Defensive alliances in spatial models of cyclical population interactions

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As a generalization of the three-strategy Rock-Scissors-Paper game dynamics in space, cyclical interaction models of six mutating species are studied on a square lattice, in which each species is supposed to have two dominant, two subordinated, and a neutral interacting partner. Depending on their interaction topologies, all imaginable systems can be classified into four (isomorphic) groups exhibiting significantly different behaviors as a function of mutation rate. In three out of four cases three (or four) species form defensive alliances that maintain themselves in a self-organizing polydomain structure via cyclic invasions. Varying the mutation rate, this mechanism results in an ordering phenomenon analogous to that of magnetic Ising systems. The model explains a very basic mechanism of community organization, which might gain important applications in biology, economics, and sociology.

The Rock-Scissors-Paper (RSP) game is certainly one of the least sophisticated games to play, yet one of the most interesting subjects of game theoretical studies [1]. The rules of the game are indeed very simple: each of two opponents choose a strategy from the strategy set R, S, P, neither knowing the choice of the other. The strategies chosen compete; the winner is determined according to a cyclic scheme of dominance: R beats S beats P beats R. If the opponents choose the same strategy, the outcome is a draw.

The RSP game and its generalizations have received considerable attention as models of cyclic interactions in biology and in economics [2,3]. Added to the classical textbook example of the cyclic preference system of mating partner choice in females of the lizard species *Uta stansburiana* [4], a multispecies version of the RSP game has been used recently as a model for cyclic interference competition among different strains of bacteriocin-producing bacteria [5,6]. The strategies are assumed to be genetically determined traits in most biological applications: the individuals pass their strategy over to their offspring (i.e., the strategies are heritable). The basic assumption of such applications of the generalized RSP game as models of population interactions is that pairs of individuals of a population repeatedly play the RSP game (or a similar game of cyclical interaction topology) against each other, receiving payoffs according to the outcome of the interaction.

Some theoretical aspects of cyclic dominance in multispecies RSP models have already been thoroughly investigated [1,7–9]. The analyses have justified that site invasions based on payoff asymmetry (i.e., takeovers of the loser's site by the winner) maintain a self-organizing domain structure within a d-dimensional lattice if n, the number of strategies (species) is less than a (d dependent) threshold value for $d \geq 2$ [10]. Our analysis will be restricted to sufficiently large systems in which drift due to finite system size does not play a decisive role.

Further generalization of the multistrategy RSP model is possible by allowing for a reticulate topology of the still cyclic dominance graph, so that each strategy can have more than one dominant and more than one subordinated opponents within the strategy set. In a previous paper [5] we have studied a model of bacteriocin-mediated competition among nine strains of toxin-producing bacteria, which is an example to this type of generalization. We also allowed for strains to mutate into each other in that model, with mutation rates set according to loss rates of toxin and resistance genes. Numerical analysis of the model has revealed that this system undergoes a critical phase transition belonging to the universality class of that of the three-state Potts model [11,12], if mutation rates decrease below a critical value. For high mutation rates, all the nine species are present with the same probability. For low mutation rates, however, one of three equivalent "coalitions" or "defensive alliances" takes over in finite time, due to unlimited domain expansion within the finite grid. The alliances consist of three species each, and their stability is related to cyclic within-domain invasions [8] providing protection against external intruders.

A defensive alliance is a directed circuit in the interaction graph, each member of which is defended against its external dominant by its within-alliance (internal) dominant. More precisely, if R, S, and P are the members of a defensive alliance, and X is an external intruder dominant over R (X beats R), then P is dominant over X (P beats X).

To specify somewhat more general criteria of stability in such systems of cyclical competition in terms of the topology of the interaction graph, we have studied the simplest possible reticulate systems with defensive alliances. The number of interacting strategies (species) has been reduced to five and six, and required each species to have exactly two dominant and two subordinated competitors among the remaining species. The dynamical behavior of the only possible five-species system is very similar to one of the six-species cases, so we concentrate on the six-species models in what follows. Any six-species system satisfying these conditions can be characterized by a directed graph and each one is isomorphic to one of the four graphs shown in Fig. 1.

We have systematically tested these four classes of interaction topologies for the emergence of defensive alliances in
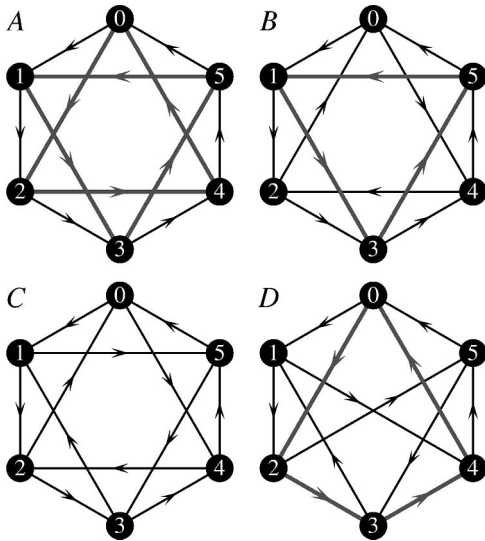
FIG. 1. The interaction topologies are characterized by the directed graphs A, B, C, and D. The bullets represent species labeled by figures. The arrows show the direction of competitive invasion. The species connected by thicker edges form defensive alliances.

FIG. 2. Average stationary concentrations of species as a function of mutation rate for graphs A (pluses), B (closed triangles), C (bullets), and D (open diamonds).

a way similar to that of the previous nine-species model. In the present spatial model each site of a square lattice is occupied by one of the six species. System evolution is governed by nearest neighbor invasion and local mutation. The latter means that a site transforms itself to one of the two dominant species of the actual resident species independently of neighborhood composition. For simplicity, the mutation rate P is the same for all the species, thus P is the only parameter of the model.

The random sequential update consists of the following steps: (1) Random choice of the focal site, (2) decision on mutation, with P being the probability of a mutation event to occur on the focal site; which of the two dominants replaces the focal species is determined at random, (3) if no mutation occurs, one of the nearest neighbors of the focal site is chosen at random and the species on the two sites play a round of the game. If one dominates the other, both sites will be occupied by the dominant (i.e., the dominant species invades the site of the other); nothing changes otherwise.

Notice that each graph of Fig. 1 has a directed Hamiltonian circuit positioned along the peripheries [13]. Graphs A, B, and C have two additional three-edge circuits (with different directions) composed of the remaining six ''internal'' edges, each of which embraces three species potentially forming a defensive alliance.

In case A the system has indeed just these two equivalent defensive alliances consisting of species $0+2+4$ and $1+3$ $+5$. Such an association of the corresponding three species maintains a self-organizing polydomain structure in the spatial model [8], and cyclic invasions prevent the invasion of species external to the alliance. For example, species 1 can invade the territory of species 2 in the $0+2+4$ association, but species 0 is dominant over both 1 and 2. Consequently species 1, the external invader, is soon abolished from the $0+2+4$ domain by 0, the very same species that dominates species 2 within the alliance. *Mutatis mutandis*, the same
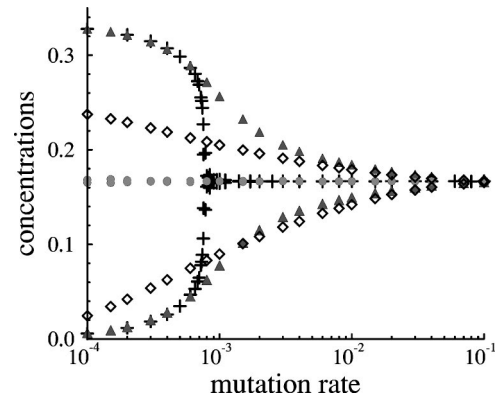
argument applies to the other two (3 and 5) external invaders of alliance $0+2+4$, and the situation is completely symmetric with respect to the defensive mechanism of the $1+3$ $+5$ alliance against 0, 2, and 4 as external invaders.

Graph B admits only one such defensive alliance ($1+3$ $+5$), and any distinguished three-species association is missing from graph C. In this latter case one can find eight equivalent three-species circuits in the corresponding directed graph, but neither is an alliance in the above sense.

The situation is quite different in graph D that has four three-species directed circuits ($1+2+3$, $3+4+5$, $0+1$ $+4$, and $0+2+5$), but neither of the corresponding associations are protected against external invaders in the sense mentioned above. However, this topology exhibits three directed four-species circuits as well, and one of them ($0+2$ $+3+4$) seems to be self-protected.

It is worth mentioning here that graph A involves three additional four-species directed circuits that are also protected, i.e., it is not straightforward to determine from the graph topologies alone, which species or associations would persist in the long run.

We used Monte Carlo (MC) analyses to predict the stationary distribution of competing species for each of the four graphs. The MC simulations have been performed on a square lattice of size $L \times L$ with periodic boundary conditions for different mutation rates P and interaction topologies. System size varied from $L=300$ to 2000. We used larger grids to suppress the undesired consequences of increased fluctuations we have found in some cases. The initial configurations have been assembled at random, each species having the same chance to occupy a site. After some thermalization we have recorded the concentrations of the species, averaging over a sampling time ranging from 10^4 to 5 $\times 10^5$ MC steps per site, as required by the actual fluctuations.

The results of the simulations are summarized in Fig. 2. The simplest case is C, where all the species are present in equal abundances in the stationary state if $P>0$ and the lattice is sufficiently large. The same applies to the five-species case mentioned above. System A behaves similarly if the mutation rate exceeds a critical value ($P>P_c$). Below this transition point one of the defensive alliances ($0+2+4$ or

$1+3+5$) takes over. In each of graphs B and D there exists only one defensive alliance whose dominance increases smoothly as the mutation rate decreases towards 0.

Figure 2 clearly demonstrates that in the limit $P \rightarrow 1$ (when mutation governs system evolution alone) the species concentrations become equal. Apart from this limiting case, the species belonging to the dominating alliance (if there exists such) are present in the same abundance (concentration). That is, in the limit $P \rightarrow 0$ the ''allied'' species concentrations tend to either 1/3 (for graphs A and B) or 1/4 (D).

For model A the detailed analysis shows that the P dependence of average concentrations can be described by introducing an order parameter as

$$\langle c_0 \rangle = \langle c_2 \rangle = \langle c_4 \rangle = \tfrac{1}{6}(1 \pm m),$$

$$\langle c_1 \rangle = \langle c_3 \rangle = \langle c_5 \rangle = \tfrac{1}{6}(1 \mp m), \qquad (1)$$

where $m=0$ if $P > P_c$, otherwise the order parameter is larger than zero ($0 < m \leqslant 1$). The results of our MC simulations support the fact that the order parameter follows a power law behavior [$m \propto (P_c - P)^{\beta}$] below the critical point in the close vicinity of P_c. The best fit is found for $\beta = 0.127(8)$ and $P_c = 0.0007515(5)$. Within the statistical error, this value of β agrees with that found for the two-dimensional Ising model ($\beta_{\text{Ising}} = 1/8$) [14,12]. In the present case the ordered phase is twofold degenerated because only one of the two defensive alliances survives (with the same probabiliy) in the limit $P \rightarrow 0$. It is therefore not surprising that the corresponding critical transition belongs to the universality class of the Ising model [15].

In order to have further numerical evidences concerning this critical transition we have studied the concentration fluctuation defined as

$$\chi = L^2 \sum_s \langle (c_s - \langle c_s \rangle)^2 \rangle, \qquad (2)$$

where summation runs over the species ($s = 0, \ldots, 5$). For model A this quantity diverges at the critical transition on large lattices. More precisely, our MC data can be well approximated by a power law, $\chi \approx |P - P_c|^{-\gamma}$ in the vicinity of P_c. Below and above the critical point, numerical fitting yields $\gamma = 1.0(2)$ and $\gamma' = 1.1(2)$, respectively, in agreement with the theoretical expectation $\gamma_{\text{Ising}} = \gamma'_{\text{Ising}} = 1$ [12].

Figure 3 compares the P dependence of χ we obtained by MC simulations for the different interaction graphs. χ remains low for graphs B and D, but this quantity diverges for C (as well as for the five-species system), in which case the power law fit yields $\chi \propto P^{-\gamma}$ with $\gamma = 0.72(3)$ in the limit $P \rightarrow 0$. This behavior implies a critical transition at $P=0$. Consequently, in the absence of mutation some ordering process is expected that is studied via considering the time dependence of correlation length at zero mutation rate [16].

If the system is started from a random initial state, then the visualization of the species distribution exhibits an ordering process for all these models at $P=0$. The situation is easy to understand for graphs B and D. In these cases the
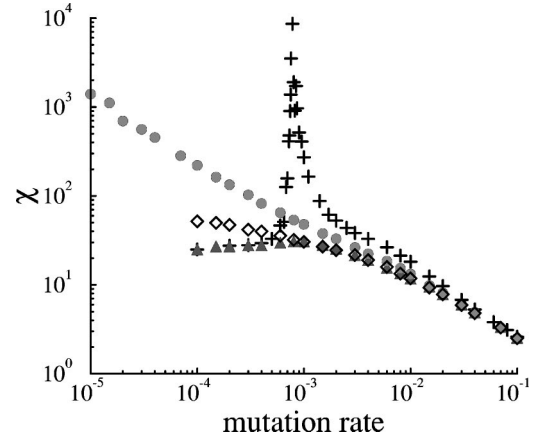

FIG. 3. Concentration fluctuations vs mutation rate for the four models. The MC data are indicated by the same symbols as in Fig. 2.

models admit only a single defensive alliance that emerges in the whole system homogeneously. Therefore the species concentrations tend exponentially towards the stationary values plotted in Fig. 2. For graph A, however, there exist two equivalent defensive alliances both forming domains of increasing size, in close analogy to the Ising models for zero magnetic field. It is emphasized that inside the domain of a defensive alliance, cyclic invasions maintain a self-organizing three-color pattern, just as in another multicycle RSP model [5]. The numerical analysis of the ''first zero'' of the equal-time pair correlation function ($C[\xi_0(t), t] = 0$) supports the fact that the deduced characteristic linear size of domains follows the usual growth law, namely, $\xi_0(t) \propto \sqrt{t}$ [16].

As mentioned above, graph C has eight equivalent three-species cycles and each one can dominate the system with the same chance in the stationary state for finite lattice size if $P=0$. The visualization of species distribution again indicates spatial ordering. The most striking feature is the extinction of several species from certain regions, and that the size of such regions increases with time. The quantitative analysis of the equal-time pair correlation function confirms the expected results, i.e., the corresponding correlation length increases as $\xi(t) \propto \sqrt{t}$. Here the correlation length is derived by fitting an exponential function ($e^{x/\xi(t)}$) to the MC data of $C(x,t)$ obtained by averaging over five runs for $L=5000$.

In all these finite-size systems the number of surviving species is reduced to three (or four for graph D) via a domain growth mechanism, and the coexistence of the surviving species is maintained by cyclic invasions. Although the interaction graphs studied may admit many possible cycles, we found that evolution favors certain topological structures that we call ''defensive alliances'' capable of protecting themselves from external invasion.

System behavior can be predicted by thoroughly studying the potential alliances within the interaction graph of the model in question. In two of four graphs (B and D) there is only a single defensive alliance, and that one inevitably dominates the system in spite of the permanent attacks by mutants and external invaders. If the interaction graph admits

two equivalent defensive alliances (A), the population undergoes a critical phase transition (accompanied with spontaneous symmetry breaking) when varying the mutation rate. This means that above a critical rate of mutations ($P > P_c$) all the species persist with the same average concentration in the stationary state, whereas below P_c the members of one of the defensive alliances take over, driving all other species extinct.

It is interesting that the four-species alliances of graph A do not show up at all in the system. The reason for this might be twofold: (1) the four-species alliances are overlapping, that is, each species is a member of more than one alliance; (2) it is topologically easier to maintain a three-species alliance within a two-dimensional lattice, because the neighborhood relations of the allies chasing each other is more probable to persist in space among three rather than among four species. In the fourth case (C) the graph has eight equivalent three-species cycles whose self-organizing patterns are easily destroyed by external invaders and mutants, because none of them form defensive alliances. Consequently, external invasions and the appearance of mutants stop domain growth (which can be observed locally for $P = 0$) and maintain a global state with equal species concentrations.

Just as in many other models of ecological processes [17], pattern formation plays a crucial role in the self-protection of defensive alliances: an external intruder is quickly abolished from the domain of an alliance, because the internal enemy of the intruder is close by—it is chasing the attacked species over the lattice. Similar spatiotemporal patterns have been observed in other models (e.g., in models of forest fires [18], evolutionary games [19], etc.) in which the invasion speeds were different for different pairs of interacting species.

The present systematic study has justified that forming defensive alliances is a powerful mechanism of stable population coexistence in the case of symmetric food-web topology. Species belonging to a defensive alliance attain higher concentrations than those not defended by other species. In systems with more than one equivalent defensive alliances for a given food web, symmetry-breaking phase transition can occur along mutation rate as the control parameter. We expect nonsymmetric topologies to admit defensive alliances as well, implying stable coexistence in real multispecies systems.

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