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Networks with dispersed degrees save stable coexistence of species in cyclic competition

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Coexistence of individuals with different species or phenotypes is often found in nature in spite of competition between them. Stable coexistence of multiple types of individuals have implications for maintenance of ecological biodiversity and emergence of altruism in society, to name a few. Various mechanisms of coexistence including spatial structure of populations, heterogeneous individuals, and heterogeneous environments, have been proposed. In reality, individuals disperse and interact on complex networks. We examine how heterogeneous degree distributions of networks influence coexistence, focusing on models of cyclically competing species. We show analytically and numerically that heterogeneity in degree distributions promotes stable coexistence.

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I. INTRODUCTION

How to maintain or prevent coexistence of competing multiple types of individuals is a key issue in various areas. For example, coexistence of multiple species in ecological habitats implies stable biodiversity realized in nature [1,2]. Coexistence of multiple types of players in evolutionary games implies survival of altruistic players in the sea of selfish players [3]. Coexistence of disease-free and infected individuals implies an endemic state that should be suppressed usually [4].

Mechanisms of coexistence have been a central theoretical question because complexity of a population state (i.e., coexistence) and stability are often contradicting requirements [5–7]. Coexistence in population dynamics has been explained by, for example, nonequilibrium-state interpretation, habitat subdivision, heterogeneity in species such as heterogeneous dispersal speeds, and heterogeneity in environments [1,2,6,8]. Spatial structure such as the square lattice also limits diffusion and promotes coexistence. In this case, each species is clustered in different regions of the lattice [9–12]. However, real-world interaction quite often occurs on contact networks of individuals that are more complex than the square lattice. Most real networks have the small-world and scale-free properties (e.g., Refs. [13,14]). The small-world property is equivalent to the combination of small average distance between vertices and large clustering, or abundance of densely connected small subgraphs such as triangles. A scale-free network is defined by a degree distribution, or the distribution of the number of contacts (edges) that each vertex has, which follows a power law, $p_k \propto k^{-\gamma}$. Here p_k is the probability that a vertex has degree k. The scale-free property may be too idealistic to describe contact networks underlying real population dynamics. Even so, it seems likely that different patches or individuals are endowed with different connectivity to others.

In terms of networks, some known mechanisms of coexistence benefit from the regular lattices, the one-dimensional continuous line, the two-dimensional continuous plane, and the complete graph (mean field situation), in which all the vertices are considered to share the same degree (see the papers cited above and references therein). In random graphs, which are sometimes used in this context [5], the vertex degree obeys the Poisson distribution. However, the real degree distribution may be even broader.

Here we investigate how possibility of coexistence is affected by heterogeneous degree distributions of contact networks, not by heterogeneous environments other than network-based ones or heterogeneous individuals. Among various competitive relationships among different phenotypes, we focus on cyclic competition of three species, which is a minimal case.

Cyclic competition is actually abundant in nature. For example, tropical marine ecosystems [15] and vertebrate communities in high-arctic areas [16] include cyclic dominance relations composed of a couple of organisms (also see Ref. [7]). Real microbial communities of *Escherichia coli* [17] and color polymorphisms of natural lizards [18] also have cyclically dominating three phenotypes and show alternating wax-and-wane population densities. In evolutionary games, the public-good game with volunteering, namely, the choice of not joining the game, results in cyclic competition [19]. The susceptible-infected-recovered-susceptible model of epidemiology and models with additional types of states also include cyclic competition [4,20]. We focus on two specific predator-prey models of such cyclic interaction, that is, the standard rock-scissors-paper (RSP) model [7] and the May-Leonard (ML) model [21]. These models have neutrally stable or unstable coexistence solutions in well-mixed populations. Therefore, in a finite population, population dynamics are eventually trapped by an absorbing state corresponding to the dominance of one species [7,22]. We show that heterogeneous degree distributions stabilize coexistence of multiple types of individuals placed on networks.

II. ROCK-SCISSORS-PAPER DYNAMICS ON NETWORKS

A. Model

As a minimal model of cyclic competition, we consider the standard RSP dynamics on networks with heterogeneous contact rates. There are three species, which we call states, represented by rock, scissors, and paper; rock beats scissors, scissors beat paper, and paper beats rock. Each vertex takes state 0, 1, or 2. A pair of vertices may be connected by an edge. The degree k of a vertex is the number of edges, or the number of contacts with other vertices. State 1 outcompetes state 0 by invading onto each neighboring state with state 0 at a rate of λ. In other words, a vertex with state 0 changes its state to 1 at a rate of λn_1, where n_i is the number of vertices with state i in the neighborhood. Similarly, 1 (2) turns into 2 (0) at a rate of μn_2 (n_0). In an ecological context, we are considering the limit that dispersion rates $(=1,\lambda,\mu)$ are much larger than the natural death rate. We consider the influence of death rates later with the ML model.

For a perfectly mixed population, the mean field theory tells that there are an ensemble of neutrally stable limit cycles surrounding a neutrally stable equilibrium corresponding to coexistence of the three states. Therefore, the coexistence solution is practically unstable in finite populations. The RSP dynamics with spatial structure, such as the square lattice, accommodate many states each of which is clustered in different loci [10–12]. Here we are interested in a network mechanism that may enable stable coexistence.

B. Equilibrium

With dispersed degrees, vertices with different degrees obey different state-transition dynamics. Let us denote by $\rho_{i,k}$ the probability that a vertex with degree k takes state i $(=0,1,2)$. The probability that a vertex adjacent to an arbitrary vertex takes state i is denoted by Θ_i. This probability does not generally agree with $\rho_{i,k}$ or its average over all the vertices. This is because a vertex with more edges is more likely to be selected as a neighbor. In fact, a neighbor has degree k with probability $kp_k/\langle k\rangle$, where p_k is the probability that a vertex has degree k and $\langle k\rangle=\Sigma kp_k$ is the mean degree giving normalization. Therefore, $\Theta_i=\Sigma_k kp_k\rho_{i,k}/\langle k\rangle$ [23]. Because each vertex is occupied by one of the three species, namely, $\rho_{0,k}=1-\rho_{1,k}-\rho_{2,k}$ and $\Theta_0=1-\Theta_1-\Theta_2$, it suffices to consider the density of state 1 and that of state 2. Noting that the expected number of state-i neighbors of a vertex with degree k is equal to $k\Theta_i$, we derive

$$\dot{\rho}_{1,k}=\lambda(1-\rho_{1,k}-\rho_{2,k})k\Theta_1-\mu\rho_{1,k}k\Theta_2, \tag{1}$$

$$\dot{\rho}_{2,k}=\mu\rho_{1,k}k\Theta_2-\rho_{2,k}k(1-\Theta_1-\Theta_2). \tag{2}$$

For example, the first term in Eq. (1) corresponds to the invasion of state 1 onto vertices with state 0. In the equilibrium, we have

$$\begin{pmatrix}\rho^*_{1,k}\\ \rho^*_{2,k}\end{pmatrix}=\frac{\lambda\Theta^*_1}{(\lambda\Theta^*_1+\mu\Theta^*_2)(1-\Theta^*_1-\Theta^*_2)+\lambda\mu\Theta^*_1\Theta^*_2}\times\begin{pmatrix}1-\Theta^*_1-\Theta^*_2\\ \mu\Theta^*_2\end{pmatrix}. \tag{3}$$

The coexistence solution to Eq. (3) is given by

$$\begin{pmatrix}\Theta^*_1\\ \Theta^*_2\end{pmatrix}=\begin{pmatrix}\rho^*_{1,k}\\ \rho^*_{2,k}\end{pmatrix}=\frac{1}{\lambda+\mu+1}\begin{pmatrix}1\\ \lambda\end{pmatrix}, \tag{4}$$

for any k. The degree distribution does not affect the equilibrium population densities [20].

C. Stability of coexistence equilibrium

When $p_k=\delta_{k,\langle k\rangle}$, each vertex has the same degree equal to the mean $\langle k\rangle$. This case corresponds to well-mixed populations. Then the coexistence is neutrally stable (e.g., Refs. [11,21]), which underlies experimental and natural ecosystems showing oscillatory population dynamics [16–18]. Equation (2) indicates that the oscillation period is proportional to $1/\langle k\rangle$.

However, the stability of the coexistence and realized dynamics are considerably influenced by networks. To see this, let us consider a two-point degree distribution given by $p_k=p\delta_{k,k_1}+(1-p)\delta_{k,k_2}$. On average, a total of np vertices have degree k_1 and $n(1-p)$ vertices have degree k_2. Equations (1) and (2) for a network with the two-point degree distribution define a four-dimensional dynamical system. We set $\lambda=\mu=1$ for simplicity, although generalization to other λ and μ is straightforward. The characteristic equation evaluated at the coexistence equilibrium [Eq. (4)] is represented by

$$x^4+\frac{3k_1k_2}{\langle k\rangle}x^3+3\left(\frac{k_1k_2(k_1+k_2-\langle k\rangle)}{\langle k\rangle}+\frac{\langle k^2\rangle^2}{\langle k\rangle^2}\right)x^2+9\frac{\langle k^2\rangle}{\langle k\rangle}k_1k_2x+9k_1^2k_2^2=0, \tag{5}$$

where $\langle k\rangle=\Sigma kp_k=pk_1+(1-p)k_2$ and $\langle k^2\rangle=\Sigma k^2p_k=pk_1^2+(1-p)k_2^2$. When $k_1=k_2=k$, we turn back to the ordinary mean field case with neutrally stable oscillations: $x=\sqrt{3}ki$, $(-3\pm\sqrt{3})k/2$. More generally, the Routh-Hurwitz criteria for Eq. (5) is

$$|H_1|=1,$$

$$|H_2|=pk_2^2(\langle k\rangle-k_1/2)^2+(1-p)k_1^2(\langle k\rangle-k_2/2)^2+3k_1^2k_2^2/4>0,$$

$$|H_3|=81k_1^2k_2^2p(1-p)(k_2-k_1)^2(\langle k^2\rangle^2+2k_1k_2\langle k\rangle^2)/\langle k\rangle^4,$$

$$|H_4|=9k_1^2k_2^2|H_3|, \tag{6}$$

where $|H_i|$ is the ith principal minor. The coexistence solution is stable when $|H_3|,|H_4|>0$, that is, $k_1\neq k_2$ and $p\neq 0,1$. Dispersed contact rates stabilize coexistence.

D. Numerical results

We resort to numerical simulations to examine more general networks and to be more quantitative about the effects of degree dispersion. We compare different types of networks with $n=5000$ vertices and $\langle k\rangle=10$. The regular (R) random graph corresponding to the ordinary mean field case is generated by the configuration model [14] with $p_k=\delta_{k,\langle k\rangle}$. This is a type of random graph in which every vertex has the same degree $\langle k\rangle$. We also use the Erdös-Rényi (ER) random graph, which has the Poisson degree distribution $p_k = e^{-\langle k\rangle}\langle k\rangle^k/k!$, and the Barabási-Albert (BA) scale-free network with the parameter $m \cong \langle k\rangle/2=5$, which yields $p_k \propto k^{-3}$ $(k \geq m)$ and $p_k=0$ $(k<m)$ [13].

Typical population dynamics for these networks are shown in Figs. 1(a)–1(c). On the R random graph, the coexistence solution is neutrally stable in theory. Combined with a finite-size effect, the amplitude of the dynamical population density becomes progressively large in an oscillatory fashion. Eventually, one state dominates the whole network in an early stage [Fig. 1(a)]. On the ER random graph [Fig. 1(b)] and the BA model [Fig. 1(c)], coexistence occurs owing to the distributed k. The fluctuations in the population density is smaller on the BA model than on the ER graph, because the BA model has a broader degree distribution.

To be more systematic, we compare population density fluctuation in the coexistence equilibrium. The fluctuation is measured by the standard deviation of the time series ρ_i [see Fig. 1(b) and 1(c)] after transient, averaged over $i=0,1$, and 2. Larger fluctuation means more unstable coexistence, and we examine how the size of the fluctuation depends on the amount of degree dispersion. In addition to the networks examined above, we use two types of networks that can create a range of degree dispersion. The first is the network with the two-point degree distribution. The standard deviation of the degree $\sqrt{\langle k^2\rangle-\langle k\rangle^2}=\sqrt{p(1-p)}|k_1-k_2|$. By varying k_1/k_2 with $p=0.9$ and $\langle k\rangle=10$ fixed, we can systematically create networks with a variety of $\sqrt{\langle k^2\rangle-\langle k\rangle^2}$. The second is the network that has Gaussian p_k with mean $\langle k\rangle$, whose $\sqrt{\langle k^2\rangle-\langle k\rangle}$ can be also modulated. The results are summarized in Fig. 1(d) for four types of networks (ER, BA, two-point, and Gaussian), excluding the R random graph because it does not sustain coexistence. Regardless of the network type, more dispersed degree distributions generally lead to more stable coexistence.

In the mean field case, a smaller network with a stronger finite-size effect tends to drive the population dynamics to the absorbing equilibrium where only one state survives [22]. The network effect on stability of coexistence is more manifested in this regime. In Fig. 2, we show survival probabilities for some networks with $n=200$, where the survival is defined by existence of all the three states. Figure 2 is consistent with Fig. 1(d); coexistence is sustained for a longer period on networks with larger degree dispersion.

III. MAY-LEONARD DYNAMICS ON NETWORKS

A. Model and equilibrium

Since neutrally stable oscillations of the RSP model may be singular phenomena, we analyze another competition model proposed by May and Leonard [21]. The ML model represents dynamics of cyclically competing three species with natural death. Because of the natural death, vertices can take the vacant state. In a well-mixed population, the coexistence equilibrium and the periodic oscillation are both unstable. A trajectory of the population density approaches heteroclinic orbits on which at least one of the three species is extinct. Theoretically, one species is transiently and alternatively dominant with ever increasing periods in an infinite population. Practically, one species eventually wins due to the finite-size effect.

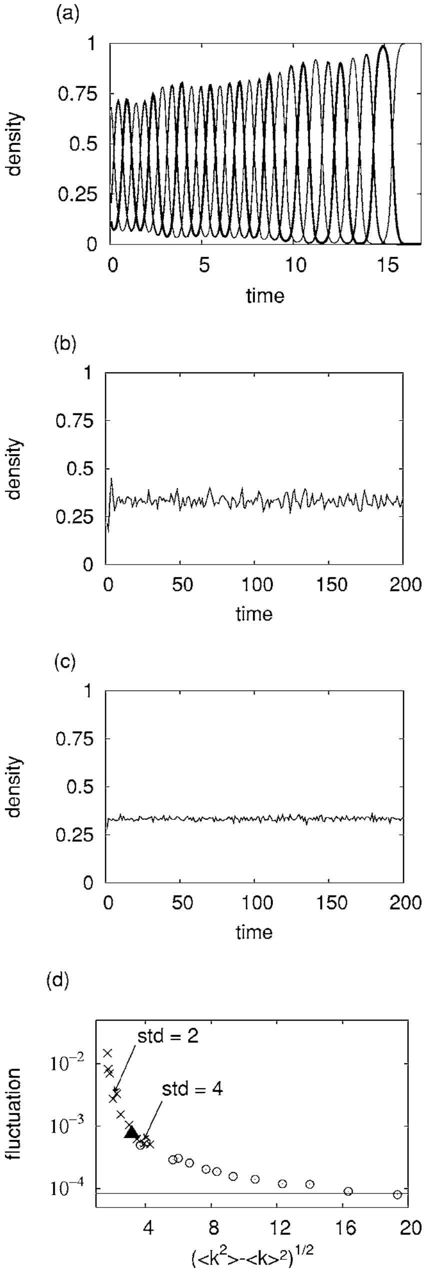

FIG. 1. RSP dynamics on networks with $n=5000$ and $\langle k\rangle=10$. The initial condition is given by the Bernoulli distribution with $\rho_0=0.7$ and $\rho_1=\rho_2=0.15$, where ρ_i is the proportion of vertices that take state i. The densities ρ_0 (thin lines), ρ_1 (moderate lines), and ρ_2 (thick lines) are shown for (a) the R random graph. For (b) the ER random graph and (c) the BA model of the same size, only ρ_0 is shown for clarity. (d) Fluctuation of population density as a function of the standard deviation of the vertex degree {ER, triangle; BA, horizontal line $[(\langle k^2\rangle-\langle k\rangle^2)^{1/2}=157.8]$; Gaussian p_k, crosses; two-point p_k, circles}. The variance of ρ_i from time 150 through 300 averaged over $i=0,1$, and 2 defines the density fluctuation.

As an interacting particle system, the ML model is a four-state system, with state 0 representing the vacant site and 1, 2, and 3 representing cyclically dominating states [12]. The

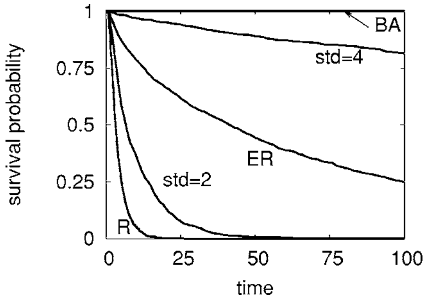

FIG. 2. Survival probabilities for the R random graph, the ER random graph, the BA model, and the networks with Gaussian p_k with standard deviation 2 and 4 [corresponding to the crosses marked by arrows in Fig. 1(d)]. We set $n=200$ and $\langle k\rangle=10$ for all the networks. The survival probabilities are calculated based on 1000 runs.

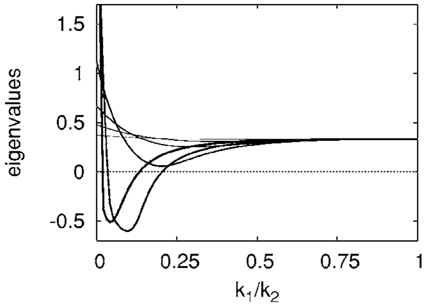

FIG. 3. Stability of the coexistence solution of the ML model. Real parts of the largest eigenvalues of the Jacobian matrix obtained from Eq. (9) with $\alpha=2/3$ and $\beta=2$ are presented for $p=0.1$ (thinnest line), $p=0.3$, $p=0.5$, $p=0.7$, $p=0.9$, and $p=0.95$ (thickest line). We set $\langle k\rangle=1$ for normalization.

ML dynamics with heterogeneous contact rates are written as

$$\dot{\rho}_{1,k} = \rho_{0,k}k\Theta_1 - (\alpha-1)\rho_{2,k}k\Theta_1 - (\beta-1)\rho_{1,k}k\Theta_3,$$

$$\dot{\rho}_{2,k} = \rho_{0,k}k\Theta_2 - (\alpha-1)\rho_{3,k}k\Theta_2 - (\beta-1)\rho_{2,k}k\Theta_1,$$

$$\dot{\rho}_{3,k} = \rho_{0,k}k\Theta_3 - (\alpha-1)\rho_{1,k}k\Theta_3 - (\beta-1)\rho_{3,k}k\Theta_2, \qquad (7)$$

where $\rho_{0,k}=1-\rho_{1,k}-\rho_{2,k}-\rho_{3,k}$. The first term in each equation indicates the rate at which a vacant site becomes colonized by state i $(1\le i\le 3)$. Supposing that $\alpha<1$ and $\beta>1$, the second term and the third term of each equation represent the population increase and decrease due to the cyclic competition, respectively. For example, in the first equation, state 1 outcompetes 2, whereas 1 is outcompeted by 3. Equation (7) has a coexistence equilibrium given by

$$\rho^*_{i,k} = \Theta^*_i = (\alpha+\beta+1)^{-1} \quad (i=1,2,3) \qquad (8)$$

for all k. With $p_k=\delta_{k,\langle k\rangle}$, the eigenvalues of the Jacobian matrix evaluated at $(\rho^*_{1,k}, \rho^*_{2,k}, \rho^*_{3,k})$, disregarding a prefactor $(\alpha+\beta+1)^{-1}$, are $x=-(1+\alpha+\beta), -1+(\alpha+\beta)/2\pm\sqrt{3}(\alpha-\beta)i/2$ [21]. When $\alpha+\beta=2$, the ML model is essentially the same as the RSP model, and the coexistence is neutrally stable $[x=-3, \pm\sqrt{3}(\alpha-\beta)i/2]$. When $\alpha+\beta>2$ and $\alpha<1$ (or $\beta<1$), the coexistence equilibrium is an unstable spiral, and the trajectory tends to a homoclinic orbit.

B. Stability of coexistence equilibrium

To investigate the network effect, we again consider the two-point degree distribution $p_k=p\delta_{k,k_1}+(1-p)\delta_{k,k_2}$. The Jacobian matrix at $(\rho^*_{1,k_1}, \rho^*_{1,k_2}, \rho^*_{2,k_1}, \rho^*_{2,k_2}, \rho^*_{3,k_1}, \rho^*_{3,k_2})^t$, where t denotes the transpose, is a block circulant matrix. Accordingly, the eigenmode has the form $(v_1, v_2, \rho v_1, \rho v_2, \rho^2 v_1, \rho^2 v_2)^t$, $v_1, v_2 \in \mathbf{C}$, where ρ is any solution to $\rho^3=1$. The corresponding characteristic equation is reduced to

$$x^2 + \left((\beta+\rho\alpha+\rho^2)(k_1+k_2) - (1-\rho^2)(\beta-1)\frac{\langle k^2\rangle}{\langle k\rangle}\right)x + (\alpha^2+\beta^2-\alpha\beta-\alpha-\beta+1)\rho^2 k_1 k_2 = 0. \qquad (9)$$

For $\rho=1$, Eq. (9) is a real equation, and two eigenvalues have the same real part that is equal to $-(\alpha+\beta+1)(k_1+k_2)/2<0$. Because an eigenvalue of Eq. (9) for $\rho=\exp(2\pi i/3)$ is conjugate of one for $\rho=\exp(4\pi i/3)$, it suffices to set $\rho=\exp(2\pi i/3)$. The larger real part of the solution to Eq. (9) is plotted in Fig. 3 for various p and $0<k_1/k_2\le 1$. The coexistence equilibrium is stabilized with negative real parts of the eigenvalues. This occurs when $k_1/k_2\cong 0.1$ and $p=0.9, 0.95$. In this situation, a small number $[=n(1-p)]$ of hubs have a large degree $(=k_2)$ in comparison with most vertices with degree k_1. This is reminiscent of long-tail p_k typical of the scale-free networks. Excess heterogeneity $(k_1/k_2<0.05)$ destroys coexistence. In this situation, a majority of vertices with degree k_1 are effectively isolated, and the network is close to the mean field case, or the R random graph with $k=k_2$. When $p<0.5$, the heterogeneity does not cause stability irrespective of k_1/k_2. This is because the contribution of the smaller subpopulation (proportion p) with the smaller degree $k=k_1(<k_2)$ to dynamics is marginal, which again results in effectively homogeneous networks with $k=k_2$.

C. Numerical results

For numerical simulations, we note that, in Eq. (7), a vacant site (state 0) is replaced by state i $(1\le i\le 3)$ at a rate of n_i. A vertex in state 1 (2, 3) kills a neighboring state 2 (3, 1) at a rate of $\beta-1$. Then, the neighboring vertex is colonized by state 1 (2, 3) with probability $(1-\alpha)/(\beta-1)$ and turns empty (state 0) otherwise [12].

Dynamics for the R and ER random graphs with $n=5000$ and $\langle k\rangle=10$ are shown in Figs. 4(a) and 4(b), respectively. Because the stability condition for the ML model is more severe than that for the RSP model, one state shortly overwhelms the others on the ER as well as R random graph. However, the transients for the ER random graph, whose degrees are more dispersed than the R random graph, are longer. The BA model and the networks with two-point p_k

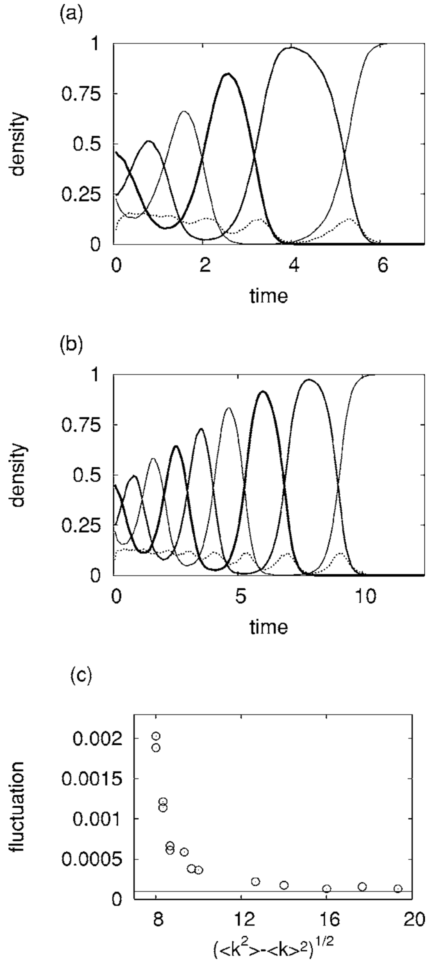

FIG. 4. ML dynamics on networks with $n=5000$, $\langle k\rangle=10$, $\alpha=2/3$, and $\beta=2$. The initial condition is given by $\rho_0=0$, $\rho_1=\rho_2=0.25$, and $\rho_3=0.5$. The R random graph (a) and the ER random graph (b) do not allow stable coexistence (ρ_0, dotted lines; ρ_1, thin solid lines; ρ_2, moderate solid lines; ρ_3, thick solid lines). (c) Fluctuation of population density {BA, horizontal line $[(\langle k^2\rangle-\langle k\rangle^2)^{1/2}=157.8]$; two-point p_k, circles}, defined by the variance of ρ_i from time 150 through 300 averaged over $i=1,2$, and 3.

with parameters realizing the stable Jacobian matrix (but not the networks with Gaussian p_k) yield coexistence. Similar to the RSP dynamics, the amount of degree dispersion is strongly correlated with the amount of density fluctuation and stability of coexistence, irrespective of the network type [Fig. 4(c)].

IV. DISCUSSION

A. Summary of the results

We have examined population dynamics with cyclic dominance relationships on networks. The steady population density is independent of degree distributions of networks. However, stability of coexistence equilibria and dynamics depend considerably on networks. Heterogeneity in degree distributions facilitates stable coexistence of different phenotypes. As touched upon in Sec. I, coexistence of competing species is desirable in, for example, ecological communities (biodiversity) and evolutionary games (survival of altruistic players).

B. Relations to synchronization of coupled oscillators

The present mechanism of coexistence is related to synchronization of coupled oscillators. With spread degree distributions, each $\rho_{i,k}$ evolves at a speed proportional to k, and $\rho_{i,1}$, $\rho_{i,2},\ldots$ are coupled by a sort of mean field feedback Θ_i. Then, the population dynamics are analogous to those of an ensemble of phase oscillators coupled by mean field interaction. In theory, coupled phase oscillators become desynchronized when the intrinsic frequency of the oscillators has a broad distribution relative to the coupling strength [24]. Oscillators with heterogeneous intrinsic frequencies correspond to vertices with heterogeneous k. In terms of competition dynamics on networks, asynchrony corresponds to stable coexistence of species where synchronous oscillations (large fluctuations in time) of the population density was suppressed. Desynchronization is known to suppress neutrally stable or unstable oscillations in ecological models with patchy populations, heterogeneous birth rates, and weak aggregation [8]. Heterogeneity in degree distributions serves to stable coexistence via desynchronization even without other kinds of heterogeneity. The correspondence between asynchrony and coexistence may be exported to more general models, particularly to ones showing oscillations in well-mixed populations; oscillatory population densities are reminiscent of cyclic competition.

C. Difference from spatial mechanisms of coexistence

The scenario to coexistence unraveled here is distinct from those based on spatial structure, heterogeneous environments, or heterogeneous individuals. In patchy habitats with heterogeneous environments or small diffusion [6], and in spatial structure with limited diffusion [9–12], multiple species can coexist by forming locally high densities of conspecifics in different subspaces [10–12]. This is the spatial mechanism of coexistence. In networks with dispersed degrees, multiple species can coexist on a network in a mixed manner without spatial segregation.

Real networks of contacts are equipped with the clustering property, as is the case for the regular lattices and small-world networks, and high clustering elicits the spatial mechanism of coexistence. In addition, many networks own broad degree distributions represented by the scale-free distributions [13,14,23]. The mechanism proposed in this work can cooperate with the spatial mechanism to promote stability of coexistence.

D. Difference from contagion dynamics

There are many possible rules for interacting particle systems. In contagion processes, such as the percolation, the susceptible-infected-recovered (SIR) model, and the contact process susceptible-infected-susceptible (SIS) model, degree dispersion affects dynamical aspects by, for example, accelerating disease propagation in initial stages [25]. More fundamentally, however, epidemic thresholds (critical infection rates) are proportional to $\langle k\rangle/\langle k^2\rangle$. Then, disease propagation on a global scale is more likely to occur on networks with more heterogeneous contact rates with small $\langle k\rangle/\langle k^2\rangle$ than on networks with rather homogeneous degrees such as the regular lattices and the random graph [4,23]. In contagion dynamics, the network influences the stationary state in addition to the dynamics, which contrasts to our results for the competition dynamics.

Generally speaking, the positions of equilibria move when we cannot neglect at least one type of state-transition event whose occurrence rate is independent of neighbors' states n_i [20]. Examples are spontaneous recovery and mutation. By contrast, the equilibria are invariant if all the state transitions are controlled by the neighbors' states, as is the case for the RSP model, the ML model, and also the voter model. However, the degree distribution does influence the stability of coexistence and hence the whole population dynamics. Our results are generalized to other population dynamics in which the rates of spontaneous transitions can be ignored.

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