundaries of $(KK + SS + RR)_c$ and $(KR + SK + RS)_c$ the two-species well-mixed states,

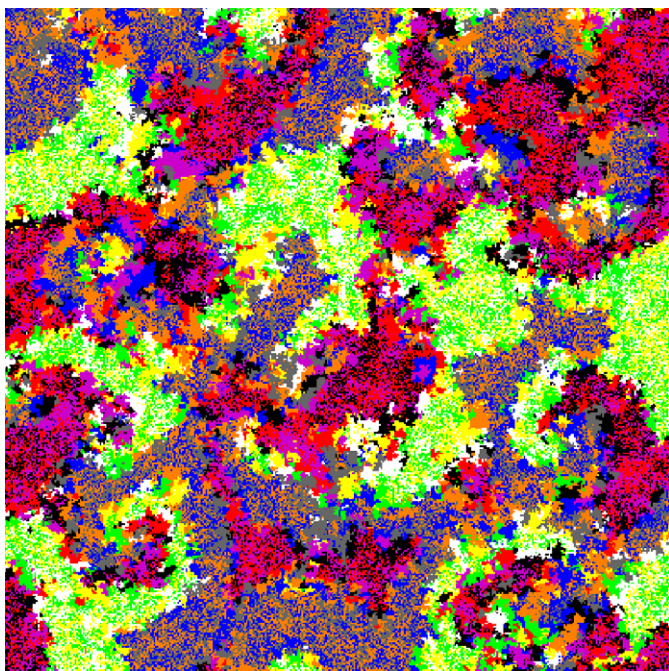


Fig. 5. Typical (400×400) snapshot in the self-organizing stationary state for $X = 0.16$. There are three coexisting domains $(KK + SR + RS)_m$, $(KS + SK + RR)_m$ and $(KR + SS + RK)_m$, each containing three mutually neutral species.

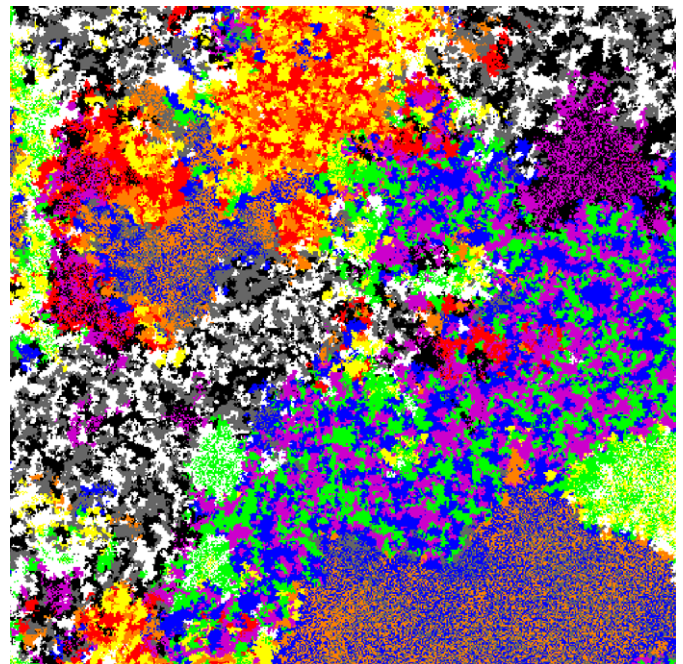


Fig. 6. A typical (500×500) snapshot of the spatial distribution of species and associations at $X = 0.066$ and $L = 2000$. Both three-species cyclic defensive alliances $(KK + SS + RR)_c$, $(KS + SR + RK)_c$ and $(KR + SK + RS)_c$ and two-species neutral domains $(KK + RS)_m$, $(SS + KR)_m$ and $(RR + SK)_m$ are present.

$[(KK + RS)_m, (SS + KR)_c]$ and $(RR + SK)_m]$ become stable. Consequently, one of the latter phases expands until encountering its mortal enemy which can defeat both of its members. Recalling the former example, the domain of $(KK + RS)_m$ can be occupied by species RK . The invasion of species RK , however, is immediately followed by the invasion of one of the competitively superior ones (species SK , SR and RR). Thus, within a short time the domain of $(KK + RS)_m$ is completely eliminated. In some time the phase boundary between $(KK + SS + RR)_c$ and $(KR + SK + RS)_c$ builds up again and a new two-species well-mixed phase pops up—the birth of a Phoenix from its ashes (Foster, 2006). In the present case, however, the newborn Phoenix may have different colors.

Notice that the intensity of diffusion is irrelevant within both types of domains and becomes relevant only at the boundary layers separating the two types of coalitions. On the one hand, neutral coalitions attain maximum stability in the well-mixed phase which is not affected by further enforced mixing: neutral coalitions are well mixed even at low values of X . On the other hand, since cyclic dominance coalitions do not contain neutral pairs at all, site swaps between neutral pairs is out of question in those. Diffusion plays a decisive role within the boundary layer, however: the larger the X value, the easier it becomes for the neutral coalitions to invade the domains of cyclic dominance coalitions.

The consecutive elimination of two-species well-mixed phases generates wild fluctuations in species densities. Fluctuation can yield the extinction of some species and finally the system approaches one of the absorbing states (with two or three mutually neutral species) at lattice sizes

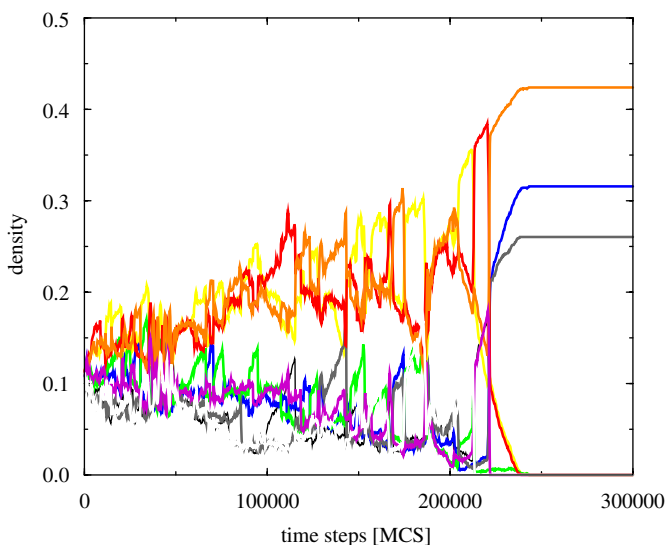


Fig. 7. Species densities as a function of time during the MC simulations at $X = 0.066$ and $L = 800$. The elimination of two-species well-mixed phases generates wild fluctuations in species densities. At lattice sizes not large enough the fluctuations may lead to the extinction of some species. Finally the system approaches one of the absorbing states with two or three mutually neutral species surviving.

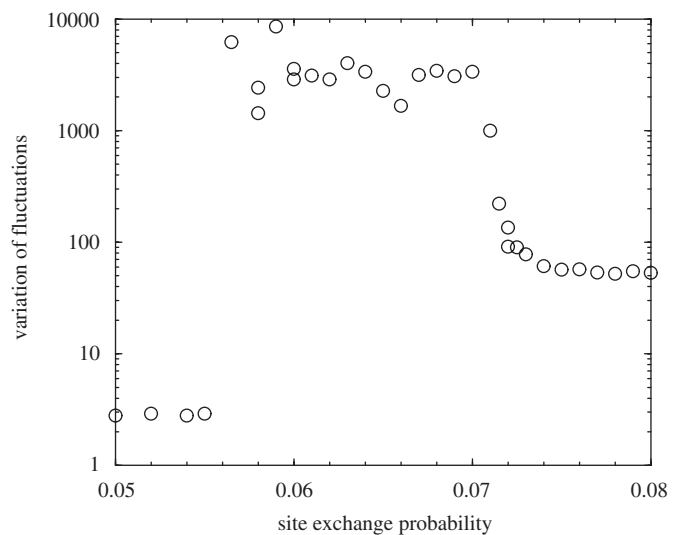


Fig. 8. Log–lin plot of the variation of fluctuation χ versus site exchange probability X . The consecutive elimination of two-species neutral domains produces high χ values in the second phase.

not large enough, as shown in Fig. 7. The catastrophic role of fluctuations can be avoided by choosing suitable lattice sizes (e.g., $L = 3200$). In this case the self-organizing patterns can be maintained for long times (the longest run time was 2×10^6 MCS).

The variation of fluctuations is quantified by the average value of χ for different mixing rates. Fig. 8 shows clearly that χ is significantly larger in the second phase compared to the other two phases. At the same time we could not detect relevant variation of χ within the second phase. The large uncertainties in χ are related to the long relaxation times. It is worth mentioning that the present data do not suggest the divergence of χ when approaching the transition points X_{c1} and X_{c2} .

The classification of the phase transitions at X_{c1} and X_{c2} requires further systematic investigations including a quantification of the ways of coexistence for many-species associations.

6. Discussion

Our model presents a surprisingly rich variety of ecological coexistence patterns, resulting from cyclic competitive relationships. With increasing the diffusion parameter X , the model exhibits three conspicuously different dynamical behaviors in turn, with two subsequent phase transitions. These phases correspond to particular “communities” which differ markedly in both the set of coexisting species and the associated spatial pattern.

A common feature of all phases is the presence of few-species domains, which contain either cyclically dominant or mutually neutral species. These domains interact with each other in various ways, resulting in a spatial structure that can be characterized by different spatial and temporal scales. This kind of embedded, multi-level spatiotemporal pattern is a general feature of natural ecosystems, which is,

however, rarely reproduced by simple population dynamical models with local interactions.

At low diffusion rates domains of defensive alliances are formed by cyclically (double) dominant species (e.g., $KK + SS + RR$). Double dominance within the alliance implies that the two possible external invaders of any member of an alliance are inferior to the next member of the alliance (the one that defeats the attacked member on both loci). For example, SS can be attacked by KS and SK , but both KS and SK are dominated by KK , the successor of SS within the alliance. And KK is always there to defend SS , because it is chasing it all the time. This means that any member of an alliance is defended by its within-alliance successor, which is its strongest competitor—i.e., its most desperate enemy. Intensive cyclic competition within the domains of the alliances maintains a self-organizing pattern and helps the allied members to protect each other against external invaders. This property warrants the integrity of these patches and their dominance over many other cyclic, three-species associations (e.g., $KK + KS + KR$). Due to the high level of symmetry within the interaction topology of the system the three cyclic defensive alliances are equivalent. Consequently, their domains expand parallel and sooner or later all except one of them goes extinct. We are currently exploring the effects of relaxing much of the symmetry assumed so far.

At high diffusion rate, the structural role of individual species and three-species domains is reversed. The domains are composed of three competitively neutral species. Surprisingly, the three domains themselves are in cyclic dominance relationship with each other. As a consequence, this spatial Rock-Scissors-Paper game between domains enables the coexistence of all the nine species.

The intermediate phase represents another, more complex structure keeping all the species coexistent. In the corresponding spatiotemporal patterns both types of coalitions (three-species cyclically dominant and neutral) are present at the same time. Along the borders separating two three-species cyclic coalitions, however, additional phases (consisting of two neutral species in a well-mixed spatial distribution) occur and expand until they meet their strongest enemy that can invade their territories. Thus the neutral, two-species coalitions are continuously eliminated and re-constituted along the borders between the cyclic defensive alliances.

From a theoretical point of view the present model represents a multi-species spatial system exhibiting many possible solutions. The large number of possible solutions comes from a simple fact; the solutions of all the possible subsystems are also solutions of the whole system. This situation raises the natural question: Which solution will be preferred by the update rules defined at the microscopic level? The Monte Carlo simulations have justified that a small number of possible solutions have a distinguished role. These favored solutions are observable on large territories of the arena and can be considered as biological entities at a larger spatial scale and of a specific internal

structure. In many cases the long-time outcome is governed by the competition between these higher-level objects (associations) as discussed by Johnson and Boerlijst (2002). At the same time, the boundary layers play only a minor role in general. Sometimes, however, the role of boundary layers becomes crucial, as they might control the composition of the separated associations—as it happens in a four-species cyclic competition model with a site swap between neutral pairs (Szabó and Sznaider, 2004). The present model demonstrates that boundary layers between species associations may catalyze the appearance and the expansion of new associations.

Our competition model is a simple description of “chemical warfare” between bacterial species. Nevertheless, in order to assess the importance of cyclic dominance networks within ecosystems in general, it is worth investigating what the cyclical competitive subsystems in our bacterial example are caused by. The implicit assumptions of our model were that both adaptation to an environment and artificially altering the environment is costly. Moreover, we assumed that the remaining energy is devoted to an efficient way of resource utilization. Due to the limited amount of metabolic resources, the resultant trade-off between the different traits guarantees a cyclic competitive dominance network between species investing differently into particular traits. These weak requirements foreshadow the generality of cyclic competitive relationships in nature.

The high number of potentially involved traits, which implies a large number of potential phenotypes, raises the question how the structural properties of the emerging network change with an increasing number of components. In the bacterial model, one toxin and resistance factor result in a Rock-Scissors-Paper type of interaction network, whereas two toxins and resistance factors result in an already much more sophisticated competitive network with longer internal loops. Our model system contains nine four-species cyclic subsystems [e.g., $(KK + SK + RS + RR)$] whose behavior was already studied for different mixing mechanisms. What turned out is that the four-species state (maintained by cyclic invasions) segregates into expanding domains of neutral pairs if mixing (X) exceeds a threshold value. Recalling the latter example, the cyclic association $(KK + SK + RS + RR)_c$ can transform into well-mixed $(KK + RS)_m$ or $(SK + RR)_m$ because these are also defensive alliances within the given four-species subsystem (Szabó and Sznaider, 2004; Szabó, 2005). Finally, we emphasize that this model involves three six-species subsystems (those containing the species of two cyclic defensive alliances) in which the phase transitions enforced by the variation of X were investigated earlier (Szabó, 2005). In general, with increasing combinations of different interference, adaptation and resource utilization traits an incrementally complicated competitive network structure is expected, with longer and longer cycles appearing in addition to short ones. Notice, however, that although the investigated competitive network contained

higher, four-species and six-species subsystems, they did not show up as spatially distinct structural units, suggesting that short cycles indeed play a special role.

The behavioral richness of the present model is related to the existence of two different types of species coalitions whose stability against each other is tuned by a single parameter (X). More complex behavior is expected for less symmetric models, e.g., by assuming different invasion rates and/or varying the topology of the interaction network. Such modifications can yield cyclic dominance relations between the associations which would be equivalent (and neutral) in the symmetric case (Perc et al., 2007). We think that cyclically dominated spatial species associations may be much more common in ecological systems than they are in the ecological literature at present.

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