

# Instability of defensive alliances in the predator-prey model on complex networks

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A model of six-species food web is studied in the viewpoint of spatial interaction structures. Each species has two predators and two preys, and it was previously known that the defensive alliances of three cyclically predating species self-organize in two dimensions. The alliance-breaking transition occurs as either the mutation rate is increased or interaction topology is randomized in the scheme of the Watts-Strogatz model. In the former case of temporal disorder, via the finite-size scaling analysis, the transition is clearly shown to belong to the two-dimensional Ising universality class. In contrast, the geometric or spatial randomness for the latter case yields a discontinuous phase transition. The mean-field limit of the model is analytically solved and then compared with numerical results. The dynamic universality and the temporally periodic behaviors are also discussed.

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The rock-scissors-paper (RSP) game [1] gives a typical three-strategy model of cyclical predator-prey food chain if rock, scissors, and paper are replaced by different competitive species in biology. In this simple game, a rock beats a pair of scissors, a pair of scissors beat a sheet of paper, and a sheet of paper beats a rock. As generalizations of the RSP game, the food webs composed of different numbers of species show a variety of interesting behaviors [2]. Especially, the models proposed by Szabó and Czárán in Refs. [3,4] have been shown to self-organize to form the defensive alliances, which become unstable as the mutation rate is increased.

In the present study, we use the model A in Ref. [3] described by the interaction topology in Fig. 1(a), where the six species weave a food web that is more complicated than the RSP game: Each species has two predators, two preys, and one neutral interacting partner. There indeed exist ecological systems showing the cyclic dominance: Examples include the three-morph mating system in the side-blotched lizard in which each morph dominates another morph when rare [5]. Another example is the system of three different populations of *Escherichia coli* [1] composed of toxin-producing ( $T$ ), toxin-resistant ( $R$ ), and toxin-sensitive ( $S$ ) strains. If the growth rate of each group satisfies  $S > R > T$ , the RSP game captures the cyclic dominance in the system:  $T$  dominates  $S$  ( $S$  is killed by  $T$ ),  $S$  dominates  $R$  due to the higher growth rate, and  $R$  dominates  $T$  for the same reason. If bacteria produce two different toxins, the food web is constructed from nine different species as has been well studied in Ref. [4].

The main interest here is to study the effect of the spatial interaction structure and for that purpose, we play the predator-prey game on the complex network structure of the

Watts-Strogatz (WS) network [6] constructed on two-dimensions (2D) as follows: (i) We first build the  $2D L \times L (N \equiv L^2)$  regular square lattice. (ii) Every bond is visited once, and with the rewiring probability  $\alpha$  it is rewired to the randomly chosen other site. The above procedure then yields a network structure which possesses characteristics such as the short characteristic path length [6,7].

Once the network is built as described above, the time evolution of the system obeys the following rules [3]: (i) Six species are scattered randomly on a square lattice as in Fig. 1(b), then (ii) the species on each randomly chosen site is mutated to one of its predating species with the mutation rate  $P$ . (iii) If no mutation occurs (with the probability  $1 - P$ ), one of the nearest neighbors is chosen to interact, and the dominant one survives and invades the subordinated one. For example, if the pair of species 0 and 1 are chosen, the species 1 is replaced by the species 0 [see Fig. 1(a)]. If two neutral partners have been chosen, i.e., no arrow connects the two species in Fig. 1(a), nothing happens. For the 2D regular square lattice corresponding to the rewiring probability  $\alpha = 0$ , it has been found that the defensive alliances composed of three species, (0,2,4) or (1,3,5), are spontaneously formed at a small mutation rate and the other species that does not belong to the alliance dies out [3] [see Fig. 1(c)]. As the mutation rate is increased, it has been shown [3] that the defensive alliance becomes unstable and there occurs well-defined phase transition of the universality class of the 2D Ising model [8], which is expected because of the existence of the  $Z_2$  symmetry: Interchange of two alliances (0,2,4)  $\leftrightarrow$  (1,3,5) do not change the game rules, which we call here *interalliance symmetry*. The spontaneous breaking of the defensive alliance originates either from the high mutation rate  $P$  or from the high degree of structural randomness controlled by the rewiring probability  $\alpha$ . In other words, the instability of the defensive alliance is induced either by the temporal randomness or by the structural randomness. In reality, these two different types of randomness may coexist. However, from the practical computational difficulty, we in

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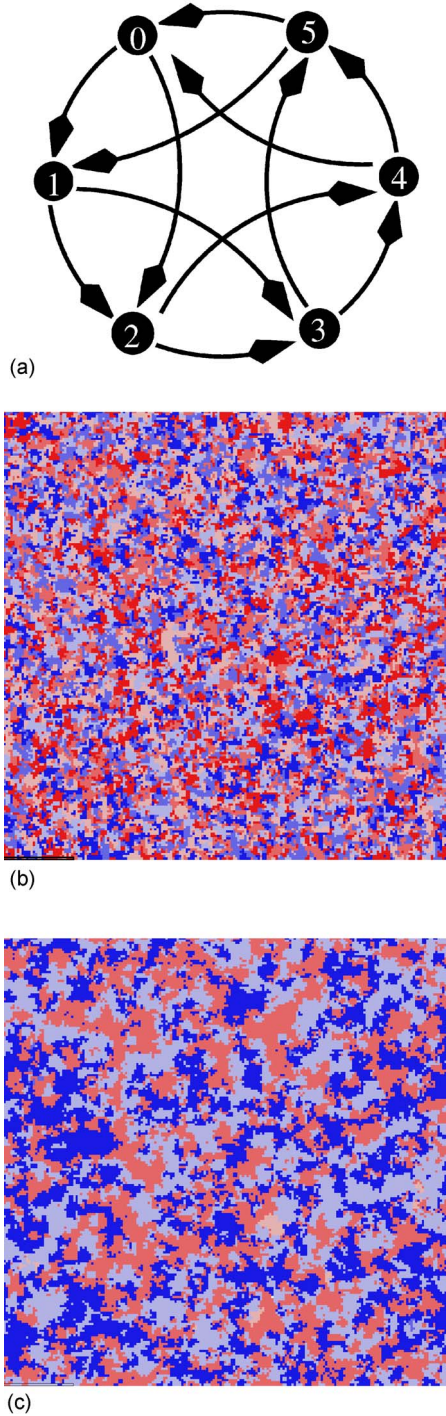


FIG. 1. (Color online) (a) The interaction topology used in this work (model A in Ref. [3]). Arrow, e.g., from 0 to 1 indicates that the species 0 is a predator to the species 1 (and thus the species 1 is the prey to the species 0). As time goes on the initial random configuration in (b) evolves to (c), where only three species [(0,2,4) or (1,3,5)] exist to form the defensive alliance. Different colors indicate different species in (b) and (c).

this paper only investigate the effect of each randomness separately.

We first investigate the phase transition for the 2D regular square lattice corresponding to the WS network with the rewiring probability  $\alpha=0$ . Although this was previously stud-

ied [3], we in this work use the extensive finite-size scaling analysis to confirm not only the 2D Ising static universality class, but also to identify the dynamic universality class detected by the dynamic critical exponent  $z$ . In order to describe the alliance breaking transition, we define the order parameter which functions as a magnetization in the Ising model as follows:

$$m = (c_0 + c_2 + c_4) - (c_1 + c_3 + c_5), \quad (1)$$

where  $c_s \equiv N_s/N$  ( $s=0, \dots, 5$ ) is the density of species  $s$  with  $N_s$  being the number of sites occupied by  $s$ . When  $P$  is sufficiently small, the defensive alliance is formed with  $c_0 \approx c_2 \approx c_4 \approx 1/3$  and  $c_1 \approx c_3 \approx c_5 \approx 0$  or vice versa, leading to  $m \approx \pm 1$  (ordered phase). When the system recovers its full symmetry at a high mutation rate, all species have the same density, yielding  $m \approx 0$ . Only for convenience, we use

$$\mu \equiv \ln(1/P) \quad (2)$$

as a control parameter. High mutation rates correspond to the small values of the mutation parameter  $\mu$ , and thus qualitatively speaking, the physical meaning of  $\mu$  resembles that of the inverse temperature in the standard statistical mechanics.

Numerical simulations are performed on systems of sizes varying from  $L=32$  to 192 with the periodic boundary conditions employed. After equilibration for  $10^4$  steps per site, which is sufficiently long enough, the thermal average is computed for later  $10^4$  steps at least. The measured quantities are  $\langle |m| \rangle$ , the Binder's cumulant [9],

$$U_L \equiv 1 - \frac{\langle m^4 \rangle}{3\langle m^2 \rangle^2}, \quad (3)$$

and the susceptibility,

$$\chi \equiv N(\langle m^2 \rangle - \langle |m| \rangle^2), \quad (4)$$

where  $\langle \dots \rangle$  denotes the thermal average. In order to study dynamic critical behavior, we also measure the autocorrelation function as a function of time  $t$  defined by

$$C(t) \equiv \langle |m(t)m(0)| \rangle - \langle |m| \rangle^2. \quad (5)$$

The finite-size scaling forms of measured quantities are written as [10]

$$\langle |m| \rangle = L^{-\beta/\nu} \tilde{m}[(\mu - \mu_c)L^{1/\nu}], \quad (6)$$

$$U_L = \tilde{U}((\mu - \mu_c)L^{1/\nu}), \quad (7)$$

$$\chi = L^{\gamma/\nu} \tilde{\chi}((\mu - \mu_c)L^{1/\nu}), \quad (8)$$

$$C(t)/C(0) = \tilde{C}(tL^{-z}), \quad (9)$$

where  $\tilde{m}$ ,  $\tilde{U}$ ,  $\tilde{\chi}$ , and  $\tilde{C}$  are suitable scaling functions,  $\mu_c$  is the critical value of  $\mu$ , and  $\beta$ ,  $\gamma$ ,  $\nu$  are standard critical exponents [8], while  $z$  is the dynamic critical exponent defined at  $\mu_c$  from the divergence of the relaxation time scale ( $\tau \sim L^z$ ).

Figure 2 summarizes the numerical results for the phase transition in the 2D regular lattice. The order parameter  $\langle |m| \rangle$  shown in Fig. 2(a) exhibits the existence of the transition,

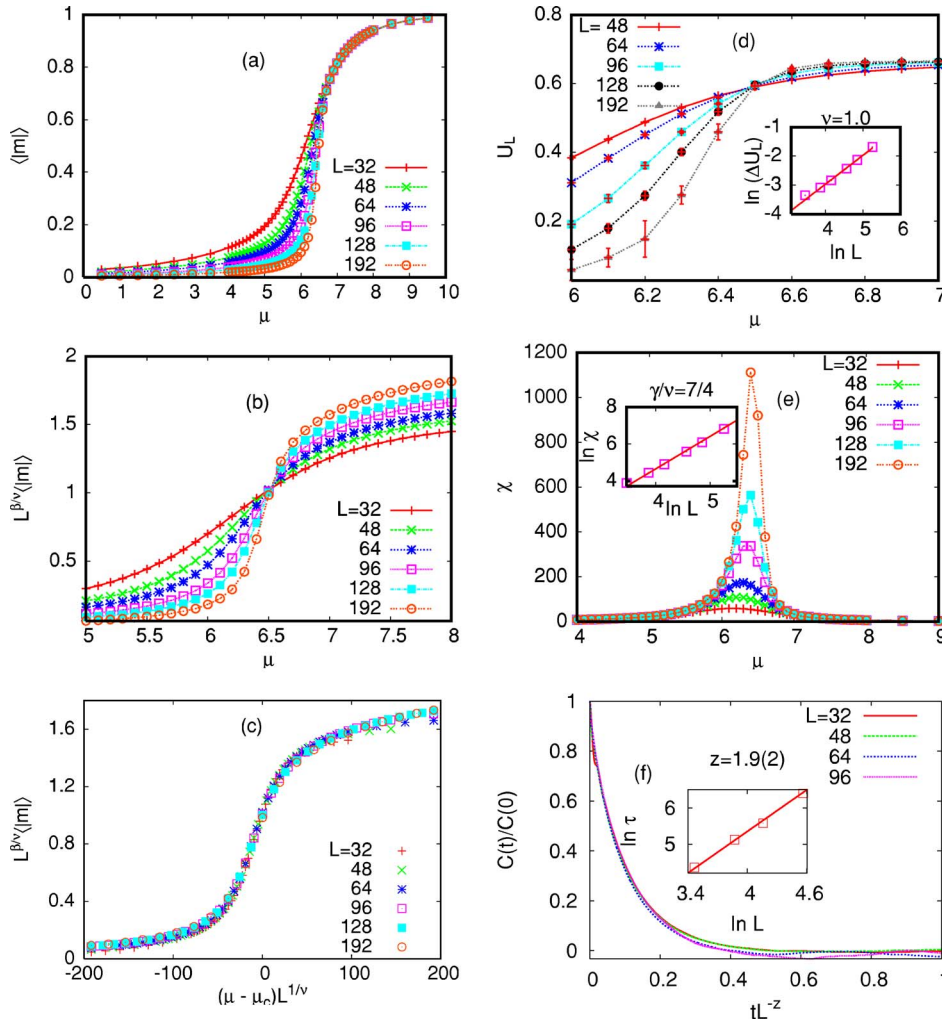


FIG. 2. (Color online) Phase transition in the 2D regular lattice in terms of the mutation parameter  $\mu$ . (a) The order parameter  $\langle |m| \rangle$  versus  $\mu$  clearly shows the existence of the alliance-breaking transition. (b) A unique crossing at  $\mu_c = 6.50(4)$  with  $\beta/\nu \approx 1/8$  is obtained from the finite-size scaling form of  $\langle |m| \rangle$ . (c) All data points for  $\langle |m| \rangle$  in (b) collapse into a smooth curve by using scaled variables. (d) Binder's cumulant at different sizes cross at  $\mu_c = 6.50(4)$  in agreement with (b). The inset in (d) shows that  $\Delta U_L \sim L^{1/\nu}$  to yield  $\nu \approx 1$ , where  $\Delta U_L \equiv U_L(\mu_1) - U_L(\mu_2)$  with  $\mu_{1,2}$  are two adjacent points near  $\mu_c$ . (e) Shows the susceptibility  $\chi$ . The inset shows a log-log plot of  $\chi$  versus  $L$  at  $\mu_c$  leading to  $\gamma \approx 7/4$ . (f) The autocorrelation function  $C(t)/C(0)$  at  $\mu_c$  versus  $tL^{-1.9}$  with  $z = 1.9$ . All curves for different sizes collapse well to a single curve, indicating that the dynamic critical exponent  $z = 1.9(2)$ .

which is analyzed in detail in Figs. 2(b) and 2(c) by using the finite-size scaling form in Eq. (6). The critical point  $\mu_c = 6.50(4)$  as well as critical exponents  $\beta \approx 1/8$  and  $\nu \approx 1$  are obtained, which are confirmed again from the finite-size scaling of the Binder's cumulant shown in Fig. 2(d). The divergence of the susceptibility in Fig. 2(e) is analyzed to get  $\gamma \approx 7/4$ . At  $\mu = \mu_c$ , we compute the autocorrelation function (5) and plot it in Fig. 2(f) in accord with the scaling form in Eq. (9): All curves at different sizes collapse well to a single curve with the dynamic critical exponent  $z \approx 2$ . All these findings clearly confirm that the alliance breaking transition induced by the mutation belongs to the 2D Ising universality class as was known in Ref. [3].

We next study the phase transition induced by the spatial randomness introduced via the long-range shortcut in the WS network model. One can motivate the study along this direction since in real systems, the spatial interaction topology among species can be much more complicated than the nearest-neighbor interaction on a regular square lattice. Distinguished from the regular network, the small-world network [6,7], which captures characteristics of many real networks very well, has a remarkably small average path length similar to the globally coupled network (or the mean-field case). The three-strategy RSP game has been studied on some small-world networks and the periodic flourishes of

three strategies were found to happen during the time evolution [11].

We fix the mutation parameter to  $\mu = 7.0$ , which is well inside the ordered phase with the defensive alliance formed for the 2D regular square lattice (see Fig. 2). Use of a very large value of  $\mu$ , corresponding to very small mutation rate, was found to make the system approach a local dynamic fixed point and then the system stays there forever. At  $\mu = 7.0$ , which is small enough to ensure the equilibration and large enough to make the system ordered at small  $\alpha$ , the system is found to undergo a phase transition at  $\alpha = \alpha_c \approx 0.28(1)$  as displayed in Fig. 3. The abrupt drop down of the order parameter  $\langle |m| \rangle$  at the transition as displayed in Fig. 3(a), together with the change of the histogram  $H(m)$ , normalized to satisfy  $\sum_m H(m) = 1$  [in Fig. 3(b)] clearly indicates that the transition is of the discontinuous nature in a sharp contrast to the finding for 2D regular lattice at  $\alpha = 0$  (see Fig. 2). In more details, the sudden change of the peak position of  $H(m)$  between  $\alpha = 0.28$  and  $0.29$  in Fig. 3(b) is interpreted as strong evidence of a discontinuous transition. Continuous transition, in general, exhibits the continuous shift of the peak position toward  $m = 0$  as the critical point is approached from the ordered phase.

In general, one can study the phase diagram of the model in the 2D parameter space of  $(\mu, \alpha)$ . Due to the practical

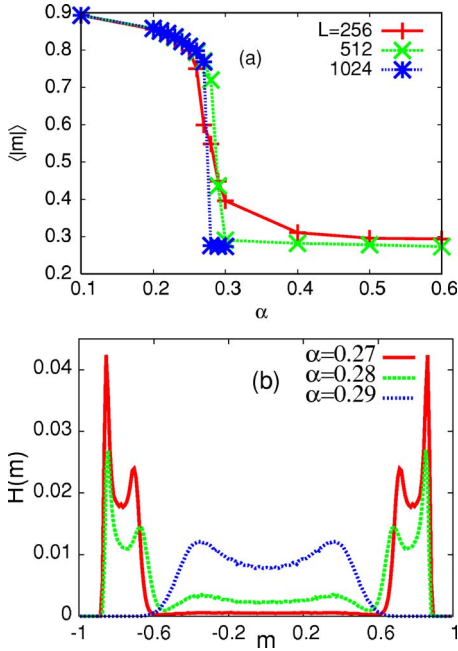


FIG. 3. (Color online) Phase transition in the WS network in terms of the rewiring probability  $\alpha$ . The mutation parameter is set to  $\mu=7.0$ . (a) The order parameter  $\langle |m| \rangle$  as a function of  $\alpha$  shows a sudden drop at  $\alpha_c \approx 0.28$ . The change of  $\langle |m| \rangle$  becomes steeper as  $L$  is increased, indicating that the transition is a discontinuous one. (b) The normalized histogram  $H(m)$  of  $m$  for  $L=1024$  is displayed at  $\alpha=0.27, 0.28$ , and  $0.29$ . The abrupt change in the form of the histogram between  $\alpha=0.28$  and  $0.29$  clearly confirms again discontinuous transition.

difficulty to cover the whole parameter space, we in this work only explore the phase transitions along the two straight lines in the  $(\mu, \alpha)$  plane: One on the axis  $(\mu, \alpha=0)$ , and the other on the line  $(\mu=7.0, \alpha)$ . Both parameters  $\mu$  and  $\alpha$  control the amounts of randomness (temporal and spatial ones, respectively), and accordingly, the ordered phase with the defensive alliance becomes unstable as either  $\mu$  is decreased (i.e., the mutation rate  $P$  is increased) or  $\alpha$  is increased. Not only the phase transitions have different natures (the continuous one belonging to the 2D Ising universality class for the former and the discontinuous one for the latter), but also the ordered and disordered phases in each case are very much different in terms of the time evolution of densities of species. In the ordered and disordered phase on the axis of  $\alpha=0$ , the density of each species does not fluctuate much but stays at almost the same level: For the ordered phase at  $\mu > \mu_c, c_s \approx 1/3$  for  $s \in \{\text{alliance}\}$  and  $c_s \approx 0$  otherwise, while for the disordered phase at  $\mu < \mu_c, c_s \approx 1/6$  for all species. In contrast, the time evolution  $c_s(t)$  for the case of the WS network at  $(\mu=7.0, \alpha)$  is strikingly different. In Fig. 4(a), the time evolutions of densities of species are shown for  $\mu=7.0$  and  $\alpha=0.27 (< \alpha_c)$ . It is clearly shown that the interalliance  $Z_2$  symmetry is broken, indicating that the system has a nonzero value of the order parameter. Another very important observation one can make from Fig. 4(a) is that each species within the alliance ( $s=0, 2, 4$ ) cyclically dominates all the others in a very regular way, and very interestingly, the species that does not belong to the domi-

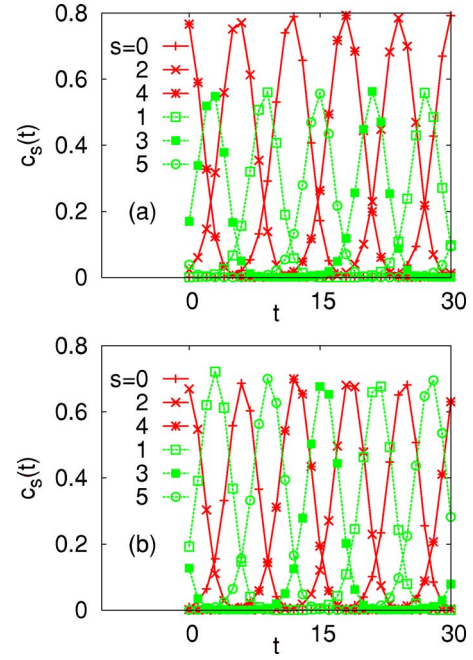


FIG. 4. (Color online) Time evolution of density of species  $c_s(t)$  for the WS network for  $L=1024$  at  $\mu=7.0$ . (a) At  $\alpha=0.27$ , the interalliance symmetry is broken, suggesting  $m \neq 0$ , and each species in the alliance dominates all the other species in a time-periodic fashion. It is interesting to note that the nondominant alliance is also formed and even the member of the nondominant alliance prevails periodically. (b) At  $\alpha=0.29$ , the system recovers its full symmetry and each species is equivalent to others. However, the time evolution of  $c_s(t)$  is still periodic, in contrast to the disordered phase in 2D regular lattice. The time  $t$  is measured after stationarity is achieved.

nant alliance also prevails in a time-periodic manner. Even in the disordered phase at  $\alpha > \alpha_c$ , the periodic dominance persists while the interalliance symmetry is fully recovered [see Fig. 4(b)].

We finally investigate the mean-field limit of the game [12], where all individual species interact with all the other species in the system. The master equation for the number  $N_s$  of species  $s$  is given by

$$\Delta N_s = P \left( -c_s + \frac{c_{i_1}}{2} + \frac{c_{i_2}}{2} \right) + 2(1-P)c_s(c_{i_1} + c_{i_2} - c_{j_1} - c_{j_2}), \quad (10)$$

where  $\Delta N_s \equiv N_s(t+1) - N_s(t)$ ,  $i_1$  and  $i_2$  ( $j_1$  and  $j_2$ ) are two preys (two predators) of  $s$ . For example, the species  $s=0$  has  $i_1=1, i_2=2, j_1=4, j_2=5$  [see Fig. 1(a)]. The term proportional to  $P$  describes the decrease of  $N_s$  by the mutation from  $s$  to its predators and increase of  $N_s$  by the mutation from its preys to  $s$ . The other term originates from the interaction of  $s$  to other species: When  $s$  meets its preys (predators)  $N_s$  is increased (decreased). The numerical factor two in front of  $(1-P)$  is due to the interaction of other species with  $s$ . If we start from the situation when  $c_0=c_2=c_4=(1+m)/6$  and  $c_1=c_3=c_5=(1-m)/6$ , with the order parameter  $m$  in Eq. (1), the above master equation is reduced to a very simple form

$$\frac{dm}{dt} = m(t+1) - m(t) = -N P m, \quad (11)$$

yielding the solution

$$m(t) = m(0)\exp(-t/\tau) \quad (12)$$

with  $\tau = PN$ . The mean-field solution indicates that there is no ordered phase at any nonzero value of the mutation rate, i.e., *the defensive alliance cannot be formed in the mean-field limit*. It is also noteworthy that the time-periodic behavior observed for the WS network in Fig. 4 ceases to exist in the mean-field case. The simulation results displayed in Fig. 5 for the mean-field model are in perfect agreement with the above analytic findings: The ordered phase that appears to exist for small system sizes drifts away toward the region of higher value of  $\mu$  as  $N$  is increased, suggesting the disappearance of the ordered phase in the thermodynamic limit [see Fig. 5(a)]. There is no time-periodic behavior of  $m$  in equilibrium as shown in Fig. 5(b), where  $t$  is measured after equilibration.

In summary, we have investigated the instability of the defensive alliances for the simple food web of six species in three different spatial interaction structures: the 2D local regular square lattice, the WS network, and the globally coupled mean-field network. The temporal randomness imposed by the mutations as well as the spatial randomness in the interaction structure tuned by the rewiring probability in the WS network has been shown to make the defensive alliance unstable. When the mutation rate is increased for the 2D square lattice, the alliance-breaking transition has been clearly identified to belong to the 2D Ising universality class due to the common  $Z_2$  symmetry. On the other hand, when the rewiring probability is increased, the transition becomes discontinuous, and around the transition the natures of the ordered and disordered phases are very different from the 2D square lattice. The mean-field model has also been studied analytically and numerically with the results that the defensive alliance cannot be formed at any value of the mutation

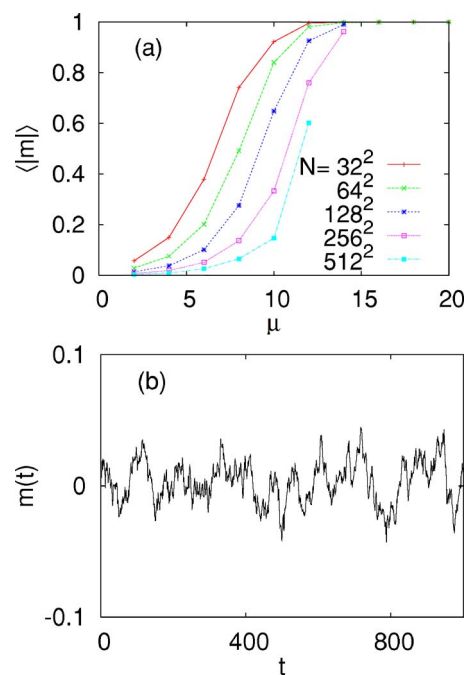


FIG. 5. (Color online) Numerical results for the mean-field case. (a) The order parameter  $\langle |m| \rangle$  versus  $\mu$  for  $N = 32^2, 64^2, \dots, 512^2$ . As  $N$  is increased, the region for the ordered phase shifts toward higher values of  $\mu$ , indicating that the defensive alliance vanishes in the thermodynamic limit at any nonzero value of the mutation rate. (b) Time evolution of the order parameter  $m(t)$  is not periodic at all, which is different from the WS network shown in Fig. 4.

rate and that the time-periodic behavior observed in the WS network is not seen any longer.

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