Multilayer network structure enhances the coexistence of competitive species

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The concept of a multiplex network can be used to characterize the dispersal paths and states of different species in a patch habitat system. The multiplex network is one of three types of multilayer networks. In this study, the effect of a multiplex network on the long-term stable coexistence of species is investigated using the concept of metapopulation. Based on the mean field approximation, the stability analysis of a two-species system shows that, compared to the single layer network, the multiplex network is more conducive to the stable coexistence of species when one species has a stronger colonization ability. That is, in such a patch habitat system, if the dispersal paths of the stronger species are different than those of the weaker species, then the larger the heterogeneity of the dispersal network of the stronger species is, the more likely the long-term stable coexistence of species. This result provides a different perspective for understanding the biodiversity in heterogeneous habitats.

I. INTRODUCTION

The mechanism of species coexistence, especially that of competitive species, remains one of the most important theoretical issues in the study of biodiversity [1–4]. Some theoretical and experimental ecological studies have shown that a heterogeneous habitat, or spatial heterogeneity of environment, is one of the most important factors affecting the long-term stable coexistence of species [5–8]. The so-called Levins metapopulation idea in ecology [9–13] assumes that the patches of habitat suitable for a species are distributed across a landscape (where, in the Levins model, the metapopulation is defined as a population of local populations inhabiting an infinitely large patch network, and the size of a metapopulation is measured by the fraction of patches occupied at any time), and that, over time, there is a dynamical process of colonization and extinction: the colonization of empty patches by occupied patches sending out colonizing propagules and the extinction of local populations on occupied patches (see also [14]). For simplicity, the Levins model assumes that all local populations are identical and hence have the same behavior [9,10,12,13]. This assumption implies that the extinctions occur completely independently in different habitat patches [12,13]. On the other hand, the Levins model

also assumes that the colonization of empty patches is not affected by distance, that is, all patches are equally connected to other patches (not necessarily to all other patches), which is called the mean-field approximation [12]. Based on these two assumptions, the Levins model shows clearly that a single species metapopulation can be long-term stable if the colonization rate (denoted by c) is larger than the extinction rate (denoted by e) [12].

In fact, according to Levins' definition of metapopulation [10], the dispersal path of a species between habitat patches determines the connection between habitat patches for this species [15,16]. This means that a patch habitat system can be regarded as a dispersal network, where (i) the nodes of the network represent the habitat patches, which have two states, occupied and unoccupied patches, respectively, and (ii) the edges between the nodes and their distribution characteristic represent the dispersal path of species between habitat patches [15–22]. Furthermore, when there are two or more species in a patch habitat system and each patch is suitable for any one of these species that may have different dispersal paths (or different dispersal networks), then this patch habitat system can be regarded as a multiplex network [23–27]. The multiplex network is one of three types of multilayer network [28], that is, a network system consisting of several component networks with the same nodes but different edge distribution characteristics.

The concept of multilayer network has not only been widely used in the analysis of social, traffic, and communication systems, etc. [23,29–32], but it has also been used

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to reveal the mechanism of biodiversity in some ecological studies [33,34]. For example, a study showed that there may be an intricate relation between interspecies competition and mutualism in a multilayer network system [33]. Moreover, a recent simulation study has shown that a multilayer network structure may promote biodiversity in a heterogeneous environment [34], which may imply a new mechanism of species coexistence in a patch habitat system. The main aim of this paper is to develop the theoretical basis that underlies these simulation results. In particular, what is the dynamic mechanism behind biodiversity in these systems? To answer this question, based on the concept of metapopulation presented by Levins [10], we present a simple multiplex network model under mean-field approximation to reveal theoretically the general principle of multiplex network in promoting, or maintaining, biodiversity in this study.

II. A TWO-SPECIES MULTIPLEX NETWORK MODEL

We here consider only two competitive species (called species 1 and 2, respectively) in a patch habitat system consisting of N patches, where N is assumed to be large and, for each species, each patch is assumed to be habitat suitable, but the two competitive species cannot simultaneously exist in one single habitat. Therefore, at any time t each patch is in exactly one of three possible states, that is, occupied by a local population of species 1, or by a local population of species 2, or not occupied (i.e., empty patch). Moreover, we also assume that (i) at any time t, each local population living in an occupied patch will go extinct with rate e [12]; (ii) at any time t, each empty patch can only be successfully colonized by the local population living in one of its neighboring occupied patches with colonization rate c [12]; and (iii) when species 1 and 2 compete for an empty patch at the same time, the colonization ability of species 1 is stronger than that of species 2 in the sense that only when species 1 fails to colonize, species 2 has the opportunity to colonize [35], that is, species 1 is the stronger species in the competition over unoccupied patches, while species 2 is the weaker species. Finally, as stated at the beginning of this paper, species 1 and 2 may have different dispersal paths between N habitat patches.

Let $G_1 = \{V, E_1\}$ and $G_2 = \{V, E_2\}$, where $V = \{1, 2, \ldots, N\}$ is the set of nodes and $E_1, E_2 \subseteq V \times V$ are two sets of edges between nodes, respectively. G_1 and G_2 are then two undirected networks with the same N nodes that are assumed to be connected, which correspond to the dispersal paths of species 1 and 2, respectively. That is, each node represents a habitat patch, and the sets E_1 and E_2 represent the dispersal paths of species 1 and species 2 between the habitat patches, respectively. Therefore, G_1 and G_2 constitute a multiplex network system [28] (see Fig. 1). Let $(g_{ij}^{(s)})_{N \times N}$ denote the adjacency matrix of G_s for $s = 1, 2$, in which $g_{ij}^{(s)} = 1$ if and only if there is an edge between node i and node j, denoted by (i, j), with $(i, j) \in E_s$, otherwise $g_{ij}^{(s)} = 0$.

Furthermore, let $\gamma_i(t)$ denote the state variable of node i at time t for $i = 1, 2, \ldots, N$, which is defined as $\gamma_i(t) = 0$ if node i is empty, $\gamma_i(t) = 1$ if node i is occupied by species

1, and $\gamma_i(t) = 2$ if node i is occupied by species 2. This implies that $\gamma_i(t)$ should be considered to be a random variable for $i = 1, 2, \ldots, N$. Let $n_0(t)$, $n_1(t)$, and $n_2(t)$ denote the numbers of empty, species 1, and species 2 nodes at time t, respectively. Then, we have $n_z(t) = \sum_{i=1}^{N} \delta_K(\gamma_i(t), z)$ for $z = 0, 1, 2$, where δ_K is the Kronecker delta function. Obviously, the frequencies of empty, species 1, and species 2 nodes at time t are $x_0(t) = n_0(t)/N$, $x_1(t) = n_1(t)/N$, and $x_2(t) = n_2(t)/N$, respectively, with $\sum_{i=0}^{2} x_i(t) = 1$. Let $d_s(i) = \sum_{j=1}^{N} g_{ij}^{(s)}$ denote the degree of node i in G_s for $s = 1, 2$. So, the average degree of G_s is $\bar{d}_s = \sum_{i=1}^{N} d_s(i)/N$ and the degree variance in G_s is $\sigma_s^2 = \sum_{i=1}^{N} [d_s(i) - \bar{d}_s]^2/N$ for $s = 1, 2$, and the covariance of G_1 and G_2 in degree is $\sigma_{1,2} = \sum_{i=1}^{N} [d_1(i) - \bar{d}_1][d_2(i) - \bar{d}_2]/N$.

Let $k_1(i)$ denote the number of neighboring nodes occupied by species 1 of node i in G_1 at time t and, similarly, $k_2(i)$ the number of neighboring nodes occupied by species 2 of node i in G_2 at time t for $i = 1, 2, \ldots, N$, which are given by

$$k_1(i) = \sum_{j=1}^{N} g_{ij}^{(1)} \delta_K(\gamma_j(t), 1),$$

$$k_2(i) = \sum_{j=1}^{N} g_{ij}^{(2)} \delta_K(\gamma_j(t), 2), \qquad (1)$$

respectively. Note that $\langle \delta_K(\gamma_i(t), z) \rangle \approx x_z(t)$ for $z = 0, 1, 2$, where the angular bracket stands for the expectation. This means that we assume that for large N, the expected probability that each node is an empty node, or a species 1 node, or a species 2 node, is the same as the frequency of empty nodes, or species 1 nodes, or species 2 nodes, in the all nodes, that is, the assumption of random uniform distribution. Based on this assumption, $\delta_K(\gamma_j(t), 1)$ and $\delta_K(\gamma_l(t), 2)$ can be also regarded as independent random variables approximately for $j, l = 1, 2, \ldots, N$ but $j \neq l$. Therefore, $k_1(i)$ and $k_2(i)$ are random variables obeying the binomial distributions $k_1(i) \sim B(d_1(i), x_1(t))$ and $k_2(i) \sim B(d_2(i), x_2(t))$, respectively, for $i = 1, 2, \ldots, N$, that is, $\langle k_s(i) \rangle = d_s(i) x_s(t)$ and $\langle k_s^2(i) \rangle = d_s^2(i) x_s^2(t) + d_s(i) x_s(t)[1 - x_s(t)]$ for $s = 1, 2$.
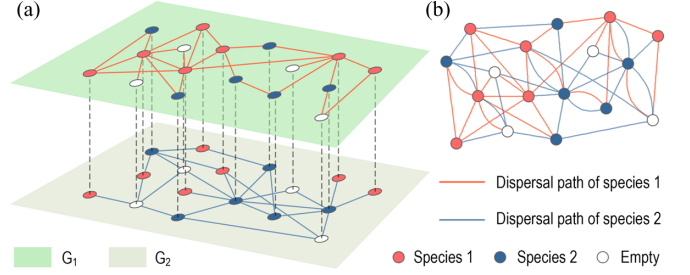

FIG. 1. The ecosystem of metapopulation with multiplex network. The red, blue, white nodes on the network represent patches which are occupied by species 1, species 2, and empty, respectively. Panel (a) illustrated the ecosystem in a multiplex network. The intralayer edges using dashed line indicate the same node on different layers. Panel (b) is the visualization of the multiplex network in the form of edge-colored multigraph

On the other hand, we have also

$$
\langle k_1(i)k_2(i)\rangle = \left\langle \sum_{j=1}^{N} g_{ij}^{(1)}\delta_K(\gamma_j(t), 1) \sum_{j=1}^{N} g_{ij}^{(2)}\delta_K(\gamma_j(t), 2) \right\rangle
$$

$$
= \sum_{j=1}^{N-1} \sum_{l=j+1}^{N} \left[g_{ij}^{(1)}g_{il}^{(2)}\langle \delta_K(\gamma_j(t), 1)\delta_K(\gamma_l(t), 2)\rangle \right.
$$
$$
\left. + g_{ij}^{(2)}g_{il}^{(1)}\langle \delta_K(\gamma_j(t), 2)\delta_K(\gamma_l(t), 1)\rangle \right]
$$
$$
= x_1(t)x_2(t)\psi(i), \tag{2}
$$

where

$$
\psi(i) = \sum_{j=1}^{N-1} \sum_{l=j+1}^{N} \left[g_{ij}^{(1)}g_{il}^{(2)} + g_{ij}^{(2)}g_{il}^{(1)} \right]
$$

$$
= \sum_{j=1}^{N} g_{ij}^{(1)} \sum_{j=1}^{N} g_{ij}^{(2)} - \sum_{j=1}^{N} g_{ij}^{(1)}g_{ij}^{(2)} \tag{3}
$$

$$
= d_1(i)d_2(i) - \sum_{j=1}^{N} g_{ij}^{(1)}g_{ij}^{(2)}.
$$

It is easy to see that the term $\sum_{j=1}^{N} g_{ij}^{(1)}g_{ij}^{(2)}$ is exactly the number of shared neighbors of node i in both G_1 and G_2. For convenience, let $\mu(i) = \sum_{j=1}^{N} g_{ij}^{(1)}g_{ij}^{(2)}$. Then, Eq. (2) can be rewritten as

$$
\langle k_1(i)k_2(i)\rangle = x_1(t)x_2(t)[d_1(i)d_2(i) - \mu(i)] \tag{4}
$$

for $i = 1, 2, \ldots, N$.

For $G_1 \neq G_2$, if node i is empty, then the probability that it is successfully colonized by species 1, denoted by $\rho_1(i)$, is $\rho_1(i) = 1 - (1 - c)^{k_1(i)}$, and the probability that it is successfully colonized by species 2, denoted by $\rho_2(i)$, is $\rho_2(i) = (1 - c)^{k_1(i)}[1 - (1 - c)^{k_2(i)}]$. We can see that for all possible $i = 1, 2, \ldots, N$, if the parameter c is large (or it is close to 1, i.e., $c \to 1$), then we must have $\rho_1(i) > \rho_2(i)$ if $k_1(i) \neq 0$ at any time t. This strongly implies that the long-term stable coexistence of species 1 and 2 in this system should be impossible if $c \to 1$. So, we here consider only the possibility of stable coexistence of species 1 and 2 when c is small. For small c, $\rho_1(i)$ and $\rho_2(i)$ can be approximated as

$$
\rho_1(i) \approx ck_1(i) - \frac{c^2}{2}k_1(i)[k_1(i) - 1],
$$

$$
\rho_2(i) \approx ck_2(i) - c^2k_1(i)k_2(i) - \frac{c^2}{2}k_2(i)[k_2(i) - 1], \tag{5}
$$

respectively. Note that $\langle k_s(i)\rangle = d_s(i)x_s(t)$ and $\langle k_s^2(i)\rangle = d_s^2(i)x_s^2(t) + d_s(i)x_s(t)[1 - x_s(t)]$ for $s = 1, 2$, and that $\langle k_1(i)k_2(i)\rangle = x_1(t)x_2(t)[d_1(i)d_2(i) - \mu(i)]$. Then the expectations of $\rho_1(i)$ and $\rho_2(i)$ can be given by

$$
\langle \rho_1(i)\rangle = \left(c + \frac{c^2}{2}\right)d_1(i)x_1(t) - \frac{c^2}{2}\left[d_1^2(i)x_1^2(t) + d_1(i)x_1(t)[1 - x_1(t)]\right],
$$

$$
\langle \rho_2(i)\rangle = \left(c + \frac{c^2}{2}\right)d_2(i)x_2(t) - c^2 x_1(t)x_2(t)[d_1(i)d_2(i) - \mu(i)] - \frac{c^2}{2}\left[d_2^2(i)x_2^2(t) + d_2(i)x_2(t)[1 - x_2(t)]\right], \tag{6}
$$

respectively.

Furthermore, the expected change rates of $x_1(t)$ and $x_2(t)$ in the time interval $(t, t + \Delta t)$ (where we take $\Delta t = 1/N$), denoted by $\langle \Delta x_1(t)\rangle/\Delta t$ and $\langle \Delta x_2(t)\rangle/\Delta t$, respectively, can be given by

$$
\frac{\langle \Delta x_1(t)\rangle}{\Delta t} = \left\langle -\sum_{i=1}^{N} \delta_K(\gamma_i(t), 1)e/N + \sum_{i=1}^{N} \delta_K(\gamma_i(t), 0)\rho_1(i)/N \right\rangle = -x_1(t)e + \left\langle \sum_{i=1}^{N} \frac{\delta_K(\gamma_i(t), 0)\rho_1(i)}{N} \right\rangle,
$$

$$
\frac{\langle \Delta x_2(t)\rangle}{\Delta t} = \left\langle -\sum_{i=1}^{N} \delta_K(\gamma_i(t), 2)e/N + \sum_{i=1}^{N} \delta_K(\gamma_i(t), 0)\rho_2(i)/N \right\rangle = -x_2(t)e + \left\langle \sum_{i=1}^{N} \frac{\delta_K(\gamma_i(t), 0)\rho_2(i)}{N} \right\rangle. \tag{7}
$$

For the terms $\langle \sum_{i=1}^{N} \delta_K(\gamma_i(t), 0)\rho_s(i)/N \rangle$ for $s = 1, 2$, based on the mean-field approximation [36] [where for each of $\rho_s(i)$ for $i = 1, 2, \cdots, N$, we replace $\rho_s(i)$ with $\sum_{j=1}^{N} \rho_s(j)/N$], we have the approximation

$$
\left\langle \sum_{i=1}^{N} \frac{\delta_K(\gamma_i(t), 0)\rho_s(i)}{N} \right\rangle \approx \left\langle \sum_{i=1}^{N} \frac{\delta_K(\gamma_i(t), 0)}{N} \sum_{j=1}^{N} \frac{\rho_s(j)}{N} \right\rangle = \left\langle x_0(t) \sum_{j=1}^{N} \frac{\rho_s(j)}{N} \right\rangle = x_0(t) \sum_{j=1}^{N} \frac{\langle \rho_s(j)\rangle}{N}. \tag{8}
$$

For convenience, let

$$
\phi_1 = \sum_{i=1}^{N} \frac{\langle \rho_1(i)\rangle}{N} = c\bar{d}_1 x_1(t) + \frac{c^2}{2}\bar{d}_1(1 - \bar{d}_1)x_1^2(t) - \frac{c^2}{2}\sigma_1^2 x_1^2(t),
$$

$$
\phi_2 = \sum_{i=1}^{N} \frac{\langle \rho_2(i)\rangle}{N} \tag{9}
$$

$$
= c\bar{d}_2 x_2(t) + \frac{c^2}{2}\bar{d}_2(1 - \bar{d}_2)x_2^2(t) - \frac{c^2}{2}\sigma_2^2 x_2^2(t) - c^2(\sigma_{1,2} + \bar{d}_1\bar{d}_2 - \bar{\mu})x_1(t)x_2(t),
$$

respectively, where $\bar{\mu} = \sum_{i=1}^{N} \mu(i)/N$. Therefore, for large N ($\Delta t \to 0$), we have

$$\frac{dx_1}{dt} = -ex_1 + x_0\phi_1 = x_1[-e + (1 - x_1 - x_2)\tilde{\phi}_1],$$

$$\frac{dx_2}{dt} = -ex_2 + x_0\phi_2 = x_2[-e + (1 - x_1 - x_2)\tilde{\phi}_2], \quad (10)$$

where $\tilde{\phi}_1 = \phi_1/x_1$ and $\tilde{\phi}_2 = \phi_2/x_2$.

III. STABILITY OF THE MULTIPLEX NETWORK DYNAMICS

For the dynamical properties of Eq. (10), it is easy to see that if $G_1 = G_2$ (i.e., species 1 and 2 have exactly the same dispersal path where we have $\bar{d}_1 = \bar{d}_2 = \bar{d}$ and $\sigma_1^2 = \sigma_2^2 = \sigma_{1,2} = \sigma^2$), then $\tilde{\phi}_1 > \tilde{\phi}_2$ for all possible $0 < x_1, x_2 < 1$ and $x_1 + x_2 \leqslant 1$, i.e., $\tilde{\phi}_1 - \tilde{\phi}_2 = c^2(x_1 + x_2)(\sigma^2 + \bar{d}^2 - \bar{d})/2 > 0$. This shows clearly that the stable coexistence of species 1 and 2 is impossible if $G_1 = G_2$, or, more specifically, under our assumptions and definitions, no stable coexistence exists for the single layer network. This result strongly implies that the differences of dispersal paths among the stronger and weaker species may play an important role in the long-term stable coexistence of species.

For the situation with $G_1 \neq G_2$, the stability analysis of Eq. (10) is summarized as follows (see also Table I, and the detailed mathematical proofs are shown in Appendix A):

(i) The trivial equilibrium $(0,0)$ is globally asymptotically stable if $-e + c\bar{d}_1 < 0$ and $-e + c\bar{d}_2 < 0$, unstable if

$-e + c\bar{d}_1 > 0$ and $-e + c\bar{d}_2 > 0$, and a saddle point if $(-e + c\bar{d}_1)(-e + c\bar{d}_2) < 0$.

(ii) If $c\bar{d}_1 - e > 0$, then the boundary equilibrium $(x_1^*, 0)$ exists with

$$x_1^* = \frac{\bar{d}_1 - cD_1/2 - \sqrt{(\bar{d}_1 - cD_1/2)^2 + 2(c\bar{d}_1 - e)D_1}}{-cD_1}$$

$$\in (0, 1), \quad (11)$$

where $D_1 = \bar{d}_1(1 - \bar{d}_1) - \sigma_1^2 < 0$. We can see that $(x_1^*, 0)$ is asymptotically stable if $A + Bx_1^* < 0$, where $A = 2(\bar{d}_1 - \bar{d}_2)/cD_2$ and $B = [D_1 + 2(\sigma_{1,2} + \bar{d}_1\bar{d}_2 - \bar{\mu})]/D_2$, where $D_2 = \bar{d}_2(1 - \bar{d}_2) - \sigma_2^2$, and that $(x_1^*, 0)$ is a saddle point if $A + Bx_1^* > 0$.

(iii) Similar to (ii), if $c\bar{d}_2 - e > 0$, then the boundary equilibrium $(0, x_2^*)$ exists with

$$x_2^* = \frac{\bar{d}_2 - cD_2/2 - \sqrt{(\bar{d}_2 - cD_2/2)^2 + 2(c\bar{d}_2 - e)D_2}}{-cD_2}$$

$$\in (0, 1). \quad (12)$$

We can see also that $(0, x_2^*)$ is asymptotically stable if $A > x_2^*$ and that it is a saddle point if $A < x_2^*$.

(iv) Let $(\hat{x}_1, \hat{x}_2)$ denote an interior equilibrium with $0 < \hat{x}_1, \hat{x}_2 < 1$ and $\hat{x}_1 + \hat{x}_2 < 1$. Then, $(\hat{x}_1, \hat{x}_2)$ satisfy $-ex_i + x_0\phi_i = 0$ for $i = 1, 2$, which are quadratic equations with solutions $\hat{x}_i^{(j)}$ for $j = 1, 2$ given by

$$\hat{x}_1^{(j)} = \frac{-(1 - A)cD_1/2 + (1 + B)\bar{d}_1}{-(1 + B)cD_1} - (-1)^j \frac{\sqrt{[(1 - A)cD_1/2 - (1 + B)\bar{d}_1]^2 + 2(1 + B)D_1[(1 - A)c\bar{d}_1 - e]}}{-(1 + B)cD_1},$$

$$\hat{x}_2^{(j)} = A + B\hat{x}_1^{(j)}. \quad (13)$$

The more detailed expressions are shown in Appendix A. We can see also that if $(\hat{x}_1^{(1)}, \hat{x}_2^{(1)})$ is an interior equilibrium, then it must be a saddle point, and if $(\hat{x}_1^{(2)}, \hat{x}_2^{(2)})$ is an interior equilibrium, then it must be asymptotically stable (see Appendix A, and see also Table I). Moreover, for the situation with $(\hat{x}_1^{(1)}, \hat{x}_2^{(1)}) = (\hat{x}_1^{(2)}, \hat{x}_2^{(2)}) = (\hat{x}_1^{(*)}, \hat{x}_2^{(*)})$, if $(\hat{x}_1^{(*)}, \hat{x}_2^{(*)})$ is an interior equilibrium, then it must be a saddle-node bifurcation (see Appendix A, and see also Table I).

Based on the above analysis, we here consider a special case to show how the difference between G_1 and G_2 in network heterogeneity influences the coexistence of species 1 and 2. In this case, for simplicity, we assume that $\bar{d}_1 = \bar{d}_2 = \bar{d}$ but $\sigma_1^2 \neq \sigma_2^2$, that is, G_1 and G_2 have the same average degree, but their network heterogeneity is not the same. Note that $A = 0$ in this case. Thus, it is easy to see that the trivial equilibrium $(0,0)$ is unstable if $-e + c\bar{d} > 0$; if $-e + c\bar{d} > 0$, then the boundary equilibrium $(x_1^*, 0)$ exists and it is asymptotically stable (or a saddle point) if $B < 0$ (or $B > 0$); the boundary equilibrium $(0, x_2^*)$ also exists if $-e + c\bar{d} > 0$ and it must be a saddle point. Furthermore, we can see also that the point $(\hat{x}_1^{(2)}, \hat{x}_2^{(2)})$ is a unique interior equilibrium if and only if

$-e + c\bar{d} > 0$ and $B > 0$ [i.e., $\sigma_1^2 > d^2 + d + 2(\sigma_{1,2} - \bar{\mu})$], and it must be also globally asymptotically stable if it exists. This result shows clearly that under the condition $-e + c\bar{d} > 0$, the increase of σ_1^2 (i.e., the increase of G_1 network heterogeneity) will promote the long-term stable coexistence of species 1 and 2. This strongly implies also that if G_1 is a regular network (i.e., $\sigma_1^2 = 0$), then the stable coexistence of species 1 and 2 is impossible even if G_2 is a heterogeneous network (i.e., $\sigma_2^2 \neq 0$). On the other hand, if G_2 is a regular network and G_1 is a heterogeneous network, then the stable coexistence of species 1 and 2 is possible.

In order to display more clearly the results of the above theoretical analysis, we show also some examples of Monte Carlo simulations (i.e., stochastic simulations based on synchronous update being independent of the mean-field approximation) in Fig. 2. G_1 and G_2 have the same average degree in all examples, and G_2 is an exponential network generated by random attachment with exponential degree distribution [37,38] and its network heterogeneity is kept to be almost the same in all examples. However, the network heterogeneity of G_1 varies in the different examples, in which G_1 is a regular random network [39] in panel (a) where the degree variance is

TABLE I. The existence and stability of equilibria in Eq. (10).

Equilibrium point	Existence Conditions	Stability Conditions	Saddle Conditions
$(0,0)$	Always exists	$c\bar{d}_1 - e < 0,$ $c\bar{d}_2 - e < 0$	$(c\bar{d}_1 - e)(c\bar{d}_2 - e) < 0$
$(0, x_2^*)$	$c\bar{d}_2 - e > 0$	$A > x_2^*$	$A < x_2^*$
$(x_1^*, 0)$	$c\bar{d}_1 - e > 0$	$A + Bx_1^* < 0$	$A + Bx_1^* > 0$
$(\hat{x}_1^{(1)}, \hat{x}_2^{(1)})$	① $c\bar{d}_1 - e > 0, c\bar{d}_2 - e > 0, A + Bx_1^* < 0, A > x_2^*$ ② $c\bar{d}_1 - e > 0, c\bar{d}_2 - e > 0, A + Bx_1^* > 0, A > x_2^*, Q_1 < 0, Q_2 > 0$	Unstable saddle	
$(\hat{x}_1^{(2)}, \hat{x}_2^{(2)})$	① $c\bar{d}_1 - e > 0, c\bar{d}_2 - e < 0, A + Bx_1^* > 0$ ② $c\bar{d}_1 - e > 0, c\bar{d}_2 - e > 0, A + Bx_1^* > 0, A < x_2^*$ ③ $c\bar{d}_1 - e > 0, c\bar{d}_2 - e > 0, A + Bx_1^* > 0, A > x_2^*, Q_1 < 0, Q_2 > 0$	Asymptotically stable	
$(\hat{x}_1^{(*)}, \hat{x}_2^{(*)})$	$c\bar{d}_1 - e > 0, c\bar{d}_2 - e > 0, A + Bx_1^* > 0, A > x_2^*, Q_1 < 0, Q_2 = 0$	Saddle-node bifurcation	

$$Q_1 = |(1-A)cD_1| + 2(1+B)\bar{d}_1; \quad Q_2 = \left((1-A)cD_1 + 2(1+B)\bar{d}_1\right)^2 - 8(1+B)D_1 e$$

zero (i.e., $\sigma_1^2 = 0$), an exponential network in panel (b) with $\sigma_1^2 > 0$ but small, and a scale-free network [37] in panels (c) and (d) with large σ_1^2. In each of the panels, the phase diagram of Eq. (10) is plotted on the left, and the simulation results on the right. We can see that the theoretical predictions can describe the properties of the simulations very well, that is, the increase of network heterogeneity corresponding to the stronger species will promote the long-term stable coexistence of competitive species.

In summary, the above analysis reveals when the long-term stable coexistence of species 1 and 2 is possible in a multiplex network system under the condition of large N through the deterministic dynamics Eq. (10). However, a more challenging question is how the coexistence of species 1 and 2 is affected by the finite size of a multiplex network. To answer this question, the effect of N on the steady-state statistics of the system is investigated using the theory of one-step process [40] (see section "steady-state statistics" in Appendix B). The
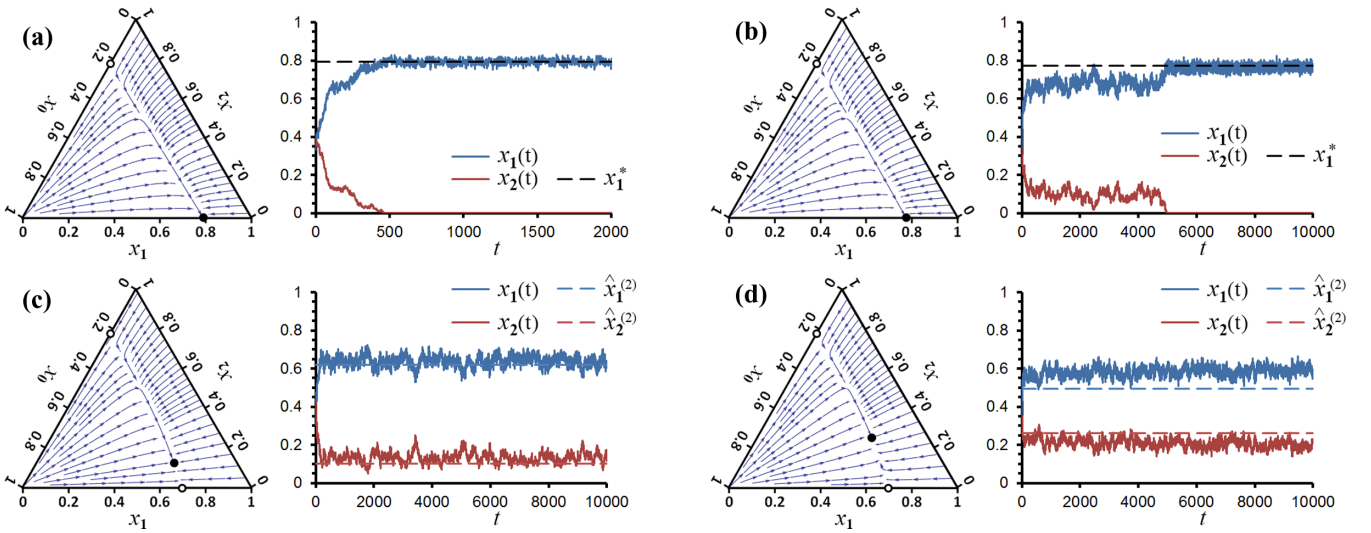

FIG. 2. Effect of heterogeneity of the dispersal network of the stronger species on species coexistence. The four examples are considered here, respectively, where (i) G_1 and G_2 have the same average degree in all examples; (ii) G_2 is an exponential network and its heterogeneity remains approximately the same in all examples; and (iii) G_1 is a regular random network in (a) with $\sigma_1^2 = 0$, an exponential network in (b) with $\sigma_1^2 > 0$ but small, and a scale-free network in (c) and (d) with large σ_1^2. In each panel, the phase diagram of Eq. (10) is plotted on the left, the simulation results in continues lines and analytical prediction in dashed lines on the right. The parameters involved in these examples are $N = 1000$, $e = c = 0.1$, and $\bar{d} = 6$; $\sigma_1^2 = \sigma_{1,2} = 0$, $\sigma_2^2 = 12.11$, and $\bar{\mu} = 0.032$ in (a); $\sigma_1^2 = 11.414$, $\sigma_2^2 = 11.628$, $\sigma_{1,2} = -0.064$, and $\bar{\mu} = 0.034$ in (b); $\sigma_1^2 = 48.148$, $\sigma_2^2 = 12.13$, $\sigma_{1,2} = -0.258$, and $\bar{\mu} = 0.038$ in (c); $\sigma_1^2 = 47.312$, $\sigma_2^2 = 11.628$, $\sigma_{1,2} = -8.25$, and $\bar{\mu} = 0.03$ in (d). For each example, the initial state of the system is taken as $(x_0(0), x_1(0), x_2(0)) = (1/3, 1/3, 1/3)$ and it obeys the random uniform distribution, that is, for each node i $(i = 1, 2, \dots, N)$, the occurrences of the events $\gamma_i(0) = 0$, or $\gamma_i(0) = 1$, or $\gamma_i(0) = 2$ have the same probability $1/3$, respectively.

results show clearly that when the system state is near a stable interior equilibrium $(\hat{x}_1, \hat{x}_2)$ of Eq. (10), the expectations of x_1 and x_2 are $\hat{x}_1$ and $\hat{x}_2$, respectively, and the variances of x_1 and x_2, denoted by $\sigma_{x_1}^2$ and $\sigma_{x_2}^2$, respectively, and the covariance of x_1 and x_2, denoted by σ_{x_1, x_2}, will tend to 0 if N is large enough, that is, for large N, the dynamical properties of the system can be described well by Eq. (10).

IV. DISCUSSION

The theory of metapopulation provides a basic theoretical framework for understanding the dynamics of population and community in heterogeneous habitats, or in patch habitat systems, in which the fundamental idea of metapopulation persistence is a stochastic balance between local extinctions and recolonizations of empty habitat patches [12,13]. The various factors affecting metapopulation dynamics have also been investigated by many theoretical studies, for example, the studies on how the metapopulation colonization rate and extinction rate vary as a function of the overall level of patch occupancy in the Levins model [9–11], the source-sink metapopulations [13,41], the model of two-species Levins metapopulations [42], and the spatially explicitly models of metapopulation [12], etc. However, none of these theoretical studies have considered whether the different dispersal paths of different species in a patch habitat system will affect the long-term stable coexistence of species. For instance, the study on two-species Levins metapopulations (including competing species, predator-prey metapopulations, and mutualism) mainly emphasizes the effects that the rate of patch turnover as well as the amount of habitat destruction has on the metapopulation persistence [13], but does not consider the influence of dispersal paths of species. However, a recent study based on numerical simulations shows that the species coexistence in a patch habitat system could be promoted by the the dispersal network heterogeneity of competitive species [34]. This result may suggest a different possible mechanism of competitive species coexistence in heterogeneous environments.

In this study, different from the classic theoretical studies of metapopulations, we present a simple multiplex network model (it is one of three types of the multilayer network [28]) to explore how the difference of dispersal paths of different species in a patch habitat system affects the long-term stable coexistence of competitive species, in which the ecological differences among different species are only reflected in their dispersal path and their priority in colonizing empty patches. Moreover, under the condition of large network size, our theoretical analysis also depends on the method of mean-field approximation which may make the result valid in the limited regime of application. Although we realize that all of our assumptions may not hold for a given ecosystem, they provide a possible theoretical way for understanding why the difference of dispersal paths of different species in a patch habitat system is conducive to species coexistence. Our main result shows clearly that, in a patch habitat system, if the dispersal paths of the species with stronger colonization ability is different than the dispersal paths of the weaker species, then the larger the heterogeneity of dispersal network of the stronger species is,

the more possible the long-term stable coexistence of species should be. This also implies that for multispecies Levins metapopulations, the difference between the dispersal patterns of different species may play a very important role in the dynamic characteristics of the metapopulations. Therefore, our theoretical analysis not only provides a different perspective for understanding the mechanism of maintaining biodiversity in a heterogeneous environment (or in patch habitat system), but also provides a challenging research direction for the development of metapopulation theory.

APPENDIX A: STABILITY ANALYSIS OF EQ. (10)

For $G_1 = G_2$, note that $d_1(i) = d_2(i) = d(i)$ and $\langle k_1(i)k_2(i) \rangle = x_1(t)x_2(t)[d^2(i) - d(i)]$ for $i = 1, 2, \ldots, N$. Then, $\langle \rho_1(i) \rangle$ and $\langle \rho_2(i) \rangle$ can be rewritten as

$$\langle \rho_1(i) \rangle = cx_1(t)d(i) + \frac{c^2}{2}x_1^2(t)d(i) - \frac{c^2}{2}x_1^2(t)d^2(i),$$

$$\langle \rho_2(i) \rangle = cx_2(t)d(i) + \left(\frac{c^2}{2}x_2^2(t) + c^2 x_1(t)x_2(t) \right)d(i)$$

$$- \left(\frac{c^2}{2}x_2^2(t) + c^2 x_1(t)x_2(t) \right)d^2(i), \quad \text{(A1)}$$

respectively, for $i = 1, 2, \ldots, N$, and we have also

$$\phi_1 = c\bar{d}x_1(t) - \frac{c^2}{2}(\sigma^2 + \bar{d}^2 - \bar{d})x_1^2(t),$$

$$\phi_2 = c\bar{d}x_2(t) - \left(\frac{c^2}{2}x_2^2(t) + c^2 x_1(t)x_2(t) \right)(\sigma^2 + \bar{d}^2 - \bar{d}),$$

$$\text{(A2)}$$

where $\bar{d} = \sum_{i=1}^{N} d(i)/N$ and $\sigma^2 = \sum_{i=1}^{N} (d(i) - \bar{d})^2/N$.

Then $\tilde{\phi}_1 > \tilde{\phi}_2$ for all possible $0 < x_1, x_2 < 1$, i.e., $\tilde{\phi}_1 - \tilde{\phi}_2 = c^2(x_1 + x_2)(\sigma^2 + \bar{d}^2 - \bar{d})/2 > 0$. This shows clearly that the stable coexistence of species 1 and 2 is impossible if $G_1 = G_2$, or, more specifically, under our assumptions and definitions, the single layer network cannot lead to the long-term stable coexistence of species.

For the situation with $G_1 \neq G_2$, the stability analysis of the boundaries of Eq. (10) is given by the following:

(i) The point (0,0) is a trivial equilibrium of Eq. (10) and it is globally asymptotically stable if $e/c > \bar{d}_i$ for $i = 1, 2$, unstable if $e/c < \bar{d}_i$ for $i = 1, 2$ and a saddle point if $(e/c - \bar{d}_1)(e/c - \bar{d}_2) < 0$ since the Jacobian matrix about $(0,0)$ is $\begin{pmatrix} -e + c\bar{d}_1 & 0 \\ 0 & -e + c\bar{d}_2 \end{pmatrix}$.

(ii) The point $(x_1^*, 0)$ with

$$x_1^* = -\left[\bar{d}_1 - \frac{c}{2}D_1 - \sqrt{\left(\bar{d}_1 - \frac{c}{2}D_1\right)^2 + 2D_1(c\bar{d}_1 - e)}\right]\Big/(cD_1) \approx 1 - e/(c\bar{d}_1),$$

where $D_1 = \bar{d}_1(1 - \bar{d}_1) - \sigma_1^2 < 0$ since $\bar{d}_1 > 1$, is a boundary equilibrium if $e/c < \bar{d}_1$. Note that the Jacobian matrix about $(x_1^*, 0)$ is

$$\begin{pmatrix} x_1^*\left[-e/(1 - x_1^*) + (1 - x_1^*)\frac{c^2}{2}D_1\right] & \partial \dot{x}_1/\partial x_2|_{(x_1^*, 0)} \\ 0 & (1 - x_1^*)\{c(\bar{d}_2 - \bar{d}_1) - \frac{c^2}{2}[D_1 + 2(\sigma_{12} + \bar{d}_1\bar{d}_2 - \mu)]x_1^*\} \end{pmatrix}.$$

Thus, $(x_1^*, 0)$ is locally asymptotically stable if $2(\bar{d}_2 - \bar{d}_1) - c[D_1 + 2(\sigma_{12} + \bar{d}_1\bar{d}_2 - \mu)]x_1^* < 0$ and a saddle point if $2(\bar{d}_2 - \bar{d}_1) - c[D_1 + 2(\sigma_{12} + \bar{d}_1\bar{d}_2 - \mu)]x_1^* > 0$.

(iii) Similar to $(x_1^*, 0)$, the point $(0, x_2^*)$ with

$$x_2^* = -\left[\bar{d}_2 - \frac{c}{2}D_2 - \sqrt{\left(\bar{d}_2 - \frac{c}{2}D_2\right)^2 + 2D_2(c\bar{d}_2 - e)}\right]\Big/(cD_2) \approx 1 - e/(c\bar{d}_2)$$

is also a boundary equilibrium if $e/c < \bar{d}_2$, where $D_2 = \bar{d}_2(1 - \bar{d}_2) - \sigma_2^2 < 0$ since $\bar{d}_2 > 1$. Note also that the Jacobian matrix about $(0, x_2^*)$ is

$$\begin{pmatrix} (1 - x_2^*)(c\bar{d}_1 - c\bar{d}_2 - \frac{c^2}{2}D_2x_2^*) & 0 \\ \partial \dot{x}_2/\partial x_1|_{(0, x_2^*)} & x_2^*\left[-e/(1 - x_2^*) + (1 - x_2^*)\frac{c^2}{2}D_2\right] \end{pmatrix}.$$

Thus, $(0, x_2^*)$ is locally asymptotically stable if $c\bar{d}_1 - c\bar{d}_2 - \frac{c^2}{2}D_2x_2^* < 0$ and a saddle point if $c\bar{d}_1 - c\bar{d}_2 - \frac{c^2}{2}D_2x_2^* > 0$.

The interior positive equilibrium of Eq. (10), denoted by $(\hat{x}_1, \hat{x}_2)$ with $0 < \hat{x}_1, \hat{x}_2 < 1$, can be obtained from the equations

$$\begin{aligned} -e + (1 - x_1 - x_2)\tilde{\phi}_1 &= 0, \\ -e + (1 - x_1 - x_2)\tilde{\phi}_2 &= 0. \end{aligned} \tag{A3}$$

Note that $\tilde{\phi}_1 = \tilde{\phi}_2 \Rightarrow x_2 = A + Bx_1$, where $A = 2(\bar{d}_1 - \bar{d}_2)/(cD_2)$ and $B = [D_1 + 2(\sigma_{1,2} - \bar{\mu} + \bar{d}_1\bar{d}_2)]/D_2$ [this means that the stability conditions of boundaries $(x_1^*, 0)$ and $(0, x_2^*)$ can be also re-expressed succinctly as $(x_1^*, 0)$ is stable if $A + Bx_1^* < 0$; and $(0, x_2^*)$ is stable if $A > x_2^*$]. Note also that the two possible solutions of Eq. (A3), denoted by $(\hat{x}_1^{(1)}, \hat{x}_2^{(1)})$ and $(\hat{x}_1^{(2)}, \hat{x}_2^{(2)})$, respectively, can be given by

$$\begin{aligned} \hat{x}_1^{(1)} &= \frac{-(1 - A)\frac{c}{2}D_1 + (1 + B)\bar{d}_1 + \sqrt{[(1 - A)\frac{c}{2}D_1 + (1 + B)\bar{d}_1]^2 - 2(1 + B)D_1e}}{-(1 + B)cD_1} \\ &= \frac{1 - A}{2(1 + B)} - \frac{\bar{d}_1}{cD_1} - \frac{\sqrt{[(1 - A)\frac{c}{2}D_1 + (1 + B)\bar{d}_1]^2 - 2(1 + B)D_1e}}{(1 + B)cD_1} \\ \hat{x}_2^{(1)} &= A + B\hat{x}_1^{(1)}, \end{aligned} \tag{A4}$$

and

$$\begin{aligned} \hat{x}_1^{(2)} &= \frac{-(1 - A)\frac{c}{2}D_1 + (1 + B)\bar{d}_1 - \sqrt{[(1 - A)\frac{c}{2}D_1 + (1 + B)\bar{d}_1]^2 - 2(1 + B)D_1e}}{-(1 + B)cD_1} \\ &= \frac{1 - A}{2(1 + B)} - \frac{\bar{d}_1}{cD_1} + \frac{\sqrt{[(1 - A)\frac{c}{2}D_1 + (1 + B)\bar{d}_1]^2 - 2(1 + B)D_1e}}{(1 + B)cD_1} \\ \hat{x}_2^{(2)} &= A + B\hat{x}_1^{(2)}. \end{aligned} \tag{A5}$$

Thus, the conditions for the existence of interior equilibrium can be shown as

(i) The interior equilibrium point $(\hat{x}_1^{(1)}, \hat{x}_2^{(1)})$ exists if $c\bar{d}_1 - e > 0$, $c\bar{d}_2 - e > 0$, $A + Bx_1^* < 0$, and $A > x_2^*$; or $c\bar{d}_1 - e > 0$, $c\bar{d}_2 - e > 0$, $A + Bx_1^* > 0$, $A > x_2^*$, $|(1 - A)D_1/2| < -(1 + B)\bar{d}_1$, and $[(1 - A)cD_1/2 + (1 + B)\bar{d}_1]^2 > 2(1 + B)D_1e$.

(ii) The interior equilibrium $(\hat{x}_1^{(2)}, \hat{x}_2^{(2)})$ exists if $c\bar{d}_1 - e > 0$, $c\bar{d}_2 - e < 0$, and $A + Bx_1^* > 0$; or $c\bar{d}_1 - e > 0$, $c\bar{d}_2 - e > 0$, $A + Bx_1^* > 0$, and $A < x_2^*$; or $c\bar{d}_1 - e > 0$, $c\bar{d}_2 - e > 0$, $A + Bx_1^* > 0$, $A > x_2^*$, $|(1 - A)D_1/2| < -(1 + B)\bar{d}_1$, and $[(1 - A)cD_1/2 + (1 + B)\bar{d}_1]^2 > 2(1 + B)D_1 e$.

In particular, if $[(1 - A)cD_1/2 + (1 + B)\bar{d}_1]^2 - 2(1 + B)D_1 e = 0$, then we have

$$\hat{x}_1^{(*)} = \hat{x}_1^{(1)} = \hat{x}_1^{(2)} = \frac{1 - A}{2(1 + B)} - \frac{\bar{d}_1}{cD_1}, \quad \hat{x}_2^{(*)} = \hat{x}_2^{(1)} = \hat{x}_2^{(2)} = A + B\hat{x}_1^{(*)}. \tag{A6}$$

It is also easy to see that the point $(\hat{x}_1^{(*)}, \hat{x}_2^{(*)})$ is an interior equilibrium if $c\bar{d}_1 - e > 0$, $c\bar{d}_2 - e > 0$, $A + Bx_1^* > 0$, $A > x_2^*$, $|(1 - A)D_1/2| < -(1 + B)\bar{d}_1$, and $[(1 - A)cD_1/2 + (1 + B)\bar{d}_1]^2 = 2(1 + B)D_1 e$.

Note that the Jacobian matrix about $(\hat{x}_1^{(i)}, \hat{x}_2^{(i)})$ for $i = 1, 2$ is

$$\begin{pmatrix} x_1\left[-\tilde{\phi}_1 + (1 - x_1 - x_2)\frac{c^2}{2}D_1\right] & -x_1\tilde{\phi}_1 \\ x_2[-\tilde{\phi}_2 - (1 - x_1 - x_2)c^2(\sigma_{1,2} - \bar{\mu} + \bar{d}_1\bar{d}_2)] & x_2\left[-\tilde{\phi}_2 + (1 - x_1 - x_2)\frac{c^2}{2}D_2\right] \end{pmatrix}\Bigg|_{(\hat{x}_1^{(i)}, \hat{x}_2^{(i)})},$$

and the eigenvalues of this matrix satisfy

$$\lambda_1 + \lambda_2 = -\tilde{\phi}_1(x_1 + x_2) + (1 - x_1 - x_2)\frac{c^2}{2}[x_1 D_1 + x_2 D_2]|_{(\hat{x}_1^{(i)}, \hat{x}_2^{(i)})} < 0$$

and

$$\begin{aligned} \lambda_1\lambda_2 &= x_1 x_2\left[-\tilde{\phi}_1 + (1 - x_1 - x_2)\frac{c^2}{2}D_1\right]\left[-\tilde{\phi}_2 + (1 - x_1 - x_2)\frac{c^2}{2}D_2\right]\Bigg|_{(\hat{x}_1^{(i)}, \hat{x}_2^{(i)})} \\ &\quad + x_1 x_2\tilde{\phi}_1[-\tilde{\phi}_1 - (1 - x_1 - x_2)c^2(\sigma_{1,2} - \bar{\mu} + \bar{d}_1\bar{d}_2)]|_{(\hat{x}_1^{(i)}, \hat{x}_2^{(i)})} \\ &= x_1 x_2(1 - x_1 - x_2)\frac{c^2}{2}\left[(1 - x_1 - x_2)\frac{c^2}{2}D_1 D_2 - \tilde{\phi}_1[D_1 + D_2 + 2(\sigma_{12} + \bar{d}_1\bar{d}_2 - \mu)]\right]\Bigg|_{(\hat{x}_1^{(i)}, \hat{x}_2^{(i)})} \\ &= x_1 x_2(1 - x_1 - x_2)\frac{c^4}{2}D_1 D_2(1 + B)\left[\frac{1 - A}{2(1 + B)} - \frac{\bar{d}_1}{cD_1} - x_1\right]\Bigg|_{(\hat{x}_1^{(i)}, \hat{x}_2^{(i)})}. \end{aligned}$$

Therefore, we have that if $(\hat{x}_1^{(1)}, \hat{x}_2^{(1)})$ is an interior equilibrium, then it must be a saddle point, if $(\hat{x}_1^{(2)}, \hat{x}_2^{(2)})$ is an interior equilibrium, then it must be asymptotically stable, and if $(\hat{x}_1^{(*)}, \hat{x}_2^{(*)})$ is an interior equilibrium, $\lambda_1\lambda_2 = 0$, then it is a saddle-node bifurcation.

These stability results are summarized in Eqs. (11)–(13) and Table I of the main text.

APPENDIX B: STEADY-STATE STATISTICS ANALYSIS OF THE TWO-SPECIES MULTIPLEX NETWORK DYNAMICS

1. One-step process

Note that for $G_1 \neq G_2$, if the node i is empty, then the probability that it is successfully colonized by species 1, denoted by $\rho_1(i)$, is $\rho_1(i) = 1 - (1 - c)^{k_1(i)}$, and the probability that it is successfully colonized by species 2, denoted by $\rho_2(i)$, is $\rho_2(i) = (1 - c)^{k_1(i)}[1 - (1 - c)^{k_2(i)}]$. Based on the theory of one-step process [40], we assume that, in each time step (or

in a small time interval), the system state can be changed at most one frequency unit (i.e., $1/N$), that is, or change from x_1 to $x_1 + 1/N$ (or to $x_1 - 1/N$) happens, or change from x_2 to $x_2 + 1/N$ (or to $x_2 - 1/N$) happens, or nothing changes. So, for the stochastic fluctuations in the frequencies of species 1 and 2 nodes, we take the one-step process with events

$$x_1 \xrightarrow{\pi_1^{\pm}} x_1 \pm 1/N,$$
$$x_2 \xrightarrow{\pi_2^{\pm}} x_2 \pm 1/N,$$

where $\pi_1^+ = \sum_{i=1}^N \delta_K(\gamma_i(t), 0)\rho_1(i)/N$ and $\pi_1^- = ex_1$ are proportional to the transition probabilities from x_1 to $x_1 + 1/N$ and from x_1 to $x_1 - 1/N$, respectively, and, similarly, $\pi_2^+ = \sum_{i=1}^N \delta_K(\gamma_i(t), 0)\rho_2(i)/N$ and $\pi_2^- = ex_2$ are proportional to the transition probabilities from x_2 to $x_2 + 1/N$ and from x_2 to $x_2 - 1/N$, respectively [40].

Let $p(x_1, x_2; t)$ denote the probability density distribution that the the frequencies of species 1 and species 2 nodes equal exactly x_1 and x_2, respectively, at time t. When the time step is taken as $1/N$, we have the master equation [40]

$$\begin{aligned} p(x_1, x_2; t + 1/N) - p(x_1, x_2, t) &= p(x_1 - 1/N, x_2; t)\pi_1^+(x_1 - 1/N, x_2) + p(x_1 + 1/N, x_2; t)\pi_1^-(x_1 + 1/N) \\ &\quad + p(x_1, x_2 - 1/N; t)\pi_2^+(x_1, x_2 - 1/N) + p(x_1, x_2 + 1/N; t)\pi_2^-(x_2 + 1/N) \\ &\quad - p(x_1, x_2; t)[\pi_1^+(x_1, x_2) + \pi_1^-(x_1)] - p(x_1, x_2; t)[\pi_2^+(x_1, x_2) + \pi_2^-(x_2)]. \end{aligned} \tag{B1}$$

Notice that

$$p(x_1, x_2; t + 1/N) \approx p(x_1, x_2; t) + \frac{1}{N} \frac{\partial p(x_1, x_2; t)}{\partial t},$$

$$p(x_1 \pm 1/N, x_2; t) \approx p(x_1, x_2; t) \pm \frac{1}{N} \frac{\partial p(x_1, x_2; t)}{\partial x_1} + \frac{1}{2N^2} \frac{\partial^2 p(x_1, x_2; t)}{\partial x_1^2},$$

$$p(x_1, x_2 \pm 1/N; t) \approx p(x_1, x_2; t) \pm \frac{1}{N} \frac{\partial p(x_1, x_2; t)}{\partial x_2} + \frac{1}{2N^2} \frac{\partial^2 p(x_1, x_2; t)}{\partial x_2^2},$$

$$\pi_1^+(x_1 - 1/N, x_2) \approx \pi_1^+(x_1, x_2) - \frac{1}{N} \frac{\partial \pi_1^+(x_1, x_2)}{\partial x_1} + \frac{1}{2N^2} \frac{\partial^2 \pi_1^+(x_1, x_2)}{\partial x_1^2},$$

$$\pi_1^-(x_1 + 1/N) \approx \pi_1^-(x_1) + \frac{1}{N} \frac{\partial \pi_1^-(x_1)}{\partial x_1} + \frac{1}{2N^2} \frac{\partial^2 \pi_1^-(x_1)}{\partial x_1^2},$$

$$\pi_2^+(x_1, x_2 - 1/N) \approx \pi_2^+(x_1, x_2) - \frac{1}{N} \frac{\partial \pi_2^+(x_1, x_2)}{\partial x_2} + \frac{1}{2N^2} \frac{\partial^2 \pi_2^+(x_1, x_2)}{\partial x_2^2},$$

$$\pi_2^-(x_2 + 1/N) \approx \pi_2^-(x_2) + \frac{1}{N} \frac{\partial \pi_2^-(x_2)}{\partial x_2} + \frac{1}{2N^2} \frac{\partial^2 \pi_2^-(x_2)}{\partial x_2^2}.$$

Furthermore, note also that

$$p(x_1, x_2; t + 1/N) - p(x_1, x_2; t) \approx \frac{1}{N} \frac{\partial p(x_1, x_2; t)}{\partial t},$$

$$
\begin{aligned}
p(x_1 - 1/N, x_2; t)\pi_1^+(x_1 - 1/N, x_2) \approx {}& p(x_1, x_2; t)\pi_1^+(x_1, x_2) + p(x_1, x_2; t)\left[-\frac{1}{N} \frac{\partial \pi_1^+(x_1, x_2)}{\partial x_1} + \frac{1}{2N^2} \frac{\partial^2 \pi_1^+(x_1, x_2)}{\partial x_1^2} \right] \\
& + \pi_1^+(x_1, x_2)\left[-\frac{1}{N} \frac{\partial p(x_1, x_2; t)}{\partial x_1} + \frac{1}{2N^2} \frac{\partial^2 p(x_1, x_2; t)}{\partial x_1^2} \right] + \frac{1}{N^2} \frac{\partial p(x_1, x_2; t)}{\partial x_1} \frac{\partial \pi_1^+(x_1, x_2)}{\partial x_1},
\end{aligned}
$$

$$
\begin{aligned}
p(x_1 + 1/N, x_2; t)\pi_1^-(x_1 + 1/N) \approx {}& p(x_1, x_2; t)\pi_1^-(x_1) + p(x_1, x_2; t)\left[\frac{1}{N} \frac{\partial \pi_1^-(x_1)}{\partial x_1} + \frac{1}{2N^2} \frac{\partial^2 \pi_1^-(x_1)}{\partial x_1^2} \right] \\
& + \pi_1^-(x_1)\left[\frac{1}{N} \frac{\partial p(x_1, x_2; t)}{\partial x_1} + \frac{1}{2N^2} \frac{\partial^2 p(x_1, x_2; t)}{\partial x_1^2} \right] + \frac{1}{N^2} \frac{\partial p(x_1, x_2; t)}{\partial x_1} \frac{\partial \pi_1^-(x_1)}{\partial x_1},
\end{aligned}
$$

$$
\begin{aligned}
p(x_1, x_2 - 1/N; t)\pi_2^+(x_1, x_2 - 1/N) \approx {}& p(x_1, x_2; t)\pi_2^+(x_1, x_2) + p(x_1, x_2; t)\left[-\frac{1}{N} \frac{\partial \pi_2^+(x_1, x_2)}{\partial x_2} + \frac{1}{2N^2} \frac{\partial^2 \pi_2^+(x_1, x_2)}{\partial x_2^2} \right] \\
& + \pi_2^+(x_1, x_2)\left[-\frac{1}{N} \frac{\partial p(x_1, x_2; t)}{\partial x_2} + \frac{1}{2N^2} \frac{\partial^2 p(x_1, x_2; t)}{\partial x_2^2} \right] + \frac{1}{N^2} \frac{\partial p(x_1, x_2; t)}{\partial x_2} \frac{\partial \pi_2^+(x_1, x_2)}{\partial x_2},
\end{aligned}
$$

$$
\begin{aligned}
p(x_1, x_2 + 1/N; t)\pi_2^-(x_2 + 1/N) \approx {}& p(x_1, x_2; t)\pi_2^-(x_2) + p(x_1, x_2; t)\left[\frac{1}{N} \frac{\partial \pi_2^-(x_2)}{\partial x_2} + \frac{1}{2N^2} \frac{\partial^2 \pi_2^-(x_2)}{\partial x_2^2} \right] \\
& + \pi_2^-(x_2)\left[\frac{1}{N} \frac{\partial p(x_1, x_2; t)}{\partial x_2} + \frac{1}{2N^2} \frac{\partial^2 p(x_1, x_2; t)}{\partial x_2^2} \right] + \frac{1}{N^2} \frac{\partial p(x_1, x_2; t)}{\partial x_2} \frac{\partial \pi_2^-(x_2)}{\partial x_2}.
\end{aligned}
$$

Therefore, the Fokker-Planck equation (i.e., a continuous-time diffusion approximation) corresponding to the master equation (B1) can be given by [40]

$$\frac{\partial p(x_1, x_2; t)}{\partial t} = -\frac{\partial}{\partial x_1}[\pi_1^+(x_1, x_2) - \pi_1^-(x_1)]p(x_1, x_2; t) + \frac{1}{2N}\frac{\partial^2}{\partial x_1^2}[\pi_1^+(x_1, x_2) + \pi_1^-(x_1)]p(x_1, x_2; t)$$

$$-\frac{\partial}{\partial x_2}[\pi_2^+(x_1, x_2) - \pi_2^-(x_2)]p(x_1, x_2; t) + \frac{1}{2N}\frac{\partial^2}{\partial x_2^2}[\pi_2^+(x_1, x_2) + \pi_2^-(x_2)]p(x_1, x_2; t). \quad \text{(B2)}$$

This is also called the forward Kolmogorov equation in mathematics.

2. Steady-state statistics

Based on Eq. (10), the terms $\pi_1^\pm$ and $\pi_2^\pm$ can be approximated as $\pi_1^+ \approx (1 - x_1 - x_2)\phi_1$, $\pi_1^- \approx x_1 e$, $\pi_2^+ \approx (1 - x_1 - x_2)\phi_2$, and $\pi_2^- \approx x_2 e$, respectively. Let $(\tilde{x}_1, \tilde{x}_2)$ denote an asymptotically stable equilibrium of Eq. (10). We now consider the statistical characteristics of the system when the system state is near $(\tilde{x}_1, \tilde{x}_2)$. In order to show this, let $\xi_1 = x_1 - \tilde{x}_1$ and $\xi_2 = x_2 - \tilde{x}_2$. This implies that the joint probability density distribution $p(x_1, x_2; t)$ can be now rewritten as the function of ξ_1 and ξ_2, i.e., $p(x_1, x_2; t) = q(\xi_1, \xi_2; t)$. Using the Taylor expansion about $(\tilde{x}_1, \tilde{x}_2)$, we have

$$\begin{aligned}\frac{\partial q(\xi_1, \xi_2; t)}{\partial t} = &-\frac{\partial}{\partial \xi_1}[a_{11}\xi_1 + a_{12}\xi_2]q(\xi_1, \xi_2; t) \\ &+ \frac{D_1}{2N}\frac{\partial^2 q(\xi_1, \xi_2; t)}{\partial \xi_1^2} \\ &- \frac{\partial}{\partial \xi_2}[a_{21}\xi_1 + a_{22}\xi_2]q(\xi_1, \xi_2; t) \\ &+ \frac{D_2}{2N}\frac{\partial^2 q(\xi_1, \xi_2; t)}{\partial \xi_2^2}\end{aligned} \quad \text{(B3)}$$

with boundary conditions $\lim_{\xi_1, \xi_2 \to \pm\infty} (q(\xi_1, \xi_2; t), \frac{\partial q(\xi_1, \xi_2; t)}{\partial \xi_1}, \frac{\partial q(\xi_1, \xi_2; t)}{\partial \xi_2}) = (0, 0, 0)$, where

$$\begin{aligned}a_{11} &= \frac{\partial}{\partial x_1}[\pi_1^+(x_1, x_2) - \pi_1^-(x_1)]\bigg|_{(\tilde{x}_1, \tilde{x}_2)}, \\ a_{12} &= \frac{\partial}{\partial x_2}[\pi_1^+(x_1, x_2) - \pi_1^-(x_1)]\bigg|_{(\tilde{x}_1, \tilde{x}_2)}, \\ a_{21} &= \frac{\partial}{\partial x_1}[\pi_2^+(x_1, x_2) - \pi_2^-(x_2)]\bigg|_{(\tilde{x}_1, \tilde{x}_2)}, \\ a_{22} &= \frac{\partial}{\partial x_2}[\pi_2^+(x_1, x_2) - \pi_2^-(x_2)]\bigg|_{(\tilde{x}_1, \tilde{x}_2)},\end{aligned} \quad \text{(B4)}$$

and

$$\begin{aligned}D_1 &= \pi_1^+(\tilde{x}_1, \tilde{x}_2) + \pi_1^-(\tilde{x}_1), \\ D_2 &= \pi_2^+(\tilde{x}_1, \tilde{x}_2) + \pi_2^-(\tilde{x}_2).\end{aligned} \quad \text{(B5)}$$

We can see that Eq. (B3) and its boundary conditions also imply that [40]

$$\begin{aligned}\frac{d\langle\xi_1\rangle}{dt} &= a_{11}\langle\xi_1\rangle + a_{12}\langle\xi_2\rangle, \\ \frac{d\langle\xi_2\rangle}{dt} &= a_{21}\langle\xi_1\rangle + a_{22}\langle\xi_2\rangle,\end{aligned} \quad \text{(B6)}$$

and

$$\begin{aligned}\frac{d\langle\xi_1^2\rangle}{dt} &= 2[a_{11}\langle\xi_1^2\rangle + a_{12}\langle\xi_1\xi_2\rangle] + \frac{D_1}{N}, \\ \frac{d\langle\xi_1\xi_2\rangle}{dt} &= a_{21}\langle\xi_1^2\rangle + (a_{11} + a_{22})\langle\xi_1\xi_2\rangle + a_{12}\langle\xi_2^2\rangle, \quad \text{(B7)} \\ \frac{d\langle\xi_2^2\rangle}{dt} &= 2[a_{21}\langle\xi_1\xi_2\rangle + a_{22}\langle\xi_2^2\rangle] + \frac{D_2}{N}.\end{aligned}$$

It is easy to see that the stationary solution of Eq. (B6), i.e., $\langle\xi_1\rangle = 0$ and $\langle\xi_2\rangle = 0$, must be also asymptotically stable [i.e., the matrix $(a_{ij})_{2\times2}$ satisfies $a_{11} + a_{22} < 0$ and $a_{11}a_{22} - a_{12}a_{21} > 0$] since the equilibrium $(\tilde{x}_1, \tilde{x}_2)$ is asymptotically stable. Thus, the statistical characteristics of the system state around the stable equilibrium $(\tilde{x}_1, \tilde{x}_2)$ can be determined by the stationary solutions of Eqs. (B6) and (B7), which are

$$\begin{aligned}\langle x_1\rangle &= \tilde{x}_1, \\ \langle x_2\rangle &= \tilde{x}_2, \\ \sigma_{x_1}^2 &= \langle\xi_1^2\rangle \\ &= -\frac{a_{12}}{a_{11}}\sigma_{x_1, x_2} - \frac{D_1}{2a_{11}N}, \\ \sigma_{x_2}^2 &= \langle\xi_2^2\rangle = -\frac{a_{21}}{a_{22}}\sigma_{x_1, x_2} - \frac{D_2}{2a_{22}N}, \\ \sigma_{x_1, x_2} &= \langle\xi_1\xi_2\rangle \\ &= \frac{1}{2N}\left[\frac{a_{21}D_1}{a_{11}} + \frac{a_{12}D_2}{a_{22}}\right]\frac{a_{11}a_{22}}{(a_{11}a_{22} - a_{12}a_{21})}, \quad \text{(B8)}\end{aligned}$$

respectively, This result means that if N is large enough, then we must have $\sigma_{x_1}^2 \to 0$, $\sigma_{x_2}^2 \to 0$, and $\sigma_{x_1, x_2} \to 0$.

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