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Predicting tipping points in mutualistic networks through dimension reduction

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Complex networked systems ranging from ecosystems and the climate to economic, social, and infrastructure systems can exhibit a tipping point (a “point of no return”) at which a total collapse of the system occurs. To understand the dynamical mechanism of a tipping point and to predict its occurrence as a system parameter varies are of uttermost importance, tasks that are hindered by the often extremely high dimensionality of the underlying system. Using complex mutualistic networks in ecology as a prototype class of systems, we carry out a dimension reduction process to arrive at an effective 2D system with the two dynamical variables corresponding to the average pollinator and plant abundances. We show, using 59 empirical mutualistic networks extracted from real data, that our 2D model can accurately predict the occurrence of a tipping point, even in the presence of stochastic disturbances. We also find that, because of the lack of sufficient randomness in the structure of the real networks, weighted averaging is necessary in the dimension reduction process. Our reduced model can serve as a paradigm for understanding and predicting the tipping point dynamics in real world mutualistic networks for safeguarding pollinators, and the general principle can be extended to a broad range of disciplines to address the issues of resilience and sustainability.

Significance

Complex systems in many fields, because of their intrinsic nonlinear dynamics, can exhibit a tipping point (point of no return) at which a total collapse of the system occurs. In ecosystems, environmental deterioration can lead to evolution toward a tipping point. To predict tipping point is an outstanding and extremely challenging problem. Using complex bipartite mutualistic networks, we articulate a dimension reduction strategy and establish its general applicability to predicting tipping points using a large number of empirical networks. Not only can our reduced model serve as a paradigm for understanding the tipping point dynamics in real world ecosystems for safeguarding pollinators, the principle can also be extended to other disciplines to address critical issues, such as resilience and sustainability.

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See Commentary on page 635.

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mutualistic, bipartite networked systems and derived a 1D reduced model. In particular, pollinator–plant networks in nature can be regarded effectively as a bipartite network, where any direct interaction in the network is between a pollinator and a plant. Pollinators or plants among themselves, of course, are also connected, albeit indirectly, where two pollinators are regarded as connected if they interact with the same plant, and the same applies to the plant–plant connections. This results in two projection networks: one for the pollinators and another for the plants. The reduced 1D model (18) applies then to either of the projection networks. It was shown that the 1D model can lead to a resilience function, a function describing the emergence of a tipping point as a properly normalized system parameter is changed continuously. The resilience function was speculated to be universal in that it resembles the actual functions obtained from a number of empirical pollinator–plant networks.

While the 1D model is simple and amenable to analysis, it is from a projection network either of the pollinators or of the plants. In the dimension reduction process, certain features of the most fundamental dynamical property of the original bipartite network are lost: mutualistic interactions. To take into account these interactions, a reduced model needs to be simple but not simpler: a 2D model is necessary to capture the bipartite and mutualistic nature, with one collective variable for the pollinators and another for the plants. Consequently, as a single parameter of the system is varied, one can define two resilience functions: one for the pollinators and another for the plants.

We proceed through a series of steps to analyze the data and predict tipping points. (i) We develop a method to obtain, for mutualistic networks of arbitrary size, a set of two nonlinear ODEs, where the dynamical variables are the average abundances of the pollinators and plants, respectively. The 2D system contains two key parameters that can be fixed for any given real bipartite mutualistic network. (ii) From the generic 2D model, we calculate the average abundances both of the pollinators and of the plants, each as a function of two key parameters that capture the variations among different empirical networks. Each function gives a 2D surface in the 3D space of the average abundance and the two parameters. Since for each real network, the values of the two parameters are fixed, we calculate the values of the average abundances. The remarkable finding is that, for the 59 available plant–pollinator networks from real data recorded over the world, all of the actual average abundance values fall on the 2D surface obtained from the reduced model, providing support for its validity and generality. (iii) We calculate, for each real network, two resilience functions by considering two types of parameter variations: (a) the fraction of removed pollinators and the associated fraction of removed links and (b) the decay rate of individual species. The motivation behind the choice of these parameters is that, because of the continuous deterioration in the environment as a result of, for example, human activities, certain pollinators would disappear and so would the associated mutualistic interactions. In the case where a species manages to survive, the increasingly hostile environment makes it difficult to be sustained, leading to an increase in its decay rate.

The approach finally leads to a method for predicting tipping points. For each real network, we compare the resilience functions with those from the corresponding reduced 2D model and find a good agreement (even in the presence of stochastic disturbances), indicating that the 2D reduced model captures the essential dynamics of the real systems and can thus be used for probabilistic prediction of the occurrence of a tipping point as some parameters reflecting the environmental deterioration change.

Results

Nonlinear Dynamical Networks of Mutualistic Interactions and a General Reduced Model in Two Dimensions. We investigate all mutualistic pollinator–plant networks available from the Web of Life database (www.Web-of-Life.es). There are altogether 59 networks, which cover a wide geographic range across different continents and climatic zones. The structures of the networks are quite different from each other, as is the number of species in each network. Despite the differences, the network dynamics can be described by a set of first-order, nonlinear ODEs, with the total number of equations (the phase space dimension) being the number of species in the network (both pollinators and plants) (13, 19). Considering a generic nonlinear dynamical system described by such ODEs with arbitrary numbers of pollinators and plants, we articulate a dimension reduction process to obtain an average system in two dimensions. As will be shown, the 2D system can capture the essential dynamical features of all 59 real mutualistic networks.

A generic mathematical model for mutualistic interactions includes the following processes: intrinsic growth and intraspecific and interspecific competition as well as mutualistic effects of plants and pollinators. We use the letters $P$ and $A$ to denote plants and pollinators, respectively. Let $S_P$ and $S_A$ be the numbers of plants and pollinators in the network, respectively, and therefore, the phase space dimension of the whole system is $S_P + S_A$. The model can be written as (13, 19)

$$
\frac{dP_i}{dt} = P_i \left( \alpha_i^{(P)} - \sum_{j=1}^{S_P} \beta_{ij}^{(P)} P_j + \frac{S_A}{S_P} \sum_{k=1}^{S_A} \gamma_{ik}^{(P)} A_k \right) + \mu_P,
$$

$$
\frac{dA_i}{dt} = A_i \left( \alpha_i^{(A)} - \kappa_i - \sum_{j=1}^{S_A} \beta_{ij}^{(A)} A_j + \frac{S_P}{S_A} \sum_{k=1}^{S_P} \gamma_{ik}^{(A)} P_k \right) + \mu_A,
$$

where $P_i$ and $A_i$ are the abundances of the $i$th plant and the $i$th pollinator, respectively; $\alpha$ is the intrinsic growth rate in the absence of intraspecific and interspecific competition as well as any mutualistic effects. The factors that affect the intraspecific and interspecific competition, such as light and nutrients for the plants at the breeding sites for animals, are characterized by the parameters $\beta_{ii}$ and $\beta_{ij}$ ($i \neq j$), respectively. Typically, intraspecific competition is stronger than interspecific competition (13, 19), and therefore, we have $\beta_{ii} \gg \beta_{ij}$. The parameters $\mu_P$ and $\mu_A$ describe the immigration of plants and pollinators, respectively, which typically assume small values and have little effect on the network dynamics (13, 20). Mutualistic interactions tend to increase the abundance (e.g., through the process where pollinators provide service to plants, while the plants provide resources to the pollinators). It is reasonable to assume that, when both mutualistic partners have a high abundance, the beneficial effect of the interactions on the population growth would saturate. The saturation effect is characterized by the half-saturation constant $h$. The parameter $\gamma$ quantifies the strength of the mutualistic interaction, where $\gamma = 0$ indicates the absence of any such interaction in the network. In general, $\gamma$ depends on the degree of the node through

$$
\gamma_{ij} = \varepsilon_{ij} \frac{\gamma_0}{(K_i h)^{\beta}},
$$

where $\gamma_0 = 1$ is a constant, $\varepsilon_{ij} = 1$ if there is an interaction between $i$ and $j$ (otherwise, $\varepsilon_{ij} = 0$), $K_i$ is the number of interactions of the species that benefit from the interactions, and $t$ determines the strength of the tradeoff between the interaction strength and the number of interactions. If there is no tradeoff ($i.e., t = 0$), the network topology will have no effect on the strength of the mutualistic interactions. In contrast, a full tradeoff ($t = 1$) means that the network topology will affect
β is a P−⟨f⟩ and and = Aii D β for the pollinator of pollinators. With respect to —the fraction of pollinators that have become f and + C ⟨⟩ correspond to network − Validity test of the reduced model in terms of the average pollinator abundance for the plant. We can then calculate, for each real data, two independent parameters, the reduced 2D model generates a surface for (A) pollinator (red) and (B) plant (green) abundances. The blue dots are the corresponding data points representing the stable steady states calculated from 59 real world networks. For each network, the parameter values of ⟨γp⟩ and ⟨γp⟩ are calculated by an unweighted average. Other parameters are h = 0.7, t = 0.5, βh0 = βh0 = 1, αh0 = αh0 = 0.3, µh = µh = 0.0001, and γ0 = 1. The data points from all 59 real networks are in the vicinity of the respective smooth surfaces from the 2D reduced system, providing preliminary validity support.

Fig. 1. Validity test of the reduced model in terms of the average pollinator and plant abundances. In the 3D plot of an average species abundance vs. the two average mutualistic interaction strengths, which are regarded as two independent parameters, the reduced 2D model generates a surface for (A) pollinator (red) and (B) plant (green) abundances. The blue dots are the corresponding data points representing the stable steady states calculated from 59 real world networks. For each network, the parameter values of ⟨γp⟩ and ⟨γp⟩ are calculated by an unweighted average. Other parameters are h = 0.7, t = 0.5, βh0 = βh0 = 1, αh0 = αh0 = 0.3, µh = µh = 0.0001, and γ0 = 1. The data points from all 59 real networks are in the vicinity of the respective smooth surfaces from the 2D reduced system, providing preliminary validity support.

the species gain from the interactions. In the ecological reality, the amount of tradeoff is somewhere between the two extreme cases.

In SI Appendix, Note 1, we detail the steps of our dimension reduction procedure, which leads to the reduced model

\[
\frac{dP_{\text{eff}}}{dt} = \alpha P_{\text{eff}} - \beta P_{\text{eff}}^2 + \frac{\langle \gamma p \rangle A_{\text{eff}}}{1 + b \langle \gamma p \rangle} P_{\text{eff}} + \mu, \\
\frac{dA_{\text{eff}}}{dt} = \alpha A_{\text{eff}} - \beta A_{\text{eff}}^2 - \kappa A_{\text{eff}} + \frac{\langle \gamma p \rangle P_{\text{eff}}}{1 + b \langle \gamma p \rangle} A_{\text{eff}} + \mu,
\]

where the dynamical variables P_{\text{eff}} and A_{\text{eff}} are the effective or average abundances of plants and pollinators, respectively; \(\alpha\) is the effective growth rate parameter for the network, \(\beta\) is a parameter characterizing the combined effects of intraspecific and interspecific competition, \(\kappa\) is the species decay rate in an averaging sense, and the parameter \(\mu\) accounts for the migration effects for the species. Of particular importance are the two effective mutualistic interaction strengths, \(\langle \gamma p \rangle\) and \(\langle \gamma p \rangle\), associated with the plants and pollinators, respectively. These two parameters can be obtained through different ways of averaging. We use three averaging methods (SI Appendix, Note 1): (i) unweighted average, (ii) degree-weighted average, and (iii) eigenvector-based average.

Does our reduced 2D system capture some basic properties of real bipartite mutualistic networks? Treating the effective mutualistic interaction strengths (\(\langle \gamma p \rangle\) and \(\langle \gamma p \rangle\)) as two independent parameters in the reduced model, we calculate the effective pollinator and plant abundances for each pair of the parameters. In the 3D plot of an effective species abundance vs. \(\langle \gamma p \rangle\) and \(\langle \gamma p \rangle\), we obtain a surface as shown in Fig. 1A for the pollinator and in Fig. 1B for the plant. We can then calculate, for each real network, the parameters \(\langle \gamma p \rangle\) and \(\langle \gamma p \rangle\) as well as the average pollinator and plant abundances, generating a data point in each case. For the reduced model to be a reasonable representation of the real network, the point must be close to the corresponding smooth surface. As shown in Fig. 1, the data points from all 59 empirical real world networks (SI Appendix, Table S1) are near the corresponding surfaces from the reduced model, providing preliminary evidence that the reduced model captures the essential behavior of the real networks from a wide geographical range across continents and climatic zones. As we will show, however, the detailed averaging process can play a role in the model’s predictive power of the average abundances and the tipping point.

Reducing the high-dimensional system (i) to the effective 2D system (iii) entails an inevitable loss of detailed information about the original system. However, since predicting the occurrence of the tipping point through the system resilience function is our goal, the primary question is whether the reduced 2D system has predictive power, despite the loss of certain details about the dynamical evolution of the original system. In the following, we present strong evidence that the answer to this question is affirmative.

A resilience function is a relationship between the average species abundance and some parameter with variations that reflect the impact on the environment caused by, for example, global warming or direct human activities, such as overuse of pesticides (21–23), where a larger impact corresponds to a higher value of the parameter. Since pollinators are more vulnerable to environmental changes than plants, we focus on two parameters: (i) \(f_p\)—the fraction of pollinators that have become extinct because of environmental deterioration and (ii) \(\kappa\)—the average pollinator decay rate. From the standpoint of plants, the disappearance of a specific pollinator means the loss of a number of links, as any pollinator typically interacts with several plants. Thus, we will also consider the parameter \(f_p\), the fraction of links destroyed as a result of the death of a fraction \(f_p\) of pollinators. With respect to \(\kappa\), we note that the parameter \(\kappa\) in the original system (i) characterizes the pollinator decay caused by a decrease in the pollinator growth rate and/or an increase in the pollinator mortality rate. Continuous deterioration of the environment leads to a gradual increase in the average decay rate \(\kappa\). While we have studied all 59 mutualistic networks derived from real data, we report the detailed validation results from 2 representative networks: network A obtained from data recorded at Tenerife, Canary Islands.

Fig. 2. Network structure of two empirical mutualistic networks from real data. A and B correspond to network A. C and D correspond to network B. The plants in A and C are marked as green, while the pollinators are marked as red. B and D are the matrix representations of networks A and B, respectively. The blue blocks indicate that the corresponding pollinator and plant have a mutualistic connection. Column and row numbers correspond to individual plant and pollinator species. Species are ordered according to their number of interactions.
and $f_n$, where the results from the resilient functions without tipping point. For networks $A$ and $B$ and $B$ ($C$ and $D$), pollinator abundance ($A$ and $C$) vs. $f_n$, the fraction of removed pollinators, and plant abundance ($B$ and $D$) vs. $f_l$, the fraction of removed mutualistic links corresponding to the value of $f_n$ in $A$ and $C$. The red curves in $A$ and $C$ and the green curves in $B$ and $D$ are the average pollinator and plant abundances, respectively, from the original system. The blue, black, and cyan curves in all of the panels are the abundances from the reduced 2D system using averaging methods $i$–$iii$, respectively. The circles and asterisks in all panels correspond to cases where the initial abundance values are relatively high (10) and low (0.01), respectively. For each value of $f_n$ (or $f_l$), results from 100 statistical realizations are displayed. The parameters are $h = 0.7, t = 0.5, \beta^{\text{fl}} = \beta^{\text{fn}} = 1, \sigma^{\text{fl}} = \sigma^{\text{fn}} = 0.3, \mu_A = \mu_B = 0.0001, \gamma_0 = 1, \text{and } \kappa = 0$. The notations SH and SL stand for the high and low initial values of the original average species abundance, respectively. UWAH, UWAL, DWAH, DWAL, EWAH, and EWAL denote unweighted average high, unweighted average low, degree-weighted average high, degree-weighted average low, eigenvalue-weighted average high, and eigenvalue-weighted average low, respectively.

(24) and network $B$ from an empirical study at Hestehaven, Denmark (25). Network $A$ has 38 pollinators and 11 plants, and there are 106 mutualistic interactions. Network $B$ has 42 pollinators and eight plants, with 79 mutualistic interactions. The structures of the two networks are shown in Fig. 2 A and C, respectively, whereas their matrix representations are shown in Fig. 2 B and D, respectively.

Resilience Functions in Systems Without a Tipping Point. We first examine the case where the system does not exhibit any tipping point. For each value of $f_n$, there are many possible network structures, rendering necessary a description based on statistical ensemble averaging. (Representative individual resilience functions are shown in SI Appendix, Fig. S1.) Fig. 3A shows, for network $A$, four types of pollinator abundances vs. $f_n$ (each with 100 statistical realizations): one from the original network (Fig. 3A, red) and three from the reduced model with different averaging methods (Fig. 3A, blue, black, and cyan) corresponding to averaging methods $i$–$iii$, respectively. We see that averaging method $i$ leads to abundance variations that are in good agreement with those from the original network, while systematic deviations exist for the results from averaging methods $ii$ and $iii$, although they agree with each other. Fig. 3B shows, for network $A$, the corresponding plant abundance vs. $f_l$, where the results from the original network are displayed in Fig. 3B, green. The averaging process $i$ leads again to average abundance variations in agreement with those from the original network. The results for network $B$ are shown in Fig. 3 C and D. We see that, for both networks in the parameter setting studied, the remaining pollinators and plants never come close to extinction, even when the fraction of removed pollinators approaches one. The reason is precisely mutualistic interactions: even if there is only one remaining pollinator, at least one plant will be connected with this pollinator. Because of the mutualistic interactions, both the pollinator and plant will survive, and the network system does not exhibit a tipping point. In this parameter regime, the small migration rate has no effect on system dynamical features, such as the absence of a tipping point. The main message of this example is that the reduced model is capable of capturing the abundance variation patterns of both pollinators and plants in the original networked systems.

A phenomenon in Fig. 3 is that, as $f_n$ is increased so that more pollinators are removed, the average plant abundance decays faster with $f_l$ than the average pollinator abundance with $f_n$. The reason is that removing one pollinator typically entails removing a number of mutualistic links, which have a more devastating effect on the plant abundance as a whole.

Power of the Reduced Model in Predicting Tipping Points. We now consider parameter regimes where the mutualistic network system exhibits a tipping point. An examination of the individual resilience functions (SI Appendix, Fig. S2) for networks $A$ and $B$ reveals that, as $f_n$ for pollinators (or the corresponding $f_l$ for plants) is increased toward unity, there exists a critical
and calculate the species abundances from the original network and from the three averages of the reduced system. The results are shown in Fig. 5. We see that, similar to the case where the network structure is altered through continuous removal of pollinators (compare with Fig. 4), the reduced model through averaging method ii or iii has a remarkable predictive power for the tipping point in that the predicted critical value of κ at which the species abundances collapse to zero agrees well with that from the original system.

In our computations, we set a relatively small value for the migration rate for all pollinator species: µ = 0.0001—the same value used in previous studies (13, 20). We find that changing this value in a small range has no effect on the tipping point dynamics. Especially before the occurrence of a tipping point, the species abundances are high, so that the changes caused by migration are negligible. After the tipping point, the injection of a small number of species will not be able to restore the abundances on the network scale.

Role of Network Randomness in the Reduced Model. Our extensive computations of the large number of empirical mutualistic networks indicate that a 2D reduced system obtained through degree- or eigenvector-weighted average can correctly predict the tipping point, while the reduced system with unweighted averaging fails to do so. One plausible reason is the lack of sufficient randomness in the network structure. In fact, despite the large variations in their size and structure, the real networks are not quite as random. For a purely random network, either unweighted or weighted averaging has the same effect on the reduced model. To test this proposition and to further show the importance of weighted averaging in the dimension reduction point past which the species abundances collapse to almost zero, signifying a tipping point. The corresponding ensemble-averaged resilience functions are shown in Fig. 4. For both networks, the 2D model tends to generate abundance values that deviate from the corresponding true values from the original system. In particular, for the reduced model derived through averaging method i, the abundance values are somewhat smaller than those from the original system, while the opposite behavior occurs for the reduced model with averaging method ii or iii. These deviations are expected, considering the drastic approximations used in deriving the reduced model. While all three types of average in the reduced model generate results indicating the occurrence of a tipping point, a key issue is the accuracy of the predicted parameter value where a tipping point is reached. In particular, if a reduced model does indeed possess predictive power for the tipping point, it should predict its occurrence at the correct critical point in the original network. In this regard, we see that the reduced model with averaging method i fails to predict the location of the tipping point, whereas the 2D model with averaging method ii or iii yields the true critical point. Since methods ii and iii are based on some sort of weighted averaging process (i.e., with respect to nodal degrees and eigenvectors), the results in Fig. 4 point at the importance of imposing weighted averaging process in the dimension reduction process. This conclusion holds not only for the two networks in Fig. 4 but also, for other networks studied.

While structural change in the network, such as gradual removal of nodes (pollinators), can trigger a tipping point, there are alternative scenarios, such as parameter changes. Here, we consider the situation where the mutualistic network structure remains intact, but the death rate of the pollinator increases because of environmental deterioration. Specifically, we increase the pollinator decay rate κ from zero and calculate the species abundances from the original network and from the three averages of the reduced system. The results are shown in Fig. 5.
Effects of Interspecific Competition. So far, we have neglected interspecific competitions, as they are generally much weaker than intraspecific competition. Mathematically, interspecific interactions can be modeled through nonzero off-diagonal elements in the competition matrices $\beta^B$ and $\beta^D$ in Eq. I, which change the structures of these matrices. It is thus useful to investigate the effects of interspecific competition. Our computations reveal that the 2D reduced model captures all essential features of the mutualistic networked systems, even in the presence of interspecific competition, as shown in Figs. 9 and 10, for the cases where tipping points are absent and present, respectively.

Fig. 9 is obtained under the same setting as that of Fig. 3, except that interspecific competition is now included. Comparing Fig. 9 with Fig. 3, we see that the competition results in somewhat lower pollinator and plant abundance, which is intuitive. For small values of $f_{\mu}$, the number of pollinators is large, and therefore, the interspecific competition among the pollinators is relatively strong. In this case, the species abundances are markedly lower than the corresponding values in the absence of interspecific competition. As $f_{\mu}$ is increased, the number of species is reduced, resulting in increasingly weak interspecific competition and consequently, smaller reductions in the abundances. As the strength $\beta_i$ of the interspecific competitive interaction is increased, simulations of both the original networked and the 2D reduced systems give lower species abundances.

The remarkable feature is that, when interspecific competition is taken into account, the 2D reduced system can still reliably predict the species abundances, with the unweighted averaging scheme giving the best result, while the degree- and eigenvector-weighted schemes predict correctly the trend of the abundance variations.

Robust Predictive Power of the Reduced Model Against Stochastic Disturbances (Noises). Is our reduced model capable of predicting the tipping point when stochastic disturbances are present in the original network? To address this question, we test the predictive power of the reduced model by considering stochastic abundance and parameter fluctuations. First, we assume that there is additive, independent white Gaussian noise in the dynamic equations for the abundance of each species. The results are shown in Fig. 7, where the color legends are the same as those in Fig. 3. We see that, despite the additive noise, the reduced model still predicts correctly the tipping point, where the performance of the model derived using the degree- and eigenvalue-averaging methods is better than that of the model based on unweighted averaging. Second, we study the case where there is randomness in the intraspecific competition rate as motivated by the consideration that, in reality, the intensity of intraspecific competition varies from one species to another. The results are shown in Fig. 8. We see that, despite the large variations in the species abundances caused by the parameter perturbation, the reduced model based on a weighted average method (averaging method ii or iii) is still capable of predicting the correct tipping point as in Fig. 4.
Fig. 9. Effect of interspecific competition on species abundance in the absence of a tipping point. For networks A (A and B) and B (C and D), ensemble-averaged pollinator abundance (A and C) vs. \( f_n \) and ensemble-averaged plant abundance (B and D) vs. \( f_i \). The legends are the same as in Fig. 3. The notions SH and SL stand for the high and low initial values of the original average species abundance, respectively. UWAH, UWAL, DWAH, DWAL, EWAH, and EWAL denote unweighted average high, unweighted average low, degree-weighted average high, degree-weighted average low, eigenvalue-weighted average high, and eigenvalue-weighted average low, respectively. The intraspecific and interspecific competitions are incorporated into the model through \( \beta_i^0 = \beta_i^p = 1 \) and \( \beta_i^0 = \beta_i^p = 0.01 \), respectively. The parameters are \( h = 0.7, t = 0.5, \alpha_i = \alpha_p = 0.3, \mu_A = \mu_B = 10^{-4}, \gamma_0 = 1.0, \) and \( \kappa = 0.0 \). The interspecific competition reduces the abundances but has no significant effect on their overall trends of variation.

Fig. 10 shows the effects of interspecific competition in the parameter regime where there is a tipping point. Comparing Fig. 10 with Fig. 4, we see that, with the inclusion of interspecific competition, the 2D reduced model derived from the degree- or eigenvector-weighting scheme predicts the tipping point accurately, which is similar to the case where such competition is absent. The mere effect of a reasonable amount of interspecific competition is simply reduced abundances. (For sufficiently large values of the interspecific interaction strength, both the original and the reduced 2D models agreeably give the result of species extinction.)

Occurrence of a Tipping Point in the 2D Parameter Space. Both structural change (removal of certain pollinator species) and parameter change (increase in \( \kappa \)) can lead to a tipping point. It is useful to examine the occurrence of a tipping point in the 2D parameter space \((f_n, \kappa)\), as both types of changes can be expected in realistic systems (21). We calculate the critical parameter value for the tipping point through both the original system and the reduced model. A representative result for network A is shown in SI Appendix, Fig. S3 for \( \kappa \in [0, 0.64] \) and \( f_n \in [0, 0.974] \). (The corresponding result for network B is presented in Fig. S4.) The general observation is that, while there are variations in the location of the tipping point in the \( f_n \) direction, the location variations in the \( \kappa \) direction are relatively smooth. In fact, our reduced model incorporating either the degree- or the eigenvector-averaging method gives an accurate prediction of the tipping point in the parameter plane.

A Mathematical Analysis of the System Dynamics with an Explanation of the Emergence of a Tipping Point. The 2D reduced model provides mathematical insights into the emergence of a tipping point. The relevant quantities are the steady-state values of the species abundances. Setting \( dP_{i,j}/dt = 0 \) and \( dA_{i,j}/dt = 0 \), we can obtain the algebraic equations for the steady-state solutions (SI Appendix, Note 3).

We first consider the parameter regime in which the system does not exhibit a tipping point (e.g., Figs. 1 and 3). In this case, we have \( \alpha > 0 \), and the physically meaningful steady-state solutions are given by

\[
P' \approx \frac{1}{\beta} \left( \alpha + \langle \gamma_A \rangle A' \right) + \frac{1}{1 + \langle \gamma_A \rangle A'}; \]

\[
A' \approx \frac{1}{\beta} \left[ \alpha - \kappa + \frac{\langle \gamma_A \rangle P'}{1 + \langle \gamma_A \rangle P'} \right].
\]

The solutions of Eq. 4 can be conveniently expressed in terms of the following algebraic equation for \( A' \):

\[
q_1 A'^2 + q_2 A' + q_3 = 0,
\]

where the coefficients \( q_1, q_2, \) and \( q_3 \) are given by

\[
q_1 \equiv -\left( h \gamma_p + h \langle \gamma_A \rangle \gamma_p + h^2 A \gamma_A \right); \]

\[
q_2 \equiv -\beta^2 - h \alpha \beta \gamma_A + h \alpha \beta \gamma_p + \langle \gamma_A \rangle \gamma_p, \]

\[
q_3 \equiv h \alpha \beta \gamma_A + h \alpha^2 \gamma_A + h \alpha \beta \gamma_p - \kappa \beta \gamma_A + h \alpha (\gamma_A) + h \alpha (\gamma_p) - \kappa \beta \gamma_A + h \alpha (\gamma_A).
\]

For \( \kappa = 0 \), we have \( q_1 < 0 \) and \( q_3 > 0 \). Of the two solutions of Eq. 5, one is positive, and another is negative. The abundance values of \( A' \) in Figs. 1 and 3 are then approximately the value of the positive solution.

We next consider the parameter regime, in which the mutu-alistic system exhibits a tipping point (Fig. 4) (i.e., \( \alpha < 0 \)). For

Fig. 10. Effect of interspecific competition on tipping point dynamics. For networks A (A and B) and B (C and D), ensemble-averaged pollinator abundance (A and C) vs. \( f_n \) and ensemble-averaged plant abundance (B and D) vs. \( f_i \). The intraspecific and interspecific competitions are incorporated into the model the same way as in Fig. 9. The parameters are \( h = 0.2, t = 0.5, \alpha_i = \alpha_p = -0.3, \mu_A = \mu_B = 10^{-4}, \gamma_0 = 1.0, \) and \( \kappa = 0.0 \). While interspecific competition somewhat reduces the species abundances, the emergence of the tipping point is not affected.
κ = 0, from the stability analysis in SI Appendix, Note 3 for an initial state with high abundances, we have \( \alpha + ((\gamma P)A)/(1 + h(\gamma P)A) > 0 \) and \( \alpha - \kappa + ((\gamma A)P)/(1 + h(\gamma A)P) > 0 \) in the parameter region where the abundance values are large (i.e., before the tipping point). In this case, the steady-state solutions are given by SI Appendix, Eqs. S14 and S16. After the tipping point has been reached, the steady-state solutions are given by SI Appendix, Eqs. S15 and S17. In this case, the physically meaningful solutions are \( A' \approx \mu \) and \( P' \approx \mu \), which correspond to the extinction state. The mathematical conditions under which the tipping point occurs are thus \( q_2^2 - q_1 q_3 = 0 \). In general, the occurrence of a tipping point is caused by the changes in the quantities \( (\gamma A) \) and \( (\gamma P) \).

For a tipping point induced by an increase in the species decay rate \( \kappa \) (Fig. 5), we have \( \alpha > 0 \). Before the tipping point, the value of \( \kappa \) is small, and we have \( \alpha - \kappa + ((\gamma A)P)/(1 + h(\gamma A)P) > 0 \) and \( \alpha + ((\gamma P)A)/(1 + h(\gamma P)A) > 0 \). In this case, we can obtain the approximate steady-state solution from Eq. 5. For larger values of \( \kappa \), the solutions of Eq. 5 become complex, which are physically unrealistic. The condition for the onset of complex solutions is \( q_2^2 - 4q_1 q_3 < 0 \). The approximate critical value \( \kappa_{c1} \) for the occurrence of the tipping point can then be calculated from the relation \( q_2^2 - 4q_1 q_3 = 0 \). However, there exists another critical value, denoted as \( \kappa_{c2} \), which can be seen as follows.

As the value of \( \kappa \) approaches \( \kappa_{c2} \), the following inequality holds: \( \alpha - \kappa + ((\gamma A)P)/(1 + h(\gamma A)P) < 0 \), under which the steady-state solutions are given by SI Appendix, Eqs. S14 and S17. In particular, we have

\[
P' \approx \frac{1}{\beta} \left[ \alpha + \frac{(\gamma P)A'}{1 + h(\gamma P)A'} \right] \quad \text{and} \quad A' \approx \mu.
\]

Since \( \mu \ll 1 \), we have \( P' \approx \alpha \). The critical value of \( \kappa \) for the emergence of this steady state can be obtained from

\[
\alpha - \kappa_{c2} + \frac{(\gamma A)P'}{1 + h(\gamma A)P'} = 0.
\]

The value of \( \kappa_{c1} \) is typically larger than that of \( \kappa_{c2} \), which gives an interval of \( \kappa \), in which the system exhibits bistability or a hysteresis behavior, as shown in Fig. 5.

Overall, the 2D reduced model thus provides a mathematical paradigm by which a number of distinct dynamical phenomena in mutualistic interacting networks can be understood. For example, as pollinators are removed one after another from the system (i.e., as \( f_\alpha \) is gradually increased), for \( \alpha < 0 \), the quantities \( (\gamma A) \) and \( (\gamma P) \) change in such a way that the system exhibits a tipping point without any hysteresis behavior. However, as the species decays faster (i.e., as the value of \( \kappa \) is increased), a hysteresis can arise. While the value of \( h \) can affect the critical parameter values and abundances, it has little effect on the occurrence of a tipping point.

The analysis leads to insights into the effect of varying the value of the parameter \( h \), the half-saturation constant. The reason that we choose different values of \( h \) for different parameter setting is to ensure that the system exhibits a tipping point as the value of \( \kappa \) or \( f \) is varied. From the mathematical analysis, for cases where a tipping point occurs, \( h \) will affect the critical values of \( \kappa, (\gamma A) \), and \( (\gamma P) \), whereas varying \( f_\alpha \) can cause the values of \( (\gamma A) \) and \( (\gamma P) \) to change. From a mathematical standpoint, the type of mutual interactions in our model belongs to Holling type II (26, 27). From an ecological point of view, the half-saturation constant \( h \) characterizes the relaxation time of the species after each mutual interaction, with strength that is described by the parameter \( \gamma \). The effect of varying \( h \) on the system dynamics is thus characteristically different from those caused by variations in \( \kappa \) and \( f \).

**Discussion**

Complex dynamical systems exhibiting a tipping point are widespread, and it is of interest to understand the dynamical mechanism of the tipping point and to develop predictive tools. To accomplish these goals, a viable solution is dimension reduction. We focus in this paper on bipartite mutualistic networks, not only as a concrete example to show the use of dimension reduction but also, because of the fundamental values of safeguarding pollinators to human survivability (28). In a mutualistic network system, a tipping point typically exists. As the environment continues to deteriorate, the system can drift toward the tipping point, where the catastrophic phenomenon of pollinator collapse will occur. The backbone that supports the functioning of such a network is mutualistic interactions between the pollinators and plants. To understand the role of the interactions with respect to the emergence of a tipping point, both species of the bipartite network must be retained in a reduced model. That is, the minimum dimension of the reduced system should be two [a 1D reduced model (18) is inadequate to describe mutualistic interactions]. With this in mind, we carry out a dimension reduction process by resorting to different types of averaging methods for species abundances. In particular, given an empirical mutualistic network, we carry out averaging processes to arrive at a 2D model with two collective dynamical variables: one for the pollinators and another for the plants. The average can be either unweighted or weighted. We show that our 2D reduced model captures the essential features of all 59 available real-world mutualistic networks, not only in terms of the average abundances but more importantly, in terms of the occurrence of the tipping point, even in the presence of stochastic disturbances. We also find that, because of the lack of sufficient randomness in real mutualistic networks, a weighted average (e.g., based on degrees or eigenvectors) is necessary for the reduced model to exhibit a tipping point at the same critical parameter value as with the original network. Our 2D model can thus serve as a generic paradigm for understanding the tipping point dynamics in real-world mutualistic networks. For example, the 2D model can be exploited to investigate a variety of nonlinear dynamical phenomena in mutually interacting networked systems, such as bifurcations (29), basin structures (30, 31), crises (32), and transient chaos (33–38), which would otherwise be infeasible with the original systems because of their high dimensionality.

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