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## Article

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# Dynamical Asymmetry Reveals Progressive Biodiversity Loss in Mutualistic Ecological Networks

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## Abstract

Understanding whether biodiversity loss occurs collectively or progressively is essential for anticipating the collapse of ecological communities. However, commonly used dimension-reduction approaches represent bipartite networks with a single collective variable and may therefore obscure differences between interacting ecological groups that follow distinct dynamics. Here, we develop a two-observable framework that retains the dynamical asymmetry between the two partitions of a bipartite network. We apply the framework to a plant–pollinator model in which competitive interactions occur among pollinators but not among plants, while mutualistic benefits are mediated by pollination-service dilution. The reduced system analytically predicts the equilibrium branches and bifurcation structure. We evaluate these predictions using ten empirical plant–pollinator networks under simulated plant and pollinator removal. The asymmetry reshapes the collapse mode beyond the critical threshold, giving rise to a progressive collapse of the community. Progressive collapse becomes more prevalent with increasing species richness, whereas the corresponding symmetric dynamics only lead to collective collapse. Our framework provides a low-dimensional approach for analysing the resilience of asymmetric bipartite systems and shows that preserving functional differences between ecological groups can reveal sequential patterns of biodiversity loss that may be obscured by aggregate descriptions.

# 1 Introduction

Ecological communities comprise large numbers of species connected through complex networks of interactions. Beyond species richness, analyses of co-occurrence networks and abundance scaling relationships provide complementary descriptions of ecological community organization [1]. Understanding whether such communities can persist under environmental change and recover from perturbations is therefore a central challenge in ecology. Empirically identified ecological response thresholds can also inform conservation and restoration priorities [2]. One of the central problems is to understand the resilience of such systems, defined as their ability to maintain or recover their functionality under perturbations, *sensu* Holling [3]. Yet, predicting the resilience of species-rich communities remains difficult because their dynamics depend jointly on numerous interacting populations and the architecture of the underlying ecological network. One promising approach to addressing this challenge is dimension reduction, namely, the projection of high-dimensional dynamics onto a low-dimensional manifold.

Existing approaches commonly use the dominant spectral properties of the interaction network to derive a one-dimensional resilience function, enabling equilibrium states, tipping points and recovery dynamics to be estimated without explicitly tracking every species [4, 5]. However, the accuracy of such reductions depends on whether a single collective variable adequately represents the dynamics of the entire community. Differences among species in their states, interactions and network positions can violate this assumption and substantially reduce predictive accuracy [6–8].

Recent studies have aimed to overcome the limitations of traditional coarse-grained approaches by retaining more information about network structure and dynamical organization. For modular and directed networks, Végúé et al. [9] proposed a framework that captures collective dynamics through observables representing groups of nodes with similar connectivity profiles. Moreover, higher assortativity, clustering, and modularity tend to enhance the accuracy of the dimension reduction resilience function [10]. For discrete-state models, network symmetries have been used to obtain exact reductions of the Markov state space, enabling otherwise large state spaces to be handled [11]. Recent advances [12] have shown that high-dimensional dynamics can be reduced to an effective low-dimensional equation by exploiting the separable nature of node-level coupling, but these methods often assume a uniform interaction structure. A recent study also developed a three-group reduction for an ecological network combining mutualistic and parasitic interactions, and used it to examine tipping behavior and control [13]. These approaches, however, cannot capture the reduced dynamics of systems in which interacting partitions obey fundamentally different dynamical laws. In this paper we investigate this central problem.

Indeed, most existing dimension-reduction approaches assume that self-dynamics and interaction terms share a common functional form across nodes. Most existing analyses of bipartite systems implicitly rely on symmetry, where both partitions feature internal connectivity and obey the same dynamical rules. Such formulations have provided important insights into how network architecture, including nestedness, influences species coexistence [14], and into how interaction structure determines community stability [15]. This trend extends to recent work on dimension reduction for bipartite systems [16–18], which is based on the same symmetric framework. However,

representing the entire network with a single collective variable implicitly assumes that the two partitions are well captured by the same macroscopic dynamics. This assumption may be appropriate when all nodes obey the same dynamical laws, but become inadequate when the two partitions are structurally and dynamically distinct.

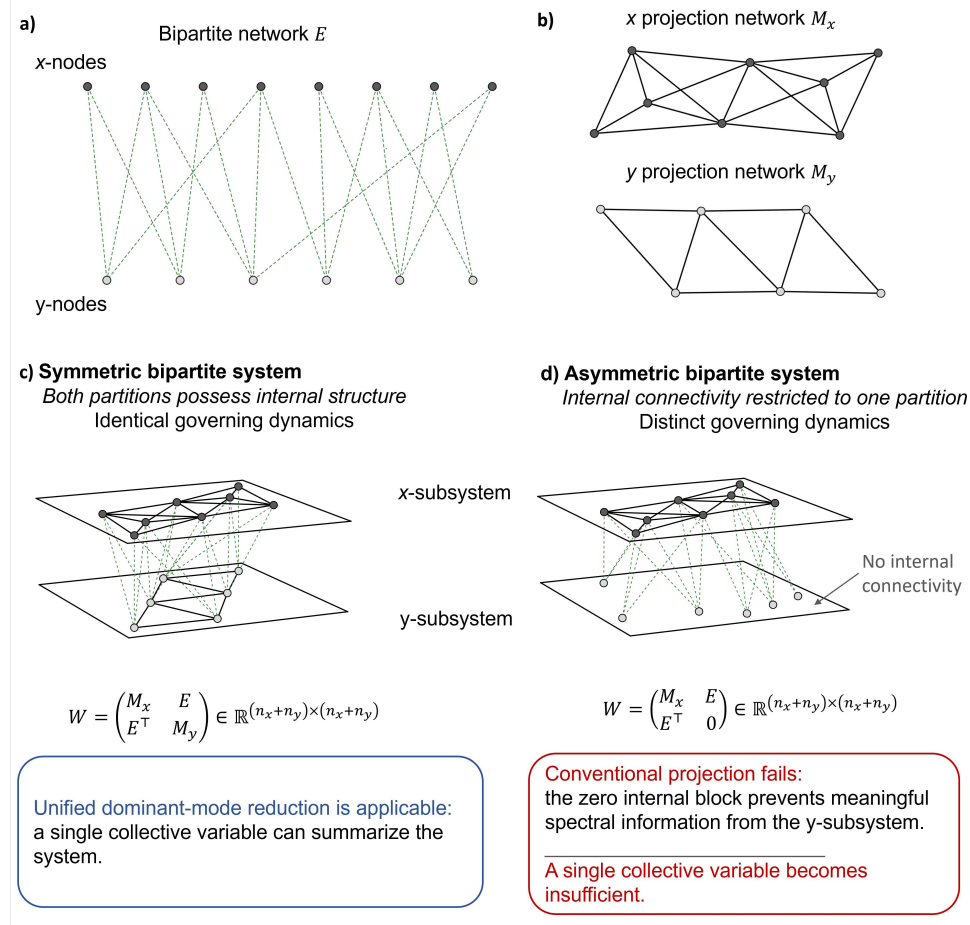


**Fig. 1 Bipartite network projections and the distinction between symmetric and asymmetric systems.** **a.** A bipartite network  $E$  consists of x- and y-nodes. **b.** The corresponding projection networks  $M_x$  and  $M_y$ , obtained by connecting nodes that share a common neighbor in the opposite partition, by linking pairs of x-nodes that share the mutual y, or y-nodes that share mutual x. **c.** A symmetric systems in which both partitions possess internal connectivity and obey identical dynamical rules, enabling conventional dominant-mode projection to define a unified collective observable. **d.** An asymmetric systems in which internal connectivity is restricted to one partition and the two partitions obey distinct governing dynamics, for which a unified dominant-mode reduction is inadequate.

Real-world systems frequently exhibit a fundamental asymmetry, where internal connectivity is restricted to a single partition, and each partition obeys distinct governing dynamics. Within multilayer ecological networks, Pilosof et al. [19] showed that interlayer edges encode the coupling between different dynamical processes, suggesting that the underlying dynamics of each layer is distinct. In real-world bipartite ecosystems, host-pathogen [20, 21], consumer-resource [22, 23] and bacteriophage-bacteria systems [24, 25] all exhibit significant asymmetry. Analogous asymmetries appear in neural networks, where excitatory and inhibitory populations differ both in their recurrent connectivity [26–28], and in the way they couple to one another, with direct consequences for the dynamics and for the propagation of localized perturbations [29–31].

As a consequence, the validity of traditional approaches becomes questionable when the symmetry assumption is violated. Specifically, these methods rely on the topological structure and spectral information to project high-dimensional variables onto one-dimensional representations. However, in asymmetric bipartite systems considered here, internal interactions occur within only one partition, whereas the internal-interaction matrix of the other partition is identically zero (as shown in Fig. 1 c and d). Therefore, the dominant-mode projection typically used in reduction methods collapses, as it cannot extract meaningful spectral information. Consequently, a single projection may fail to represent the coupled macroscopic response of the two partitions and may lead to inaccurate predictions of resilience. This limitation is particularly relevant for plant–pollinator networks because plants and pollinators perform distinct ecological functions and can experience different forms of within- and between-guild interactions.

To address this gap, we propose a general dimension-reduction framework that preserves the structural and dynamical distinctions between the two partitions of an asymmetric bipartite system. Rather than compressing the entire network into a single collective variable, our approach constructs a separate observable for each partition while retaining the coupling between them, thereby extending the applicability of the dominant-mode projection beyond symmetric constraints. For the partition lacking internal connectivity, we induce a projected interaction matrix that captures the indirect connectivity mediated by the other partition. This allows each subsystem to be represented by its own distinct observable. We further provide an analytical derivation to demonstrate that this two-observable projection is grounded in the system’s full dynamics.

As a representative ecological application, we consider plant–pollinator communities, whose bipartite organization provides a natural setting for examining interactions between functionally distinct groups [32, 33]. Empirical analyses further show that species loss can be accompanied by changes in interaction motifs and species’ structural roles within plant–animal mutualistic networks [34]. Building on a standard model of context-dependent mutualism [35], we introduce dynamical asymmetry by assigning distinct governing equations to plants and pollinators. In the model considered here, direct competitive interactions are restricted to the pollinator guild, whereas mutualistic benefits to plants incorporate the dilution of pollination services among interacting

species. We apply the method to ten empirical plant–pollinator networks and evaluate its predictions under simulated plant and pollinator removal. Our results show that asymmetric dynamics can produce progressive biodiversity loss, in which a subset of species approaches extinction before the remainder of the community, whereas the corresponding symmetric dynamics produce the collective collapse of the whole community.

The remainder of the paper is organized as follows. Section 2 introduces the two-observable reduction, derives the resilience function of the asymmetric plant–pollinator model, validates it across ecological networks, and compares collapse modes under symmetric and asymmetric dynamics. Section 3 summarizes the ecological implications and scope of the framework. Section 4 presents the general reduction and the resilience-function analysis for the plant–pollinator model; extended numerical analyses are provided in Supplementary Information.

## 2 Results

### 2.1 Resilience function of the asymmetric plant–pollinator model with dilution

To evaluate the efficacy of the proposed framework, we consider a plant–pollinator model [36], which has long been recognized as a prototypical system for studying bipartite ecological networks. Owing to its explicitly mutualistic interactions and well-characterized structure, this system provides a natural testing ground for dimension reduction methods in bipartite settings. However, the dynamics of classical plant–pollinator models is typically formulated in a symmetric manner, with internal interaction structures on both partitions. This symmetry does not fully reflect the intrinsic asymmetry between plants and pollinators in which the intensity of interactions within the two groups may be very different. To bridge this gap, we introduce a refined version of the plant–pollinator model that incorporates asymmetric dynamical mechanisms.

Mutualistic benefits are expected to saturate or become self-limiting in order to prevent unrealistic positive feedback in population growth [14, 37]. Importantly, the ecological mechanisms underlying this limitation differ between plants and pollinators. Plants act as passive resources waiting to be visited and their reproductive success depends on the visitation rate provided by pollinators. As plant density increases, pollinator services are diluted across individuals, leading to reduced per-capita visitation rates and, consequently, lower reproductive output [38, 39]. We incorporate this dilution effect explicitly in the denominator of the plant growth term to capture the resulting self-limitation mechanism. In contrast, pollinators actively search for floral resources and primarily experience limitations through competition associated with resource uptake.

Thus, we model such a system with  $N$  pollinators  $x_i$  ( $i = 1, 2, \dots, N$ ) and  $M$  plants  $y_k$  ( $k = 1, 2, \dots, M$ ). The dynamics is governed by

$$\frac{dx_i}{dt} = x_i \left( \alpha_i^{(x)} - \sum_{j=1}^N \beta_{ij} x_j \right) + x_i \cdot \frac{\sum_{k=1}^M \gamma_{ik}^{(x)} y_k}{1 + h \sum_{k=1}^M \gamma_{ik}^{(x)} y_k}, \quad (1)$$

$$\frac{dy_k}{dt} = y_k \left( \alpha_k^{(y)} - \kappa_k \right) + y_k \cdot \frac{\sum_{i=1}^N \gamma_{ki}^{(y)} x_i}{1 + h \sum_{i=1}^N \gamma_{ki}^{(y)} x_i + \eta y_k}, \quad (2)$$

where  $\alpha_i^{(x)}$  and  $\alpha_k^{(y)}$  denote intrinsic growth rates of pollinator  $i$  and plant  $k$ , respectively, and  $h$  is the saturation coefficient of the mutualistic benefit. The parameter  $\eta$  is the dilution coefficient, representing the reduction of per-capita pollination benefit with increasing plant density. In this asymmetric formulation, the  $y$ -subsystem does not include an explicit internal competition matrix. Therefore, the dilution term  $\eta y_k$  in the denominator is the only nonlinear mechanism that limits the per-capita mutualistic benefit on the plant side. The linear term  $y_k(\alpha_k^{(y)} - \kappa_k)$  alone does not provide saturation; a feasible plant equilibrium in the absence of mutualistic input requires  $\kappa_k > \alpha_k^{(y)}$ . This condition highlights the structural difference between the present asymmetric formulation. Competition among pollinators is described by the interaction matrix whose elements are  $\beta_{ij}$ , which we assume to be non-negative.

The quantities  $\gamma_{ik}^{(x)}$  and  $\gamma_{ki}^{(y)}$  represent mutualistic interaction weights from plants to pollinators and vice versa, respectively. They are constructed from the bipartite matrix  $E = [\epsilon_{ik}]$  as

$$\gamma_{ik}^{(x)} = \epsilon_{ik} \frac{\gamma_0}{K_i}, \quad \gamma_{ki}^{(y)} = \epsilon_{ik} \frac{\gamma_0}{K_k},$$

where  $\gamma_0 = 1$  is a normalization constant,  $\epsilon_{ik} = 1$  if species  $i$  (pollinator) and  $k$  (plant) interact (and 0 otherwise), and  $K_i$  and  $K_k$  denote the degrees of pollinator  $i$  and plant  $k$  in the bipartite network. All model parameters are summarized in Table 1.

**Table 1** Model parameters and their biological interpretation.

| Parameter           | Description                                 | Appears in          |
|---------------------|---------------------------------------------|---------------------|
| $\alpha_i^{(x)}$    | Growth rate of pollinator $i$               | Pollinator dynamics |
| $\alpha_k^{(y)}$    | Growth rate of plant $k$                    | Plant dynamics      |
| $\beta_{ij}$        | Competition between pollinators $i$ and $j$ | Pollinator dynamics |
| $\gamma_{ik}^{(x)}$ | Plant-to-pollinator interaction weight      | Mutualistic term    |
| $\gamma_{ki}^{(y)}$ | Pollinator-to-plant interaction weight      | Mutualistic term    |
| $h$                 | Saturation coefficient                      | Mutualistic benefit |
| $\eta$              | Dilution coefficient                        | Plant dynamics      |
| $K_i, K_k$          | Degree in bipartite network                 | Interaction weights |

The bipartite network  $E$  can be directly obtained from field observations, but interactions within the same partition are difficult to measure. Traditional mutualistic models often assume a fully connected internal network among species of the same

partition [40]. However, such a strong assumption neglects the complexity in real ecological communities. Therefore, projection in one-mode is widely used to transform the bipartite network  $E$  into internal connectivity within partitions [41, 42]. In this construction, two pollinators are connected if they share a plant partner, while two plants are connected if they share a pollinator partner, as illustrated in Fig. 1 a and b.

Given that direct competitive measurements are often empirically elusive, competition can be inferred from shared mutualistic partners [14, 43]. Following this idea, we construct the competition matrix as  $M_x = \mathcal{R}[EE^\top] = [\beta_{ij}]$ , where  $\mathcal{R}$  denotes the row-normalization operator. Specifically, for any given matrix  $A$ , its action is defined as  $\mathcal{R}[A]_{ij} = A_{ij} / \sum_k A_{ik}$ . The diagonal elements  $\beta_{ii}$  represent normalized intraspecific competition, while the off-diagonal elements  $\beta_{ij}$  quantify the relative competitive strength between pollinators  $i$  and  $j$  arising from their shared plant partners. We construct  $M_y$  using the Gram matrix [44],  $M_y = E^\top E$ , whose entries quantify structural similarity between plants.

We apply the dimension reduction framework developed in Supplemental Information, Sec. 4.1 to obtain an effective two-dimensional system that captures the collective dynamics. Specifically, we introduce the observables  $X = a^\top x$  and  $Y = b^\top y$ , where  $a$  and  $b$  are the principal eigenvectors of  $M_x^\top$  and  $M_y^\top$ , respectively. This projection yields the reduced model

$$\dot{X} = X \left( \alpha^{(x)} - \beta_{\text{eff}} X \right) + X \cdot \frac{\gamma_0^{(x)} Y}{1 + h \gamma_0^{(x)} Y}, \quad (3)$$

$$\dot{Y} = Y \left( \alpha^{(y)} - \kappa \right) + Y \cdot \frac{\gamma_0^{(y)} X}{1 + h \gamma_0^{(y)} X + \eta Y}, \quad (4)$$

where  $X$  and  $Y$  denote the effective abundances of pollinators and plants, respectively. Here,  $\alpha^{(x)}$  and  $\alpha^{(y)}$  are the effective intrinsic growth rates,  $\kappa$  is the effective plant mortality rate, and  $\beta_{\text{eff}}$  represents the effective competition strength. By analyzing the equilibria of Eqs. (3)-(4), we show in the Supplemental Information that the system undergoes a saddle-node bifurcation identified by the following critical threshold

$$\beta_c = \frac{\gamma_0^{(x)} \gamma_0^{(y)} \eta [1 - h(\kappa - \alpha^{(y)})] [1 + h\alpha^{(x)}]^2}{(\kappa - \alpha^{(y)}) \left[ \eta + \sqrt{\eta h \left\{ \gamma_0^{(x)} [1 + h\alpha^{(x)}] - \alpha^{(x)} \eta \right\}} \right]^2}. \quad (5)$$

Full details of the application of the dimension reduction framework to this model (1)-(2) are provided in Supplementary Note 2.

As shown in Fig. 2, increasing the effective competition strength  $\beta_{\text{eff}}$  progressively suppresses the high-abundance state of the reduced pollinator-plant system, leading to a simultaneous decrease in observables  $X$  and  $Y$ . Within a range of  $\beta_{\text{eff}} < \beta_c$ , the high-abundance state coexists with a stable low-abundance state, giving rise to bistability. As competition becomes stronger, the high-abundance state is increasingly weakened until, at  $\beta_{\text{eff}} = \beta_c$ , it collides with the unstable equilibrium and disappears through a saddle-node bifurcation. Consequently, for  $\beta_{\text{eff}} > \beta_c$ , the system can no

longer sustain the high-abundance state, and only the low-abundance state remains stable. Thus, the critical threshold  $\beta_c$  marks the maximum effective competition that the coupled system can withstand while maintaining a high-abundance state.

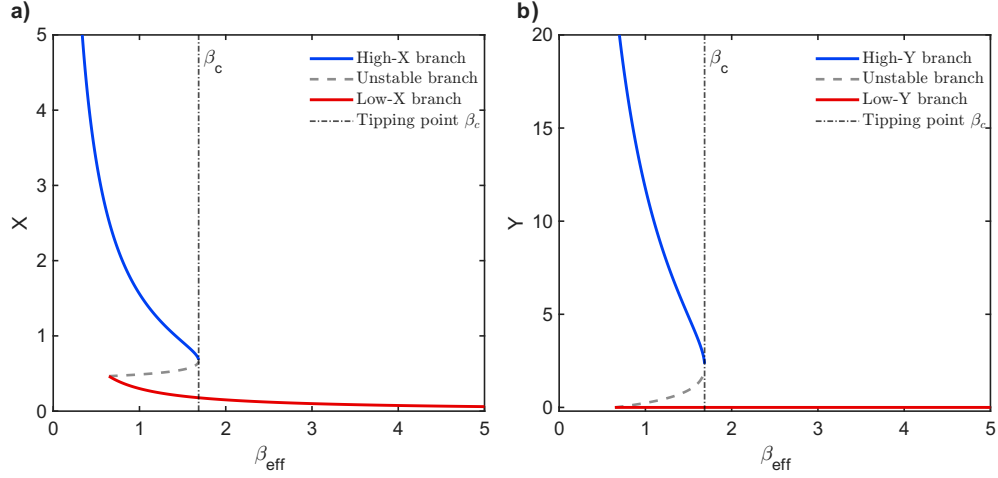


**Fig. 2 Resilience functions and saddle-node bifurcation in  $\beta_{\text{eff}}$ -space for the reduced model. a.** Pollinator observable  $X$ . **b.** Plant observable  $Y$ . Blue and red solid curves denote stable high- and low-abundance states, respectively. And gray dashed curves denote unstable equilibria. Increasing  $\beta_{\text{eff}}$  lowers the high-abundance branch until it disappears in a saddle-node bifurcation, beyond which only the low-abundance state remains. Parameters are  $\alpha^{(x)} = \alpha^{(y)} = 0.3$ ,  $\kappa = 0.5$ ,  $\gamma_0^{(x)} = 0.9$ ,  $\gamma_0^{(y)} = 0.5$ ,  $h = 0.7$ , and  $\eta = 0.2$ .

## 2.2 Validation across ecological networks

To validate these theoretical predictions on empirical systems, we perform numerical simulations based on the Web of Life database [45]. We investigate the response of the system under two perturbation strategies: (i) random removal of a fraction  $f_x$  of pollinators and (ii) random removal of a fraction  $f_y$  of plants, where  $f_x, f_y \in [0, 1]$ . After each deletion step, species with zero bipartite degree were removed from the active dynamical system. Therefore, all projected matrices were computed on the active component of the perturbed network.

Because these perturbations reconstruct the bipartite network  $E$ , we recompute the effective pollinator competition matrix  $M_x$  at each perturbation step. Let  $E^{(f)}$  denote the perturbed bipartite matrix after deletion, and define the row-normalized projected matrix  $M_{x,0}^{(f)} = \mathcal{R} [E^{(f)}(E^{(f)})^\top]$ . Previous studies have shown that mutualistic interactions can effectively reduce competition [14]. Accordingly, the loss of bipartite connectivity weakens mutualistic support and may thereby increase the effective competitive pressure experienced by the system. Here, we apply a diagonal-reinforcement rule to  $M_{x,0}^{(f)} = \mathcal{R} [E^{(f)}(E^{(f)})^\top]$ , as detailed in Supplementary Note 4.

To examine how these two perturbation strategies translate into the system response, Fig. 3 presents 20 independent numerical realizations for each scenario. The

solid black lines indicate a representative trial for each case. As shown in Fig. 3 a, the observables  $X$  and  $Y$  initially decrease gradually with increasing  $f_x$ , but undergo a sharp and abrupt collapse as  $f_x$  approaches 0.8. This threshold behavior indicates that the perturbation strategy drives the system across the saddle-node region predicted by the reduced model Eqs. (3)-(4) in  $\beta_{\text{eff}}$ -space, consistent with the transition shown in Fig. 2. In contrast, the system exhibits remarkable robustness under plant removal ( $f_y$ ), as shown in Fig. 3 b. A striking phenomenon is delayed collapse. Even with the loss of nearly all plants, the system often avoids a systemic crash. This resilience is attributed to the presence of dominant nodes. These hub plants, with many mutualistic partners, can sustain the pollinator community even when most other plant species have been removed. Consequently, a total collapse is only triggered if these specific hub species are among the randomly removed fraction, leading to the observed variance among individual trials.

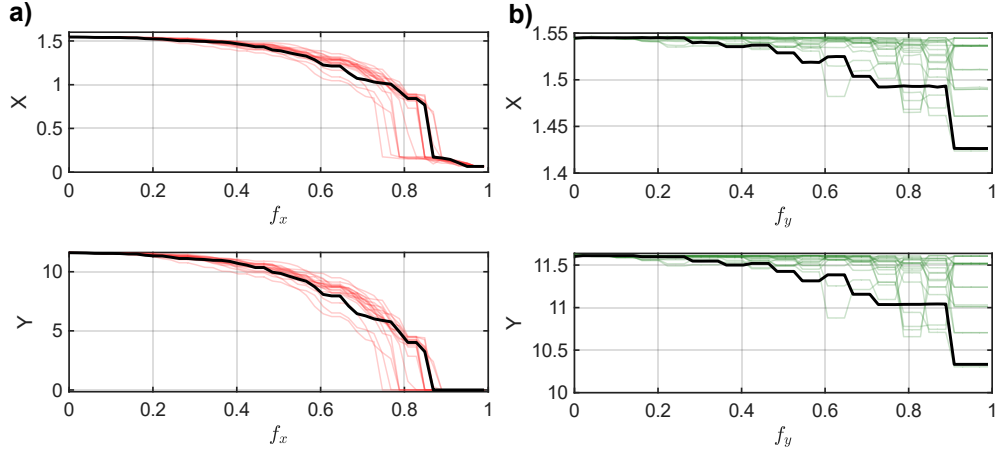


**Fig. 3 Resilience patterns of observables  $X$  and  $Y$  in network M\_PL.046.** **a.** Pollinator removal. **b.** Plant removal. For each value of  $f_x$  or  $f_y$ , 20 independent realizations are shown. Light-colored curves represent individual realizations, with one realization highlighted in black for visual clarity. The sharp collapse in a near  $f_x \approx 0.8$  is consistent with the saddle-node transition predicted by the reduced model. Parameters are  $\alpha_i^{(x)} = \alpha_i^{(y)} = 0.3$ ,  $\alpha^{(y)} =$ ,  $\kappa = 0.5$ ,  $\gamma_0^- 1$ ,  $h = 0.7$ , and  $\eta = 0.2$ .

To examine resilience across ecological networks, we analyzed ten empirical pollination networks of varying scales (shown in Table 2). For each system, we calculated  $\beta_{\text{eff}}$  based on the resulting network structure. The corresponding numerical resilience responses were then mapped onto  $\beta_{\text{eff}}$ -space, as shown in Fig. 4. We find that all data points collapse onto universal resilience curves, regardless of the size, topology, or perturbations. The collapse is more pronounced for the partition with internal connectivity, whereas the partition without explicit internal coupling shows larger deviations. This result indicates that the analytically predicted resilience function captures a universal pattern across diverse asymmetric mutualistic systems.

| Network ID | Total species | Number of links | Connectance |
|------------|---------------|-----------------|-------------|
| M_PL_032   | 40            | 65              | 0.281       |
| M_PL_046   | 60            | 278             | 0.395       |
| M_PL_064   | 22            | 32              | 0.286       |
| M_PL_009   | 142           | 242             | 0.085       |
| M_PL_018   | 144           | 393             | 0.094       |
| M_PL_026   | 159           | 204             | 0.036       |
| M_PL_001   | 185           | 361             | 0.043       |
| M_PL_055   | 259           | 431             | 0.035       |
| M_PL_015   | 797           | 2933            | 0.034       |
| M_PL_062   | 1500          | 15255           | 0.032       |

**Table 2** Structural properties of the ten empirical plant–pollinator networks. Data are sourced from the Web of Life database [45] and represent a gradient of network scales (22 to 1500 species). For each network, the total number of species, mutualistic interactions, and connectance are provided.

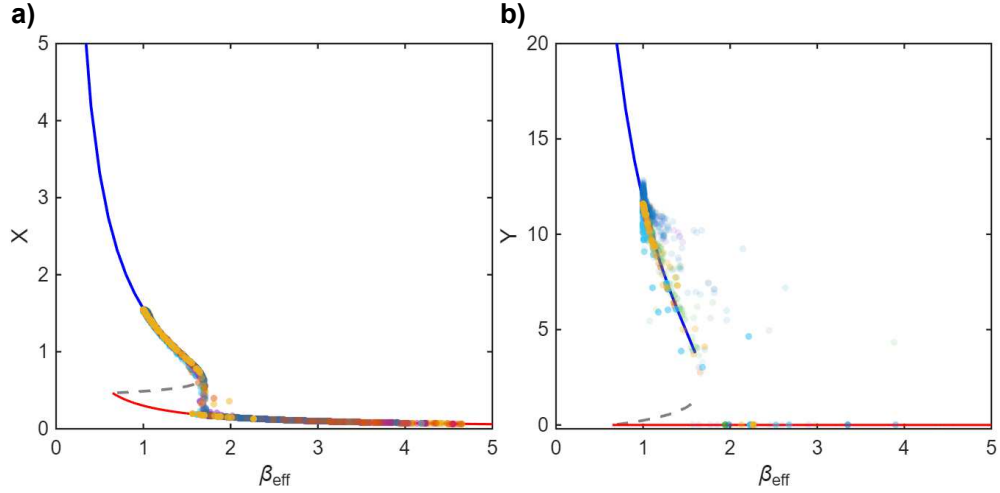


**Fig. 4 Validation across empirical networks.** Analytical resilience functions (lines) predict the transition of the system state as a function of  $\beta_{\text{eff}}$ . Data from ten empirical plant–pollinator networks (points), shown in Fig. 3 and Supplementary Note 3, follow the predicted resilience curves across networks of different sizes and structures. The agreement between empirical data and analytical predictions is stronger for partitions retaining internal connectivity, whereas partitions without internal connectivity exhibit larger deviations from the predicted curves.

### 2.3 Collapse modes under symmetric and asymmetric dynamics

By analyzing the dynamical evolution of the system near the critical threshold  $\beta_c$ , we observed two distinct modes of collapse. In some cases, all species in both partitions

enter the extinction regime after the tipping point, resulting in a collective collapse. In other cases, a small number of species go extinct first, and further removals lead to the gradual loss of additional species, resulting in a progressive collapse. The pollinator and plant subsystems generally exhibit the same collapse mode under a given removal strategy. To further examine what influences the emergence of progressive collapse, we calculated its probability for each network, defined as the proportion of removal trials exhibiting progressive rather than collective collapse at the critical threshold. As shown in Fig. 5, the probability of progressive collapse increases with total species richness, indicating that larger ecological networks are more prone to progressive collapse near the critical threshold.

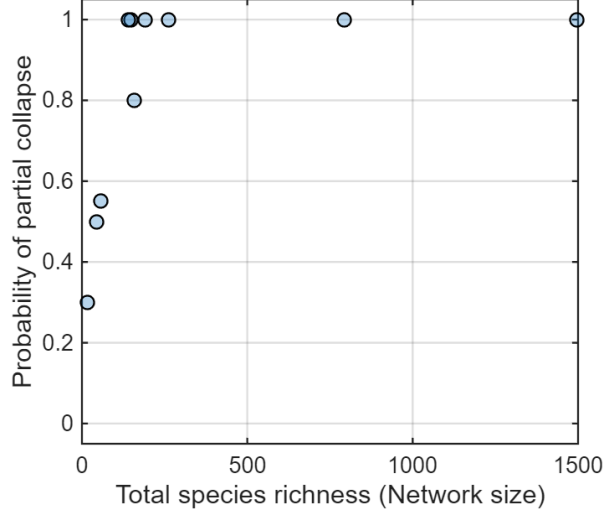


**Fig. 5 Observed relationship between the proportion of progressive-collapse trials and total species richness.** For each of the ten empirical networks, whose structural properties are summarized in Table 2, 20 independent pollinator-removal trials were performed using the same dynamical parameters as in Fig. 3. Points indicate the fraction of trials exhibiting progressive. Across the empirical networks, the fraction of progressive collapse trials increases with total species richness.

To illustrate these two collapse modes, we consider the bipartite networks M\_PL\_001 and M\_PL\_009 as representative examples. Their topological structures are shown in Fig. 6. We then examine their dynamical evolution after crossing the critical threshold  $\beta_c$ , as shown in Fig. 7. The relatively large network M\_PL\_001 exhibits progressive collapse, whereas M\_PL\_009 undergoes collective collapse.

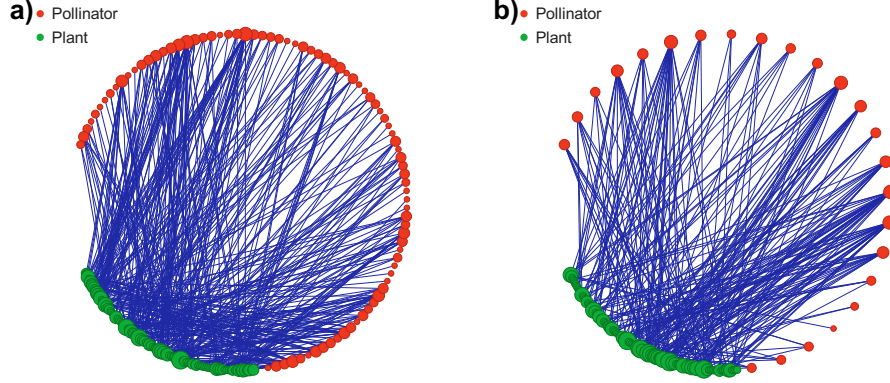


**Fig. 6 Network structures of two empirical mutualistic plant–pollinator networks. a.** M\_PL.001. **b.** M\_PL.009. Green and red nodes denote plants and pollinators, respectively, and blue links represent mutualistic interactions between them. Node sizes are proportional to the number of mutualistic interactions.

To assess the role of dynamical asymmetry in shaping the collapse mode, we compare our results with the corresponding symmetric model introduced in [16]. Using the same networks and removal protocols, we perform the same analysis for M\_PL.001 and M\_PL.009 and examine their dynamics beyond the critical threshold. As shown in Fig. 8, both networks exhibit collective collapse after the transition, with species in the two partitions entering the extinction regime together.

### 3 Discussion

Our results show that, despite the structural and dynamical asymmetries between the two partitions, the collective behavior of the system can still be captured by the proposed dimension reduction framework. The reduced model derived for the asymmetric plant–pollinator system successfully predicts the equilibrium branches and bifurcation structure of the original system.

We further find that, in contrast to symmetric systems where only collective collapse occurs, asymmetry significantly alters the collapse dynamics beyond the critical threshold, allowing either progressive collapse or collective collapse to emerge. Moreover, the collapse mode shows a clear dependence on system size. As species richness increases, progressive collapse becomes increasingly prevalent and approaches certainty in the larger networks examined here. For these larger asymmetric systems, biodiversity loss beyond the critical threshold therefore unfolds progressively.

Meanwhile, the reduced model exhibits a clear difference in predictive accuracy between the two partitions. For the partition with internal connectivity, the reduced model more accurately reproduces the collective behavior of the original system, whereas larger deviations between the reduced and full systems are observed for the partition without internal connectivity. The current construction of  $M_y$  based on the Gram matrix may be an important factor limiting the reduction accuracy for this partition. Therefore, a more appropriate method for constructing  $M_y$  is needed to fully

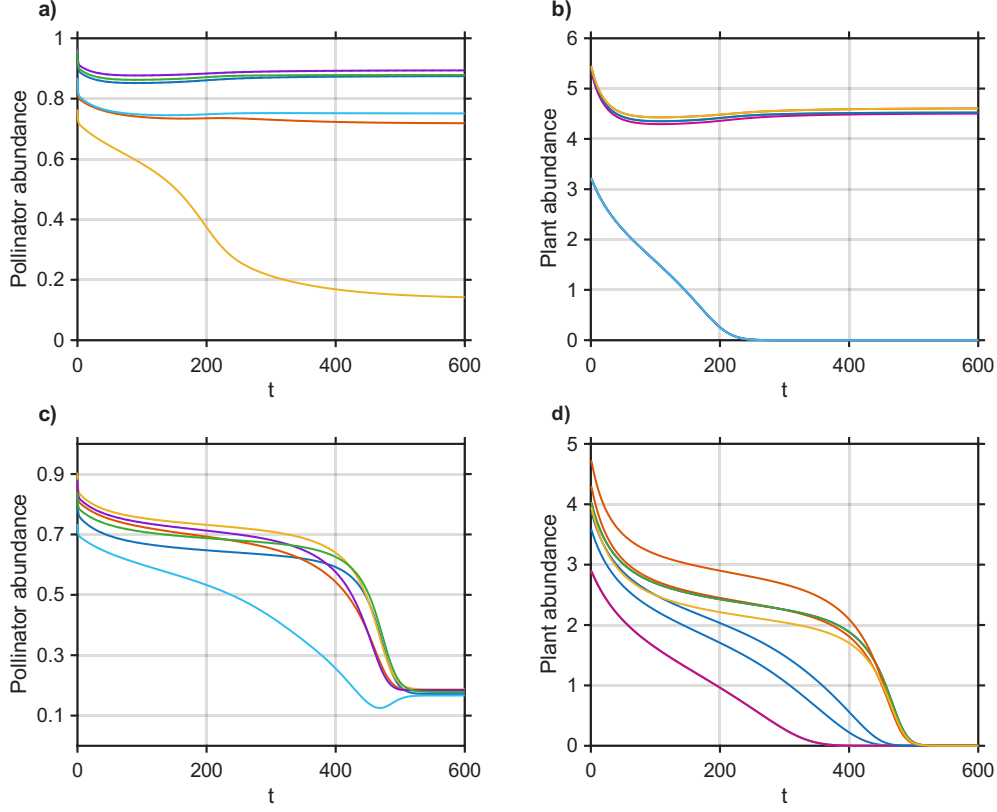


**Fig. 7 Critical dynamics under the asymmetric model for two empirical networks. a. b.** Temporal abundance trajectories of individual pollinator and plant species, respectively, in network M\_PL\_001, showing progressive collapse. **c. d.** Corresponding trajectories in network M\_PL\_009, showing collective collapse. Each curve represents an individual species. Parameters are  $\alpha_i^{(x)} = \alpha_i^{(y)} = 0.3$ ,  $\alpha^{(y)} =$ ,  $\kappa = 0.5$ ,  $\gamma_0^- 1$ ,  $h = 0.7$ , and  $\eta = 0.2$ .

capture the collective behavior. Improving and generalizing the applicability of the current framework is an important direction of future research.

## 4 Methods

### 4.1 Two-observable reduction for asymmetric bipartite systems

The diversity of dynamical forms exhibited by asymmetric bipartite systems calls for a general analytical treatment. In this section, we formulate our approach using a generic dynamical model that encodes the asymmetry. We consider an asymmetric bipartite system composed of an  $x$ -subsystem and a  $y$ -subsystem, containing  $N$  and  $M$  dynamical variables, respectively. The state variables are denoted by  $x = (x_1, \dots, x_N) \in \mathbb{R}^N$

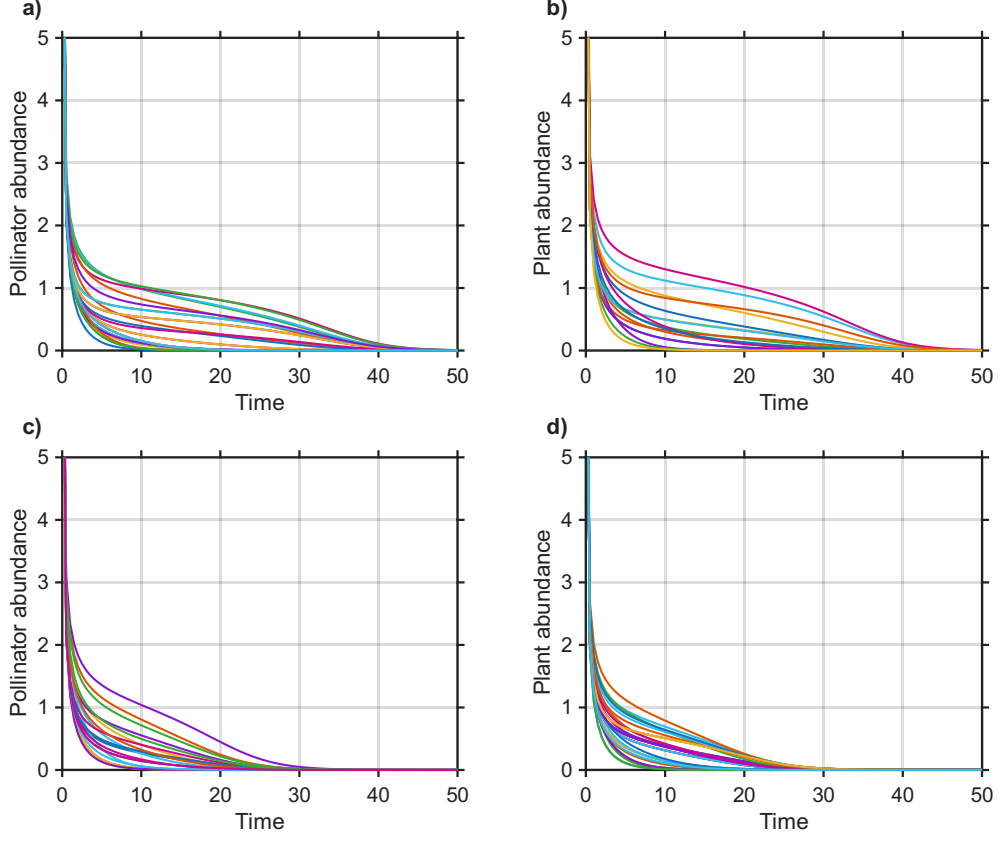


**Fig. 8 Critical dynamics under symmetric model dynamics for two empirical networks.** **a. b.** Temporal abundance trajectories of pollinator and plant species, respectively, in network M\_PL\_001. **c. d.** Corresponding trajectories in network M\_PL\_009. Each colored curve represents an individual species. Both networks exhibit collective collapse, with species in both partitions declining toward the extinction regime after the transition. The symmetric model and parameterization follow Ref. [16].

and  $y = (y_1, \dots, y_M) \in \mathbb{R}^M$ , whose time evolution is governed by the following equations

$$\dot{x}_i = F_1(x_i) + H_1(h_1(\mathbf{y}), x_i) + \sum_{j=1}^N \beta_{ij} G(x_i, x_j), \quad (6)$$

$$\dot{y}_k = F_2(y_k) + H_2(h_2(\mathbf{x}), y_k), \quad (7)$$

where  $F_1(x_i)$  and  $F_2(y_k)$  represent the intrinsic dynamics of  $x_i$  and  $y_k$ , respectively. The quantities  $h_1(\mathbf{y})$  and  $h_2(\mathbf{x})$  denote bipartite effective fields obtained by aggregating inputs from the opposite subsystem. The functions  $H_1(\cdot)$  and  $H_2(\cdot)$  describe the local, node-wise response to these fields. The term  $\sum_{j=1}^N \beta_{ij} G(x_i, x_j)$  describes

the pairwise interactions among the variables  $x_i$ . The coefficients  $\beta_{ij}$  represent the interaction strength from  $x_j$  to  $x_i$ , and we collect them into the interaction matrix  $M_x = [\beta_{ij}] \in \mathbb{R}^{N \times N}$ . Throughout this work, we assume that  $M_x$  is nonnegative and irreducible. We introduce the bipartite incidence matrix  $E = [\epsilon_{ik}] \in \{0, 1\}$ , where  $\epsilon_{ik} = 1$  if  $x_i$  interacts with  $y_k$ , and 0 otherwise.

This asymmetry motivates separate constructions for the two subsystems. We introduce two macroscopic observables

$$X = \sum_{i=1}^N a_i x_i = a^\top \mathbf{x}, \quad Y = \sum_{k=1}^M b_k y_k = b^\top \mathbf{y},$$

where  $a_i, b_k \in \mathbb{R}^+$  satisfy  $\sum_{i=1}^N a_i = 1$  and  $\sum_{k=1}^M b_k = 1$ . Thus,  $X$  and  $Y$  represent weighted average activities, with weights reflecting the relative contribution of nodes to the collective dynamics.

Taking the weighted average of Eq. (6), and applying the closure assumptions detailed in Supplementary Note 1, we obtain the generic reduced equation

$$\dot{X} = F_1(X) + \mathcal{I}_1(Y, X) + \alpha G(\theta X, X), \quad (8)$$

where  $\mathcal{I}_1(Y, X)$  denotes the closed contribution of the bipartite field acting on the  $x$ -subsystem. The closure involves two distinct approximations. The first is a Taylor expansion around the macroscopic observables  $X$  and  $Y$ . The second is a mean-field replacement of local degree-normalized bipartite averages by the corresponding global spectral averages. This replacement is accurate when the microscopic variables are sufficiently homogeneous, or when the bipartite structure is sufficiently regular so that local averages are close to the global observables.

The structural parameters in Eq. (8) are determined by the internal interaction matrix  $M_x = [\beta_{ij}]$ . Since  $\beta_{ij}$  denotes the interaction strength from  $x_j$  to  $x_i$ , the row sum  $k_i^{\text{in}} = \sum_{j=1}^N \beta_{ij}$  represents the total input strength received by node  $i$ . We define the diagonal matrix  $K$  by  $K_{ii} = k_i^{\text{in}}$ .

As shown in Supplementary Note 1, cancellation of the leading-order term associated with the second argument of  $G(\cdot)$  is obtained by choosing  $a$  as a normalized eigenvector of the transposed interaction matrix,

$$M_x^\top a = \alpha a.$$

We therefore choose  $a$  as the principal eigenvector of  $M_x^\top$ . The Perron-Frobenius theorem guarantees that, since  $M_x$  is nonnegative and irreducible, the principal eigenvalue is real and the corresponding eigenvector can be chosen with positive components, ensuring physical interpretability [44].

The corresponding eigenvalue defines the weighted total input strength,

$$\alpha = \sum_{i=1}^N a_i k_i^{\text{in}} = a^\top k^{\text{in}}.$$

The remaining mismatch in the first argument of  $G(\cdot)$  gives rise to a residual correction quantified by

$$\theta = \frac{1}{\alpha} \frac{a^\top K a}{a^\top a}.$$

The numerical evaluations in Supplementary Note 1 show that  $\theta$  remains extremely close to unity. We therefore use the approximation  $\theta \simeq 1$  in the analysis below.

For the  $y$ -subsystem, no analogous eigenvector condition arises from an explicit internal interaction term, because this partition lacks internal connectivity. We therefore introduce the Gram matrix [44]

$$M_y = E^\top E.$$

This matrix quantifies the structural similarity between the  $y$ -variables induced by their shared coupling to the  $x$ -subsystem. Using the induced Gram-matrix closure for the  $y$ -subsystem, we obtain

$$\dot{Y} = F_2(Y) + \mathcal{I}_2(X, Y), \quad (9)$$

where  $\mathcal{I}_2(X, Y)$  denotes the closed contribution of the bipartite field acting on the  $y$ -subsystem. As  $M_y$  is symmetric and element-wise non-negative, its leading eigenvector can be chosen to have non-negative components according to the Perron-Frobenius theorem [44]. We use this dominant eigenmode as the weight vector  $b$  to define the macroscopic observable  $Y$ , thereby extracting the principal collective pattern induced by bipartite coupling.

For the Holling type-II mutualistic model considered below, the bipartite response terms are separable in the abundance of the focal species. Therefore,

$$\mathcal{I}_1(Y, X) = X H_1(Y), \quad \mathcal{I}_2(X, Y) = Y H_2(X),$$

and Eqs. (8) and (9) reduce to the model-specific form used in the following analysis.

For the specific model studied below, the coupled reduced equations provide a two-dimensional description of the equilibrium branches and their loss of stability. The control parameter acts directly on the  $x$ -subsystem, while the response of the  $y$ -subsystem is transmitted through the bipartite coupling. The resulting bifurcation structure is examined numerically in the next section; the general framework does not require the two partitions to possess identical critical thresholds.

## 4.2 Approximation of the mutualistic term and the diagonal-reinforcement rule

The mutualistic inputs can be written as degree-normalized local neighbour averages,

$$\sum_{k=1}^M \gamma_{ik}^{(x)} y_k = \gamma_0^{(x)} \left( \frac{1}{K_i} \sum_{k=1}^M \epsilon_{ik} y_k \right), \quad (10)$$

$$\sum_{i=1}^N \gamma_{ki}^{(y)} x_i = \gamma_0^{(y)} \left( \frac{1}{K_k} \sum_{i=1}^N \epsilon_{ik} x_i \right). \quad (11)$$

We then apply an additional mean-field closure by replacing these local degree-normalized neighbour averages with leading-eigenvector-weighted averages,

$$\frac{1}{K_i} \sum_{k=1}^M \epsilon_{ik} y_k \approx Y = b^\top y, \quad (12)$$

$$\frac{1}{K_k} \sum_{i=1}^N \epsilon_{ik} x_i \approx X = a^\top x. \quad (13)$$

Unlike the  $x$ -projection, the choice of  $b$  is not forced by a cancellation condition; we adopt it because it is the dominant right singular vector of  $E$ . It is expected to be accurate when the bipartite structure is sufficiently regular or when the microscopic variables  $x_i$  and  $y_k$  are sufficiently homogeneous so that the local neighbor averages are close to the global observables. Under this closure,

$$\sum_{k=1}^M \gamma_{ik}^{(x)} y_k \approx \gamma_0^{(x)} Y, \quad (14)$$

$$\sum_{i=1}^N \gamma_{ki}^{(y)} x_i \approx \gamma_0^{(y)} X. \quad (15)$$

These approximations map the original high-dimensional system onto the two-dimensional form introduced in Section 4.1.

Because the microscopic mapping from lost mutualistic links to increased self-limitation is not directly measured, we introduce a diagonal-reinforcement rule based on the modeling assumption. This rule is designed to satisfy two minimal requirements: no additional reinforcement in the unperturbed network, and a monotonic increase of effective self-limitation as average bipartite connectivity is lost. To model this effect, we reinforce only the diagonal entries of  $M_{x,0}^{(f)}$ . We define the connectivity ratio

$$r(f) = \frac{\langle K \rangle_f}{\langle K \rangle_0},$$

where  $\langle K \rangle_0$  and  $\langle K \rangle_f$  are the average bipartite degrees before and after perturbation, respectively. The strength of the diagonal reinforcement is taken as

$$\rho(f) = \alpha_{\max} [1 - r(f)]^{\gamma_p}.$$

The exponent  $\gamma_p$  controls how sharply self-limitation increases after the loss of mutualistic connectivity. The prefactor  $\alpha_{\max}$  sets the maximum strength of this reinforcement.

Unless stated otherwise, we use  $\alpha_{\max} = 2$  and  $\gamma_p = 2$  in the simulations. The updated competition matrix is then

$$M_x^{(f)} = M_{x,0}^{(f)} + \rho(f) \operatorname{diag} \left( d^{(f)} + \bar{d}^{(f)} \mathbf{1} \right),$$

where

$$d_i^{(f)} = (M_{x,0}^{(f)})_{ii}, \quad \bar{d}^{(f)} = \frac{1}{N_f} \sum_i d_i^{(f)}.$$

Equivalently,

$$(M_x^{(f)})_{ii} = (M_{x,0}^{(f)})_{ii} + \rho(f) \left[ (M_{x,0}^{(f)})_{ii} + \bar{d}^{(f)} \right],$$

while the off-diagonal entries are unchanged.

## Data availability

This study uses the original bipartite adjacency matrices for ten plant–pollinator networks obtained from the Web of Life database [45]. The network identifiers and structural summaries are provided in Table 2.

## Code availability

The custom code used to generate the simulations and figures is central to the quantitative results and is available to editors and reviewers of the corresponding authors upon request. Public release will be considered after acceptance.

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## Author contributions

M.Y. conceived the study, performed the experiments, and wrote the main manuscript text. Y.S. secured the funding, contributed to data analysis, and revised the manuscript. S.A. supervised the project and provided guidance. All authors reviewed and approved the final manuscript.

## Competing interests

The authors declare no competing interests.

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