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Stability and selective extinction in complex mutualistic networks

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We study species abundance in the empirical plant-pollinator mutualistic networks exhibiting broad degree distributions, with uniform intragroup competition assumed, by the Lotka-Volterra equation. The stability of a fixed point is found to be identified by the signs of its nonzero components and those of its neighboring fixed points. Taking the annealed approximation, we derive the nonzero components to be formulated in terms of degrees and the rescaled interaction strengths, which lead us to find different stable fixed points depending on parameters, and we obtain the phase diagram. The selective extinction phase finds small-degree species extinct and effective interaction reduced, maintaining stability and hindering the onset of instability. The nonzero minimum species abundances from different empirical networks show data collapse when rescaled as predicted theoretically.

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I. INTRODUCTION

A community of randomly interacting species can become unstable as the number of species and their interaction connectivity together go beyond a threshold [1]. Such a random-interaction model can be informative with the help of the random matrix theory, and it has been instrumental in the theoretical study of ecological systems, illuminating their features from the perspective of stability [2–8]. Recently available datasets point out the complex organization of interspecific interactions, neither completely random nor ordered [9–18], and they have drawn the attention of researchers to the origins and implications of overrepresented network structural features [19–22]. Contrary to the unstructured communities in which every species is subject to the identical randomness in its interaction profile, individual species can be in fundamentally different states under structured interactions. For instance, the mutualistic partnership between flowering plants and pollinating bees is characterized by different numbers of partners, called degrees, from species to species. Considering also the intrinsic competitions among plants and among pollinators due to limited resources [20,23–29], one finds that the abundance of a species increases due to the benefit from mutualistic partners but also decreases due to the cost from competition, the imbalance of which may lead some species to flourish but others to become extinct [26,27]. The mechanism driving such different fates across species remains to be elucidated [30–33].

Here we investigate the different abundances and different likelihood of extinction of individual species in heterogeneous mutualistic networks from the perspective of stability. We consider the Lotka-Volterra-type (LV) equation for species abundance on plant-animal mutualistic networks, with the mutualistic interaction constructed from an empirical dataset [34], which is heterogeneous, and all-to-all intragroup competition assumed [4,20,23–29]. The strengths of mutualism and competition are set to be uniform. We restrict ourselves to the stationary state and study the stable fixed points. Exponentially many fixed points exist with zero components at different species, but only the stable one is relevant to the stationary state.

To find the stable fixed point, we first show that stability can be assessed by the signs of the nonzero components of the considered fixed point and its neighboring fixed points. Next, approximating the adjacency matrix to be in factorized form, we derive the nonzero components of each fixed point to be formulated in terms of degrees and the rescaled interaction strengths. Using these results, we devise an algorithm to classify species into surviving and extinct ones and thereby formulate the stable fixed point, which turns out to work well, as supported by good agreement with numerical solutions. The extinction or the diverging abundances of selected species happens depending on parameters, the analytic understanding of which allows us to obtain the phase diagram, including the full coexistence, selective extinction, and unstable phase. In the selective extinction phase, small-degree species go extinct, which results in reducing the effective interaction among the surviving species and suppressing the onset of instability. Our study enables a principled discrimination between surviving and extinct species and the prediction of the abundances of the surviving species, helping us to understand the interplay of stability, species abundance, and extinction in structured ecological communities.

II. MODEL

We consider a system of $N^{(\mathrm{P})}$ flowering plant species and $N^{(\mathrm{A})}$ pollinating animal species. Their abundances x_i's evolve

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with time under the LV equation as

$$\frac{dx_i(t)}{dt} = x_i\left(\alpha_i + \sum_{j=1}^{S} B_{ij}x_j\right), \tag{1}$$

where $S = N^{(\mathrm{P})} + N^{(\mathrm{A})}$ is the total number of species, $\alpha_i = 1$ is the intrinsic growth rate, and $\mathbb{B} = (B_{ij})$ is the $S \times S$ interaction matrix,

$$\mathbb{B} \equiv -\mathbb{I} - c(\mathbb{J}^{(0)} - \mathbb{I}) + m\mathbb{A}. \tag{2}$$

Here $\mathbb{I} \equiv \begin{pmatrix} \mathbf{I}^{(\mathrm{PP})} & \mathbf{0} \\ \mathbf{0} & \mathbf{I}^{(\mathrm{AA})} \end{pmatrix} = \mathbf{I}^{(\mathrm{PP})} \oplus \mathbf{I}^{(\mathrm{AA})}$ is the identify matrix representing intraspecific regulation, $\mathbb{J}^{(0)} \equiv \begin{pmatrix} \mathbf{J}^{(\mathrm{PP})} & \mathbf{0} \\ \mathbf{0} & \mathbf{J}^{(\mathrm{AA})} \end{pmatrix} = \mathbf{J}^{(\mathrm{PP})} \oplus \mathbf{J}^{(\mathrm{AA})}$ consists of the matrices of 1's ($J_{pp'} = J_{aa'} = 1$ for all p, p', a, a') representing all-to-all competition among plants and among pollinators along with strength $0 < c < 1$, and $\mathbb{A} \equiv \begin{pmatrix} \mathbf{0} & \mathbf{A}^{(\mathrm{PA})} \\ \mathbf{A}^{(\mathrm{AP})} & \mathbf{0} \end{pmatrix} = \mathbf{A}^{(\mathrm{PA})} \oplus \mathbf{A}^{(\mathrm{AP})}$ is the symmetric adjacency matrix ($A_{pa} = A_{ap} = 0, 1$) with $\mathbf{A}^{(\mathrm{AP})} = \mathbf{A}^{(\mathrm{PA})\mathsf{T}}$ representing the mutualistic interaction along with the mutualism strength $m > 0$. The useful properties of the matrices of 1's, which are given in Appendix A, enable various analytic calculations. There are $L \equiv \sum_{p,a} A_{pa}$ mutualistic partner pairs.

We select a real-world community [35] in a database [34] to construct the adjacency matrix $\mathbb{A}$, and use it to define $\mathbb{B}$ by Eq. (2), and we build all our theoretical framework, which will be applied later to other communities. Notice that the elements of $\mathbb{B}$ are not random numbers but represent the interaction relationships among different species with a uniform interaction strength c or m. The whole interaction network encoded in $\mathbb{B}$ and the distributions of the mutualism degrees, $k_p \equiv \sum_a A_{pa}$ of plants and $k_a \equiv \sum_p A_{pa}$ of animals, are presented in Figs. 1(a) and 1(b), respectively. Different degrees of species are a fundamental heterogeneity in their mutualistic interaction profiles, which have been neglected in the random-interaction model assuming the interaction strength between each pair of species to be an independent and identically distributed random variable [1–8], but they are of main concern in the present study.

Integrating Eq. (1) up to $T = 10^3$ with the initial condition $x_i(0) = 1$, we find, as shown in Fig. 1(c), that $x_i(t)$'s for different species i exhibit different behaviors as functions of time. They become stationary in the long-time limit, and we approximate the stationary-state abundance by the species abundance at the final time step T,

$$x_i^{(\mathrm{st})} \equiv \lim_{t\to\infty} x_i(t) \simeq x_i(T). \tag{3}$$

Some species show $x_i^{(\mathrm{st})} = 0$, implying their extinction. Also, as shown in Fig. 1(d), $x_i^{(\mathrm{st})}$ tends to grow with degree k_i. This correlation will be clarified in the next sections. Another remarkable feature is that the effect of mutualism on the species abundance can be drastically different depending on species [26,27,29]. The species with large degrees find their abundances increasing with m, but the abundances of the species having small degrees decrease with m [Fig. 1(d)]. In the next sections, we develop the analytic approach to understand the nature and origin of such heterogeneity in the species abundance depending on parameters.

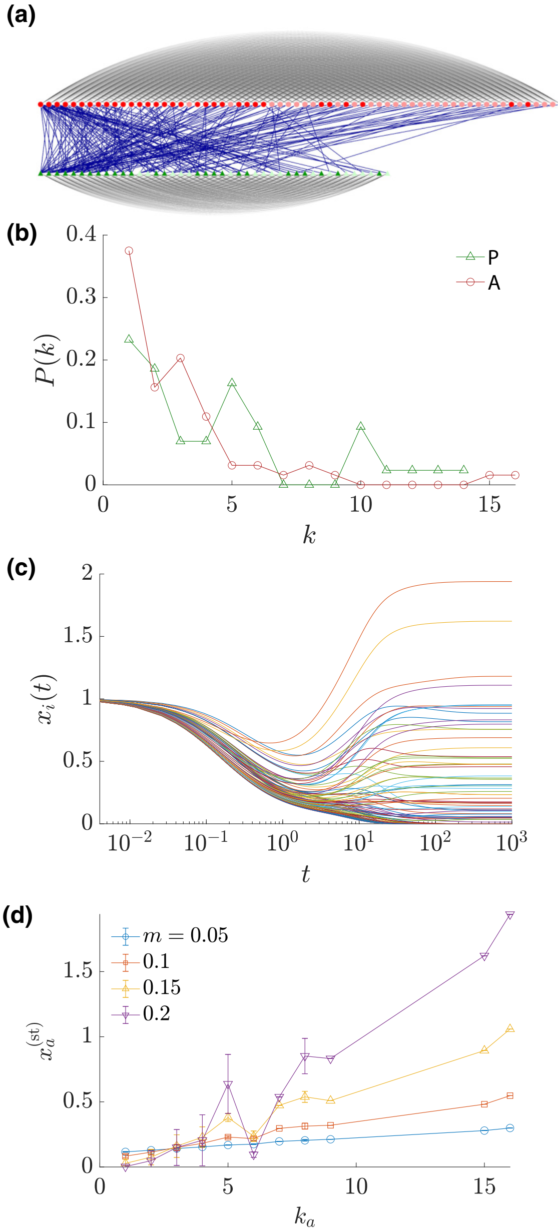

FIG. 1. Interaction network and species abundance of the selected community. (a) Interaction network of $N^{(\mathrm{P})} = 43$ plant species (green triangle) and $N^{(\mathrm{A})} = 64$ animal species (red circle) connected by $L = 196$ mutualistic interaction links (blue) and all-to-all intragroup competition links (gray). Nodes of light red and light green represent extinct species for $c = 0.1$ and $m = 0.2$. (b) Mutualism degree distributions for plants (triangle) and animals (circle). (c) Abundances of individual species (different lines) for $c = 0.1$ and $m = 0.2$. (d) The stationary-state abundance vs degree for animal species with $c = 0.1$ and selected m's.

III. STABILITY

The state of a dynamical system, like Eq. (1), is expected to converge to a stable fixed point in the long-time limit. If a stable fixed point exists and is unique, its components will give the stationary-state abundances that we obtain numerically.

Depending on which components are zero, there are 2^S different fixed points of Eq. (1). A fixed point $\vec{x}^* = (x_i^*)$ has components

$$x_i^* = \begin{cases} 0 & \text{for } i \in \mathcal{S}^{(0)}, \\ -\sum_{j\in\mathcal{S}^{(+)}}[(B^{(+)})^{-1}]_{ij} & \text{for } i \in \mathcal{S}^{(+)}, \end{cases} \tag{4}$$

where $\mathcal{S}^{(0)}$ and $\mathcal{S}^{(+)}$ are the set of the species with zero and nonzero components in the considered fixed point, respectively, and $[(B^{(+)})^{-1}]_{ij}$ is the inverse of the effective interaction matrix $\mathbb{B}^{(+)}$ obtained by eliminating the rows and columns of the species of $\mathcal{S}^{(0)}$ in $\mathbb{B}$ [8]. We keep the indices i or j of the original interaction matrix $\mathbb{B}$ such that $B_{ij}^{(+)} = B_{ij}$ as long as $i, j \in \mathcal{S}^{(+)}$.

The fixed point in Eq. (4) is stable if a small perturbation $\delta x_i = x_i - x_i^*$ does not grow persistently with time but vanishes in the long-time limit. The time evolution of the perturbation is given by $\frac{d}{dt}\delta x_i = H_{ij}\delta x_j$, which involves the Jacobian matrix at the fixed point $\vec{x}^* = (x_i^*)$ given by

$$H_{ij} = \delta_{ij}\left[1 + \sum_{\ell=1}^{S} B_{i\ell}x_\ell^*\right] + x_i^* B_{ij}. \tag{5}$$

For $i \in \mathcal{S}^{(0)}$, it holds that $x_i^* = 0$, and therefore one can see that $H_{ij} = \delta_{ij}[1 + \sum_{\ell=1}^{S} B_{i\ell}x_\ell^*]$. For $i \in \mathcal{S}^{(+)}$, it holds that $1 + \sum_\ell B_{i\ell}x_\ell^* = 1 + \sum_{\ell\in\mathcal{S}^{(+)}} B_{i\ell}^{(+)}x_\ell^* = 0$, leading to $H_{ij} = x_i^* B_{ij}$. If all the eigenvalues λ_i's of $\mathbb{H} = (H_{ij})$ have negative real parts, then the small perturbation will die out and the fixed point can be considered as stable.

We derive the approximate expression for the eigenvalues of $\mathbb{H}$. For $i \in \mathcal{S}^{(0)}$, let us consider a neighboring fixed point $\vec{x}^{*\prime} = (x_\ell^{*\prime})$ with $\mathcal{S}^{(+)\prime} = \mathcal{S}^{(+)} \cup \{i\}$, which satisfies $1 + \sum_\ell B_{i\ell}x_\ell^{*\prime} = 1 + \sum_{\ell\in\mathcal{S}^{(+)}} B_{i\ell}x_\ell^{*\prime} + B_{ii}x_i^{*\prime} = 0$. Assuming that $x_\ell^{*\prime} \simeq x_\ell^*$ for $\ell \in \mathcal{S}^{(+)}$ and using $B_{ii} = -1$, we find $H_{ij} \simeq \delta_{ij}x_i^{*\prime}$. Therefore, with rows and columns rearranged, the Jacobian matrix $\mathbb{H}$ contains one zero submatrix, say, $H_{ij}^{(0+)} = 0$, and three nonzero block submatrices $H_{ij}^{(00)} \simeq x_i^{*\prime}\delta_{ij}$, $H_{ij}^{(+0)} = x_i^* B_{ij}$, and $H_{ij}^{(++)} = x_i^* B_{ij}^{(+)}$ such that

$$\mathbb{H} = \begin{pmatrix} \mathbf{H}^{(00)} & \mathbf{0} \\ \mathbf{H}^{(+0)} & \mathbf{H}^{(++)} \end{pmatrix} = \begin{pmatrix} (\delta_{ij}x_i^{*\prime}) & \mathbf{0} \\ (x_i^* B_{ij}) & (x_i^* B_{ij}^{(+)}) \end{pmatrix}. \tag{6}$$

Given the zero block submatrix, all the eigenvalues of $\mathbb{H}$ come from the diagonal blocks, $H_{ij}^{(00)} \simeq x_i^{*\prime}\delta_{ij}$ and $H_{ij}^{(++)} = x_i^* B_{ij}^{(+)}$. $\mathbf{H}^{(00)}$ is already diagonalized, with $x_i^{*\prime}$'s as its eigenvalues. To obtain the eigenvalues of $\mathbf{H}^{(++)}$, we decompose it as $H_{ij}^{(++)} = -x_i^*\delta_{ij} + V_{ij}$ with $V_{ij} \equiv -cx_i^*(1-\delta_{ij}) + mx_i^* A_{ij}$ and apply the perturbation theory with V_{ij} taken as a perturbation to obtain the approximate eigenvalues $-x_i^*$'s for small c and m as described in Appendix B and Ref. [33]. Therefore, we find that the eigenvalues λ_i's of $\mathbb{H}$ are approximately

$$\lambda_i \simeq \begin{cases} x_i^{*\prime} & \text{for } i \in \mathcal{S}^{(0)}, \\ -x_i^* & \text{for } i \in \mathcal{S}^{(+)}. \end{cases} \tag{7}$$

A concrete example of constructing the Jacobian matrix and deriving Eq. (7) for a small community is presented in Appendix B.

Using Eq. (7), we can see that all the eigenvalues are negative, and the fixed point in Eq. (4) is stable when the following conditions are met: (i) every species i that would have a negative fixed-point abundance ($x_i^{*\prime} < 0$) if it were added to $\mathcal{S}^{(+)}$ has zero abundance ($x_i^* = 0$) and is in $\mathcal{S}^{(0)}$, and (ii) every species i in $\mathcal{S}^{(+)}$ has a positive fixed-point abundance ($x_i^* > 0$). If the components of a fixed point are known, one can use these stability conditions to predict which species go extinct and which species survive. In the next section, we derive the approximate analytic formula for the components of a fixed point and use it along with Eq. (7) to infer the stable fixed point.

IV. ANALYTIC APPROACHES TO THE FIXED POINT

In this section, we assume that all species survive, $\mathcal{S}^{(0)} = \emptyset$, and we obtain the components of the corresponding fixed point in Eq. (4). While the inverse of a matrix is not available in a closed form in general, here we first consider the case of zero or weak mutualism and then take an approximation for the adjacency matrix to derive the components of the fixed point. The obtained results will be generalized straightforwardly to the case of $\mathcal{S}^{(0)} \neq \emptyset$ in Sec. V B.

A. No mutualism

Let us consider the case of no mutualism but competition only. The interaction matrix for $m = 0$ is given in a simple form as

$$\mathbb{B} = \mathbb{B}_0 \equiv -(1-c)\mathbb{I} - c\mathbb{J}^{(0)}. \tag{8}$$

Trying $\mathbb{B}_0^{-1} = -\frac{1}{1-c}(\mathbf{I}^{(\mathrm{PP})} \oplus \mathbf{I}^{(\mathrm{AA})} \ominus b^{(\mathrm{P})}\mathbf{J}^{(\mathrm{PP})} \ominus b^{(\mathrm{A})}\mathbf{J}^{(\mathrm{AA})})$ as its inverse and inserting it into $\mathbb{B}_0\mathbb{B}_0^{-1} = \mathbb{I}$, we find that $b^{(\mathrm{P})} = \frac{\tilde{c}^{(\mathrm{P})}}{N^{(\mathrm{P})}}$ and $b^{(\mathrm{A})} = \frac{\tilde{c}^{(\mathrm{A})}}{N^{(\mathrm{A})}}$, where the rescaled competition strengths $\tilde{c}^{(\mathrm{P})}$ and $\tilde{c}^{(\mathrm{A})}$ are defined as

$$\tilde{c}^{(\mathrm{G})} \equiv \frac{cN^{(\mathrm{G})}}{cN^{(\mathrm{G})} + 1 - c} \tag{9}$$

with G representing either P or A. The properties of the matrix of 1's, such as $\mathbf{J}^{(\mathrm{PP})}\mathbf{J}^{(\mathrm{PP})} = N^{(\mathrm{P})}\mathbf{J}^{(\mathrm{PP})}$, are used for derivation. The rescaled competition $\tilde{c}^{(\mathrm{G})}$ ranges between 0 and 1, and grows with c and $N^{(\mathrm{G})}$ as long as $0 < c < 1$.

The inverse matrix $\mathbb{B}_0^{-1}$ is represented in a compact form as

$$\mathbb{B}_0^{-1} = (1-c)^{-1}(-\mathbb{I} + \tilde{\mathbb{c}}\tilde{\mathbb{J}}^{(0)}) \tag{10}$$

with $\tilde{\mathbb{c}} \equiv \tilde{c}^{(\mathrm{P})}\mathbf{I}^{(\mathrm{PP})} \oplus \tilde{c}^{(\mathrm{A})}\mathbf{I}^{(\mathrm{AA})}$ and $\tilde{\mathbb{J}}^{(0)} \equiv \frac{\mathbf{J}^{(\mathrm{PP})}}{N^{(\mathrm{P})}} \oplus \frac{\mathbf{J}^{(\mathrm{AA})}}{N^{(\mathrm{A})}}$. Then the component of the fixed point in Eq. (4) with $\mathcal{S}^{(0)} = \emptyset$ is given by

$$x_i^{*(0)} = x_0^{(\mathrm{G}_i)} \equiv \frac{1 - \tilde{c}^{(\mathrm{G}_i)}}{1-c} = \frac{1}{cN^{(\mathrm{G}_i)} + 1 - c}, \tag{11}$$

where G_i is the group the species i belongs to, either P or A. The superscript (0) means the zeroth-order approximation. The first-order correction will be presented as well in the next subsection, and then we move to the approximation for general m. For $0 < c < 1$, Eq. (11) is positive for all i. Therefore, all the eigenvalues of the Jacobian in Eq. (7) with $\mathcal{S}^{(0)} = \emptyset$ are negative, and the fixed point with Eq. (11) for all i is the stable fixed point. The increase of the competition strength c

or of the number of species $N^{(\mathrm{G}_i)}$ leads to the decrease of the abundance $x_i^{*(0)}$.

B. Weak mutualism

Suppose that the mutualism strength m is not zero but small. Expanding the inverse $\mathbb{B}^{-1}$ as

$$\mathbb{B}^{-1} = (\mathbb{B}_0 + m\mathbb{A})^{-1} = \mathbb{B}_0^{-1}\sum_{n=0}^{\infty}\left(-m\mathbb{A}\mathbb{B}_0^{-1}\right)^n \tag{12}$$

with $\mathbb{B}_0$ given in Eq. (8), and utilizing the relations like $\mathbf{A}^{(\mathrm{PA})}\mathbf{J}^{(\mathrm{AA})} = \mathbf{K}^{(\mathrm{PP})}\mathbf{J}^{(\mathrm{PA})}$ with $K_{pp'} = k_p\delta_{pp'}$ a block in the degree matrix,

$$\mathbb{K} \equiv \mathbf{K}^{(\mathrm{PP})} \oplus \mathbf{K}^{(\mathrm{AA})}, \tag{13}$$

one can evaluate the first-order term in m in Eq. (12) to obtain the first-order approximation

$$x_i^{*(1)} \simeq x_0^{(\mathrm{G}_i)}\left[1 + \frac{m}{1-c}\frac{1-\tilde{c}^{(\bar{\mathrm{G}}_i)}}{1-\tilde{c}^{(\mathrm{G}_i)}}\left(k_i - \tilde{c}^{(\mathrm{G}_i)}\langle k\rangle^{(\mathrm{G}_i)}\right)\right] \tag{14}$$

with the mean degree $\langle k\rangle^{(\mathrm{G})} \equiv \frac{L}{N^{(\mathrm{G})}}$. This first-order approximation works if $||\mathbb{A}\mathbb{B}_0^{-1}||$ is sufficiently small. See Appendix C for more details.

The formula in Eq. (14) allows us to understand the origin of the ambivalent effects of mutualism on the species abundance as observed in Fig. 1(d). The two terms in the parentheses in Eq. (14) represent the mutualistic benefit of a species i (in group G_i) from its k_i mutualistic partners in group $\bar{\mathrm{G}}_i$, and the competition with other species in the same group G_i that also benefit from mutualism, respectively. Their difference may be positive or negative depending on degree k_i. It is the species with $k_i > \tilde{c}^{(\mathrm{G})}\langle k\rangle^{(\mathrm{G}_i)}$ that finds abundance increasing with increasing m; the abundance of the species with $k_i < \tilde{c}^{(\mathrm{G})}\langle k\rangle^{(\mathrm{G}_i)}$ decreases with m, as its mutualistic benefit is overwhelmed by the competition with the species in the same group to the extent proportional to m in the first-order approximation.

One caveat is that Eq. (14) can be negative depending on parameters, which suggests that the fixed point with all species surviving is unstable and that some species will turn out to have zero abundance in the stable fixed point. This will be explored in Sec. V B.

C. Annealed approximation for general *m*

Each term for $n \geqslant 1$ in Eq. (12) represents the sum of the influences of other species on the abundance of a species built up over the pathways involving n mutualistic pairs. To analytically track such higher-order contributions, we consider the *annealed* adjacency matrix $\tilde{A}_{pa} \equiv \frac{k_p k_a}{L}$, meaning the probability to connect p and a in the network ensemble for a given degree sequence [36], and equivalently

$$\widetilde{\mathbb{A}} = L^{-1}\mathbb{K}\mathbb{J}^{(1)}\mathbb{K}, \tag{15}$$

where $\mathbb{K}$ is the degree matrix introduced in Eq. (13), and $\mathbb{J}^{(1)}$ contains the matrices of 1's at the off-diagonal blocks as $\mathbb{J}^{(1)} \equiv \mathbf{J}^{(\mathrm{PA})} \oplus \mathbf{J}^{(\mathrm{AP})}$ with $J_{pa} = J_{ap} = 1$ for all p and a. Then, after some algebra utilizing the properties of the matrices of 1's as detailed in Appendix D, we find each term $\mathbb{B}_0^{-1}(-m\widetilde{\mathbb{A}}\mathbb{B}_0^{-1})^n$ reduced to

$$\mathbb{B}_0^{-1}\left(-m\widetilde{\mathbb{A}}\mathbb{B}_0^{-1}\right)^n = \begin{cases} -\frac{\tilde{m}^n}{1-c}\widetilde{\mathbb{K}}\widetilde{\mathbb{J}}^{(1)}\widetilde{\mathbb{K}} & \text{for } n = 1, 3, 5, \ldots, \\ -\frac{\tilde{m}^n}{1-c}\widetilde{\mathbb{K}}\widetilde{\mathbb{J}}^{(0)}\widetilde{\mathbb{K}} & \text{for } n = 2, 4, 6, \ldots, \end{cases} \tag{16}$$

where we introduced $\widetilde{\mathbb{J}}^{(1)} \equiv \frac{\mathbf{J}^{(\mathrm{PA})}}{\sqrt{N^{(\mathrm{P})}N^{(\mathrm{A})}}} \oplus \frac{\mathbf{J}^{(\mathrm{AP})}}{\sqrt{N^{(\mathrm{P})}N^{(\mathrm{A})}}}$, $\widetilde{\mathbb{K}} \equiv \frac{\frac{\mathbf{K}^{(\mathrm{PP})}}{\langle k\rangle^{(\mathrm{P})}} - \tilde{c}^{(\mathrm{P})}\mathbf{I}^{(\mathrm{PP})}}{\sqrt{\xi^{(\mathrm{P})} - \tilde{c}^{(\mathrm{P})}}} \oplus \frac{\frac{\mathbf{K}^{(\mathrm{AA})}}{\langle k\rangle^{(\mathrm{A})}} - \tilde{c}^{(\mathrm{A})}\mathbf{I}^{(\mathrm{AA})}}{\sqrt{\xi^{(\mathrm{A})} - \tilde{c}^{(\mathrm{A})}}}$, and the rescaled mutualism strength $\tilde{m}$,

$$\tilde{m} \equiv \frac{m}{1-c}\sqrt{\langle k\rangle^{(P)}\langle k\rangle^{(A)}(\xi^{(P)} - \tilde{c}^{(P)})(\xi^{(A)} - \tilde{c}^{(A)})} \tag{17}$$

with the ratio of the first two moments of the mutualism degree

$$\xi^{(\mathrm{G})} \equiv \frac{\langle k^2\rangle^{(\mathrm{G})}}{\langle k\rangle^{(\mathrm{G})2}} \tag{18}$$

quantifying the heterogeneity of degree [22]. The rescaled mutualism $\tilde{m}$ is the key parameter governing the species abundance, capturing the effects of network structural heterogeneity on the species abundance.

All the terms for $n \geqslant 1$ in Eq. (12) are proportional to either $\widetilde{\mathbb{J}}^{(0)}$ or $\widetilde{\mathbb{J}}^{(1)}$, with $\tilde{m}^n$ in the coefficient. Consequently, the sum of the influences of interspecific interactions over all possible pathways in Eq. (12) is reduced to two infinite geometric series, manifesting the advantage of the annealed approximation. Then the inverse matrix is expressed in a closed form as

$$\widetilde{\mathbb{B}}^{-1} = \mathbb{B}_0^{-1} - \frac{1}{1-c}\frac{\tilde{m}}{1-\tilde{m}^2}\widetilde{\mathbb{K}}(\tilde{m}\widetilde{\mathbb{J}}^{(0)} + \widetilde{\mathbb{J}}^{(1)})\widetilde{\mathbb{K}}. \tag{19}$$

Substituting Eq. (19) in Eq. (4), we obtain the fixed point

$$\tilde{x}_i^* = x_0^{(\mathrm{G}_i)}\left(1 + \bar{k}_i\tilde{m}\frac{\tilde{m} + \eta^{(\mathrm{G}_i\bar{\mathrm{G}}_i)}}{1-\tilde{m}^2}\right) \tag{20}$$

with the rescaled degree

$$\bar{k}_i \equiv \frac{\frac{k_i}{\langle k\rangle^{(\mathrm{G}_i)}} - \tilde{c}^{(\mathrm{G}_i)}}{\xi^{(\mathrm{G}_i)} - \tilde{c}^{(\mathrm{G}_i)}}, \tag{21}$$

and the asymmetry factor

$$\eta^{(\mathrm{PA})} \equiv \frac{1-\tilde{c}^{(\mathrm{A})}}{1-\tilde{c}^{(\mathrm{P})}}\sqrt{\frac{\langle k\rangle^{(\mathrm{P})}(\xi^{(\mathrm{P})} - \tilde{c}^{(\mathrm{P})})}{\langle k\rangle^{(\mathrm{A})}(\xi^{(\mathrm{A})} - \tilde{c}^{(\mathrm{A})})}} = \frac{1}{\eta^{(\mathrm{AP})}}. \tag{22}$$

The formula in Eq. (20) is the main result of the present work, representing the abundance of individual species under heterogeneous mutualistic interactions and uniform intragroup competition. It is the cornerstone of the results that follow in the next sections. The abundance is given by a nonlinear function of the rescaled mutualism $\tilde{m}$ in Eq. (17), revealing how the higher-order contributions of interspecific interactions are combined with the network structure. The increase of mean connectivity $\langle k\rangle^{(\mathrm{P,A})}$ or the increase of the degree heterogeneity $\xi^{(\mathrm{P,A})}$ enhances the rescaled mutualism strength. As $\tilde{m}$ increases, $\tilde{x}_i^*$ may increase or decrease, depending on the sign of the rescaled degree $\bar{k}_i$. The rescaled degree quantifies the imbalance of the mutualism benefit and the competition cost; $\tilde{x}_i^*$ increases (decreases) with $\tilde{m}$ if $\bar{k}_i$ is positive (negative) as long as $0 < \tilde{m} < 1$.

One can notice that $\tilde{x}_i^*$ in Eq. (20) can be negative for some species i depending on parameters and degree, implying then that Eq. (20) is not the stable fixed point and invoking the necessity to classify correctly surviving and extinct species. The divergence of Eq. (20) at $\tilde{m} = 1$ suggests the onset of instability, which can be suppressed up to a larger value of $\tilde{m}$ than 1, along with the extinction of selected species, as we will see.

V. PHASE DIAGRAM

Some of the formulated abundances in Eq. (20) can be negative depending on parameters. Then, by Eq. (7), some species may have to have zero abundance, and the remaining surviving species should have positive abundances different from Eq. (20) as the interspecific interaction among the surviving species should be considered to formulate their abundances. In this section, we investigate the stable fixed point depending on parameters by identifying the species to go extinct, if any, and recalculating the abundance of the surviving species, and we obtain the phase diagram.

A. Full coexistence phase

Let us call it *full coexistence* if there is no extinct species, i.e., if $x_i^{(\mathrm{st})} > 0$ for all i. For sufficiently small $\tilde{m}$, the numerically and analytically obtained values for the stationary-state abundance, $x_i^{(\mathrm{st})}$ and $\tilde{x}_i^*$ in Eq. (20), are in good agreement. This agreement implies that in the full-coexistence phase (i) the annealed approximation works, $x_i^{(\mathrm{st})} \simeq \tilde{x}_i^{(\mathrm{st})}$, and (ii) Eq. (20) is stable, $\tilde{x}_i^{(\mathrm{st})} = \tilde{x}_i^*$, where $\tilde{x}_i^{(\mathrm{st})}$ is the stationary-state abundance from the solution to Eq. (1) with the annealed adjacency matrix $\tilde{A}_{ij}$ used. See Appendix E for different kinds of species abundances used in this paper.

From Eq. (7), the full-coexistence fixed point in Eq. (20) is stable only if all $\tilde{x}_i^*$'s are positive. This holds for $\tilde{m} < \tilde{m}_e^*(c) \equiv \min(\tilde{m}_e^{*(\mathrm{P})}(c), \tilde{m}_e^{*(\mathrm{A})}(c))$ with

$$\tilde{m}_e^{*(\mathrm{G})}(c) \equiv \begin{cases} 1 & \text{for } c < c_{\min}^{*(\mathrm{G})}, \\ \dfrac{\sqrt{4\left(1-\bar{k}_{\min}^{(\mathrm{G})}\right)+\left(\bar{k}_{\min}^{(\mathrm{G})}\eta^{(\mathrm{G}\bar{\mathrm{G}})}\right)^2}+\bar{k}_{\min}^{(\mathrm{G})}\eta^{(\mathrm{G}\bar{\mathrm{G}})}}{2\left(1-\bar{k}_{\min}^{(\mathrm{G})}\right)} & \text{for } c > c_{\min}^{*(\mathrm{G})}. \end{cases} \tag{23}$$

Here $\bar{k}_{\min}^{(\mathrm{G})}$ is the rescaled degree of the group-G species having the smallest degree $k_{\min}^{(\mathrm{G})}$, and $c_{\min}^{*(\mathrm{G})}$ is defined as

$$c_{\min}^{*(\mathrm{G})} \equiv \frac{k_{\min}^{(\mathrm{G})}}{N^{(\mathrm{G})}\left(\langle k\rangle^{(\mathrm{G})} - k_{\min}^{(\mathrm{G})}\right) + k_{\min}^{(\mathrm{G})}}, \tag{24}$$

such that $\bar{k}_{\min}^{(\mathrm{G})} < 0$ for $c > c_{\min}^{(\mathrm{G})}$.

The predicted boundary of the full coexistence phase $\tilde{m}_e^*(c)$ is shown by a dashed line in Fig. 2(a), which is fixed at 1 for $c < c_{\min}^* \equiv \min(c_{\min}^{*(\mathrm{P})}, c_{\min}^{*(\mathrm{A})})$ and decreases with c for $c > c_{\min}^*$. For $c < c_{\min}^*$, all species have positive rescaled degrees, $\bar{k}_i > 0$, and their fixed-point abundances $\tilde{x}_i^*$ increase with $\tilde{m}$ until diverging at $\tilde{m} = \tilde{m}_e^*(c) = 1$. Considering the fraction of diverging-abundance species $r_u \equiv S^{-1}\sum_i \theta(x_i^{(\mathrm{st})} - M)$ with $M = 10^5$, we call it the *unstable* phase if $r_u > 0$. We define the instability threshold $\tilde{m}_u(c)$ such that $r_u > 0$ for $\tilde{m} \geqslant \tilde{m}_u(c)$. One finds in Eq. (20) that the theoretical prediction for the instability threshold is given by $\tilde{m}_u^*(c) = 1$ for $c < c_{\min}^*$, which agrees with the boundary of the full coexistence phase $\tilde{m}_e^*(c) = 1$ in Eq. (23). Notice that the unstable phase meets the full coexistence phase at $\tilde{m} = 1$ for $c < c_{\min}^*$ [Fig. 2(a)].

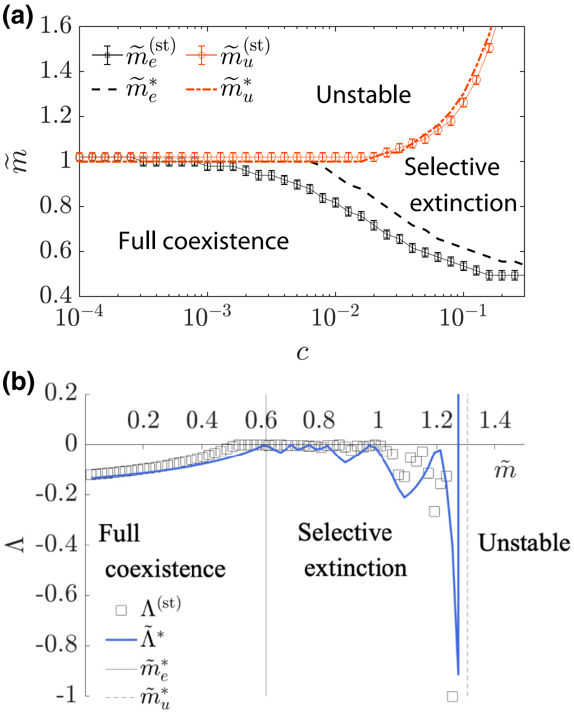

FIG. 2. Phase diagram and stability for the selected community [35]. (a) The phase boundaries $\tilde{m}_e^{(\mathrm{st})}$ and $\tilde{m}_u$ based on the stationary-state abundances are compared with the theoretical prediction $\tilde{m}_e^*$ and $\tilde{m}_u^*$ from Eq. (23) and the condition $\tilde{m}^{(+)}|_{\tilde{m}_u^*} = 1$, respectively. (b) The largest real part $\Lambda^{(\mathrm{st})}$ of the eigenvalues of the Jacobian matrix at $\vec{x}^{(\mathrm{st})}$ and that at $\vec{x}^*$ approximated as $\tilde{\Lambda}^* = \max_{i\in\mathcal{S}^{(0)}, j\in\mathcal{S}^{(+)}}(\tilde{x}_i^{*\prime}, -\tilde{x}_j^*, -1)$ are shown as functions of $\tilde{m}$ for $c = 0.1$.

When c is larger than $c_{\min}^*$ and $\tilde{m}$ is larger than $\tilde{m}_e^*(c)$, there appear some species i with $\tilde{x}_i^* < 0$ according to Eq. (20), implying that they should go extinct, having zero abundance in the true stable fixed point. Computing the fraction of extinct species in terms of their stationary-state abundances as

$$r_e^{(\mathrm{st})} \equiv S^{-1}\sum_{i=1}^{S}\theta\left(\epsilon - x_i^{(\mathrm{st})}\right), \tag{25}$$

with $\epsilon = 10^{-5}$ introduced under finite precision of numerics and the Heaviside step function $\theta(x) = 1$ for $x > 0$ and 0 otherwise, we find that $r_e^{(\mathrm{st})}$ becomes nonzero as $\tilde{m}$ exceeds the extinction threshold $\tilde{m}_e^{(\mathrm{st})}(c)$ for $c > c_{\min}^*$, which is well approximated by the predicted threshold $\tilde{m}_e^*(c)$ in Eq. (23) [Fig. 2(a)]. Let us call it *selective extinction* if there exist extinct species ($r_e^{(\mathrm{st})} > 0$) but no abundance-diverging species ($r_u = 0$). Our analysis shows that the full-coexistence phase meets the selective extinction phase at $\tilde{m}_e^{(\mathrm{st})} \simeq \tilde{m}_e^*$ for $c > c_{\min}^*$. While we showed that the full-coexistence phase ends at $\tilde{m}_e^{(\mathrm{st})}$, it remains to be explored which species go extinct and what happens for the remaining surviving species. This will be addressed in the next subsection in details.

In Fig. 2(b), the largest real part $\Lambda^{(\mathrm{st})}$ of the eigenvalues of the Jacobian $\mathbb{H}$ computed at the stationary-state abundance $\vec{x}^{(\mathrm{st})} = (x_i^{(\mathrm{st})})$ is shown to be negative in the full-coexistence phase, demonstrating the stability of $\vec{x}^{(\mathrm{st})}$. The analytically obtained fixed point $\vec{\tilde{x}}^* = (\tilde{x}_i^*)$ is stable as well; the largest eigenvalue $\tilde{\Lambda}^*$ of the Jacobian $\tilde{H}_{ij} = \delta_{ij}[1 + \sum_{\ell=1}^{S} \tilde{B}_{i\ell}\tilde{x}_\ell^*] + \tilde{x}_i^*\tilde{B}_{ij}$ is evaluated as $\tilde{\Lambda}^* = \max_i(-\tilde{x}_i^*, -1)$, from Eq. (7) and the property that $\tilde{H}_{ij}$ has the eigenvalue -1 (Appendix B), and it remains negative in the full-coexistence phase. Moreover, we see a good agreement between Λ and $\tilde{\Lambda}^*$.

B. Selective extinction phase

If the set $\mathcal{S}^{(0)}$ of extinct species is known, one can apply Eq. (20) to the subcommunity of the surviving species and obtain their abundances analytically. Removing the rows and columns of the species belonging to $\mathcal{S}^{(0)}$ in the full matrix $\tilde{\mathbb{B}}$ and also in the adjacency matrix $\tilde{\mathbb{A}}$, one can obtain the effective interaction matrix $\tilde{\mathbb{B}}^{(+)}$ and the effective adjacency matrix $\tilde{\mathbb{A}}^{(+)}$ for the surviving-species community, from which we can compute the effective quantities such as $x_0^{(\mathrm{G},+)}$, $\bar{k}_i^{(+)}$, $\tilde{m}^{(+)}$, and $\eta^{(\mathrm{PA},+)}$ as described in Appendix F. Using them in Eq. (20), one can obtain the approximate stable fixed point

$$\tilde{x}_i^* = \begin{cases} 0 & \text{for } i \in \mathcal{S}^{(0)}, \\ x_0^{(\mathrm{G}_i,+)}\left(1 + \bar{k}_i^{(+)}\tilde{m}^{(+)}\frac{\tilde{m}^{(+)}+\eta^{(\mathrm{G}_i\bar{\mathrm{G}}_i,+)}}{1-(\tilde{m}^{(+)})^2}\right) & \text{for } i \in \mathcal{S}^{(+)}. \end{cases} \tag{26}$$

The sets of extinct and surviving species, $\mathcal{S}_{\mathrm{stable}}^{(0)}$ and $\mathcal{S}_{\mathrm{stable}}^{(+)}$, for the *stable* fixed point are not given *a priori*. Examining all possible sets $\mathcal{S}^{(0)}$ and identifying the one yielding all negative eigenvalues as given in Eq. (7) could be done, but it takes a very long time.

Our analytic results, Eqs. (7) and (26), give a clue to proceed. Suppose that we have a pair of disjoint sets $\mathcal{S}^{(0)}$ and $\mathcal{S}^{(+)}$ with $\mathcal{S} \equiv \mathcal{S}^{(0)} \cup \mathcal{S}^{(+)}$ the set of all species. If a species in $\mathcal{S}^{(+)}$ with a small (large) effective degree has a negative (positive) value of $\tilde{x}_i^*$ from Eq. (26), then it will be likely to be in the right set $\mathcal{S}_{\mathrm{stable}}^{(0)}$ ($\mathcal{S}_{\mathrm{stable}}^{(+)}$) for the stable fixed point according to Eq. (7). Using this reasoning, we can update iteratively $\mathcal{S}^{(0)}$ and $\mathcal{S}^{(+)}$ towards obtaining $\mathcal{S}_{\mathrm{stable}}^{(0)}$ and $\mathcal{S}_{\mathrm{stable}}^{(+)}$ as follows.

Initially we begin with $\mathcal{S}^{(0)} = \emptyset$, $\mathcal{S}^{(+)} = \mathcal{S}$, $\tilde{\mathbb{B}}^{(+)} = \tilde{\mathbb{B}}$, and $\tilde{x}_i^*$ evaluated by Eq. (26). Then, the following procedures are repeated until stopping at step (iii):

(i) We label as new extinct species all the plant (animal) species p_e's (a_e's) with their fixed-point abundances $\tilde{x}_{p_e}^*$ ($\tilde{x}_{a_e}^*$) having a *different* sign from that of the hub plant species $\tilde{x}_{p_{\mathrm{hub}}}^*$ (animal species $\tilde{x}_{a_{\mathrm{hub}}}^*$), the one having the largest effective degree.

(ii) Go to step (iv) if there are such new extinct species, or

(iii) Stop if there are none.

(iv) We remove those new extinct species from $\mathcal{S}^{(+)}$ and add them to $\mathcal{S}^{(0)}$ and update $\tilde{\mathbb{B}}^{(+)}$ by eliminating their rows and columns, and

(v) Set $\tilde{x}_{p_e}^* = \tilde{x}_{a_e}^* = 0$, and evaluate $\tilde{x}_i^*$'s for the remaining surviving species i by Eq. (26) using the new $\tilde{\mathbb{B}}^{(+)}$.

Note that the effective rescaled mutualism strength $\tilde{m}^{(+)}$ can be larger than 1, making the hub abundances negative according to Eq. (26) in the middle of the above procedures, which is why we compare the sign of the abundance of a species with that of hub species to identify extinct species. At the end of these procedures we are given $\mathcal{S}_{\mathrm{stable}}^{(0)}$ and $\mathcal{S}_{\mathrm{stable}}^{(+)}$, which we use to obtain the stable fixed point $\tilde{x}_i^*$'s from Eq. (26) [37].

As shown in Fig. 3(a), the predicted abundance $\tilde{x}_i^*$ approximates reasonably the stationary-state abundance $x_i^{(\mathrm{st})}$. It grows with degree k_i and takes a zero value for the species with the smallest degrees, demonstrating the crucial role of degree on extinction. Its origin can be understood by examining the rescaled degree, the imbalance of the mutualistic benefit, and the competition cost, the former of which is proportional to the raw degree. The stable fixed point $\tilde{x}_i^*$ predicts whether a species survives or goes extinct correctly for 80% of species across parameters; the predicted fraction $\tilde{r}_e^* \equiv S^{-1}\sum_i \theta(\epsilon - \tilde{x}_i^*)$ of extinct species is in good agreement with the true value $r_e^{(\mathrm{st})}$ in Eq. (25), which plays the role of the order parameter distinguishing the full-coexistence phase ($r_e = 0$) and the selective extinction phase ($r_e > 0$) [Fig. 3(b)].

Deviations stem from the annealed approximation. The stationary-state abundance $\tilde{x}_i^{(\mathrm{st})}$ under the annealed adjacency matrix agrees perfectly with $\tilde{x}_i^*$ (Appendix G), and the predicted fraction of extinct species $\tilde{r}_e^*$ explains very well the true value $\tilde{r}_e$ under the annealed adjacency matrix (Appendix H). Instead of using $\tilde{\mathbb{B}}$ and Eq. (26), one can also use $\mathbb{B}$ and Eq. (4) in the above procedures to identify the set of extinct and surviving species and obtain the stable fixed point x_i^* from Eq. (4), which agrees very well with $x_i^{(\mathrm{st})}$ as shown in Fig. 3(a).

One might have expected instability to arise at $\tilde{m} = 1$ from Eq. (20). However, the extinction of the small-degree species effectively reduces $\tilde{m}$ to $\tilde{m}^{(+)}$ [Fig. 3(b)] and the abundances of the surviving species are evaluated by Eq. (26). The effective rescaled mutualism strength $\tilde{m}^{(+)}$ is kept smaller than 1, preventing the onset of instability, up to $\tilde{m}_u(c)$ for $c > c_{\min}^*$. As the smallest-degree species go extinct, we find that the degree heterogeneity is reduced in the interaction network of the surviving species, which drives the reduction of the effective rescaled mutualism strength (Appendix F). Like in the full coexistence phase, the largest real part of the eigenvalues Λ at $\vec{x}^{(\mathrm{st})}$ and $\tilde{\Lambda}^* = \max_{i\in\mathcal{S}_{\mathrm{stable}}^{(0)}, j\in\mathcal{S}_{\mathrm{stable}}^{(+)}}(\tilde{x}_i^{*\prime}, -\tilde{x}_j^*, -1)$ at the stable fixed point $\tilde{x}_i^*$ remains negative in the selective extinction phase, demonstrating stability [Fig. 2(b)].

The selective extinction phase meets the unstable phase at $\tilde{m}_u(c)$ where the fraction of abundance-diverging species r_u becomes nonzero. The instability threshold $\tilde{m}_u(c)$ coincides with its theoretical prediction $\tilde{m}_u^*$ at which $\tilde{m}^{(+)} = 1$ and $\tilde{x}_i^*$ in Eq. (26) diverges [Fig. 3(b)]. For $\tilde{m} > \tilde{m}_u^*$, the nonzero components of the stable fixed point become negative, featuring the nonzero fraction $\tilde{r}_u^* \equiv S^{-1}\sum_i \theta(-\epsilon - \tilde{x}_i^*)$ of the species having negative $\tilde{x}_i^*$.

Lastly, to demonstrate the general applicability of our analytic results, we study the minimum stationary-state abundance of the surviving species $x_{\min}^{(\mathrm{st})}$ in 46 large empirical mutualistic networks with $N^{(\mathrm{P})}, N^{(\mathrm{A})} \geqslant 20$ [34]. As in Sec. II, we assume the uniform intragroup competition with strength c, and we use the datasets to construct the mutualism adjacency matrices with the mutualism strength m.

From the theoretical framework developed in the previous sections, $x_{\min}^{(\mathrm{st})}$ can be approximated by the nonzero minimum

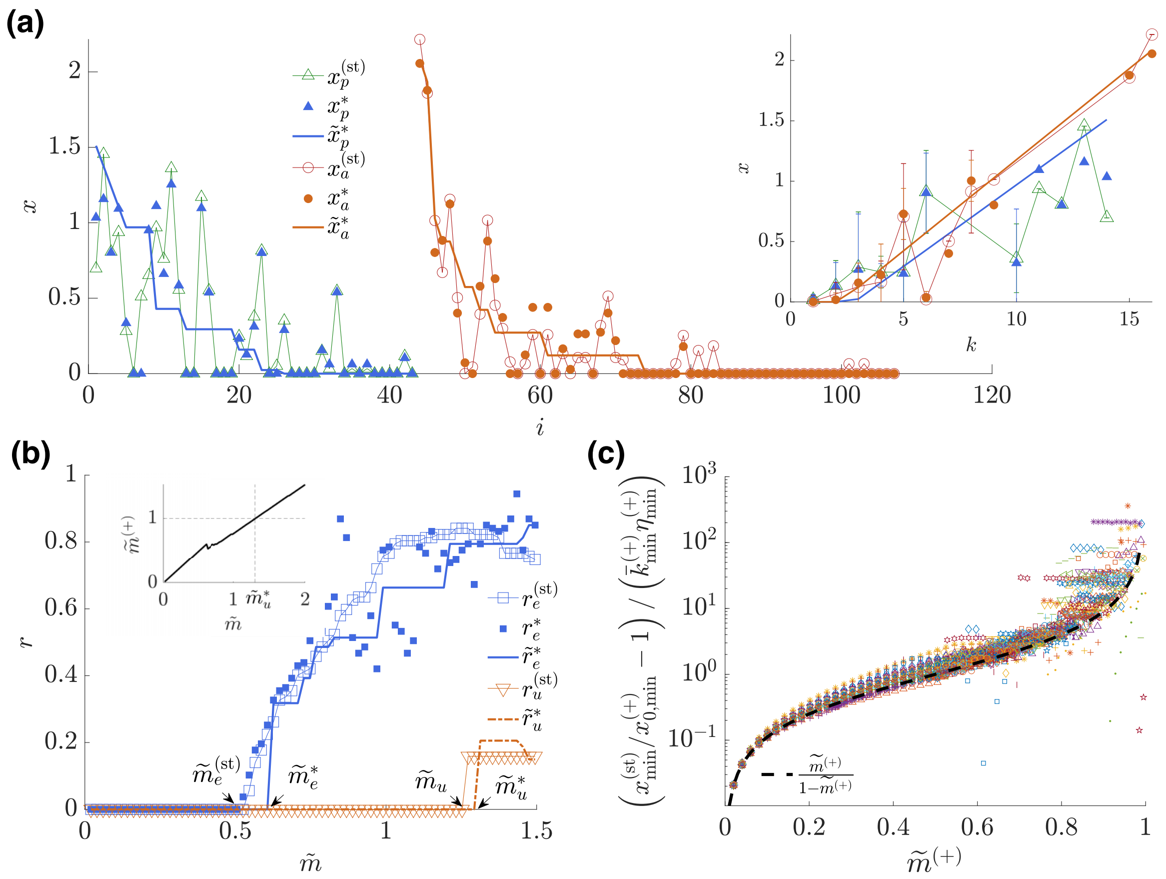

FIG. 3. Selective extinction phase. (a) Stationary-state abundances $x_i^{(st)}$ are compared with the stable fixed-point ones x_i^*'s and $\tilde{x}_i^*$'s for $c = 0.1$ and $\tilde{m} = 0.8$. The species index i is arranged in descending order of degree among plants and animals. Inset: Abundance vs degree. (b) Fraction $r_e^{(st)}$ of extinct species and r_u of the abundance-diverging species based on the stationary-state abundance for $c = 0.1$. They are compared with $\tilde{r}_e^*$ and $\tilde{r}_u^*$ based on the stable fixed point $\tilde{x}_i^*$'s and also with r_e^* based on x_i^*'s. The critical points are also marked, $\tilde{m}_e^{(st)} \simeq 0.53$ and $\tilde{m}_e^* \simeq 0.61$. Inset: The effective rescaled mutualism strength $\tilde{m}^{(+)}$ reaches 1 at $\tilde{m} = \tilde{m}_u^* \simeq 1.3$ for $c = 0.1$. (c) The collapse of the nonzero minimum abundances $x_{\min}^{(st)}$ rescaled as in Eq. (27) in 46 real-world communities as functions of $\tilde{m}^{(+)}$.

component of the stable fixed point, $\tilde{x}^*_{\min} = \min_{i\in\mathcal{S}^{(+)}_{\text{stable}}} \tilde{x}^*_i = \tilde{x}^*_{i_{\min}}$ representing the predicted abundance of species $i_{\min}$. From Eq. (26), we find that $\tilde{x}^*_{\min}$ behaves as a function of $\tilde{m}^{(+)}$ as

$$\frac{\frac{\tilde{x}^*_{\min}}{x^{(+)}_{0,\min}} - 1}{\bar{k}^{(+)}_{\min}\eta^{(+)}_{\min}} \simeq \frac{\tilde{m}^{(+)}}{1-\tilde{m}^{(+)}}, \tag{27}$$

where $\bar{k}^{(+)}_{\min} \equiv \bar{k}_{i_{\min}}$, $x^{(+)}_{0,\min} \equiv x_0^{(\mathrm{G}_{i_{\min}},+)}$, and $\eta^{(+)}_{\min} \equiv \eta^{(\mathrm{G}_{i_{\min}}\bar{\mathrm{G}}_{i_{\min}},+)}$, and we approximate $1 + \tilde{m}^{(+)}/\eta^{(+)}_{\min}$ by $1 + \tilde{m}^{(+)}$ on the right-hand-side. In Fig. 3(c), the plots of the rescaled minimum abundance given by the left-hand-side of Eq. (27) with $x^{(st)}_{\min}$ in place of $\tilde{x}^*_{\min}$ versus $\tilde{m}^{(+)}$ for $c = 0.1$ in 46 empirical mutualistic networks collapse reasonably onto $\frac{\tilde{m}^{(+)}}{1-\tilde{m}^{(+)}}$ in agreement with Eq. (27). There are outliers, though. About 6% of the data points have their rescaled minimum abundances negative, and they are thus neglected in Fig. 3(c). Some of the outliers seen in Fig. 3(c) are attributed to the annealed approximation, which returns close to the theoretical curve in the annealed network [see Fig. 6(e)]. Outliers seen for $\tilde{m}^{(+)} \simeq 1$ in Fig. 6(e) suggest the possible relevance of network characteristics beyond the degree sequence, which needs further investigation.

VI. SUMMARY AND DISCUSSION

While various theoretical approaches have been established for studying the stability and biodiversity of random unstructured communities, the relation between the structured interaction, universal in the real world, and the emergent phenomena of the community has been little understood, partly due to the lack of an analytically tractable model. Here we considered a model community of two groups of species—plants and pollinators—under uniform intragroup competition and empirical heterogeneous intergroup mutualism, and we investigated analytically and numerically the abundance and extinction of individual species in that community.

Deriving the stability condition and the stable fixed point of the LV equation, we quantified the influences of the structural heterogeneity. The strength of mutualism is rescaled by the degree heterogeneity. The species with few mutualistic partners are driven to extinction by their little benefit of mutualism compared with the high cost of competition. As the mutualism strength increases, more species find benefit falling short of cost, resulting in the increase of the number of extinct species. The effective rescaled mutualism among the surviving species is reduced with respect to the original one, which enables the community of the surviving species to be stable for a wide range of parameters, delaying the onset of instability. The number of extinct species and the fraction of the abundance-diverging species play the roles of the order parameter in the phase diagram.

Going beyond the annealed approximation to identify further network characteristics than degree may provide rich concepts and methods to characterize the structure-function relationship of ecological communities. Contrary to the unstructured communities where the interspecific interaction patterns and strengths are random and distributed identically across species, the number of mutualistic partners is different from species to species in the structured community that we study in the present work. We showed how the abundance and the likelihood of extinction depend on the degree of a species. Real-world communities should exhibit both nonuniform interaction strengths and heterogeneous connection patterns. If our analytic framework can be generalized to handle not only heterogeneity but also the randomness of the interaction matrix, it will help us to better understand how structural heterogeneity and randomness together govern the stability and species extinction of real-world communities.

ACKNOWLEDGMENTS

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APPENDIX A: PROPERTIES OF THE MATRICES OF 1'S

The matrix of 1's denoted by $\mathbf{J}$ having all elements equal to 1, $J_{ij} = 1$ for all i and j, is used in the present work to represent the all-to-all uniform competition among plants and among animals via $\mathbf{J}^{(\mathrm{PP})}$ and $\mathbf{J}^{(\mathrm{AA})}$ of dimension $N^{(\mathrm{P})} \times N^{(\mathrm{P})}$ and $N^{(\mathrm{A})} \times N^{(\mathrm{A})}$, respectively, and also to represent the uniform coupling between plants and animals, appearing in the annealed adjacency matrix, via $\mathbf{J}^{(\mathrm{PA})}$ and $\mathbf{J}^{(\mathrm{AP})}$ of dimension $N^{(\mathrm{P})} \times N^{(\mathrm{A})}$ and $N^{(\mathrm{A})} \times N^{(\mathrm{P})}$, respectively. We also consider its integrated versions in block-matrix form

$$\begin{aligned} \mathbb{J}^{(0)} &\equiv \begin{pmatrix} \mathbf{J}^{(\mathrm{PP})} & \mathbf{0} \\ \mathbf{0} & \mathbf{J}^{(\mathrm{AA})} \end{pmatrix} = \mathbf{J}^{(\mathrm{PP})} \oplus \mathbf{J}^{(\mathrm{AA})}, \\ \mathbb{J}^{(1)} &\equiv \begin{pmatrix} \mathbf{0} & \mathbf{J}^{(\mathrm{PA})} \\ \mathbf{J}^{(\mathrm{AP})} & \mathbf{0} \end{pmatrix} = \mathbf{J}^{(\mathrm{PA})} \oplus \mathbf{J}^{(\mathrm{AP})}, \end{aligned} \tag{A1}$$

with $\oplus$ representing the direct sums of two matrices of 1's defined on different groups of nodes, and the rescaled matrices given by

$$\begin{aligned} \widetilde{\mathbb{J}}^{(0)} &\equiv \begin{pmatrix} \frac{\mathbf{J}^{(\mathrm{PP})}}{N^{(\mathrm{P})}} & \mathbf{0} \\ \mathbf{0} & \frac{\mathbf{J}^{(\mathrm{AA})}}{N^{(\mathrm{A})}} \end{pmatrix} = \frac{\mathbf{J}^{(\mathrm{PP})}}{N^{(\mathrm{P})}} \oplus \frac{\mathbf{J}^{(\mathrm{AA})}}{N^{(\mathrm{A})}}, \\ \widetilde{\mathbb{J}}^{(1)} &\equiv \begin{pmatrix} \mathbf{0} & \frac{\mathbf{J}^{(\mathrm{PA})}}{\sqrt{N^{(\mathrm{P})}N^{(\mathrm{A})}}} \\ \frac{\mathbf{J}^{(\mathrm{AP})}}{\sqrt{N^{(\mathrm{P})}N^{(\mathrm{A})}}} & \mathbf{0} \end{pmatrix} = \frac{\mathbf{J}^{(\mathrm{PA})} \oplus \mathbf{J}^{(\mathrm{AP})}}{\sqrt{N^{(\mathrm{P})}N^{(\mathrm{A})}}}. \end{aligned} \tag{A2}$$

In this Appendix, we present their useful properties, which are used to derive the analytic results presented in the main text.

Let us denote the matrices of 1's of dimension $N_1 \times N_2$ by $\mathbf{J}^{(N_1 \times N_2)}$. If one multiplies $\mathbf{J}^{(N_1 \times N_2)}$ and $\mathbf{J}^{(N_2 \times N_3)}$, then she obtains $\mathbf{J}^{(N_1 \times N_2)}\mathbf{J}^{(N_2 \times N_3)} = N_2\mathbf{J}^{(\mathrm{N}_1 \times \mathrm{N}_3)}$, since $\sum_{j=1}^{N_2} J_{ij}^{(\mathrm{N}_1 \times \mathrm{N}_2)} J_{jk}^{(\mathrm{N}_2 \times \mathrm{N}_3)} = \sum_{j=1}^{N_2} 1 = N_2$ for all $1 \leqslant i \leqslant N_1$ and $1 \leqslant k \leqslant N_3$. Therefore, we have

$$\mathbf{J}^{(\mathrm{G}_1\mathrm{G}_2)}\mathbf{J}^{(\mathrm{G}_2\mathrm{G}_3)} = N^{(\mathrm{G}_2)}\mathbf{J}^{(\mathrm{G}_1\mathrm{G}_3)}, \tag{A3}$$

where $\mathrm{G}_1, \mathrm{G}_2, \mathrm{G}_3 \in \{\mathrm{P}, \mathrm{A}\}$. Using this result, one can see that the rescaled block matrices of 1's satisfy

$$\begin{aligned} &\widetilde{\mathbb{J}}^{(0)}\widetilde{\mathbb{J}}^{(0)} = \widetilde{\mathbb{J}}^{(0)}, \\ &\widetilde{\mathbb{J}}^{(1)}\widetilde{\mathbb{J}}^{(1)} = \widetilde{\mathbb{J}}^{(0)}, \\ &\widetilde{\mathbb{J}}^{(0)}\widetilde{\mathbb{J}}^{(1)} = \widetilde{\mathbb{J}}^{(1)}\widetilde{\mathbb{J}}^{(0)} = \widetilde{\mathbb{J}}^{(1)}. \end{aligned} \tag{A4}$$

The multiplication of $\mathbf{J}$ with the adjacency matrix $\mathbf{A}^{(\mathrm{PA})}$ or $\mathbf{A}^{(\mathrm{AP})} = \mathbf{A}^{(\mathrm{PA})\mathsf{T}}$ is evaluated as

$$\begin{aligned} \mathbf{A}^{(\mathrm{G}_1\mathrm{G}_2)}\mathbf{J}^{(\mathrm{G}_2\mathrm{G}_3)} &= \mathbf{K}^{(\mathrm{G}_1)}\mathbf{J}^{(\mathrm{G}_1\mathrm{G}_3)}, \\ \mathbf{J}^{(\mathrm{G}_1\mathrm{G}_2)}\mathbf{A}^{(\mathrm{G}_2\mathrm{G}_3)} &= \mathbf{J}^{(\mathrm{G}_1\mathrm{G}_3)}\mathbf{K}^{(\mathrm{G}_3)}, \end{aligned} \tag{A5}$$

where we use, for instance, that $\sum_{a'} A_{pa'}J_{a'a} = \sum_{a'} A_{pa'} = k_p$ and $\sum_{p'} J_{pp'}A_{p'a} = k_a$. Note that $K_{pp'} = k_p\delta_{pp'}$ and $K_{aa'} = k_a\delta_{aa'}$. The block adjacency matrix defined as

$$\mathbb{A} \equiv \begin{pmatrix} \mathbf{0} & \mathbf{A}^{(\mathrm{PA})} \\ \mathbf{A}^{(\mathrm{AP})} & \mathbf{0} \end{pmatrix} = \mathbf{A}^{(\mathrm{PA})} \oplus \mathbf{A}^{(\mathrm{AP})}, \tag{A6}$$

the block rescaled matrices of 1's $\widetilde{\mathbb{J}}^{(0)}$ and $\widetilde{\mathbb{J}}^{(1)}$, and the block degree matrix defined as

$$\mathbb{K} \equiv \begin{pmatrix} \mathbf{K}^{(\mathrm{PP})} & \mathbf{0} \\ \mathbf{0} & \mathbf{K}^{(\mathrm{AA})} \end{pmatrix} = \mathbf{K}^{(\mathrm{PP})} \oplus \mathbf{K}^{(\mathrm{AA})} \tag{A7}$$

satisfy the following equalities:

$$\begin{aligned} &\mathbb{A}\widetilde{\mathbb{J}}^{(0)} = \mathbb{K}\widetilde{\mathbb{N}}\widetilde{\mathbb{J}}^{(1)}, \ \widetilde{\mathbb{J}}^{(0)}\mathbb{A} = \widetilde{\mathbb{J}}^{(1)}\widetilde{\mathbb{N}}\mathbb{K}, \\ &\mathbb{A}\widetilde{\mathbb{J}}^{(1)} = \mathbb{K}\widetilde{\mathbb{N}}\widetilde{\mathbb{J}}^{(0)}, \ \widetilde{\mathbb{J}}^{(1)}\mathbb{A} = \widetilde{\mathbb{J}}^{(0)}\widetilde{\mathbb{N}}\mathbb{K} \end{aligned} \tag{A8}$$

with $\widetilde{\mathbb{N}} \equiv (\begin{smallmatrix} \sqrt{\frac{N^{(\mathrm{P})}}{N^{(\mathrm{A})}}}\mathbf{I}^{(\mathrm{PP})} & \mathbf{0} \\ \mathbf{0} & \sqrt{\frac{N^{(\mathrm{A})}}{N^{(\mathrm{P})}}}\mathbf{I}^{(\mathrm{AA})} \end{smallmatrix}) = \sqrt{\frac{N^{(\mathrm{P})}}{N^{(\mathrm{A})}}}\mathbf{I}^{(\mathrm{PP})} \oplus \sqrt{\frac{N^{(\mathrm{A})}}{N^{(\mathrm{P})}}}\mathbf{I}^{(\mathrm{AA})}$.

Multiplying the degree matrices $\mathbf{K}^{(\mathrm{PP})}$ and $\mathbf{K}^{(\mathrm{AA})}$ by $\mathbf{J}$ matrices yields

$$\begin{aligned} &\mathbf{J}^{(\mathrm{G}_1\mathrm{G}_2)}\mathbf{K}^{(\mathrm{G}_2)}\mathbf{J}^{(\mathrm{G}_2\mathrm{G}_3)} = L\mathbf{J}^{(\mathrm{G}_1\mathrm{G}_3)}, \\ &\mathbf{J}^{(\mathrm{G}_1\mathrm{G}_2)}(\mathbf{K}^{(\mathrm{G}_2)})^2\mathbf{J}^{(\mathrm{G}_2\mathrm{G}_3)} = N^{(\mathrm{G}_2)}\langle k^2\rangle^{(\mathrm{G}_2)}\mathbf{J}^{(\mathrm{G}_1\mathrm{G}_3)}, \end{aligned} \tag{A9}$$

where we used $\sum_{a_1a_2} J_{aa_1}K_{a_1a_2}J_{a_2p} = \sum_{a_1} k_{a_1} = L$ and $\sum_{p_1,p_2,p_3} J_{pp_1}K_{p_1p_2}K_{p_2p_3}J_{p_3a} = \sum_{p_1} k_{p_1}^2 = N^{(\mathrm{P})}\langle k^2\rangle^{(\mathrm{P})}$, and $\langle k^2\rangle^{(\mathrm{G})} = \sum_{i\in\mathcal{S}^{(\mathrm{G})}} k_i^2/N^{(\mathrm{G})}$ is the mean of the square of the degree of species of group G with $\mathcal{S}^{(\mathrm{G})}$ the set of group-G species. The block matrices satisfy

$$\begin{aligned} &\widetilde{\mathbb{J}}^{(0)}\mathbb{K}\widetilde{\mathbb{J}}^{(0)} = \widetilde{\mathbb{J}}^{(0)}\langle\mathbb{K}\rangle, \\ &\widetilde{\mathbb{J}}^{(0)}\mathbb{K}\widetilde{\mathbb{J}}^{(1)} = \langle\mathbb{K}\rangle\widetilde{\mathbb{J}}^{(1)}, \\ &\widetilde{\mathbb{J}}^{(1)}\mathbb{K}\widetilde{\mathbb{J}}^{(0)} = \widetilde{\mathbb{J}}^{(1)}\langle\mathbb{K}\rangle, \\ &\widetilde{\mathbb{J}}^{(1)}\mathbb{K}\widetilde{\mathbb{J}}^{(1)} = \langle k\rangle^{(\mathrm{P})}\langle k\rangle^{(\mathrm{A})}\langle\mathbb{K}\rangle^{-1}\widetilde{\mathbb{J}}^{(0)}, \\ &\widetilde{\mathbb{J}}^{(1)}\mathbb{K}^2\widetilde{\mathbb{J}}^{(1)} = \langle k^2\rangle^{(\mathrm{P})}\langle k^2\rangle^{(\mathrm{A})}\langle\mathbb{K}^2\rangle^{-1}\widetilde{\mathbb{J}}^{(0)}, \end{aligned} \tag{A10}$$

with $\langle\mathbb{K}\rangle \equiv \langle k\rangle^{(\mathrm{P})}\mathbf{I}^{(\mathrm{PP})} + \langle k\rangle^{(\mathrm{A})}\mathbf{I}^{(\mathrm{AA})}$ being the sum of the identity matrices multiplied by the group averages. These relations are valid also for a function $f(\mathbb{K})$ of $\mathbb{K}$ as

$$\begin{aligned}
&\widetilde{\mathbb{J}}^{(0)} f(\mathbb{K}) \widetilde{\mathbb{J}}^{(0)} = \widetilde{\mathbb{J}}^{(0)} \langle f(\mathbb{K}) \rangle, \\
&\widetilde{\mathbb{J}}^{(0)} f(\mathbb{K}) \widetilde{\mathbb{J}}^{(1)} = \langle f(\mathbb{K}) \rangle \widetilde{\mathbb{J}}^{(1)}, \\
&\widetilde{\mathbb{J}}^{(1)} f(\mathbb{K}) \widetilde{\mathbb{J}}^{(0)} = \widetilde{\mathbb{J}}^{(1)} \langle f(\mathbb{K}) \rangle, \\
&\widetilde{\mathbb{J}}^{(1)} f(\mathbb{K}) \widetilde{\mathbb{J}}^{(1)} = \langle f(\mathbb{K}) \rangle^{(\mathrm{P})} \langle f(\mathbb{K}) \rangle^{(\mathrm{A})} \langle f(\mathbb{K}) \rangle^{-1} \widetilde{\mathbb{J}}^{(0)}, \qquad \text{(A11)}
\end{aligned}$$

where

$$\begin{aligned}
\langle f(\mathbb{K}) \rangle &\equiv \frac{\operatorname{Tr} f(\mathbf{K}^{(\mathrm{PP})})}{N^{(\mathrm{P})}} \mathbf{I}^{(\mathrm{PP})} \oplus \frac{\operatorname{Tr} f(\mathbf{K}^{(\mathrm{AA})})}{N^{(\mathrm{A})}} \mathbf{I}^{(\mathrm{AA})} \\
&= \langle f(\mathbb{K}) \rangle^{(\mathrm{P})} \mathbf{I}^{(\mathrm{PP})} \oplus \langle f(\mathbb{K}) \rangle^{(\mathrm{A})} \mathbf{I}^{(\mathrm{AA})} \qquad \text{(A12)}
\end{aligned}$$

is the sum of the group averages of $f(\mathbb{K})$, and its inverse means $\langle f(\mathbb{K}) \rangle^{-1} = \frac{1}{\langle f(\mathbb{K}) \rangle^{(\mathrm{P})}} \mathbf{I}^{(\mathrm{PP})} \oplus \frac{1}{\langle f(\mathbb{K}) \rangle^{(\mathrm{A})}} \mathbf{I}^{(\mathrm{AA})}$. For general z, $\langle f(\mathbb{K}) \rangle^{z} = (\langle f \rangle^{(\mathrm{P})})^{z} \mathbf{I}^{(\mathrm{PP})} \oplus (\langle f \rangle^{(\mathrm{A})})^{z} \mathbf{I}^{(\mathrm{AA})}$. The multiplication of $\langle f(\mathbb{K}) \rangle$ and $\widetilde{\mathbb{J}}^{(1)}$ is not commutative:

$$\begin{aligned}
&\langle f(\mathbb{K}) \rangle \widetilde{\mathbb{J}}^{(1)} = \langle f(\mathbb{K}) \rangle^{(\mathrm{P})} \langle f(\mathbb{K}) \rangle^{(\mathrm{A})} \widetilde{\mathbb{J}}^{(1)} \langle f(\mathbb{K}) \rangle^{-1}, \\
&\widetilde{\mathbb{J}}^{(1)} \langle f(\mathbb{K}) \rangle = \langle f(\mathbb{K}) \rangle^{(\mathrm{P})} \langle f(\mathbb{K}) \rangle^{(\mathrm{A})} \langle f(\mathbb{K}) \rangle^{-1} \widetilde{\mathbb{J}}^{(1)}, \qquad \text{(A13)}
\end{aligned}$$

which can be seen by considering, for instance, the P-block of $\langle f(\mathbb{K}) \rangle \widetilde{\mathbb{J}}^{(1)} \mathbb{X}$ as $\langle f \rangle^{(\mathrm{P})} \mathbf{J}^{(\mathrm{PA})} \mathbf{X}^{(\mathrm{A})} = \langle f \rangle^{(\mathrm{P})} \langle f \rangle^{(\mathrm{A})} \mathbf{J}^{(\mathrm{PA})} \frac{1}{\langle f \rangle^{(\mathrm{A})}} \mathbf{X}^{(\mathrm{A})}$ with $\mathbb{X} = \mathbf{X}^{(\mathrm{P})} \oplus \mathbf{X}^{(\mathrm{A})}$.

APPENDIX B: EIGENVALUES OF THE JACOBIAN MATRIX

To help understand Eq. (7), here we construct the Jacobian matrix for a small community as a concrete example, and we present the eigenvalue perturbation theory that we used in the main text.

1. Jacobian matrix for a small community

Let us consider a community consisting of $S = 4$ species and a fixed point $\vec{x}^* = (x_1^* \neq 0, 0, 0, x_4^* \neq 0)$ of the LV equation for the community, which corresponds to $\mathcal{S}^{(0)} = \{2, 3\}$ and $\mathcal{S}^{(+)} = \{1, 4\}$. As shown in Eq. (4), the nonzero components (abundances) of species 1 and 4 in $\mathcal{S}^{(+)}$ satisfy

$$\mathbb{B}^{(+)} \begin{pmatrix} x_1^* \\ x_4^* \end{pmatrix} = \begin{pmatrix} B_{11} & B_{14} \\ B_{41} & B_{44} \end{pmatrix} \begin{pmatrix} x_1^* \\ x_4^* \end{pmatrix} = -\begin{pmatrix} 1 \\ 1 \end{pmatrix},$$

where we introduced the effective interaction matrix $\mathbb{B}^{(+)}$ by eliminating the rows and columns of the species, 2 and 3, of $\mathcal{S}^{(0)}$ in the original 4×4 interaction matrix $\mathbb{B}$ while keeping the original indices of rows and columns. Using Eq. (5) and rearranging the order of indices as (2 3 1 4), we find the Jacobian matrix at the considered fixed point given by

$$\mathbb{H} = \begin{pmatrix} 1+B_{21}x_1^*+B_{24}x_4^* & 0 & 0 & 0 \\ 0 & 1+B_{31}x_1^*+B_{34}x_4^* & 0 & 0 \\ x_1^* B_{12} & x_1^* B_{13} & x_1^* B_{11} & x_1^* B_{14} \\ x_4^* B_{42} & x_4^* B_{43} & x_4^* B_{41} & x_4^* B_{44} \end{pmatrix},$$

which is represented as in Eq. (6) in terms of the block matrices

$$\mathbf{H}^{(00)} = \begin{pmatrix} H_{22} & 0 \\ 0 & H_{33} \end{pmatrix}$$

$$= \begin{pmatrix} 1 + B_{21}x_1^* + B_{24}x_4^* & 0 \\ 0 & 1 + B_{31}x_1^* + B_{34}x_4^* \end{pmatrix}$$

and

$$\mathbf{H}^{(++)} = \begin{pmatrix} H_{11} & H_{14} \\ H_{41} & H_{44} \end{pmatrix} = \begin{pmatrix} x_1^* B_{11} & x_1^* B_{14} \\ x_4^* B_{41} & x_4^* B_{44} \end{pmatrix}.$$

Note that $B_{ij}^{(+)} = B_{ij}$ if $i, j = 1$ or 4 in our example.

The diagonal elements H_{22} and H_{33} are the eigenvalues of $\mathbf{H}^{(00)}$, as $\mathbf{H}^{(00)}$ is a diagonal matrix. The diagonal elements can be further simplified. Let us first consider $H_{22} = 1 + B_{21}x_1^* + B_{24}x_4^*$. A clue is obtained by considering a neighboring fixed point $\vec{x}^{*\prime} = (x_1^{*\prime}, x_2^{*\prime}, 0, x_4^{*\prime})$ with $\mathcal{S}^{(0)\prime} = \{3\}$ and $\mathcal{S}^{(+)\prime} = \{1, 2, 4\}$, where species 2 has a nonzero component, as well as species 1 and 4. Their abundances satisfy

$$\begin{pmatrix} B_{11} & B_{12} & B_{14} \\ B_{21} & B_{22} & B_{24} \\ B_{41} & B_{42} & B_{44} \end{pmatrix} \begin{pmatrix} x_1^{*\prime} \\ x_2^{*\prime} \\ x_4^{*\prime} \end{pmatrix} = -\begin{pmatrix} 1 \\ 1 \\ 1 \end{pmatrix}.$$

Among the three equalities from this equation is $B_{21}x_1^{*\prime} + B_{22}x_2^{*\prime} + B_{24}x_4^{*\prime} = -1$. Rearranging the terms and recalling $B_{22} = -1$, we find that $x_2^{*\prime} = 1 + B_{21}x_1^{*\prime} + B_{24}x_4^{*\prime}$. If we assume that $x_1^{*\prime} \simeq x_1^*$ and $x_4^{*\prime} \simeq x_4^*$, i.e., that the nonzero components of species 1 and 4 are similar between the two fixed points $\vec{x}^*$ and $\vec{x}^{*\prime}$, then we find that

$$H_{22} = 1 + B_{21}x_1^* + B_{24}x_4^* \simeq 1 + B_{21}x_1^{*\prime} + B_{24}x_4^{*\prime} = x_2^{*\prime}.$$

The assumption is expected to be valid if S is large and the number of species having nonzero components is sufficiently large at the fixed point, for which allowing one more species to have a nonzero component would not change much the nonzero components of other species. Similarly, one can simplify H_{33} as $H_{33} \simeq x_3^{*\prime}$ by using another neighboring fixed point corresponding to $\mathcal{S}^{(0)\prime} = \{2\}$ and $\mathcal{S}^{(+)\prime} = \{1, 3, 4\}$. In general, one can obtain the approximate expression $H_{ii} \simeq x_i^{*\prime}$ for every $i \in \mathcal{S}^{(0)}$ by considering the neighboring fixed point corresponding to $\mathcal{S}^{(0)\prime} = \mathcal{S}^{(0)} - \{i\}$ and $\mathcal{S}^{(+)\prime} = \mathcal{S}^{(+)} \cup \{i\}$. Therefore, given a fixed point corresponding to $\mathcal{S}^{(0)}$ and $\mathcal{S}^{(+)}$, $x_i^{*\prime}$ for $i \in \mathcal{S}^{(0)}$ means the abundance that the species i would have if it had a nonzero component like the species of $\mathcal{S}^{(+)}$.

2. Eigenvalues of $H_{ij}^{(++)}$ and its largest one

To obtain the eigenvalues $\lambda_i^{(+)}$'s of the $S^{(+)} \times S^{(+)}$ matrix $H_{ij}^{(++)} \equiv x_i^* B_{ij}^{(+)}$ at x_i^*, we decompose $H_{ij}^{(++)}$ as $H_{ij}^{(++)} = -x_i^* \delta_{ij} + V_{ij}$ with $V_{ij} \equiv -c x_i^* (1 - \delta_{ij}) + m x_i^* A_{ij}$. Considering the eigenvalue expansion $\lambda_i^{(+)} \simeq -x_i^* + V_{ii} + \sum_{j \neq i} \frac{x_j^* V_{ji} V_{ij} x_i^*}{x_i^* - x_j^*} \simeq -x_i^*$ and noting that $V_{ii} = 0$, one finds that the eigenvalues can be approximated by the zeroth-order term as $\lambda_i^{(+)} \simeq -x_i^*$ when V_{ij} is sufficiently small.

It should also be noted that $H_{ij}^{(++)}$ has $\vec{x}^* = (x_i^*)$ as an eigenvector with eigenvalue -1; $\sum_j H_{ij}^{(++)} x_j^* = \sum_j x_i^* B_{ij}^{(+)} (-\sum_\ell [(B^{(+)})^{-1}]_{j\ell}) = -x_i^*$. Therefore, the largest real part of the eigenvalues $\lambda_i^{(+)}$'s is approximated by $\max(-x_i^*, -1)$.

APPENDIX C: $\mathbb{B}^{-1}$ TO THE FIRST ORDER IN m

For $\mathbb{B} = \mathbb{B}_0 + m\mathbb{A}$, one can expand its inverse $\mathbb{B}^{-1}$ in terms of the mutualism strength m as

$$\begin{aligned}\mathbb{B}^{-1} &= \mathbb{B}_0^{-1}\sum_{n=0}^{\infty}\left(-m\mathbb{A}\mathbb{B}_0^{-1}\right)^n \\ &= \mathbb{B}_0^{-1} - m\mathbb{B}_0^{-1}\mathbb{A}\mathbb{B}_0^{-1} + O(m^2).\end{aligned} \tag{C1}$$

Using Eqs. (A8), (A10), and (10), one can evaluate $\mathbb{B}^{-1}$ up to the first order of m as

$$\begin{aligned}\mathbb{B}^{-1} &\simeq \mathbb{B}_0^{-1} - \frac{m}{(1-c)^2}\big[-\mathbb{I} + \tilde{\mathbb{c}}\widetilde{\mathbb{J}}^{(0)}\big]\mathbb{A}\big[-\mathbb{I} + \tilde{\mathbb{c}}\widetilde{\mathbb{J}}^{(0)}\big] \\ &= \mathbb{B}_0^{-1} - \frac{m}{(1-c)^2}\big[\mathbb{A} - \mathbb{A}\tilde{\mathbb{c}}\widetilde{\mathbb{J}}^{(0)} - \tilde{\mathbb{c}}\widetilde{\mathbb{J}}^{(0)}\mathbb{A} + \tilde{\mathbb{c}}\widetilde{\mathbb{J}}^{(0)}\mathbb{A}\tilde{\mathbb{c}}\widetilde{\mathbb{J}}^{(0)}\big] \\ &= \mathbb{B}_0^{-1} - \frac{m}{(1-c)^2}\big[\mathbb{A} - \mathbb{K}\widetilde{\mathbb{N}}\widetilde{\mathbb{J}}^{(1)}\tilde{\mathbb{c}} - \tilde{\mathbb{c}}\widetilde{\mathbb{J}}^{(1)}\widetilde{\mathbb{N}}(\mathbb{K} - \langle\mathbb{K}\rangle\tilde{\mathbb{c}})\big].\end{aligned} \tag{C2}$$

Then the abundance of a plant species p is given by

$$\begin{aligned}x_p^{*(1)} &= -\sum_j (B^{-1})_{pj} = x_0^{(\mathrm{P})} \\ &\quad + \frac{m}{(1-c)^2}\left[k_p - k_p\tilde{c}^{(\mathrm{A})} - \tilde{c}^{(\mathrm{P})}\frac{L}{N^{(\mathrm{P})}} + \tilde{c}^{(\mathrm{P})}\frac{L}{N^{(\mathrm{P})}}\tilde{c}^{(\mathrm{A})}\right] \\ &= x_0^{(\mathrm{P})} + \frac{m}{(1-c)^2}(1-\tilde{c}^{(\mathrm{A})})(k_p - \tilde{c}^{(\mathrm{P})}\langle k\rangle^{(\mathrm{P})}) \\ &= x_0^{(\mathrm{P})}\left[1 + \frac{m}{1-c}\frac{1-\tilde{c}^{(\mathrm{A})}}{1-\tilde{c}^{(\mathrm{P})}}(k_p - \tilde{c}^{(\mathrm{P})}\langle k\rangle^{(\mathrm{P})})\right],\end{aligned} \tag{C3}$$

and that of an animal species a is

$$x_a^{*(1)} = x_0^{(\mathrm{A})}\left[1 + \frac{m}{1-c}\frac{1-\tilde{c}^{(\mathrm{P})}}{1-\tilde{c}^{(\mathrm{A})}}(k_a - \tilde{c}^{(\mathrm{A})}\langle k\rangle^{(\mathrm{A})})\right]. \tag{C4}$$

APPENDIX D: $\mathbb{B}^{-1}$ UNDER THE ANNEALED APPROXIMATION FOR THE ADJACENCY MATRIX

In the annealed approximation, the adjacency matrix element A_{ij} is approximated by the probability that the two nodes i and j are connected by a link in the ensemble of networks preserving the given degree sequence $\{k_i\}$ as

$$\tilde{A}_{ij} = \frac{k_i k_j}{L} \tag{D1}$$

with L the total number of links. Equivalently, the block adjacency matrix takes the form

$$\widetilde{\mathbb{A}} = \frac{1}{L}\mathbb{K}\mathbb{J}^{(1)}\mathbb{K} = \frac{1}{\sqrt{\langle k\rangle^{(\mathrm{P})}\langle k\rangle^{(\mathrm{A})}}}\mathbb{K}\widetilde{\mathbb{J}}^{(1)}\mathbb{K}. \tag{D2}$$

Using this, one finds that the terms $\mathbb{B}_0^{-1}(-m\widetilde{\mathbb{A}}\mathbb{B}_0^{-1})^n$ appearing in Eq. (12) are simplified. Evaluating the first three terms, one can find the expression for general n by induction. Let us first consider the term with $n = 1$, which is evaluated as

$$\begin{aligned}&\mathbb{B}_0^{-1}(-m\widetilde{\mathbb{A}})\mathbb{B}_0^{-1} \\ &= \frac{-m}{(1-c)^2}\frac{(-\mathbb{I} + \tilde{\mathbb{c}}\widetilde{\mathbb{J}}^{(0)})\mathbb{K}\widetilde{\mathbb{J}}^{(1)}\mathbb{K}(-\mathbb{I} + \tilde{\mathbb{c}}\widetilde{\mathbb{J}}^{(0)})}{\sqrt{\langle k\rangle^{(\mathrm{P})}\langle k\rangle^{(\mathrm{A})}}} \\ &= \frac{-m}{(1-c)^2} \\ &\quad\times\frac{\mathbb{K}\widetilde{\mathbb{J}}^{(1)}\mathbb{K} - \tilde{\mathbb{c}}\langle\mathbb{K}\rangle\widetilde{\mathbb{J}}^{(1)}\mathbb{K} - \mathbb{K}\widetilde{\mathbb{J}}^{(1)}\tilde{\mathbb{c}}\langle\mathbb{K}\rangle + \tilde{\mathbb{c}}\langle\mathbb{K}\rangle\widetilde{\mathbb{J}}^{(1)}\langle\mathbb{K}\rangle\tilde{\mathbb{c}}}{\sqrt{\langle k\rangle^{(\mathrm{P})}\langle k\rangle^{(\mathrm{A})}}} \\ &= \frac{-m}{(1-c)^2}\frac{(\mathbb{K} - \tilde{\mathbb{c}}\langle\mathbb{K}\rangle)\widetilde{\mathbb{J}}^{(1)}(\mathbb{K} - \tilde{\mathbb{c}}\langle\mathbb{K}\rangle)}{\sqrt{\langle k\rangle^{(\mathrm{P})}\langle k\rangle^{(\mathrm{A})}}} \\ &= -\frac{\tilde{m}}{1-c}\widetilde{\mathbb{K}}\widetilde{\mathbb{J}}^{(1)}\widetilde{\mathbb{K}},\end{aligned} \tag{D3}$$

where Eq. (A11) is used and the rescaled degree matrix is introduced,

$$\widetilde{\mathbb{K}} \equiv \frac{\mathbb{K} - \tilde{\mathbb{c}}\langle\mathbb{K}\rangle}{\sqrt{\langle\mathbb{K}(\mathbb{K} - \tilde{\mathbb{c}}\langle\mathbb{K}\rangle)\rangle}} = \frac{\mathbb{K} - \tilde{\mathbb{c}}\langle\mathbb{K}\rangle}{\langle\widetilde{\mathbb{K}}\mathbb{K}\rangle}, \tag{D4}$$

and the rescaled mutualism strength $\tilde{m}$, defined in Eq. (17) in the main text, is also represented here as

$$\tilde{m} = \frac{m}{1-c}\frac{\langle\mathbb{K}\widetilde{\mathbb{K}}\rangle^{(\mathrm{P})}\langle\mathbb{K}\widetilde{\mathbb{K}}\rangle^{(\mathrm{A})}}{\sqrt{\langle\mathbb{K}\rangle^{(\mathrm{P})}\langle\mathbb{K}\rangle^{(\mathrm{A})}}}. \tag{D5}$$

Notice that $\langle k\rangle^{(\mathrm{P})} = \langle\mathbb{K}\rangle^{(\mathrm{P})}$ and $\langle\mathbb{K}\widetilde{\mathbb{K}}\rangle^{(\mathrm{P})} = \langle k^2\rangle^{(\mathrm{P})} - \tilde{c}^{(\mathrm{P})}(\langle k\rangle^{(\mathrm{P})})^2 = (\langle k\rangle^{(\mathrm{P})})^2(\xi^{(\mathrm{P})} - \tilde{c}^{(\mathrm{P})})$ from Eq. (A12).

The term with $n = 2$ is evaluated as

$$\begin{aligned}&\mathbb{B}_0^{-1}(-m\widetilde{\mathbb{A}})\mathbb{B}_0^{-1}(-m\widetilde{\mathbb{A}})\mathbb{B}_0^{-1} \\ &= \frac{-\tilde{m}}{1-c}\widetilde{\mathbb{K}}\widetilde{\mathbb{J}}^{(1)}\widetilde{\mathbb{K}}\frac{-m}{\sqrt{\langle k\rangle^{(\mathrm{P})}\langle k\rangle^{(\mathrm{A})}}}\mathbb{K}\widetilde{\mathbb{J}}^{(1)}\mathbb{K}\frac{-\mathbb{I} + \tilde{\mathbb{c}}\widetilde{\mathbb{J}}^{(0)}}{1-c} \\ &= \frac{\tilde{m}}{1-c}\widetilde{\mathbb{K}}\frac{m\langle\widetilde{\mathbb{K}}\mathbb{K}\rangle^{(\mathrm{P})}\langle\widetilde{\mathbb{K}}\mathbb{K}\rangle^{(\mathrm{A})}\langle\widetilde{\mathbb{K}}\mathbb{K}\rangle^{-1}\widetilde{\mathbb{J}}^{(0)}}{\sqrt{\langle k\rangle^{(\mathrm{P})}\langle k\rangle^{(\mathrm{A})}}}\frac{-\mathbb{K} + \tilde{\mathbb{c}}\langle\mathbb{K}\rangle}{1-c} \\ &= -\frac{\tilde{m}^2}{1-c}\widetilde{\mathbb{K}}\widetilde{\mathbb{J}}^{(0)}\widetilde{\mathbb{K}}.\end{aligned} \tag{D6}$$

The term with $n = 3$ is

$$\begin{aligned}&\mathbb{B}_0^{-1}(-m\widetilde{\mathbb{A}})\mathbb{B}_0^{-1}(-m\widetilde{\mathbb{A}})\mathbb{B}_0^{-1}(-m\widetilde{\mathbb{A}})\mathbb{B}_0^{-1} \\ &= \frac{-\tilde{m}^2}{1-c}\widetilde{\mathbb{K}}\widetilde{\mathbb{J}}^{(0)}\widetilde{\mathbb{K}}\frac{-m}{\sqrt{\langle k\rangle^{(\mathrm{P})}\langle k\rangle^{(\mathrm{A})}}}\mathbb{K}\widetilde{\mathbb{J}}^{(1)}\mathbb{K}\frac{-\mathbb{I} + \tilde{\mathbb{c}}\widetilde{\mathbb{J}}^{(0)}}{1-c} \\ &= \frac{\tilde{m}^2}{1-c}\widetilde{\mathbb{K}}\frac{m\langle\widetilde{\mathbb{K}}\mathbb{K}\rangle\widetilde{\mathbb{J}}^{(1)}}{\sqrt{\langle k\rangle^{(\mathrm{P})}\langle k\rangle^{(\mathrm{A})}}}\frac{-\mathbb{K} + \tilde{\mathbb{c}}\langle\mathbb{K}\rangle}{1-c} \\ &= -\frac{\tilde{m}^2}{1-c}\widetilde{\mathbb{K}}\frac{m\langle\widetilde{\mathbb{K}}\mathbb{K}\rangle^{(\mathrm{P})}\langle\widetilde{\mathbb{K}}\mathbb{K}\rangle^{(\mathrm{A})}}{(1-c)\sqrt{\langle k\rangle^{(\mathrm{P})}\langle k\rangle^{(\mathrm{A})}}}\widetilde{\mathbb{J}}^{(1)} \\ &\quad\times\langle\mathbb{K}\widetilde{\mathbb{K}}\rangle^{-1}(\mathbb{K} - \tilde{\mathbb{c}}\langle\mathbb{K}\rangle) \\ &= -\frac{\tilde{m}^3}{1-c}\widetilde{\mathbb{K}}\widetilde{\mathbb{J}}^{(1)}\widetilde{\mathbb{K}}.\end{aligned} \tag{D7}$$

From Eqs. (D3), (D6), and (D7), one can obtain by induction Eq. (16), and we find that the inverse of the interaction

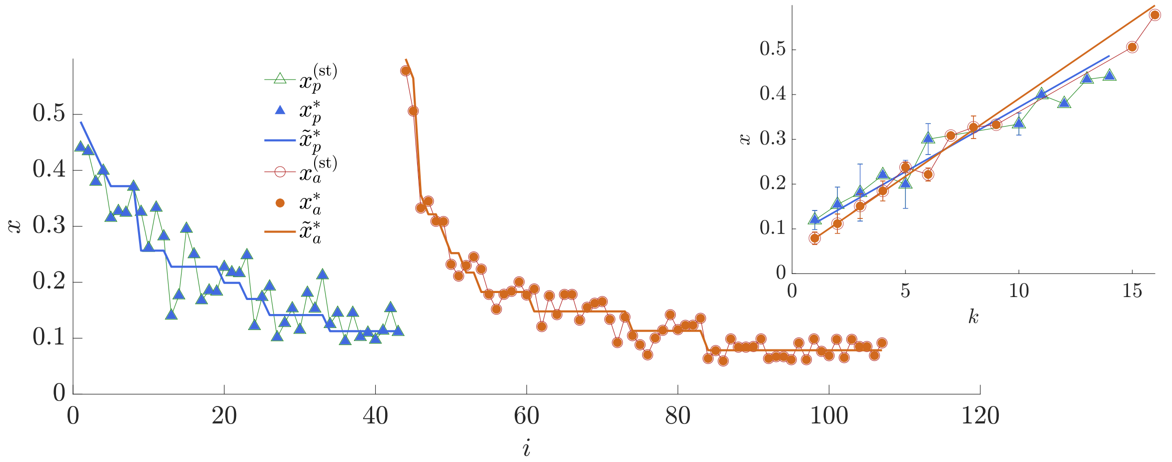

FIG. 4. Species abundance in the full-coexistence phase. Stationary-state abundances $x_i^{(\mathrm{st})}$ of individual species i are compared with the stable fixed-point ones x_i^*'s and $\tilde{x}_i^*$'s for $c = 0.1$ and $\tilde{m} = 0.4$. The species index i is arranged in descending order of degree among plants and among animals. Inset: abundance vs degree.

matrix is evaluated as

$$\widetilde{\mathbb{B}}^{-1} = \mathbb{B}_0^{-1} - \frac{1}{1-c}\widetilde{\mathbb{K}}\left(\widetilde{\mathbb{J}}^{(1)}\sum_{n=1,3,5,\ldots}\tilde{m}^n + \widetilde{\mathbb{J}}^{(0)}\sum_{n=2,4,6,\ldots}\tilde{m}^n\right)\widetilde{\mathbb{K}}$$
$$= \mathbb{B}_0^{-1} - \frac{1}{1-c}\frac{\tilde{m}}{1-\tilde{m}^2}\widetilde{\mathbb{K}}(\tilde{m}\widetilde{\mathbb{J}}^{(0)} + \widetilde{\mathbb{J}}^{(1)})\widetilde{\mathbb{K}}, \qquad \text{(D8)}$$

which is given also in Eq. (19).

APPENDIX E: DIFFERENT MEASURES OF THE SPECIES ABUNDANCE IN THE LONG-TIME LIMIT

In the present study, a couple of different measures of the species abundance appear, being numerical or analytical solutions to the LV equations. We summarize their notations here to help distinguish and understand them.

(i) $x_i^{(\mathrm{st})}$: It is defined in Eq. (3) and represents the numerical solution $x_i(T)$ at the final step to the LV equation in Eq. (1) using the interaction matrix $\mathbb{B}$ constructed from the original adjacency matrix $\mathbb{A}$.

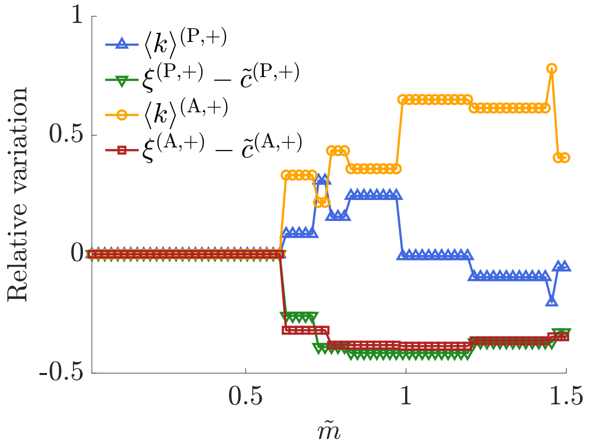

FIG. 5. Relative variations of the network structural properties with the rescaled mutualism strength $\tilde{m}$ for $c = 0.1$. Shown are the relative variations of the mean degree $\langle k\rangle$ and the degree heterogeneity minus the rescaled competition $\xi - \tilde{c}$ for plants and animals. The relative variation is evaluated, e.g., as $\frac{\langle k\rangle^{(\mathrm{P},+)} - \langle k\rangle^{(\mathrm{P})}}{\langle k\rangle^{(\mathrm{P})}}$.

(ii) $\tilde{x}_i^{(\mathrm{st})}$: It represents the numerical solution $\tilde{x}_i(T)$ at the final step to the LV equation in Eq. (1) using the interaction matrix $\widetilde{\mathbb{B}}$ constructed from the factorized adjacency matrix $\widetilde{\mathbb{A}}$ in Eq. (15) under the annealed approximation.

(iii) x_i^*: It is defined in Eq. (4) and represents the stable fixed point to the LV equation in Eq. (1) using $\mathbb{B}$. The sets of surviving and extinct species, $\mathcal{S}^{(+)}$ and $\mathcal{S}^{(0)}$, can be obtained by updating iteratively $\mathbb{B}^{(+)}$ and x_i^*, using Eq. (4), as described in Sec. V B.

(iv) $\tilde{x}_i^*$: It represents the stable fixed point to the LV equation in Eq. (1) using $\widetilde{\mathbb{B}}$ under the annealed approximation. While it can be evaluated numerically by Eq. (4) using $\widetilde{\mathbb{B}}$, its analytic expression is available in Eq. (26). The sets of surviving and extinct species, $\mathcal{S}^{(+)}$ and $\mathcal{S}^{(0)}$, can be obtained by updating iteratively $\widetilde{\mathbb{B}}^{(+)}$ and $\tilde{x}_i^*$, using Eq. (26), as described in Sec. V B.

In Fig. 4. we present $x_i^{(\mathrm{st})}$, x_i^*, and $\tilde{x}_i^*$ for $c = 0.1$ and $\tilde{m} = 0.4$ in the full-coexistence phase.

APPENDIX F: EFFECTIVE QUANTITIES IN EQ. (26)

The effective interaction matrix $\widetilde{\mathbb{B}}^{(+)}$ for the surviving species is obtained by removing the rows and columns corresponding to the species belonging to $\mathcal{S}^{(0)}$ in the full interaction matrix $\widetilde{\mathbb{B}}$. For later use, we introduce $\mathcal{S}^{(\mathrm{P},+)}$ and $\mathcal{S}^{(\mathrm{A},+)}$ to denote the set of plant and animal species, respectively, in $\mathcal{S}^{(+)}$ to be assigned nonzero components, and $\mathcal{S}^{(\mathrm{P},0)}$ and $\mathcal{S}^{(\mathrm{A},0)}$ to denote the set of plant and animal species, respectively, in $\mathcal{S}^{(0)}$ to be assigned zero components. Their sizes are $N^{(\mathrm{P},+)}$, $N^{(\mathrm{A},+)}$, $N^{(\mathrm{P},0)}$, and $N^{(\mathrm{A},0)}$. The effective interaction matrix $\widetilde{\mathbb{B}}^{(+)}$ is of size $S^{(+)} \times S^{(+)}$ with $S^{(+)} = N^{(\mathrm{P},+)} + N^{(\mathrm{A},+)}$ and takes the form

$$\widetilde{\mathbb{B}}^{(+)} = -\mathbb{I}^{(+)} + c(\mathbb{J}^{(0,+)} - \mathbb{I}^{(+)}) + m\widetilde{\mathbb{A}}^{(+)}, \qquad \text{(F1)}$$

where $\widetilde{\mathbb{A}}^{(+)}$ is the effective adjacency matrix for the plant and animal species in $\mathcal{S}^{(+)}$.

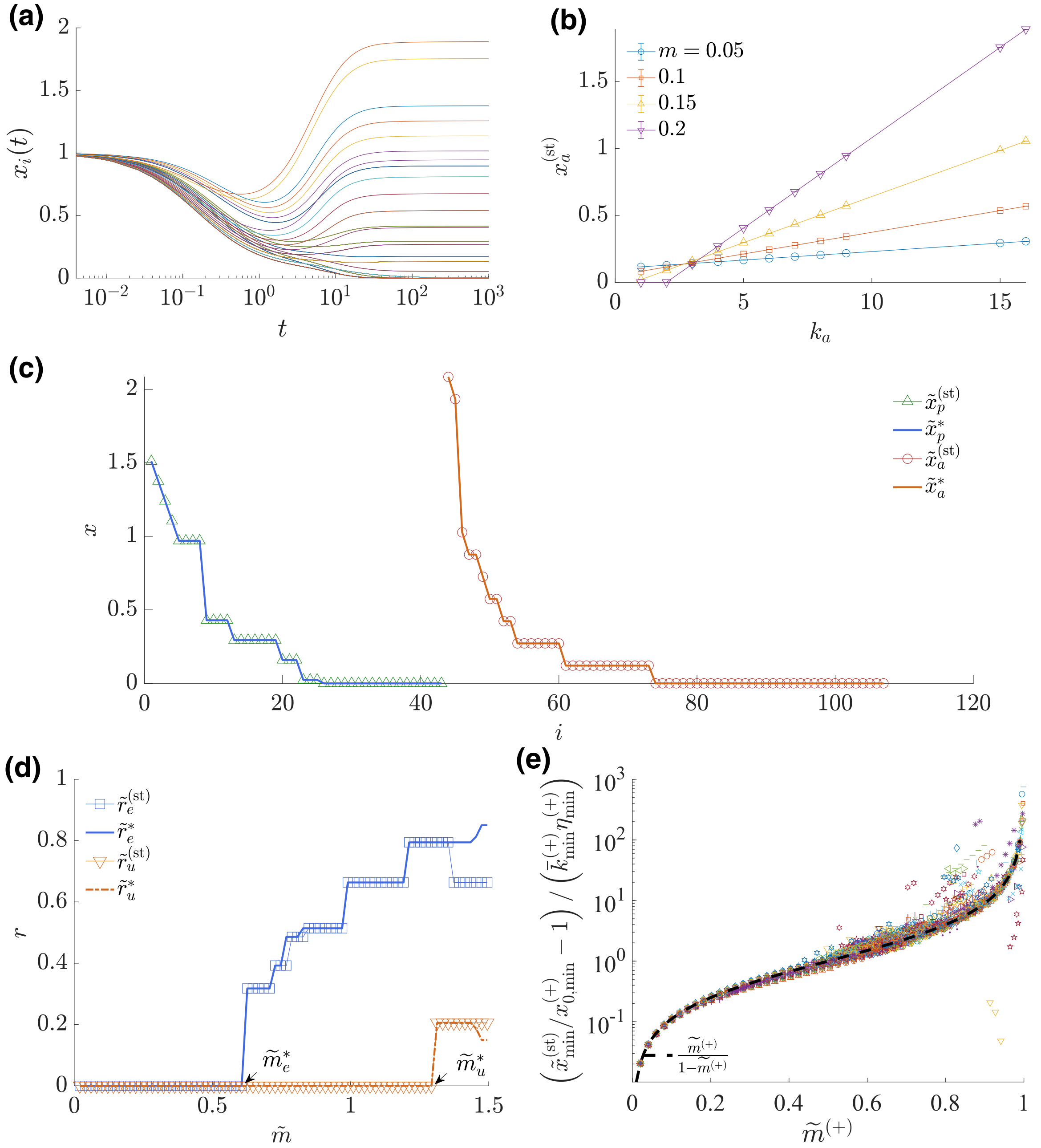

FIG. 6. Species abundance under the annealed adjacency matrix. (a) Time evolution of the abundances of individual species (different lines) obtained by numerically integrating Eq. (1) with the annealed adjacency matrix $\tilde{A}_{ij}$ used for $c = 0.1$ and $m = 0.2$. (b) The stationary-state abundance vs degree for animal species with $c = 0.1$. (c) Stationary-state abundances $\tilde{x}_i^{(\mathrm{st})}$ of individual species i are compared with the stable fixed-point components $\tilde{x}_i^*$'s for $c = 0.1$ and $\tilde{m} = 0.8$ belonging to the selective extinction phase. (d) Fraction $\tilde{r}_e^{(\mathrm{st})}$ of extinct species and $\tilde{r}_u$ of the abundance-diverging species based on the stationary-state abundance $\tilde{x}_i^{(\mathrm{st})}$. They are compared with the theoretical predictions $\tilde{r}_e^*$ and $\tilde{r}_u^*$ based on the stable fixed point $\tilde{x}_i^*$'s. (e) The collapse of the minimum abundances $\tilde{x}_{\min}^{(\mathrm{st})}$ rescaled as in Eq. (27) in 46 real-world communities as functions of $\tilde{m}^{(+)}$.

The effective adjacency matrix $\widetilde{\mathbb{A}}^{(+)} = \tilde{\mathbf{A}}^{(\mathrm{PA},+)} \oplus \tilde{\mathbf{A}}^{(\mathrm{AP},+)}$ is obtained by removing in $\widetilde{\mathbb{A}}$ the rows and columns of the species in $\mathcal{S}^{(0)}$. Therefore, it holds that $\tilde{A}_{pa}^{(+)} = \tilde{A}_{pa} = k_p k_a / L$ if p and a are in $\mathcal{S}^{(+)}$. Once $\widetilde{\mathbb{A}}^{(+)}$ is given, the effective network quantities such as the effective degree can be derived from $\widetilde{\mathbb{A}}^{(+)}$. Moreover, $\widetilde{\mathbb{A}}^{(+)}$ maintains the factorized form in terms of the effective degrees and the effective number of links. Therefore, the effective quantities can be inserted into Eq. (20), developed originally with the factorized adjacency matrix, to yield Eq. (26). Below, we illustrate how to evaluate them specifically.

(i) The effective rescaled competition strength is $\tilde{c}^{(\mathrm{G},+)} \equiv \frac{cN^{(\mathrm{G},+)}}{cN^{(\mathrm{G},+)}+1-c}$ with G being P or A.

(ii) The effective zeroth-order abundance is $x_0^{(\mathrm{G},+)} \equiv \frac{1-\tilde{c}^{(\mathrm{G},+)}}{1-c}$.

(iii) The total number of links is $L^{(+)} \equiv \sum_{p\in\mathcal{S}^{(\mathrm{P},+)},a\in\mathcal{S}^{(\mathrm{A},+)}} \tilde{A}_{pa}^{(+)} = \frac{1}{L}\sum_{p\in\mathcal{S}^{(\mathrm{P},+)}} k_p \sum_{a\in\mathcal{S}^{(\mathrm{A},+)}} k_a = L\ell^{(\mathrm{P},+)}$

$\ell^{(\mathrm{A},+)}$, with $\ell^{(\mathrm{P},+)} \equiv \frac{1}{L}\sum_{p\in\mathcal{S}^{(\mathrm{P},+)}} k_p$ and $\ell^{(\mathrm{A},+)} \equiv \frac{1}{L}\sum_{a\in\mathcal{S}^{(\mathrm{A},+)}} k_a$ denoting the ratio of the links incident on the plant and animal species of $\mathcal{S}^{(+)}$, respectively, to the original number of links $L = \sum_p k_p = \sum_a k_a$.

(iv) The effective degree of a plant or animal species in $\mathcal{S}^{(+)}$ is evaluated as $k_p^{(+)} \equiv \sum_{a\in\mathcal{S}^{(\mathrm{A},+)}} \tilde{A}_{pa}^{(+)} = k_p \sum_{a\in\mathcal{S}^{(\mathrm{A},+)}} \frac{k_a}{L} = k_p \ell^{(\mathrm{A},+)}$ and $k_a^{(+)} \equiv \sum_{p\in\mathcal{S}^{(\mathrm{P},+)}} \tilde{A}_{pa}^{(+)} = k_a \ell^{(\mathrm{P},+)}$, satisfying $L^{(+)} = \sum_{p\in\mathcal{S}^{(\mathrm{P},+)}} k_p^{(+)} = \sum_{a\in\mathcal{S}^{(\mathrm{A},+)}} k_a^{(+)}$.

(v) The effective adjacency matrix maintains its factorized form $\tilde{A}_{pa}^{(+)} = \tilde{A}_{pa} = \frac{k_p k_a}{L} = \frac{k_p^{(+)} k_a^{(+)}}{L^{(+)}}$ in terms of the effective degrees and the effective numbers of links defined above.

(vi) The effective degree heterogeneity is evaluated as $\xi^{(\mathrm{P},+)} = \frac{\langle k^2\rangle^{(\mathrm{P},+)}}{\langle k\rangle^{(\mathrm{P},+)}}$ with the moments given by $\langle k^n\rangle^{(\mathrm{P},+)} = \frac{1}{N^{(\mathrm{P},+)}}\sum_{p\in\mathcal{S}^{(\mathrm{P},+)}} (k_p^{(+)})^n$. $\xi^{(\mathrm{A},+)}$ and $\langle k^n\rangle^{(\mathrm{A},+)}$ are evaluated in the same manner.

(vii) The effective rescaled degree is evaluated by $\bar{k}_i^{(+)} \equiv \frac{\frac{k_i^{(+)}}{\langle k\rangle^{(\mathrm{G}_i,+)}} - \tilde{c}^{(\mathrm{G}_i,+)}}{\xi^{(\mathrm{G}_i,+)} - \tilde{c}^{(\mathrm{G}_i,+)}}$.

(viii) The effective asymmetry factor is evaluated by $\eta^{(\mathrm{PA},+)} \equiv \frac{1-\tilde{c}^{(\mathrm{A},+)}}{1-\tilde{c}^{(\mathrm{P},+)}}\sqrt{\frac{\langle k\rangle^{(\mathrm{P},+)}(\xi^{(\mathrm{P},+)}-\tilde{c}^{(\mathrm{P},+)})}{\langle k\rangle^{(\mathrm{A},+)}(\xi^{(\mathrm{A},+)}-\tilde{c}^{(\mathrm{A},+)})}} = \frac{1}{\eta^{(\mathrm{AP},+)}}$.

(ix) The effective rescaled mutualism strength $\tilde{m}^{(+)}$ is evaluated by

$$\tilde{m}^{(+)} \equiv \frac{m}{1-c} \times \sqrt{\langle k\rangle^{(P,+)}\langle k\rangle^{(A,+)}(\xi^{(P,+)} - \tilde{c}^{(P,+)})(\xi^{(A,+)} - \tilde{c}^{(A,+)})} \tag{F2}$$

exactly in the same manner as Eq. (17) using the effective quantities.

The relative variations of the effective quantities with respect to their original values are shown in Fig. 5. While the extinction of small-degree species may make the effective mean degree $\langle k\rangle^{(+)}$ larger than the original one $\langle k\rangle$, the hub plants and animals lose their significant portions of partners, resulting in the reduction of the effective degree heterogeneity. The rescaled competition $\tilde{c}^{(+)}$ decreases as more species go extinct with increasing $\tilde{m}$. These quantities together determine the effective rescaled mutualism $\tilde{m}^{(+)}$, which turns out to be smaller than $\tilde{m}$ as shown in Fig. 3(b).

APPENDIX G: SPECIES ABUNDANCE UNDER THE ANNEALED ADJACENCY MATRIX

Here we present the plots of the species abundances, the fraction of extinct and abundance-diverging species, and the rescaled minimum abundance in the case of the annealed interaction matrix $\widetilde{\mathbb{B}}$ and the annealed adjacency matrix $\widetilde{\mathbb{A}}$ in Fig. 6.

APPENDIX H: ACCURACY IN THE PREDICTION OF THE EXTINCTION OF INDIVIDUAL SPECIES

We consider a species extinct if its abundance is smaller than $\epsilon = 10^{-5}$ and surviving otherwise. The criterion is used to assess the stationary-state abundance $x_i^{(\mathrm{st})}$ and $\tilde{x}_i^{(\mathrm{st})}$ and discriminate the fate of i evolving under the original and the annealed interaction matrix, respectively. To illuminate the predictive power of the stable fixed-point abundance $\tilde{x}_i^*$ for the fate—survival or extinction—of individual species, we compute the fraction of the species that are correctly predicted, i.e., found to be surviving in both abundances, $x_i^{(\mathrm{st})} \geqslant \epsilon$ and $\tilde{x}_i^* \geqslant \epsilon$, or found to be extinct in both, $x_i^{(\mathrm{st})} < \epsilon$ and $\tilde{x}_i^* < \epsilon$, which we can consider as the accuracy of the stable fixed-point abundances in the prediction of species extinction and we present in Fig. 7(a). We also do the same analysis with $\tilde{x}_i^{(\mathrm{st})}$ and $\tilde{x}_i^*$ and show the result in Fig. 7(b). On the average across parameters in the selective extinction phase, the accuracy of $\tilde{x}_i^*$ in predicting extinction/survival amounts to 79.3% for $x_i^{(\mathrm{st})}$ under the original interaction matrix and 99.2% for $\tilde{x}_i^{(\mathrm{st})}$ under the annealed interaction matrix.

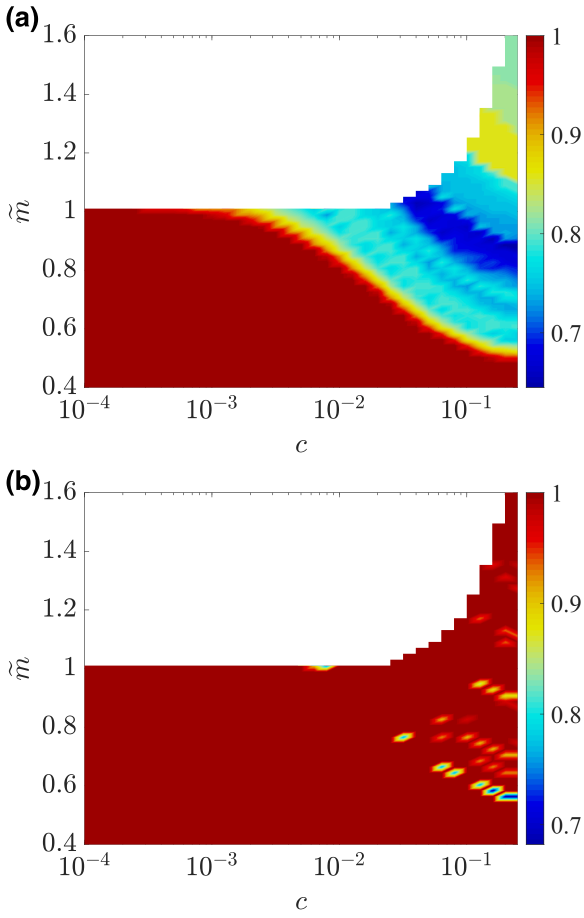

FIG. 7. Accuracy of the analytic formula of the stable fixed-point abundances in predicting the extinction or survival of individual species. Shown in the $(c, \tilde{m})$ plane is the fraction of the species whose survival or extinction is predicted identically by (a) both the stationary-state abundance $x_i^{(\mathrm{st})}$ under the original interaction matrix $\mathbb{B}$, and the stable fixed point $\tilde{x}_i^*$, and (b) both $\tilde{x}_i^{(\mathrm{st})}$ under the annealed interaction matrix $\widetilde{\mathbb{B}}$, and the stable fixed point $\tilde{x}_i^*$.

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