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Fractional core-based collapse mechanism and structural optimization in complex systems

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Abstract Catastrophic and major disasters in real-world systems ranging from financial markets and ecosystems, often show generic early-warning signals that may indicate a collapse. Hence, understanding the collapse mechanism of a complex network and predicting its process are of uttermost importance. However, these challenges are often hindered by the extremely high dimensionality of the underlying system. We present here the concept of the fractional core (F-core) that considers the contribution of the network topology and dynamics to systematically analyze the collapse process in such networks, and encompass a broad range of dynamical systems, from mutualistic ecosystems to regulatory dynamics. We offer testable predictions on the tipping point, and, in particular, prove that the extinction of the maximum F-core of a network is an efficient indicator of whether a system completely collapses. The results show that the death of species or cells in a low-order F-core may improve the average density and have little influence on the tipping point. Generally, the principle of the F-core demonstrates how complex systems collapse and opens an innovative optimization strategy to uncover the optimal structure of systems.

Keywords collapse mechanism, tipping point, structural optimization, complex systems, phase transition

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1 Introduction

Understanding how complex systems, ranging from ecosystems and climate to economic, social, and infrastructure systems, collapse is a pressing scientific challenge [1–5]. The breakdown of a complex system is always induced by a rather small perturbation from the system itself [6–8] to the external environment [4, 9]. Examples of such collapse are the crash of financial markets, the degradation of coral reefs caused by regional stressors, and massive jamming in urban traffic systems. In fact, these collapses are the consequence of gradual changes in systems, which often cause disastrous consequences for humans, and are rarely predictable and often irreversible. The collapse mechanism is caused by the dynamical and structural parameters in complex networked systems. However, the collapse mechanism is hard to identify, due to the difficulties encountered in quantifying the contribution of nodes on the system performance and, in particular, considering the self-dynamics of each node and the dynamic interactions between them. Hence, it remains a challenging problem. A good understanding of the collapse mechanism in complex networked systems can effectively support the prediction of the collapse process, the tipping point, and the structural optimization of systems.

To capture the collapse mechanisms in such systems, early-warning signals [10–14], which are generic symptoms, may occur when complex dynamical systems approach a critical point. The critical slowing

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down [13] is the most important clue in predicting that a system is getting close to a tipping point. Skewness and flickering before transitions are also indicators of whether a system is getting close to a catastrophic bifurcation as tipping [15–17]. However, these indicators are far from being able to predict thresholds in most complex systems [18]. Simpson-Porco et al. [19] found that voltage collapse and related instabilities are identified as contributing factors in several recent large-scale blackouts of power grids, including those in Scandinavia (2003), the Northeastern United States (2003), Athens (2004), and Brazil (2009). Obura et al. [20] found that the coral reef state is globally based on one key indicator, namely, live coral cover, that is conceptually straightforward and accessible to measure, making it a leading indicator of ecosystem health in the ocean. To overcome the analytical framework of resilience multi-dimensional systems, a dimension reduction process to derive effective one-dimensional dynamics for multi-dimensional systems was proposed to predict the systems' tipping point [4].

Indeed, previous approaches have not provided exact analytical results that relate network properties to the collapse mechanism in complex networked systems. Recently, Morone et al. [21] revealed that the maximum k-core of a network is the root of collapse with regard to the collapse mechanism in complex networked systems. The method presented an analytic solution of the fixed point for a nonlinear model of mutualistic dynamical systems in terms of a topological invariant of the network, the k-core number. To capture the effectiveness of the k-core, some studies have applied the k-core to different networks and achieved promising results. Zhang et al. [22] found the key users regarding the stability of a whole network through the collapsed coreness problem in social networks. Burleson-Lesser et al. [23] proposed a new k-core-based robustness that is based on theory rather than individual examinations of discrete networks, and a method of determining a network's tipping point of collapse in ecological and financial networks. Although the k-core is simple and amenable to analysis, it is limited in the following aspects: (1) Certain features of the most fundamental dynamical property of the original network are lost in the analytical results, particularly weighted interactions. (2) The process of species extinction becomes inaccurate as the mutualistic interaction strength weakens. (3) The structure of the ecosystem is non-optimal.

To address these problems, a piecewise function is introduced to capture the value of a node's contribution resulting from the alteration of the most fundamental dynamical property. Then, a fresh concept, i.e., fractional core (F-core), is proposed to provide evidence for node classification, considering its structure feature and dynamical behavior. For different dynamics, the F-core structure would be different in revealing the collapse mechanism. The effectiveness of the F-core is tested in real mutualistic and biological networks. The results show that the F-core is very effective in the prediction of the collapse process, tipping point, and structural optimization of the system. We offer a general predictive framework for the collapse mechanism using the F-core that can treat a broad range of dynamical models from ecological and biological networks to finance systems. The main contributions of our work are as follows:

- A fresh concept, i.e., F-core is proposed. The F-core could provide evidence for a classification of the species or cells from ecological to biological networks, considering the contribution of the network topology and dynamics. For different dynamics, one node would fall in a different F_{shell} by the F-core, but it always falls in a fixed k_{shell} by the k-core.
- The F-core could allow accurate monitoring of the species or cell extinction process as the mutualistic interaction strength weakens, but the results by the k-core cause larger errors.
- The extinction of some species or cells in a low F-shell may improve the average density of a system, but there is no difference in the tipping point of the system. However, we could not find these phenomena through the k-core method.

The remaining parts of this paper are organized as follows: Section 2 briefly summarizes related work. Section 3 defines the F-core and establishes the relationship between the F-core and fixed points in mutualistic ecosystems and gene regulatory dynamics. Section 4 validates the results of the F-core in the prediction of the collapse process, tipping point, and structural optimization of the system. We also perform a comparison with the k-core in Section 4. Section 5 discusses the limitations of this work. Finally, Section 6 presents the conclusion of our work.

2 Related work

Considering that the tipping point can capture the system's sudden shifts to the irrecoverable state, the point that can be a function of the dynamical and structural parameters of the system should be derived [21]. May [24] discussed how alternate stable states can arise in simple one-dimensional systems.

Scheffer et al. [7] proposed a minimal model of ecosystem catastrophic shifts to predict how smooth changes can be interrupted by sudden drastic switches to a contrasting state by diverse events. Mumby et al. [25] combined ecosystem thresholds and stochastic disturbance models to evaluate targets for the restoration of ecosystem processes through the coral reef model. Xiong et al. [26] modeled the cell fate induction process using the ordinary differential equation to explain the irreversibility of maturation. Gardner et al. [27] proposed a synthetic, bistable gene-regulatory network considering a double-negative feedback loop to predict the conditions necessary for bistability.

In the real world, as systems with a high dimensionality property, such as ecosystems, biological systems, social systems, and critical infrastructure systems, have several components and interactions, the tipping point cannot be easily determined [28]. Gao et al. [4] proposed a dimension reduction method to derive an analytical solution to compute the tipping point. Laurence et al. [29] enhanced the dimension-reduction method through a weighted spectrum of the adjacency matrix, extending the application to networks of arbitrary degree distributions with high accuracy. To analyze the influence of mutualistic interactions, i.e., the most fundamental dynamical property of the original bipartite network on the tipping point of a system, a 2D dimension reduction model was proposed to capture its bipartite and mutualistic nature [30]. However, these proposed models still cannot easily identify the contribution of each node in weighted networks, and then predict the collapse process in a changeable environment. Hence, it is necessary to relate the network properties to the fixed point of a dynamical system to reveal the root cause of a system collapse.

3 Materials and methods

3.1 F-core

We illustrate the concept of the F-core by focusing on the dynamics of an ecosystem with N species, where each species i is characterized by a density, i.e.,

$$\dot{x}_i\left(t\right) = -dx_i - sx_i^2 + \sum_{j=1}^{N} A_{ij}\gamma_{ij}\frac{x_i x_j}{\alpha + \sum_{k=1}^{N} A_{ik}x_k}, \tag{1}$$

which provides a rather general deterministic description of an ecosystem governed by mutualistic interactions. Here, d is the death rate of species, $s > 0$ is the self-limitation parameter modeling the intraspecific competition that limits a species' growth once x_i exceeds a certain value, a is the half-saturation constant, A_{ij} is the adjacency matrix of the system, and γ_{ij} is the mutualistic interaction strength between species i and j.

Next, we explain the definition of the $F_{\text{core}} = T$, which is the maximal sub-graph, not necessarily globally connected, consisting of a node with strength greater than T (Figure 1(b)). The nodes fall in $F_{\text{shell}} = T$, which means that their contribution to the system will transit from a finite value to 0 in Figure 1(c). In an ecosystem, each species has a value w which represents the strength of species [31]. Here, w_i could be calculated by $w_i = \sum_{j=1}^{N} A_{ij}\Psi(w_j - T)$. The process of obtaining the F-core structure is as follows: (i) For a given value T, we eliminate the variables w which satisfies $w \leqslant T$, and keep other variables w for which $w > T$. (ii) The contribution of w for which $T < w \leqslant T + \Delta T$ is $(w - T)/\Delta T$, and the contribution of others is 1, as shown in (2). (iii) After (i) and (ii), species have a smaller value w', and if $w' \leqslant T$ or $T < w' \leqslant T + \Delta T$, (i) or (ii) is repeated until the contribution of each remaining species is constant. This process is identical to the algorithm for extracting the F-core of the network. The pseudocode of the F-core is presented in Algorithm 1.

$$\Psi\left(w - T\right) = \begin{cases} 0, & w \leqslant T, \\ \frac{w-T}{\Delta T}, & T < w \leqslant T + \Delta T, \\ 1, & w > T + \Delta T. \end{cases} \tag{2}$$

Remark 1. Note that Eq. (2) was required to get the F-core of a network. A schematic representation of a network as successive enclosed F-cores is listed in Figure 1(b), and here ΔT in (2) is equal to 1. For different dynamical systems, the optimal ΔT is needed to be derived by the minimum mean square error method.

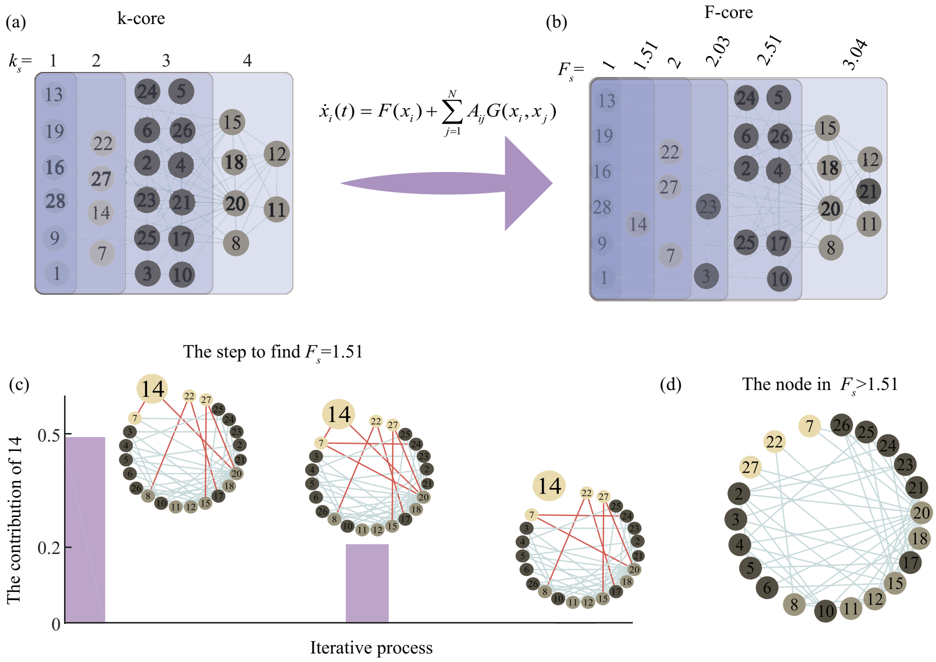

Figure 1 (Color online) Illustration of the fractional core (F-core) in a network. The network includes 28 nodes and 59 links. (a) Schematic representation of a network as the k-core. (b) Schematic representation of the network as the F-core. (c) Process of finding the node which is in $F_s = 1.51$. First, we find that the strength of the nodes belongs to $1.51 < w \leqslant 2.51$, and the contribution of these nodes is $(w - 1.51)/1$, so the links of nodes 14, 22, and 27 are red. The strength of node i is calculated by $w_i = \sum_{j=1}^{N} A_{ij}\Psi(w_j - T)$. Then, the strength of each node is updated, and the process is repeated until the contribution of each remaining species is constant. Finally, the contribution of node 14 is 0, but the contribution of others is a finite value, so node 14 is in $F_s = 1.51$. (d) Schematic representation of the network that includes the nodes in $F_s > 1.51$.

Algorithm 1 F-core

```
Require: Network $G = (V, E)$, death rate $d$, the interaction strength $\gamma$;
for $i \Leftarrow 1$ to length($\gamma$) do
    Calculate $y^s$ through (8) at step $i$;
    $w(1, :)$ = degree($G$);
    for $t \Leftarrow 1$ to 100 do
        $\Delta T = 0.01 \cdot t \cdot K_\gamma$;
        for $j \Leftarrow 2$ to 200 do
            Calculate $w$ through (2) at step $j$;
            if $w(j, :) == w(j-1, :)$ then
                $y(t, :) = w(j, :)$;
                Calculate the mean square error between $y^s$ at step $i$ and $y(t, :)$;
                Break;
            end if
        end for
    end for
    Determine the optimal $\Delta T$ through LSM in (2);
    $y^*(i, :) = y(t1, :)$; //$t1$ is the optimal $\Delta T$ through LSM.
end for
Return $y^*$. //$y^*$ is the F-core of the network.
```

3.2 Analysis of the fixed-point of mutualistic ecosystems

To test the relationship between the F-core and mutualistic interaction strength in mutualistic ecosystems, the fixed-point equations for this system can be written in terms of the Hill function,

$$y_i^* = \sum_{j=1}^{N} A_{ij} H_1\left(y_j^* - \frac{\alpha d s}{(\gamma - d)^2}, \frac{\alpha \gamma s}{(\gamma - d)^2}\right), \tag{3}$$

where $y_i^* = {}^{s}/_{(\gamma - d)} \sum_{j=1}^{N} A_{ij} x_j^*$. To determine the analytical solution for this fixed point, we use the logic approximation of the Hill function $H_n(x, T) \approx \Psi(x - T)$ in (3). The fixed-point equations can be written as

$$\begin{cases} y_i^* = \sum_{j=1}^{N} A_{ij}\Psi\left(y_j^* - K_\gamma\right), \\ K_\gamma = \dfrac{\alpha s\left(\gamma + d\right)}{\left(\gamma - d\right)^2}. \end{cases} \tag{4}$$

The optimal ΔT for this piecewise function should be found. The objective function of the optimal ΔT can be written as

$$\min \sum_{j=1}^{N} \left(\frac{(\gamma - d)^2 y_j^s - ads}{(\gamma - d)^2 y_j^s - ads + a\gamma s} - \Psi\left(y_j^* - \frac{as(\gamma + d)}{(\gamma - d)^2} \right) \right)^2, \tag{5}$$

where y_j^s can be solved as follows.

Through the dimension reduction method, the dynamical equation of (1) when it reaches the steady state could be written as

$$f\left(\beta_{\text{eff}}, x_{\text{eff}}\right) = -dx_{\text{eff}} - sx_{\text{eff}}^2 + \gamma\beta_{\text{eff}}\frac{x_{\text{eff}}^2}{\alpha + \beta_{\text{eff}}x_{\text{eff}}} = 0. \tag{6}$$

The dynamical equation of (1) when it reaches the steady state could be written as

$$-dx_i - sx_i^2 + \gamma k_i \frac{x_i x_{\text{eff}}}{\alpha + k_i x_{\text{eff}}} = 0. \tag{7}$$

The activity of node i can be obtained as $x_i = \gamma k_i x_{\text{eff}}/(1 + k_i x_{\text{eff}}) - d$, so we have

$$y_j^s = \frac{s\alpha\left(sx_i + d\right)}{\left(\gamma - d - sx_i\right)\left(\gamma - d\right)}. \tag{8}$$

Remark 2. Eq. (3) is derived from (1) in the steady state. Through a logic approximation of the Hill function in (3), the analytical solution for mutualistic ecosystems can relate the F-core to the fixed point. The minimum mean square error method is required to derive the optimal ΔT for mutualistic ecosystems.

3.3 Analysis of the fixed-point of gene regulatory dynamics

Next, we explore it in gene regulatory networks governed by the Michaelis-Menten equation,

$$\dot{x}_i\left(t\right) = -dx_i^f + \gamma\sum_{j=1}^{N} A_{ij}\frac{x_j^n}{a^n + x_j^n}. \tag{9}$$

The first term on the right-hand describes the degradation ($f = 1$) or dimerization ($f = 2$), and d is the mortality rate of the genes. The second term captures the genetic activation between genes, where the Hill coefficient n describes the cooperation level in gene regulation and γ is the maximal interaction strength between a pair of genes.

To test the relationship between the F-core and the mutualistic interaction strength in the gene regulatory dynamics, the fixed-point equations for this system can be written in terms of the Hill function,

$$y_i^* = \sum_{j=1}^{N} A_{ij} H_n\left(y_j^*, K_\gamma\right), \tag{10}$$

where $y_j^* = \frac{x_j d}{\gamma}$. To identify the analytical solution for this fixed point we use the logic approximation of the Hill function in (10). The optimal ΔT for this piecewise function should be found. The fixed-point equations can be written as

$$\begin{cases} y_i^* = \sum_{j=1}^{N} A_{ij}\Psi\left(y_j^* - K_\gamma\right), \\ K_\gamma = (ad)/\gamma. \end{cases} \tag{11}$$

The objective function of the optimal ΔT can be written as

$$\min \sum_{j=1}^{N} \left(\frac{\left(\gamma y_j^s\right)^n}{(da)^n + \left(\gamma y_j^s\right)^n} - \Psi\left(y_j{}^* - K_\gamma\right) \right)^2, \tag{12}$$

where y_j^s can be solved as follows.

Through the dimension reduction method, the dynamical equation of (9) when it reaches the steady state could be written as

$$f\left(\beta_{\text{eff}}, x_{\text{eff}}\right) = -d x_{\text{eff}} + \gamma \beta_{\text{eff}} H_n\left(x_{\text{eff}}, \alpha\right) = 0. \tag{13}$$

The dynamical equation of (9) when it reaches the steady could be written as

$$x_i = \frac{\gamma}{d} k_i \frac{x_{\text{eff}}^n}{\alpha^n + x_{\text{eff}}^n} = 0, \tag{14}$$

so we have

$$y_j^s = k_i \frac{x_{\text{eff}}^n}{\alpha^n + x_{\text{eff}}^n}. \tag{15}$$

Remark 3. Eq. (10) was derived from (9) in the steady state. Through a logic approximation of the Hill function in (10), the analytical solution for the gene regulatory dynamics can relate the F-core to the fixed point. The minimum mean square error method is required to obtain the optimal ΔT for gene regulatory dynamics.

4 Results

4.1 Collapse mechanism of complex systems

Here we argue that the contribution of each node is not 0 or 1 in each shell and it will decrease as the mutualistic interaction strength weakens. For illustration, as mutualistic interactions caused by the phenological change weaken [32], e.g., the contribution from bees to the overall pollen transfer within the network decreases, the density of plants decreases [33]. To capture the contribution of each node and test the relationship between the F-core and mutualistic interaction strength, we use a weighted mutualistic ecosystem that includes five bees and four flowers (Figure 2 and (1)). The weighted mutualistic ecosystem collapses as the mutualistic interaction strength weakens. The fixed-point equation for this system is discussed in Section 3. The analytical results in the perspectives of the F-core in Figures 2(j)–(m) show that the number 2 bee and the number 2 flower are always in $F_{\text{shell}} = 2.3$, but their contribution decreases as the mutualistic interaction strength weakens. The same phenomenon was found in the number 1 bee and the number 3 flower. Of note, the analytical results in the perspectives of the k-core in Figures 2(f)–(i) could not capture these phenomena. However, the analytical results by the F-core can predict the beginning of the collapse in Figures 2(d) and (l), and the total collapse in Figures 2(e) and (m). However, the prediction of the analytical results by the k-core is overoptimistic.

Performance in the Erdos Renyi (ER) and scale-free (SF) networks. In ER networks, the topological structure is homogeneous. Here we use $\langle k \rangle$ to replace β_{eff} in (6). Below, we discuss the influence of the average degree $\langle k \rangle$ on the collapse process of mutualistic ecosystems in Figures 3(a)–(c). We also test the influence of the weight on the collapse process of mutualistic ecosystems. Three weight patterns are considered in Figures 3(d)–(f): (1) the weight of the link obeys the uniform distribution (U), (2) the weight of a link is correlated to its degree, and (3) the weight of the link obeys the power-law distribution (λ).

The degree distribution of the SF network obeys a power law, and it is drawn from a probability distribution $p(k_i) = C{k_i}^{-\lambda}$; here [34],

$$\lambda = 1 + n \left[\sum_{i=1}^{n} \ln k_i / (k_{\min} - 0.5) \right]^{-1}. \tag{16}$$

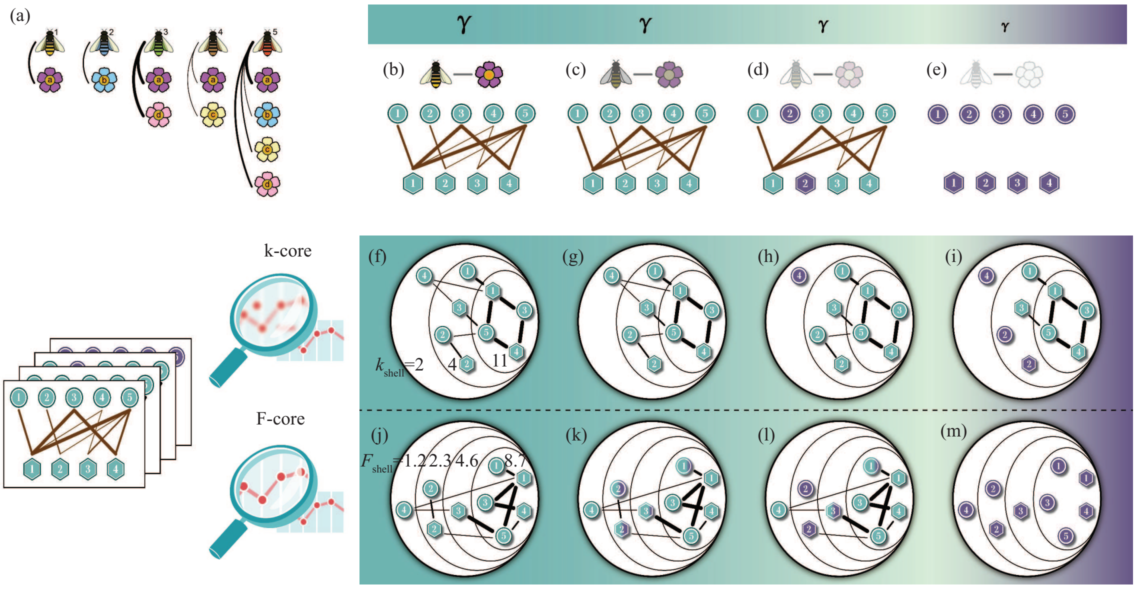

Figure 2 (Color online) Predicting the structural collapse of a weighted mutualistic ecosystem in three perspectives: (1) binary network, (2) k-core, and (3) fractional core (F-core). (a) Bipartite network between plants and animal pollinators. The ecosystem includes five bees and four flowers. The thickness of the lines represents the different preferences of each species. The collapse of weighted ecosystems occurs as the mutualistic interaction strength weakens from the binary network (b)–(e), k-core (f)–(i), and F-core (j)–(m) perspectives. Comparing the results in (e) and (m), the system completely collapses. However, in (i) the species that belong to $k_{\text{shell}} = 4$ and 11 survived. Comparing the results in (d) and (l), the number 2 bee and the number 2 flower become extinct, but in (h), they survived, and the number 4 bee is extinct.

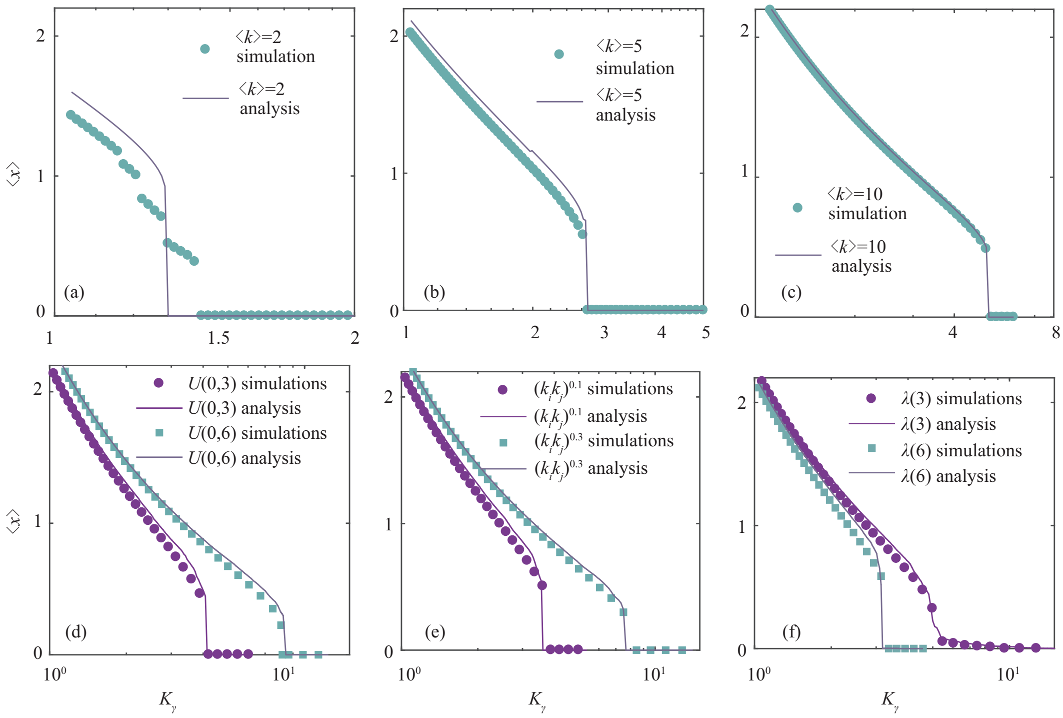

Figure 3 (Color online) Performance in Erdos Renyi (ER) networks, where dots, blocks, and solid lines are used to indicate the simulation results and the analytical solutions. (a)–(c) We test the influence between the average activity $\langle x\rangle$ and K_γ under different average degrees $\langle k\rangle$ in ER networks. (a) $\langle k\rangle = 2$; (b) $\langle k\rangle = 5$; (c) $\langle k\rangle = 10$. (d)–(f) We test the influence between the average activity $\langle x\rangle$ and K_γ based on the weighted ER networks. (d) The weight of the link obeys the uniform distribution; the dots mean that the weight of the link obeys $U(0, 3)$, while the blocks mean that the weight of the link obeys $U(0, 6)$. (e) The weight of the link is correlated to its degree; the dots mean that the weight of the link obeys $(k_i k_j)^{0.1}$, while the blocks mean that the weight of the link obeys $(k_i k_j)^{0.3}$. (f) The weight of the link is correlated to the power-law distribution (λ); the dots mean that the weight of the link obeys $\lambda(3)$, while the blocks mean that the weight of the link obeys $\lambda(6)$.

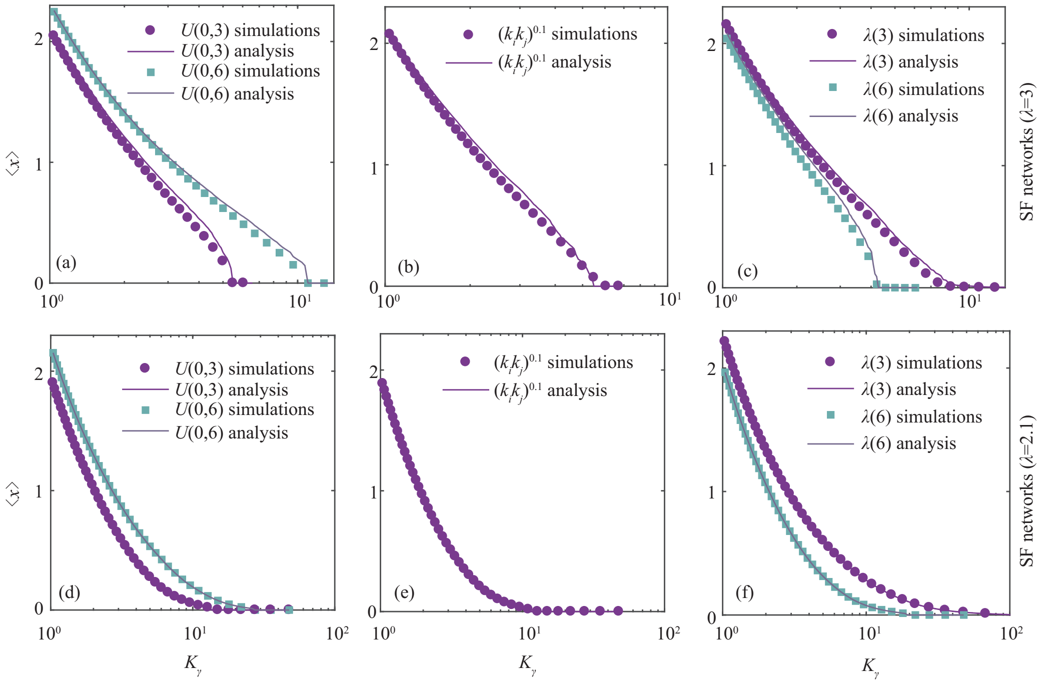

Figure 4 (Color online) Performance in scale-free (SF) networks, where dots, blocks, and solid lines are used to indicate the simulation results and the analytical solutions. (a)–(c) We test the influence between the average activity $\langle x\rangle$ and K_γ based on the weighted SF networks, where the power exponent is 3. (a) The weight of the link obeys the uniform distribution; the dots mean that the weight of the link obeys $U(0,3)$, while the blocks mean that the weight of the link obeys $U(0,6)$. (b) The weight of the link is correlated to its degree; the dots mean that the weight of the link obeys $(k_ik_j)^{0.1}$. (c) The weight of the link is correlated to the power-law distribution (λ); the dots mean that the weight of the link obeys $\lambda(3)$, while the blocks mean that the weight of the link obeys $\lambda(6)$. (d)–(f) Similar to (a)–(c), here the power exponent is 2.1.

The key is how to confirm $k_{\min}$. A variety of measures are used for quantifying the distance between two probability distributions, but for non-normal data, the most common measure is the Kolmogorov-Smirnov (KS) statistic, which is the maximum distance between the cumulative distribution functions (CDFs) of the data and the fitted model,

$$D = \max_{k \geqslant k_{\min}} |S(k) - P(k)|, \tag{17}$$

where $S(k)$ is the CDF of the degree for the observations with value at least $k_{\min}$, $P(k)$ is the CDF for the power-law model that best fits the data in the region $k > k_{\min}$. Our estimate $\widehat{k}_{\min}$ is then the value of $k_{\min}$ that minimizes D. For different positive interaction strengths, we use the KS statistic to confirm $k_{\min}$.

Below, we discuss the influence of weight on the collapse process of mutualistic ecosystems in SF networks. Three weight patterns are considered in Figure 4: (1) the weight of the link obeys the uniform distribution (U), (2) the weight of the link is correlated to its degree, and (3) the weight of the link obeys the power-law distribution (λ).

Performance in real networks. The above example shows that the F-core could determine nodes' contribution as the mutualistic interaction strength weakens. In addition, the F-core is effective in predicting species extinction in a mutualistic ecosystem. In real ecosystems, the decline of the system with anemone fish and host sea anemones is an important issue of great concern [35–37]. We use mutualistic interactions which include 10 anemone fish and 26 host sea anemones, as shown in Figure 5(a) [38], to compare the usefulness between the F-core and k-core in predicting the collapse of real mutualistic ecosystems, as the mutualistic interaction strength weakens. To illustrate the universality of the F-core for complex systems, we apply the gene regulatory dynamics in (9) with $d = 0.5$, $f = 1$, and $n = 2$ to the transcription networks of S. cerevisiae in Figure 5(d) [39].

We selected two points, where the first indicates when the system begins to collapse (Figures 5(b) and (e)) and the other indicates when the system collapses completely (Figures 5(e) and (f)), to map out the collapse process. The F-core can capture the beginning of a collapse, but there is no species or cell by the k-core, as shown in Figures 5(b) and (e). Meanwhile, the prediction of the tipping point, i.e., the

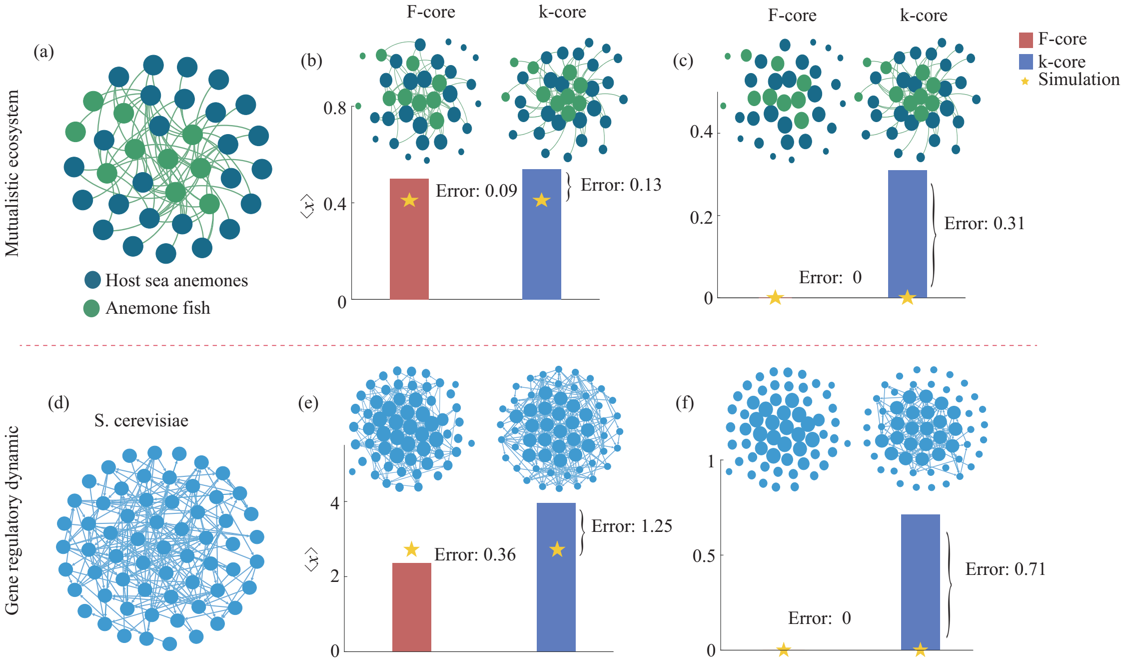

Figure 5 (Color online) Collapse process in two complex systems. Here, the stars represent the simulation results, and the histogram is the theoretical result by the F-core and k-core. (a) The ecosystem includes 10 anemone fish and 26 host sea anemones. The blue circles represent the host sea anemones, and the green circles represent the anemone fish. (b) The system begins to collapse by the F-core, but there is no species being extinct by the k-core. (c) The system completely collapses by the F-core when $\gamma = 0.8$, but there are species being survived by the k-core. (d) We ran the Michaelis-Menten dynamics on the transcription regulatory networks of S. cerevisiae [39] to model the dynamics of genetic regulation. (e) The system begins to collapse by the F-core, but there is no species being extinct by the k-core when $\gamma = 0.5$. (f) The system completely collapses by the F-core when $\gamma = 0.4$, but there are species being survived by the k-core.

complete collapse by the F-core is more reliable (Figures 5(c) and (f)). The error between the analytical and simulation results (Figures 5(b)–(c) and (e)–(f)) shows that the analytical results by the F-core are reliable. In sum, the theoretical results of the F-core approach are universal and precise in the prediction of the system collapse process. The F-core is helpful for monitoring the process and is able to perform measurements before the system totally collapses.

4.2 Tipping point of complex systems in three perturbations

Many factors, such as climate change, nutrient enrichment, habitat fragmentation, overhunting, exotic species introductions, or loss of third species, may cause a change in the network structure, particularly the link weight, or mutualistic interaction strength [40]. Here, we introduce three kinds of perturbations: (i) A fraction f_n of nodes is removed in a random way, capturing species extinctions or cell death. (ii) A fraction f_l of links is removed in a random way, capturing the interaction between species or cell disappearance. (iii) All weights of A_{ij} are reduced by a fraction f_w to mimic global environmental changes. Next, the influence of the three perturbations' strength and mutualistic interaction strength on the process is analyzed. Using the same mutualistic network in Figure 5(a) and the regulatory network in Figure 5(d), similarly, three perturbations are introduced, and the death rate $d = 0.5$ is set. To quantify the influence of the perturbation strength, Figures 6(a)–(c) and (h)–(j) show that the average density and average expression level of the system $\langle x \rangle$ decrease as the mutualistic interaction strength weakens, where a similar fraction is considered in the three perturbations, i.e., $f = 0.01$, $f = 0.2$, $f = 0.4$, and $f = 0.6$.

As the interaction strength decreases, once γ reaches γ_c (K_{γ_c} reaches the max F-core of the system), the system completely collapses, indicating the occurrence of a tipping point. Obviously, if $\gamma < \gamma_c$, or $y_i < K_{\gamma_c}$, one obtains

$$K_{\gamma_c} = k^{\max}_{\text{F-core}} = \frac{\alpha s \beta \left(2d\beta + 2\sqrt{d\beta} + 1\right)}{\left(2\sqrt{d\beta} + 1\right)^2}, \tag{18}$$

where $\beta = \frac{\langle k^2 \rangle}{\langle k \rangle}$, no mutualistic benefit is exchanged among species or genes, because the corresponding

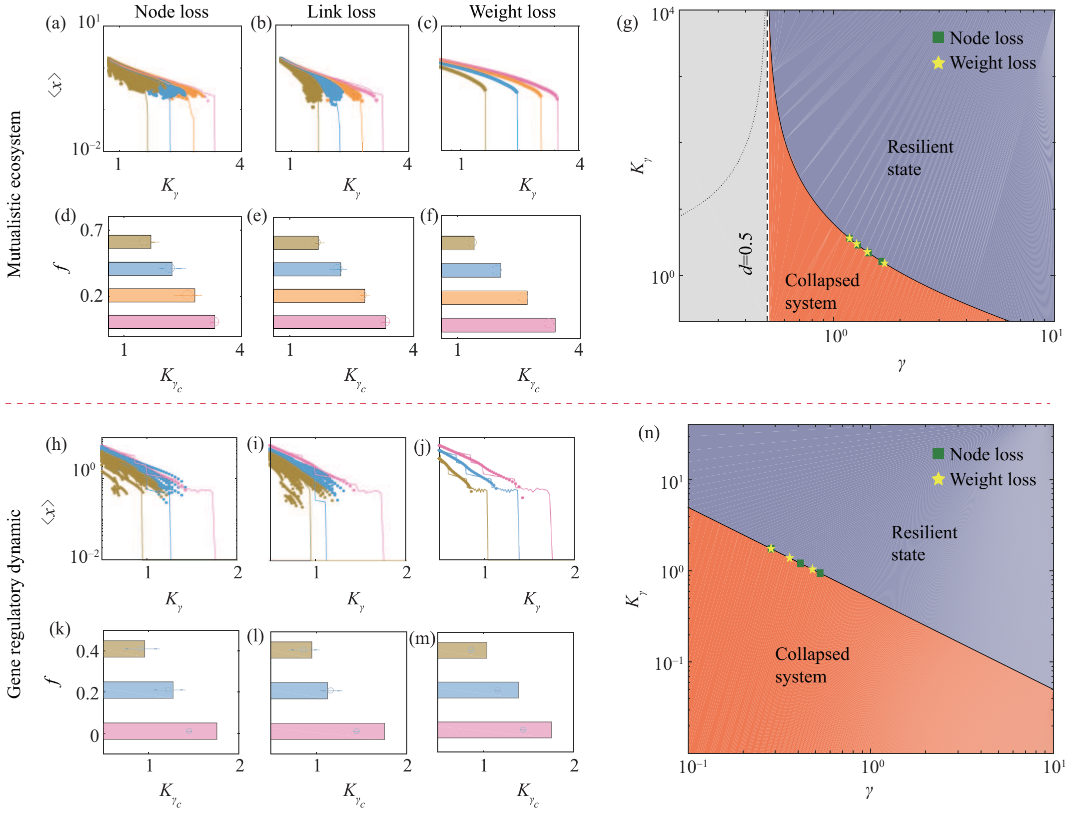

Figure 6 (Color online) Tipping point of a mutualistic ecosystem under three perturbations. We tested the relation between the average density or activity $\langle x\rangle$ and K_γ against (1) the extinction of a fraction f_n of species or cells in a random way; (2) a fraction f_l of interactions between species or cells disappearing in a random way; (3) all weights on average to a fraction f_w decreasing to their original value, simulating a global change in the environmental conditions on the system when $d = 0.5$. Here the same strengths of perturbations $f = 0.01, f = 0.2, f = 0.4$, and $f = 0.6$ are considered. (a) Dots and solid lines are used for indicating the simulation results and analytical solutions against node loss, respectively. (b) and (c) A similar diversity characterizes the system's response to the link perturbation f_l and global perturbation f_w. (d)–(f) Tipping point against three perturbations when $d = 0.5$. (g) Phase diagram for mutualistic dynamics in the γ-K_γ plane. In the resilient state phase, the system has a single stable fixed point. In the collapsed system phase, the system completely collapses. (h)–(n) Similar diversities characterized in the gene regulatory network.

critical threshold is too large, and the system collapses.

In Figures 6(d)–(f) and (k)–(m), as the removed fraction increases, or as the fraction of all weights decreases, the tipping point forwards, i.e., the resilience of the system becomes low. These considerations lead to the phase diagram of feasible and stable mutualistic ecosystems and the gene regulatory network depicted in Figures 6(g) and (n) in the space (γ, K_γ). The phase diagram features the predicted tipping line of instability defined by (18). The point is the relation between γ_c and K_{γ_c}. Our finding is not specific to the network shown in Figures 5(a) and (d). We also analyzed the influence of the perturbation strength on the system resilience in other mutualistic networks, such as weighted scale-free networks, and obtained similar conclusions, as presented in Appendix B.

4.3 Structural optimization of complex systems

Once the collapse mechanism is revealed through the F-core, we can derive the tipping point (18) and average density (19) for each structure of the ecosystem,

$$\langle x\rangle = \sum_{i=1}^{N}\frac{x_i^*}{N} = \sum_{i=1}^{N}\frac{\sum_{j=1}^{N}A_{ij}\Psi\left(y_j^*-K_\gamma\right)(\gamma-d)^2-asd}{N(s^2a+s\sum_{j=1}^{N}A_{ij}\Psi\left(y_j^*-K_\gamma\right)(\gamma-d))}, \tag{19}$$

where y_j^* can be obtained by (8) and (15). In a real ecosystem, some redundant species that do not influence the system are removed from the system [41–43]. However, these species cannot be easily identified. Here, we propose a method to retrieve the influence of species on system resilience including

Table 1 Mutualistic networks

Network ID	Species	N	$\langle s\rangle$
Net 1	Anemones fish	36	4
Net 2	Plants ants	92	14
Net 3	Plants pollinators	371	4.97
Net 4	Plants pollinators	141	5.4
Net 5	Plants pollinators	47	2.5
Net 6	Plants pollinators	209	6.8
Net 7	Plants pollinators	772	6.2
Net 8	Plants pollinators	76	5
Net 9	Parasite host	31	83
Net 10	Plants pollinators	45	23
Net 11	Plants ants	64	87

the tipping point and average density. It could also provide an idea to determine the optimal structure of a system for limited resources. The results on gene regulatory networks are discussed in Subsection 3.3.

Remark 4. The statistics of the datasets used in this study are shown in Figure 5(d) and Table 1. All real mutualistic networks of plant-pollinator and plant-seed dispersers are publicly available at the Interaction Web database [21]. The biological network is publicly available in the BioModels database1).

The analysis of resilience in the real network in Figure 7(a) reveals three patterns concerning the influence of species on system resilience: (1) The species below $k_F = 1.01$ are negative in terms of the density of the system and have no influence on the tipping point (as shown in Figures 7(b), (d), and (j)). (2) The species below $k_F = 2.51$ are negative for the density of the system but beneficial for the tipping point (as shown in Figures 7(b), (e), (f), and (j)). (3) Other species are beneficial for the density of the system and the tipping point (as shown in Figures 7(b), (g), (h), (i), and (j)). The results show that the average density is optimal when the species below $k_F = 2.51$ are extinct, and the corresponding network structure is shown in Figure 7(f). Meanwhile, the tipping point of the network with no species extinction is the same as the tipping point of removing the species below $k_F = 1.01$.

We analyzed 11 real networks in Table 1, and determined the tipping point and average density for each ecosystem structure (Appendix B). This approach is further supported by our finding that redundancy can be disadvantageous in a local ecosystem. The average density of Nets 1–8 and 11 in Figure 7(k) first rises and then descends, similar to the results in Figure 7(b). The average density of Nets 9 and 10 has a slight fluctuation when species below $k_F = 2$ are removed; i.e., these species are redundant. The optimal network structure for each network is shown in Figure 7(k). The tipping point decreases, when the species go extinct as its F-core extinction (Figure 7(l)).

4.4 Comparison with the k-core

Thus far, we have studied the effectiveness of the F-core on the prediction of the collapse process, the tipping point, and the optimization of ecosystems and regulatory systems. Hence, it is important to perform a comparison with the k-core to predict the collapse process, the tipping point, and optimization in ecosystems.

Here we compared our theoretical solution with the k-core that has been used to predict the tipping point. Figure 8 shows how the maximum F-core and maximum k-core correlate with K_{γ_c}. R^2 which is the coefficient of determination, was used to evaluate the validity of the tipping point prediction. The larger the R^2 is, the better the method is. The results in different ecosystems listed in Table 1 show that the value of R^2 by the F-core is larger than the value of R^2 by the k-core. Hence, the F-core is more effective in the prediction of the tipping point. Intriguingly, the tipping point obtained by the k-core is always an integer, but the tipping point by the F-core can be fractional.

Then, we compared our theoretical solution with the k-core for optimization. Figure 9 shows how the average activity $\langle x\rangle$ as the F-core extinction fluctuates from low to high. The results of the F-core show that the species in the low F-shell are negative for the average density of the system, and there is an optimal structure for the average density as the F-core extinction fluctuates from low to high. However, the results by the k-core show that the average density is optimal until the species in the maximum F-core survive, and it does not match the numerical integration results. In addition, the results of the

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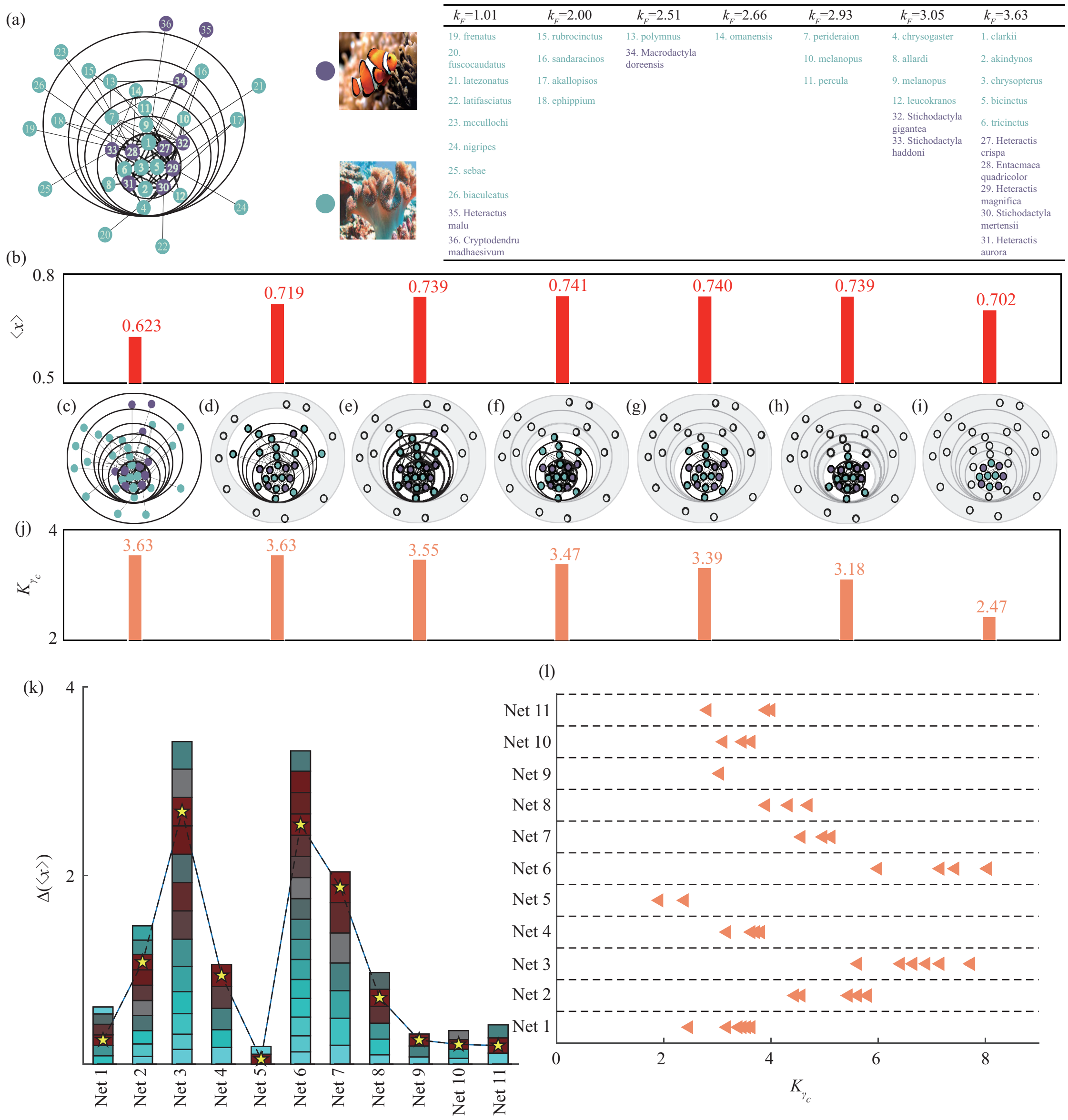
1) ftp://ftp.ebi.ac.uk/pub/databases/biomodels/.



k_F=1.01	k_F=2.00	k_F=2.51	k_F=2.66	k_F=2.93	k_F=3.05	k_F=3.63
19. frenatus	15. rubrocinctus	13. polymnus	14. omanensis	7. perideraion	4. chrysogaster	1. clarkii
20. fuscocaudatus	16. sandaracinos	34. Macrodactyla doreensis		10. melanopus	8. allardi	2. akindynos
21. latezonatus	17. akallopisos			11. percula	9. melanopus	3. chrysopterus
22. latifasciatus	18. ephippium				12. leucokranos	5. bicinctus
23. mccullochi					32. Stichodactyla gigantea	6. tricinctus
24. nigripes					33. Stichodactyla haddoni	27. Heteractis crispa
25. sebae						28. Entacmaea quadricolor
26. biaculeatus						29. Heteractis magnifica
35. Heteractus malu						30. Stichodactyla mertensii
36. Cryptodendru madhaesivum						31. Heteractis aurora

Figure 7 (Color online) Optimal network structure as the fractional core (F-core) extinction. (a) F-core structure of the ecosystem. The table lists the F-core of each species. (c)–(i) Network structures as the F-core extinction. (b) When the species below $k_F = 2.51$ are extinct, the average density is best; i.e., the network structure is optimal. (j) When the species goes extinct as its F-core extinction, the tipping point decreases. (k) 11 mutualistic ecosystems (Appendix B) are considered, where the yellow pentacles refer to the optimal network structure for each network. (l) The orange arrow of each line represents the tipping point of the mutualistic ecosystem (Appendix B).

F-core show that the species in the low F-shell have little influence on the tipping point of the system, and there is an optimal structure for the tipping point as the F-core extinction fluctuates from low to high (Appendix B). However, the results by the k-core show that the tipping point is fixed until the species in the maximum F-core survive, and it does not match the numerical integration results. In a word, the extinction of some species may improve the average density, and there is no difference in the tipping point of the system. The F-core method can help recognize these species and explore the optimal structure of systems. Meanwhile, the k-core method would lead to a large error.

Remark 5. In the numerical results, we numerically integrated the dynamic equations ((1) and (9)) using a fourth-order Runge-Kutta algorithm until all the variables $x_i(t)$ reach the steady state. In the Runge-Kutta algorithm, we set the truncation error as 0.00001 and initialized the activity $x_i(0) = 1$ at time $t = 0$. For mutualistic ecosystems, we used $s = 1$, $\alpha = 1$ in (1). For the gene regulatory dynamic, we used $f = 1$, and $n = 1$ in (9). The influence of the mutualistic interaction strength is discussed in Figures 3 and 4. The influence of the death rate is discussed in Appendix B.

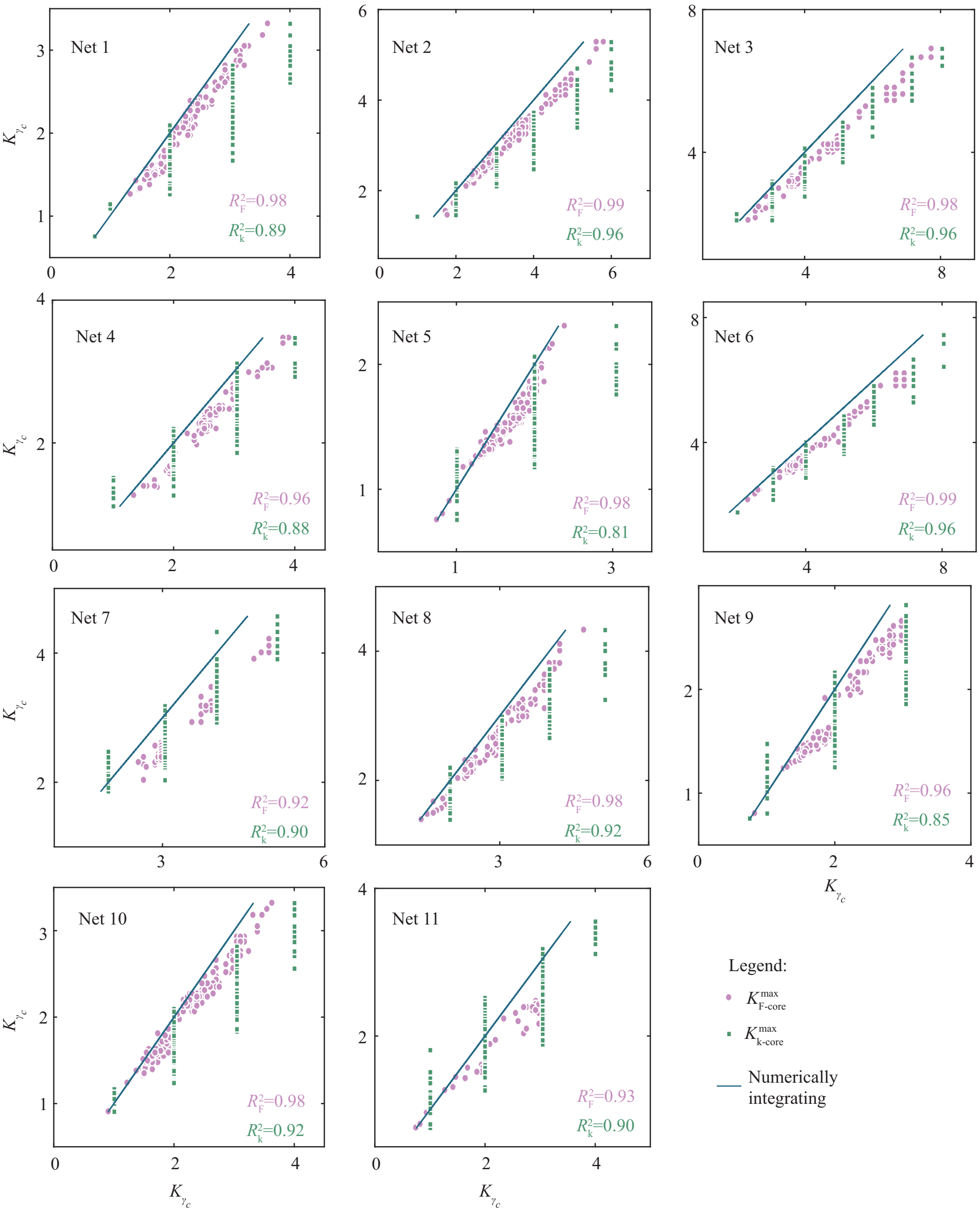


Figure 8 (Color online) Comparison between the tipping point K_{γ_c} by the fractional core (F-core) and K_{γ_c} by the k-core for different ecosystems in Table 1. In each panel, each pink point represents the result of the tipping point by the F-core vs. the result of the tipping point by numerically integrating for a specific network under perturbation. Each green point represents the result of the tipping point by the k-core vs. the result of the tipping point by numerically integrating for a specific network under perturbation. Then, we plot the line representing $K_{\gamma_c} = K_{\gamma_c}$. The coefficient of determination R^2 is used to evaluate the validity of tipping point prediction. Overall, the results show that $K^{\max}_{\text{F-core}}$ correlates better with K_{γ_c} than $K^{\max}_{\text{k-core}}$.

5 Limitations of this work

Because the logic approximation is used to test the relationship between the F-core and mutualistic interaction strength in this work, our theoretical results are applicable to a large class of systems governed by the nonlinear Hill, logistic or sigmoidal interactions. These interactions are widely distributed in neural circuitry, financial and banking ecosystems, microbial ecosystems, and gene regulatory networks.

An important condition for the applicability of the F-core solution is that the system must be mutualistic. However, this work did not examine the collapse mechanism and structural optimization of the systems which considers the condition of positive and negative interactions. These interactions are common in real networks, such as activations and inhibitions in neuronal or gene regulatory networks, and

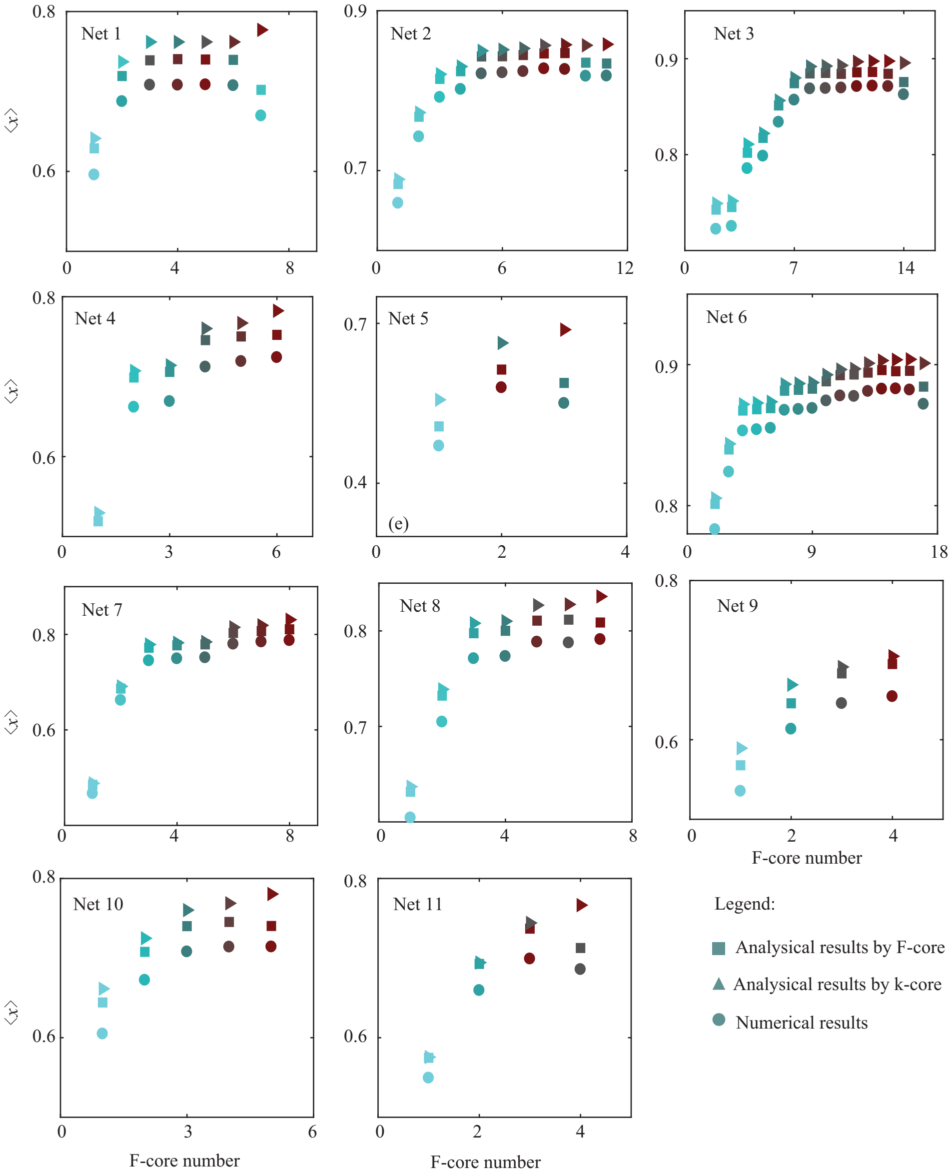


Figure 9 (Color online) Comparison between the $\langle x\rangle$ as the fractional core (F-core) extinction and $\langle x\rangle$ as the F-core extinction for different ecosystems in Table 1. We test the relation between the average activity $\langle x\rangle$ as the F-core extinction from low to high. In each panel, each square dot represents the network structure when species that belong to the corresponding F-core go extinct vs. the result of the average density by the F-core. Each triangular dot represents the network structure when the species belonging to the corresponding F-core go extinct vs. the result of the average density by the k-core. Each circular dot represents the numerical results. Overall, the F-core method and numerical integration results show the same tendency, i.e., increasing first and then decreasing, but the average activity by the k-core method always rises.

cooperation and competition or even conflicts in social and ecological networks. The interplay between positive and negative interactions is crucial in affecting the evolution pattern and final steady states or oscillations of network dynamics, which determine the network resilience. Only a few models support the two interactions to analyze a complex system's tipping point. Therefore, the application of the proposed scheme on systems, where positive and negative interactions co-exist, can be performed in the future.

6 Conclusion

Here we have presented the concept of the F-core to predict the structural collapse of weighted mutualistic ecosystems and gene regulatory networks. In terms of understanding the concept of the F-core and comparison with the k-core, our results lead to three key findings: (i) We provide evidence for a classification of species or cells in networks and accurately monitor the species or cell extinction process, as the mutualistic interaction strength weakens, while considering that the prediction of the analytical results by the k-core is overoptimistic. (ii) An analytic solution of the tipping point under three realistic perturbations is presented. The findings show that the tipping point would forward as the increase of the perturbation fraction; i.e., the resilience of the system is worse. (iii) We explore the optimal structure of systems as the F-core extinction, but the k-core method helps find these phenomena. Our results identify three patterns concerning the effect of species or cells on system resilience. In particular, the extinction of some species or cells may improve the average density of a system, but there is no difference in the tipping point of the system. Hence, the maintenance of a proper structure in systems is necessary to promote system density.

The role of the F-core is a key factor affecting systems' collapses, and accurately dividing the systems to find potential keystone species [44, 45]. It provides testable predictions for the collapse process of system responses to different perturbations from climate change and other factors [46]. It also suggests potential intervention strategies to avoid the collapse of systems, and optimal removal strategies to make systems keep the maximum density under different perturbations [47, 48]. The proposed scheme is applicable to a large class of dynamics such as mutualistic coupling, gene regulation, and neural networks. These dynamics are widely distributed in neural circuitry systems, financial and banking ecosystems, microbial ecosystems, and gene regulatory systems.

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Supporting information Appendixes A and B. The Appendix includes experimental setup and results. The supporting information is available online at info.scichina.com and link.springer.com. The supporting materials are published as submitted, without typesetting or editing. The responsibility for scientific accuracy and content remains entirely with the authors.

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