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Prediction of collapse process and tipping points for mutualistic and competitive networks with *k*-core method

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Ecosystems generally have the self-adapting ability to resist various external pressures or disturbances, which is always called resilience. However, once the external disturbances exceed the tipping points of the system resilience, the consequences would be catastrophic, and eventually lead the ecosystem to complete collapse. We capture the collapse process of ecosystems represented by plant-pollinator networks with the *k*-core nested structural method, and find that a sufficiently weak interaction strength or a sufficiently large competition weight can cause the structure of the ecosystem to collapse from its smallest *k*-core towards its largest *k*-core. Then we give the tipping points of structure and dynamic collapse of the entire system from the one-dimensional dynamic function of the ecosystem. Our work provides an intuitive and precise description of the dynamic process of ecosystem collapse under multiple interactions, and provides theoretical insights into further avoiding the occurrence of ecosystem collapse.

Keywords: complex networks, tipping points, dimension reduction, *k*-core

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1. Introduction

Species depend on and interact with each other to maintain ecosystem stability and achieve ecosystem functions through complex dynamic networks.[1–3] In fact, perturbations such as climate change, human activity, and habitat fragmentation are constantly altering the strength and number of these interactions.[4–6] Ecosystems usually have some ability to self-sustain, self-regulate, and resist these perturbations. The concern, however, is that ecosystems could collapse and cause mass extinctions if the magnitude of the disturbance exceeds a tipping point.[7,8] A typical example is the risk assessment of anthropogenic deforestation of the Amazon forest. Researchers predicted that at 40% deforestation, the Amazon forest could change its structure into a savannah, especially in the southeastern Amazon.[9–12]

Indeed, ecosystems with different structural characteristics have significantly different tipping points for their catastrophic transition due to the complexity and heterogeneity of interactions between species.[13–15] Therefore, identifying the role of species in an ecosystem can effectively improve our understanding of tipping points in ecosystems. Think of an ecosystem as a network where the nodes represent the species present in the system and the connections between species are considered connections. Degree of a node is the number of connections between the node and other nodes. The *k*-core, which is the network subgraph with degree of all nodes at least *k*, provides a way to effectively capture the topological invariance of the interaction network between species and is widely used.[16–18] Based on *k*-core decomposition, Garcia *et al.*[19,20] proposed a method to rank key species in mutualistic networks and a structured way to visualize bipartite ecological networks. Using *k*-core as a predictor of mutualistic ecosystem structure collapse, Morone *et al.*[21] revealed that the root cause of system collapse is the extinction of species located in the largest *k*-core of the network. The *k*-core mainly investigates the static topology and connectivity patterns of ecosystems, which is a useful tool to describe the structure of ecosystems. However, *k*-core cannot consider factors affecting population changes, such as birth rate, mortality rate, competition, mutualism and environmental factors, and thus cannot effectively analyze species dynamics.

For a particular ecosystem, tipping points are determined by its network structure as well as its dynamics. However, mathematical analysis of tipping points in ecosystems consisting of a large number of species and their complex interactions is a challenge. The development of network dimension reduction theory has provided new insights into the analysis of large-scale components of complex ecosystems. Based on the input (the number of connections directed towards the node) and output degrees (the number of connections directed away from the node), Gao *et al.*[22] first proposed a general dimension reduction framework for *N*-dimensional systems to obtain efficient one-dimensional dynamics which we can analyze using traditional mathematical methods. Jiang *et al.*[23] further analyzed the degree weighted method and eigenvectors weighted method, and proposed a two-dimensional dimension

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reduction method to helpfully predict tipping points of mutualistic ecosystems. In many such works, dimension reduction methods based on network science have been applied to obtain efficient low-dimensional dynamic equations for complex ecosystems.[24–26] However, for complex ecosystems containing multiple interactions, precise analysis of how the evolution of their interactions affects ecosystem tipping points is still lacking.

In this paper, we analyze the tipping points of ecosystems with both mutualistic and competitive interactions and their collapse processes during the evolution of interactions. We use the topological invariant of the system k-core to capture the structural features of ecosystems during the evolution of interactions. We find that as the interaction strength weakens or the competition weight increases, the outer species in k-core go extinct because they cannot gain enough interest in the interaction. We then analyze the efficient one-dimensional dynamic function of ecosystems, which solely relies on a single variable. This function represents the change of system average activity with network structural parameters, such as competition weight and interaction strength. By doing so, we derive the tipping points for the structure and dynamic collapse of ecosystems. To test our insights, we further observe the collective activity of 10 real plant-pollinator networks during the evolution of interactions. Our results show that interaction strength and competition weights among species play key roles in mediating tipping points of ecosystems.

2. Model and methods

2.1. Model of the mutualistic and competitive ecosystem

We consider the following nonlinear differential equation to describe the population of species i of plant-pollinator ecosystems:[21,27,28]

$$\frac{\mathrm{d}x_i}{\mathrm{d}t} = -d_i x_i - s_i x_i^2 + \gamma_1 \sum_{j=1}^{N} A_{ij}^{+} \frac{x_i x_j}{\alpha + \sum_{k=1}^{N} A_{ij} x_k} - \gamma_2 \sum_{j=1}^{N} A_{ij}^{-} \frac{x_i x_j}{\alpha + \sum_{k=1}^{N} A_{ij} x_k}, \tag{1}$$

where N represents the number of species in the community, x_i is the population of the i-th species, d_i is the death rate of the i-th species, s_i is the restriction coefficient of intraspecific competition on the population of species i, and α is the half-saturation constant. The third term of the above equation represents the response function of mutualistic interaction. The structure of the mutualistic interaction between species can be denoted as A_{ij}^{+}. Here γ_1 is the intensity of mutualistic interaction between species. The last item corresponds to the impact of interspecies competitive interaction on population. A_{ij}^{-} describes the interspecies competitive interaction between species. The intensity of interspecies competitive interaction between species is captured by γ_2.

We use mixed matrix A_{ij} to code mutualistic and competitive interactions between species. To distinguish mutualistic and competitive interactions in matrix A_{ij}, we employ 1 to describe the existence of the mutualistic relationship between two species, -1 to represent the existence of their competitive relationship, and 0 if there is no interaction. Throughout the work, except when studying the effects of specific parameters, we set the parameters of the species in the ecosystem $d_i = d$, $s_i = s$, and $\gamma_1 = \gamma_2$.

2.2. Dimension reduction method

Equation (1) describes a complex system consisting of a set of N-dimensional coupled differential equations. As the number of species N increases, the population of N-species obtained by direct solution does not provide many general properties of the original ecosystem and it is difficult to analyze the population with mathematical tools that analyze low-dimensional equations. Therefore, it is necessary to reduce the N-dimensional system to directly observable objects.

In this study, we introduce the method of analytic dimension reduction to obtain the one-dimensional equation of the original system (as shown in Fig. 1). The analytic dimension reduction method is first proposed by Duan *et al.*[29] Through dimension reduction, the state of the original system is captured by the collective average activity of the system. Compared with other dimension reduction methods,[22,23] the analytic dimension reduction method can directly obtain the collective average activity of the system through the interaction network of the system without solving the N-dimensional dynamic equation. In the following we will use the analytic dimension reduction method to obtain the one-dimensional equation of Eq. (1).

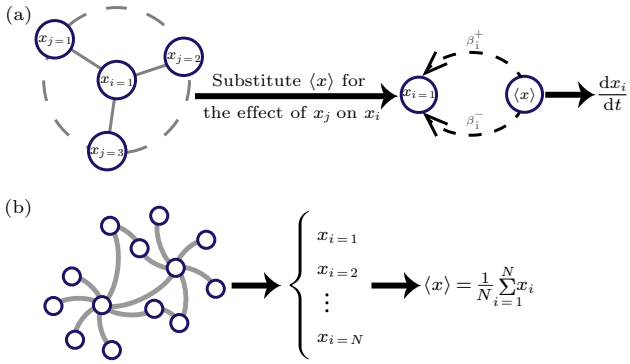


Fig. 1. Dimension reduction method based on analytical solutions. Here $\langle x \rangle$ is the collective average activity of the ecosystem, β_i^{+} is the number of mutualistic interactions of species i, and β_i^{-} is the number of competitive interactions of species i. (a) The activity of the individual species i is influenced by its associated species j. Substituting the effect of species j on i by $\langle x \rangle$, we can obtain approximate activity for individual species. The result is expressed by Eq. (3). (b) By capturing the activity of all species using the method in (a), we can in turn obtain the collective average activity of the ecosystem. The result is expressed by Eq. (5).

We first consider the average activity $\langle x \rangle$ to observe the

collective dynamics of the system:

$$\langle x\rangle = \frac{1}{N}\sum_{i=1}^{N} x_i. \tag{2}$$

The observation $\langle x\rangle$ depends on the activity of each node in the ecosystem and captures the global state of the system. In the plant-pollinator system, $\langle x\rangle$ can be quantified as the average population of all species, including plants and pollinators. In an ecosystem, the state of species i is affected by its associated species j. We assume that the number of species that have an effect of species j on i is approximately $\langle x\rangle$. Equation (1) can then be written as

$$\frac{\mathrm{d}x_i}{\mathrm{d}t} = -dx_i - sx_i^2 + \frac{\gamma_1\beta_i^+ x_i\langle x\rangle}{\alpha+\beta_i\langle x\rangle} - \frac{\gamma_2\beta_i^- x_i\langle x\rangle}{\alpha+\beta_i\langle x\rangle}, \tag{3}$$

where $\langle x\rangle$ captures all activity of j on i, $\beta_i^+ = \sum_{i=1}^{N} A_{ij}^+$ is the sum of the mutualistic interactions of species i, $\beta_i^- = \sum_{i=1}^{N} A_{ij}^-$ is the sum of the competitive links of species i, and $\beta_i = \sum_{i=1}^{N} A_{ij}^+ + \sum_{i=1}^{N} A_{ij}^-$ is the weight of all links of species i. We then introduced Lyapunov stability.[30] Let $f(x_i,\beta_i^+,\beta_i^-) = \mathrm{d}x_i/\mathrm{d}t$, according to Lyapunov stability, the system is in a equilibrium state if $f(x_i,\beta_i^+,\beta_i^-) = 0$. We can further obtain the analytical solution of x_i in equilibrium:

$$x_i = \frac{1}{s}\left(\frac{\gamma_1\beta_i^+\langle x\rangle}{\alpha+\beta_i\langle x\rangle} - \frac{\gamma_2\beta_i^-\langle x\rangle}{\alpha+\beta_i\langle x\rangle}\right) - \frac{d}{s}. \tag{4}$$

Then by substituting Eq. (4) into Eq. (2), we in turn obtain the collective average activity $\langle x\rangle$ of the ecosystem:

$$\langle x\rangle = \frac{1}{N}\sum_{j=1}^{N}\left[\frac{1}{s}\left(\frac{\gamma_1\beta_i^+\langle x\rangle}{\alpha+\beta_i\langle x\rangle} - \frac{\gamma_2\beta_i^-\langle x\rangle}{\alpha+\beta_i\langle x\rangle}\right) - \frac{d}{s}\right]. \tag{5}$$

With the above steps, we can obtain the collective activity of the ecosystem through the structure of the system without solving the dynamic solution of each node. This method reduces the complexity of mathematical calculations. Next, we further simplify the parameters of Eq. (5).

In Eq. (5), we can see that collective average activity $\langle x\rangle$ of an ecosystem is mainly influenced by β_i^+, β_i^-, and β_i. We approximate the number of interaction links β_i for all species using the collective average degree of the ecosystem $\langle\beta\rangle = \frac{1}{N}\sum_{j=1}^{N}\beta_i$. For a particular ecosystem, the number of mutualistic links and the number of competitive links can be viewed as a linear relationship. We define the weight of competitive links in the ecosystem as p, that is, the number of competitive links can be approximated as $p\langle\beta\rangle = \frac{1}{N}\sum_{j=1}^{N}\beta_i^-$, and the number of mutualistic links can be expressed as $(1-p)\langle\beta\rangle = \frac{1}{N}\sum_{j=1}^{N}\beta_i^+$.

For the competition weight p of ecosystem, we first obtain the primary competition weight of the system by the framework of Gao *et al.*,[22] and p can be written as

$$p = \frac{\mathbf{1}^{\mathrm{T}}A\boldsymbol{c}}{\mathbf{1}^{\mathrm{T}}A\mathbf{1}}, \tag{6}$$

where $\mathbf{1}$ is the unit vector $\mathbf{1} = (1,\ldots,1)^{\mathrm{T}}$, and the vector $\boldsymbol{c} = (c_1,c_2,\ldots,c_N)^{\mathrm{T}}$; c_i is the ratio of the number of competitive links of the i-th species to the number of all links of the i-th species. Since there are significant differences in the interactions of different species, and these differences make p unable to accurately capture the competition weight of the ecosystem. If $c_i > 0$, we reduce the heterogeneity of the competition intensity of the species i by using p instead of the c_i and obtain a new vector $\boldsymbol{c}$. Then we substitute this $\boldsymbol{c}$ into Eq. (6) again and obtain the competition weight p of the system.

Finally, we obtain the one-dimensional representation of Eq. (1) as

$$\langle x\rangle \approx \frac{1}{s}\frac{\gamma_1(1-p)\langle\beta\rangle\langle x\rangle}{\alpha+\langle\beta\rangle\langle x\rangle} - \frac{1}{s}\frac{\gamma_2 p\langle\beta\rangle\langle x\rangle}{\alpha+\langle\beta\rangle\langle x\rangle} - \frac{d}{s}. \tag{7}$$

Equation (7) analytically obtains the collective average activity of the ecosystem. Furthermore, as a one-dimensional equation, Eq. (7) allows us to analyze it using traditional mathematical analysis methods. To verify that Eq. (7) can effectively capture the state of the system, we conduct extensive tests usingErdős–Rényi (ER) networks and real plant-pollinator networks. The results are shown in Subsection 3.1.

2.3. The k-core and the threshold K_γ to benefit from interactions

As an indicator, k-core can divide the graph into subgraphs. Due to the linear complexity and intuitive interpretability of the k-core structure, it has many application fields including economics, social sciences, and bioinformatics. The k-core refers to the network subgraph with all nodes in a network whose degree is at least k. To obtaining k-core, first check whether there are nodes in the network with a degree less than k, if there are, remove the nodes and remove their edges, and re-check the network until all nodes meet the degree of at least k. In Fig. 2(a), for example, the 3-core is shown by the orange balls. The k-core is used as the topological logic invariant of the network, starting from the periphery of the network, 1 core contains 2 cores, 2 core contains 3 cores, and so on, until the innermost core of the network. We define the innermost core of k-core as $k_{\max}$, while k-shell (k_{s}) is the shell of k-core. According to the definition of k-core, k-core is a nested structure. If the $(k+1)$-core structure can be found in the k-core structure, then k_{s} can be expressed as the set composed of the remaining nodes after removing the $(k+1)$-core structure from the k-core. In Fig. 2(a), the 1_{s} is shown by the purple balls. In other words, the subset of species in the k-core consists of the periphery k_{s} and the remaining $(k+1)$-core.

Morone *et al.*[21] studied the k-core nested structure of mutualistic ecosystems and proposed a threshold $K_\gamma = \frac{\alpha s(\gamma_1+d)}{(\gamma_1-d)^2}$ at which species benefit from mutualistic interactions. As shown in Fig. 2(b), with the increase of K_γ, the species

gradually becomes extinct from the outermost layer to the innermost layer. The species in the k-core can only benefit from the mutualistic interaction of other associated species when it is higher than K_γ. Here, k-core can be denoted as $\lceil K_\gamma \rceil$-core. However, the more common ecosystems involving multiple interactions have not yet been studied.

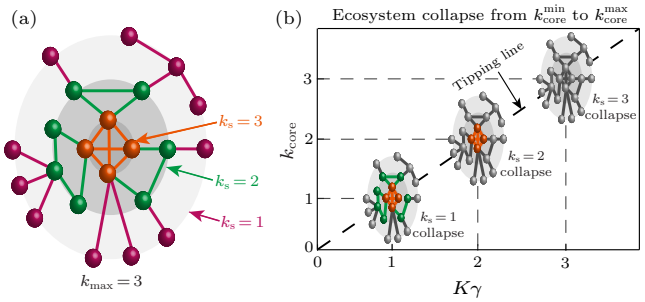


Fig. 2. The k-core structure and k-core collapse process of ecological networks. Spheres represent species, and solid lines represent interactions between species. (a) Schematic diagram of the k-core nested structure of a simple ecosystem. The k-core is the network subgraph with degree of all nodes at least k, and this ecosystem contains 1-core (purple, green and orange spheres), 2-core (green and orange spheres) and 3-core (orange spheres) subgraph structures. k-shell (k_s) is defined as the set of peripheral nodes of k-core. The maximum core of this entire network $k_{max} = 3$, which corresponds to the sub-network with the largest k-core. (b) The illustration of collapse process of the ecosystem. Grey discs and lines represent extinct species and their dissipating interactions. K_γ serves as a threshold for species in the ecosystem to benefit from mutualistic interactions. Morone *et al.*[21] found that all species in the ecosystem can gain sufficient benefit from the mutualistic interactions when $K_\gamma < 1$. Species at $k_s = 1$ cannot benefit from mutualistic interactions with other species if interactions evolve such that K_γ is greater than 1 and less than 2. By analogy, when K_γ is further increased so that it exceeds k_{max}, the species of the whole system cannot obtain enough benefits from the mutualistic interaction, and the whole system collapses.

In this study, we consider the collapse process of ecosystems with mutualistic and competitive interactions. We firstly introduce a coupling factor $\gamma = (1-p)\gamma_1 - p\gamma_2$, which takes into account not only the mutualistic interaction strength between species, but also the competitive interaction strength between species and the competition weight of the entire ecosystem. Then we further obtain K_γ under the interactions of mutualist and competition as

$$K_\gamma = \frac{\alpha s(\gamma + d)}{(\gamma - d)^2}. \tag{8}$$

In order to verify that K_γ can accurately capture the interaction evolution process, we use the real ecosystem for verification. The comparisons between the analytical solution and the simulation solution of the real ecosystem are shown in Figs. 4 and 5. Furthermore, we analyze the roles of γ and p in K_γ, and the results of the influence of variables γ and p on K_γ are shown in Fig. 6.

2.4. Database of plant-pollinator networks and acquisition of competitive interactions

We select 10 real plant-pollination networks from the web-of-life (https://www.web-of-life.es). As shown in Table 1, this database covers a wide geographic range and different climates. The number of species in this database ranged from 27 to 185. However, these networks only provide data on the mutualistic relationship between species, and do not cover the competitive relationship between species.

Table 1. Plant-pollinator networks from the web of life.

ID	Species	Interactions	Location
M_PL_001[31]	185	361	Chile
M_PL_002[31]	107	196	Chile
M_PL_008[32]	49	106	Canary Islands
M_PL_010[33]	107	456	Zackenberg
M_PL_011[34]	27	52	Mauritius
M_PL_030[35]	81	109	Venezuela
M_PL_031[36]	97	156	Venezuela
M_PL_033[37]	47	141	Canada
M_PL_040[38]	72	114	Jamaica
M_PL_046[39]	60	278	Denmark

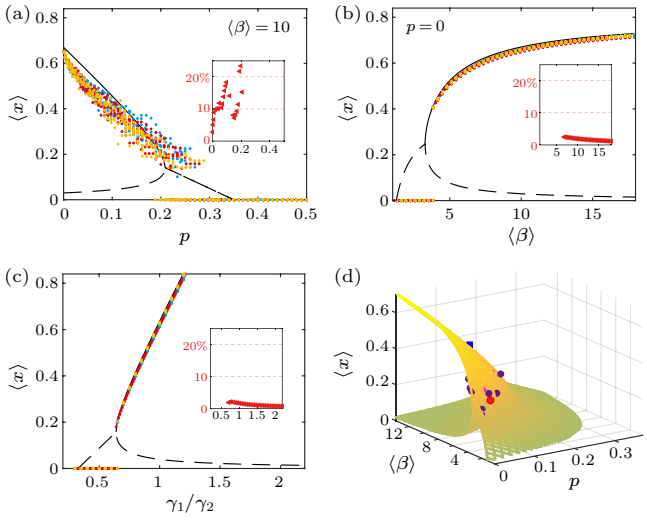


Fig. 3. Statistical characteristics of local ecosystem. (a)–(c) Competition weight p, collective average degree $\langle\beta\rangle$ and interaction strength γ_1/γ_2 versus collective average activity $\langle x\rangle$. The nonlinear bifurcating resilience function is obtained from Eq. (7), and Eq. (1) is solved for the simulation solution. The scattered points in the figure represent simulation solutions, and the black curve represents analytical solutions. The error analysis between the analytical solution and the simulation solution is shown in the subgraph, where the red triangle is the relative error in the form of percentage. (a) We verify the predictive power of the analytical solution using a fully connected mutualistic network with $\langle\beta\rangle = 10$. Each step randomly changes the mutualistic link to the competitive link until the mutualistic network becomes a competitive network, and $\langle x\rangle$ and p are calculated in each step. [(b), (c)] ER network is used as the original network for numerical simulation. We introduce a variable w and change the weights of links in the network by $A \longmapsto w \cdot A$, so the statistical characteristics of the adjacency matrix are distributed to different regions. (d) The three-dimensional space presents the relationship of $\langle x\rangle$ with p and $\langle\beta\rangle$ and. Mapping of 10 real-world ecosystems in 3D space from Table 1.

Here, we use the coupled framework of mutualism and competition developed by Gracia–Lazaro *et al.*,[40] in which species in different groups benefit from each other through pollination, and species in the same group compete for food or space. In this work, we assume that competition occurs when the common mutualistic links of species i and j reach 0.7 of all their links. In addition, we can also obtain networks

of different competition weights by adjusting the proportion of mutualistic links required.

3. Results

3.1. Statistical characteristics of local ecosystems

We use analytic methods to map high-dimensional complex ecosystems into a one-dimensional representation. The basic idea of this method is shown in Figs. 1(a) and 1(b). The activity of the individual species is influenced by the activity of its neighbors. First, we substitute the activity of the neighbor species x_j with the collective average activity $\langle x\rangle$ of the local ecosystem. Then, we in turn get $\langle x\rangle$ according to Eq. (2). In this way, we can obtain the collective average activity of the entire network through the structural characteristics of the network without computing Eq. (1).

Through dimension reduction, we can characterize a particular local ecosystem by three statistical features: $\langle x\rangle$ captures the collective average activity of ecosystem, $\langle\beta\rangle$ represents the collective average degree of ecosystem, and p is the competition weight of the ecosystem. The interaction function of $\langle x\rangle$ related to $\langle\beta\rangle$ and p is expressed in Eq. (7), which predicts the bifurcation function of the form of Figs. 3(a) and 3(b). We can see that as p increases or $\langle\beta\rangle$ decreases, the collective average activity of the ecosystem gradually decreases and suddenly jumps to a low-abundance state at the bifurcation point. To verify that Eq. (7) can effectively represent the activity of the original ecosystem, we conduct extensive tests. We first verify the relationship between $\langle x\rangle$ and p by fixing the $\langle\beta\rangle$ of the system and gradually converting the mutualistic links to competing links. We then verify the relationship of $\langle\beta\rangle$ to $\langle x\rangle$ by introducing a factor w that uniformly changes the collective average degree $\langle\beta\rangle$ of the system by $A \to w\cdot A$. In addition, we formalize the relationship between γ and $\langle x\rangle$ in Fig. 3(c). We find that the ecosystem jumps from a high abundance state to a low abundance state when γ is small. We use ER networks to verify it and show that the analytical solution accurately predicts the simulation solution. Found by error analysis shown in the subfigure of Fig. 3, the relative error of most of the results of high abundance state is below 20%. If we identify the low abundance state of the analytical result as a system crash, that is, 0, the error will be further narrowed. Therefore, the error is within the acceptable range.

We finally represent the relationships of $\langle x\rangle$ to $\langle\beta\rangle$ and p in three spaces and fit them using the real ecosystems in Table 1 [Fig. 3(d)]. Our extensive validation shows that the activity of the original system can be effectively captured by the analytic dimension reduction method.

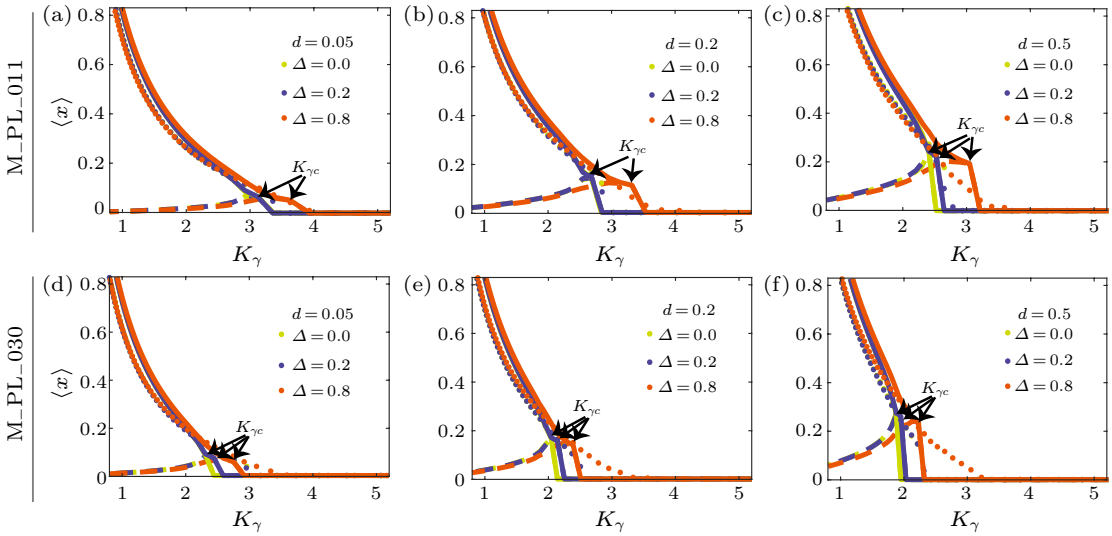


Fig. 4. Numerical simulation and analytical solutions of real networks with different parameters. (a) Collective activity $\langle x\rangle$ of the ecosystem as a function of K_γ, which is captured by Eq. (8). K_γ decreases as the interaction strength γ increases. We use a variable w and change γ of the network by $A \longmapsto w\cdot A$. Line is the analytical solution obtained by Eq. (7). The point is the numerical solution to Eq. (1) solved using the ODE45 algorithm. We add perturbations that follows the normal distribution with mean 0 and variance $\triangle$ to species interactions when death rate $d = 0.05$. $K_{\gamma c}$ is the tipping point of ecosystem collapse. [(b), (c)] Same as (a), but using $d = 0.2, 0.5$, respectively. [(d), (f)] Relationship between collective activity $\langle x\rangle$ and K_γ in the M_PL_030 network.

3.2. The K_γ captures ecosystem collapse under the interaction of mutualist and competition

Morone *et al.*[21] first proposed a threshold for species benefit from interactions: K_γ. Specifically, only species larger than K_γ-core in the k-core nested structure can benefit from the interaction. However, previous research has only dealt with mutualistic ecosystems. In this work, we extend K_γ to capture the structural features of ecosystems with mutualistic and competitive interactions in Subsection 2.3. As shown in Eq. (8), K_γ is affected by interaction strength γ_1/γ_2, competition weight p and dynamic parameters. We formalized the collective average activity $\langle x\rangle$ as a function of K_γ in Fig. 4. The results show that with the increase of K_γ, the collective average activity $\langle x\rangle$ of the ecosystems gradually decreases and

there is a tipping point $K_{\gamma c}$ where the ecosystems collapse.

To verify the consistency of the simulated and analytical solutions, we conducted tests using the real ecosystems. The simulation solution is obtained by solving Eq. (1), and the analytical solution is obtained by Eq. (7). We verify the predictive power of the analytical solution by adjusting the dynamic parameters and adding perturbations. As shown in Fig. 4, our analytical solution can fit well with the simulation solution even with different d (usually d is in the range of 0.1–0.3[21,41,42]) and different perturbations added.

In addition, we further illustrate the broad applicability of K_γ using more real ecosystems with different geographic ranges and climates in Fig. 5. The results show that K_γ captures the collapse process of the ecosystem under the interactions of mutualist and competition.

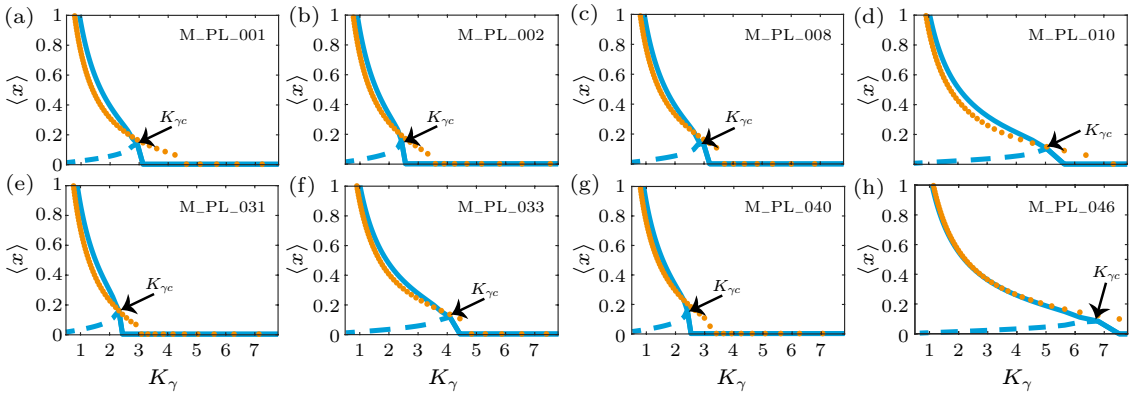


Fig. 5. Numerical simulation and analytical solution of different real networks. Using $\langle x \rangle$ as a function of K_γ, we further verify analytical and simulated solutions for a large number of ecosystems from Table 1. Line is the analytical solution obtained by Eq. (7). The point is the numerical solution of Eq. (1) solved using the ODE45 algorithm. $K_{\gamma c}$ is the tipping point of ecosystem collapse; $d = 0.2$, $\triangle = 0.0$; and the others are the same as those in Fig. 4.

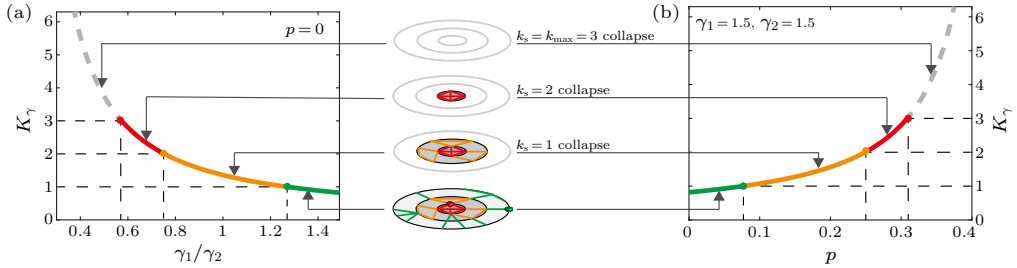


Fig. 6. The effect of interaction strength and competition weights on k-core collapse. (a) The effect of interaction strength on the ecosystem. For the small γ_1/γ_2 such that $K_\gamma > 3$, all species in the ecosystem cannot obtain sufficient survival resources from the interaction and go extinct. As γ_1/γ_2 increases such that $3 > K_\gamma > 2$, species with $k_s < 3$ cannot get enough benefits and become extinct. When γ_1/γ_2 is further increased such that K_γ is less than 1, all species in the ecosystem can gain sufficient benefits from their interactions. (b) The relationship between the competitive intensity of the ecosystem and the k-core collapse process. Here p is the competitive intensity of ecosystem. Contrary to the effect of the interaction strength γ_1/γ_2, as the competition strength p increases, the species in the ecosystem collapse from the minimum k_s to the maximum k_{max}. Parameters are set as $d = 0.1$, $s = 1$, and $\alpha = 1$.

3.3. Effect of interaction strength and competition weights on k-core collapse

K_γ is the threshold for species to benefit from interaction. For a local ecosystem containing the interactions of mutualist and competition, K_γ depends not only on the intensity of interaction, but also on the weight of competition. In order to accurately capture the threshold of k-core collapse, we formalize the relationship between γ_1/γ_2 and p on K_γ by Eq. (8) in Fig. 6. The results show that all species can benefit from the interaction only when the interaction strength γ_1/γ_2 of species is large enough. Conversely, if γ_1/γ_2 is so small that $K_\gamma > k_{max}$, the species will not gain enough benefits from the interactions to survive, and the ecosystem will collapse.

In addition, the weight of competition also affects the threshold of k-core collapse. As shown in Fig. 6(b), for strong competition weight p such that $K_\gamma > k_{max}$, all species in the ecosystem cannot gain enough benefits from the interactions to go extinct. When the competition intensity is further reduced such that $k_2 < K_\gamma < k_{max}$, species in the 3-shell can benefit from the interaction. For a sufficiently small weight of competition so that $K_\gamma < 1$, all species can survive.

3.4. Critical conditions for local ecosystem collapse

So far, we have realized that the ecosystem collapses from the shell of k-core (k_s) to the innermost core of k-core (k_{max}), and the ecosystem reaches the tipping point of collapse if species located at k_{max} start to become extinct. However, accurate prediction of tipping points in complex ecosystems is a long-term research challenge. In this section, we develop a framework to address this challenging problem. Through

dimension reduction, we first obtain the one-dimensional dynamic equation of the ecosystem (see Subsection 2.2). We then introduce Lyapunov stability. According to Lyapunov stability, the dynamics and structure of the ecosystem reach equilibrium when $\frac{\partial\langle\beta\rangle}{\partial\langle x\rangle}|_{\langle x\rangle=\langle x\rangle_\gamma}=0$. Then, we can obtain the tipping point of dynamics and structure at equilibrium:

$$\langle x\rangle_\gamma=\frac{\sqrt{d\gamma}-d}{s}, \tag{9}$$

$$\langle\beta\rangle_\gamma=\frac{\alpha s}{d+\gamma-2\sqrt{d\gamma}}=\frac{\alpha s}{(\sqrt{\gamma}-\sqrt{d})^2}, \tag{10}$$

where $\langle x\rangle_\gamma$ represents the tipping point of system dynamics, and $\langle\beta\rangle_\gamma$ is the tipping point of system structure; γ is the coupling factor of the interaction strength γ_1/γ_2 and the competition weight p.

Equations (9) and (10) possess a high degree of comprehensiveness because they consider not only the intrinsic dynamic parameters but also the interaction intensity and competition weights within the ecosystem. These considerations are reflected in the state phase diagram of the ecosystem as shown in Fig. 7. The characteristics of the phase diagram are defined by Eqs. (9) and (10), which separate the extinction-resilient phases of the ecosystem. We tested these phase diagrams using real plant-pollinator networks. The predicted phase diagrams for γ and p with $\langle x\rangle$ and $\langle\beta\rangle$ are shown in Fig. 7, and all ecosystem states can be accurately captured by these phase diagrams even after changing dynamic parameters, interaction strength and competition weight.

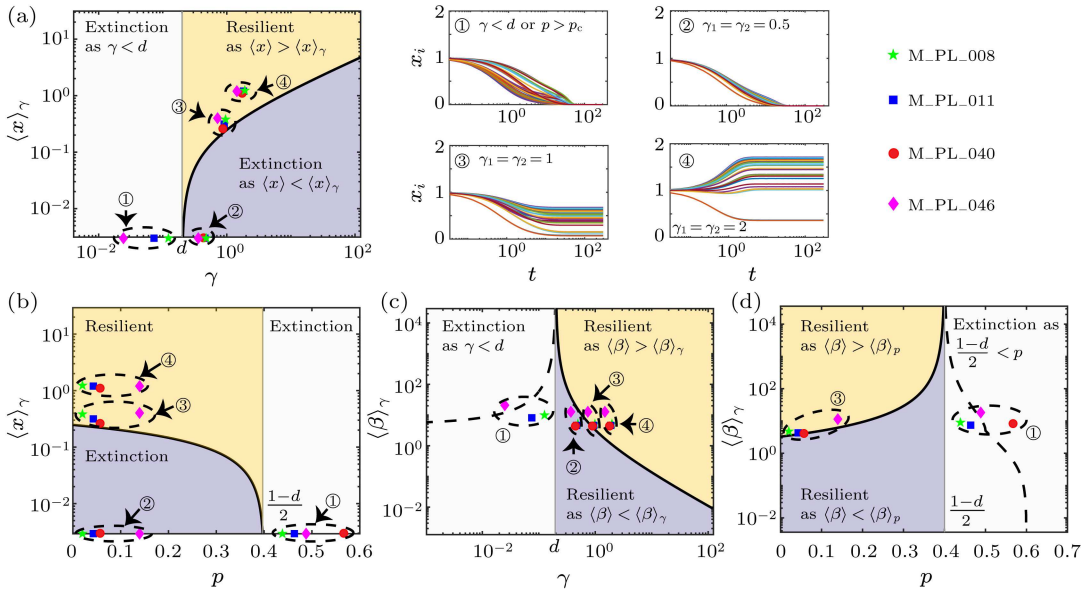


Fig. 7. Phase diagram of tipping points of ecosystems. (a) Predicted phase diagram of γ with $\langle x\rangle$ for $\gamma=(1-p)\gamma_1-p\gamma_2$, which encodes the effects of the interaction strength γ_1/γ_2 and the competition weight p, with d being the death rate of species. The characteristics of the phase diagram are separated by Eq. (9). We validate the predictive power of the phase diagrams using 4 real ecosystems listed in Table 1. We obtain the ①, ②, ③, and ④ states of the species population of the M_PL_008 ecosystem by adjusting the interaction strength γ_1/γ_2 and competition weight p. (b) The phase diagram of competition weight p with $\langle x\rangle$. Equation (9) separates the extinction-resilient phases of ecosystems. [(c), (d)] Phase diagram of γ with $\langle\beta\rangle$, and phase diagram of p with $\langle\beta\rangle$. The extinction-resilient phases of the ecosystem are separated by Eq. (10).

4. Discussion and conclusions

In this work, we establish a dimensionality reduction algorithm for mutualistic and competitive coupled ecosystems. By using the analytical dimensionality reduction method, we can simplify the N-dimensional nonlinear rate equation to a one-dimensional rate equation, and then obtain the collective average activity of the system by knowing the ecosystem structure. Under the plant-pollinator network dynamics model, the theoretical solutions agree well with the simulation results. The study demonstrates that the analytic dimension reduction methods can be used to accurately characterize the control and state parameters of the ecosystem.

Through the topological invariant of the ecosystem, k-core, we obtain the collapse characteristics of the ecosystems under interactions of mutualism and competition. Studies have shown that the evolution of interactions may cause species extinction and decline in ecosystem function, or even lead to ecosystem collapse.[43,44] Specifically, as the strength of interaction weakens or the weight of competition increases, species in the ecosystem will become extinct from the outermost shell to the largest core of the k-core structure. The ecosystem will reach the tipping point of collapse when species in the largest k-core begin to become extinct due to interactive evolution. In previous studies, due to the lack of intrinsic dynamical information and effective analytical tools for large-scale systems, the critical point of system collapse was considered to be highly unpredictable.[22,45,46] However, our work finds that through the analysis of the one-dimensional efficiency

model of the ecosystem, the analytical solution of the tipping point of the ecosystem under the interaction of reciprocity and competition can be obtained, as shown in Eqs. (9) and (10). Thus, by establishing early warning mechanisms, it is possible to open up new opportunities for proactive conservation and management of ecosystems before they collapse by introducing mutualistic interactions and identifying and protecting critical nodes.

Overall, our work elucidates the process of species collapse during the evolution of interactions in ecosystems with mutualistic and competitive interaction types, and obtains the tipping point of ecosystem collapse. Since similar k-core collapses are ubiquitous in real-world networks, our findings can be applied to many complex systems: social networks, disease transmission networks and supply chain systems. Our future work will further investigate the impact of different types of interactions on ecosystem collapse and gain insight into their role in ecosystems, which has profound implications for understanding complex ecosystems.

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