Understanding pesticide-induced tipping in plant-pollinator networks across geographical scales: Prioritizing richness and modularity over nestedness

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Mutually beneficial interactions between plants and pollinators are crucial for biodiversity, ecosystem stability, and crop production. A threat to a mutualistic network is the occurrence of a tipping point at which the species abundances collapse to a near zero level. In modern agriculture, there is widespread use of pesticides. What are the effects of extensive pesticide use on mutualistic networks? We develop a plant-pollinator-pesticide model and study its dynamics using 123 mutualistic networks across the globe. We demonstrate that pesticide exposure can lead to a tipping point. Furthermore, while the network characteristics such as richness and modularity exhibit a strong association with pesticide-induced tipping, nestedness shows a weak association. A surprising finding is that the mutualistic networks in the African continent are less pesticide tolerant than those in Europe. We articulate and test a pragmatic intervention strategy through targeted management of pesticide levels within specific plant species to delay or avert the tipping point. Our study provides quantitative insights into the phenomenon of pesticide-induced tipping for safeguarding mutualistic networks that are fundamental to agriculture and ecosystems.

I. INTRODUCTION

A mutualistic network arises from interactions between two classes of species that mutually benefit each other, playing a fundamental role in supporting terrestrial biodiversity [1] and ensuring human food security [2,3]. A mutualistic network can have a complex bipartite structure and the pollinator-plant interactions can be highly nonlinear [4–15], yet the permissible states or attractors of the system can be quite simple: only stable steady states. A typical situation is where two stable steady states coexist in the phase space: one corresponding to a survival state with healthy abundance levels of all pollinator and plant species and another associated with extinction of the pollinator species, each with its own basin of attraction. As a control or bifurcation parameter changes (e.g., increases), an inverse saddle-node bifurcation occurs at which the survival steady states disappear, leaving the extinction state as the only attractor in the system—the generic dynamical mechanism leading to a tipping point [11,16–26]. It is the simplicity of the asymptotic dynamical states of complex nonlinear mutualistic networks in spite of their high dimensionality, i.e., stable steady states or fixed-point attractors, which justifies the use of dimensional reduction for understanding the generic tipping-point dynamics. For example, it was demonstrated that a high-dimensional mutualistic network can effectively be reduced to a two-dimensional system with the "mean-field" plant and pollinator abundances as the two dynamical variables, which makes a geometric analysis of the tipping-point transition and its accurate prediction feasible [11]. Previously, strategies to manage or mitigate a tipping point were also investigated [9,13,27–29]. Complex networks in natural and engineering systems can undergo a tipping point from normal functioning to a catastrophic state as a parameter changes through a critical point [7,11–13,24,27,29–53]. Ecological networks are particularly vulnerable to tipping as their parameters may be drifting towards a critical point due to the impact of global climate change and other human influences [7,48,54]. A class of ecological networks fundamental to agriculture and biodiversity is mutualistic pollinator-plant networks [4–14].

From the point of view of network dynamics, the role of the structure of a mutualistic network in the coexistence of plant and pollinator species and tipping is a pertinent issue. A previous study identified network nestedness as a key structural factor underlying the network dynamics [55]. In particular, it was found that mutualistic networks tend to exhibit a high level of nestedness, which, in turn, fosters species competition and leads to greater species diversity within the community. In another influential work [7], an association was established between the drivers of pollinator decline and the emergence of a tipping point that leads to a sudden and simultaneous collapse of the pollinator populations. These works highlighted the importance of connectance and/or nestedness in promoting the survival of pollinator populations in challenging ecological landscapes. In a more general sense, identifying the potential drivers influencing ecological systems is important [25]. It has been recognized that, beyond the natural drivers associated with species' physiological parameters and

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noise, the role of human-induced anthropogenic drivers are crucial. For complex mutualistic networks, depending on the structural properties of the network, such as nestedness, connectance, richness, and modularity, climate warming can serve as a pivotal driver in the early occurrence of a tipping point.

Among the various human influences, the widespread use, overuse, and even abuse of pesticides in the past arguably would have a negative impact on these mutualistic networks, but such impacts have not been well understood at a quantitative level. Pesticide usage can be detrimental to plant-pollinator mutualistic networks because, practically, it may be the most common reason that such a network can experience a tipping point [56–59]. The adverse effects of pesticides on plant-pollinator networks are predominantly direct and immediate, which can alter and significantly advance the tipping point of the original network in the absence of pesticide use. In general, pollinators' movements are not limited to cultivated plants or domestic crops alone; they also forage for wild plants. Intensified agriculture and increased agrochemical use expose pollinators to toxic substances, including commonly used pesticides [59], fungicides, herbicides [60], and heavy-metal contamination from soil fertilizers [61]. Pollinators face multiple exposure routes, such as ingesting contaminated pollen and nectar or encountering contaminated nesting sites [62,63]. The accumulated pesticides have various adverse effects, including reduced growth [64] and increased mortality rates in pollinators and their larvae [65,66]. Pesticide accumulation impairs critical biological behaviors, including memory, navigation, foraging, and feeding [59,67,68]. Delayed larval and pupal development leads to decreased overlap between seasonal flowering plants and pollinator activity [69]. These factors weaken the plant-pollinator mutualism by altering visitation rates and can be considered sublethal effects. Moreover, chemical pesticide exposure compounds the impact of other stressors on pollinator populations, such as habitat loss and exposure to pathogens and diseases [70,71].

The pesticide body burden of pollinators directly linked to the pesticide exposure from the plants they visit, resulting in various lethal and sublethal effects that elevate mortality and weaken mutualistic interaction strength, which can ultimately accelerating community collapse through a tipping point. Thus, managing pesticide levels in key plants within the network could help mitigate these adverse outcomes and support overall community persistence.

Drawing from our available data on real-world plant-pollinator networks, our study endeavors to tackle multiple objectives. In particular, will the large-scale use of pesticides eventually lead to a tipping point of mutualistic networks at which the pollinator species become extinct on a relatively short timescale? Are pollinator-plant mutualistic networks from different parts of the world equally vulnerable to pesticide-induced tipping and whether this root cause remains consistent across different geographical scales, spanning continents, and hemispheres? Can pragmatic but effective control or mitigation strategies be devised to prevent or delay the pesticide-induced tipping if it is inevitable? The purpose of this paper is to address these questions by incorporating the effects of pesticides in mutualistic network models and analyzing a large number of empirical networks from different continents of the world.

II. METHODS

A. Dataset

We studied 123 real mutualistic networks from four continents: Africa, Europe, and North and South America [72]. (Asia and Oceania have too few networks available, so they are excluded from our study.) Here we present the detailed results for four specific networks: Ⓐ ($S_A = 61$, $S_P = 17$ and the number of links $L = 146$) from Hicking, Norfolk, UK; Ⓑ($S_A = 38$, $S_P = 11$, and $L = 106$) from Tenerife, Canary Islands; Ⓒ ($S_A = 44$, $S_P = 13$, and $L = 143$) from North Carolina, USA; and Ⓓ ($S_A = 42$, $S_P = 8$, and $L = 79$) from Hestehaven, Denmark. In the database, the IDs of the four networks are 6, 8, 25, and 38, respectively. The primary reason for this selection bias is to maintain parity with previous works [13,48]. However, it is worth noting that these networks are also chosen due to their significant size and higher nestedness values.

B. Multidimensional plant-pollinator-pesticide model and its two-dimensional reduction

An ecologically realistic mathematical model is employed to study these mutualistic communities, encompassing intrinsic growth, intra- and interspecific competition, and mutualistic interactions between plants and pollinators. Let P_i and A_i be the abundance of the ith plant and pollinators, respectively. Following Ref. [55], the equations for the rate of change of P_i and A_i are given by:

$$\frac{dP_i}{dt} = P_i\left(\alpha_i^P - \sum_{j=1}^{S_P}\beta_{ij}^P P_j + \sum_{j=1}^{S_A}m_{ij}^P\right) + u^P$$

$$\frac{dA_i}{dt} = A_i\left(\alpha_i^A - \sum_{j=1}^{S_A}\beta_{ij}^A A_j + \sum_{j=1}^{S_P}m_{ij}^A\right) - \kappa^A A_i + u^A, \quad (1)$$

where S_P and S_A are the plant and pollinator richness in the community. Description of the other parameters are the following: α^P and α^A are the intrinsic growth rate of plant and pollinators, respectively, in the absence of competition and mutualism. The degree of the mutualism can be categorize in two ways, obligate and facultative, depending the sign of α. If the population persists in the absence of mutualism, then it is called facultative mutualism and α is positive in this case. Conversely, α is negative for the case of obligate mutualism, where species cannot persists in the absence of mutualism. We assumed a common value α as the intrinsic growth rate of all species for the sake of simplicity. $\beta_{ij}^{P,A}$ represents the intra- (for $i = j$) and interspecific (for $i \neq j$) competition between plant or pollinators. Usually $\beta_{ii} \gg \beta_{ij}$ and so we assumed $\beta_{ii} = 1$ and $\beta_{ij} = 0$ for all plant and pollinators. $m_{ij}^P(= \frac{\gamma_{ij}^P A_j}{1 + h\sum_{j=1}^{S_A}\gamma_{ij}^P A_j})$ is the per-capita mutualistic benefit received by plant i from the pollinator j and similarly $m_{ij}^A(= \frac{\gamma_{ij}^A P_j}{1 + h\sum_{j=1}^{S_P}\gamma_{ij}^A P_j})$ is the per-capita mutualistic benefit received by pollinator i from the plant j. The parameters γ_{ij}^P and
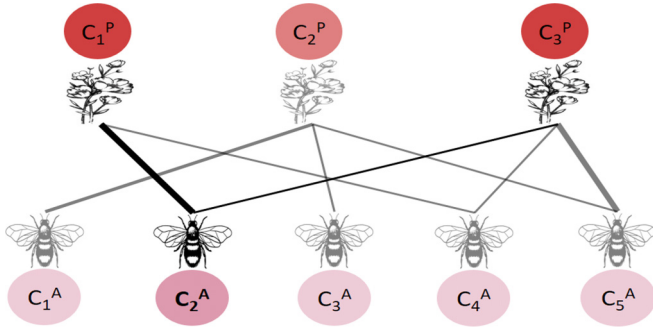
FIG. 1. A visual depiction of our model system, showcasing a mutualistic network featuring three plant species and five pollinators. The width of the connecting lines in the illustration reflects the intensity of mutualistic interactions. Shown are the pesticide body burdens of both plants and pollinators using circles attached to each species. As an illustrative instance, consider second pollinator, which engages in interactions with the first and third plant species (emphasized with a bold color). Consequently, the pesticide body burden of the second pollinator is influenced by the combined pesticide burdens of the first and third plants, as well as the strength of their mutualistic relationships.

γ_{ij}^{A} are the strength of mutualistic interactions, which takes the following form: $\gamma_{ij}^{P,A} = \delta_{ij}\frac{\gamma}{d_i^\rho}$. Here δ_{ij}'s are the elements of the adjacency matrix of the network, $\delta_{ij} = 1$ if plant i and pollinator j is connected and $\delta_{ij} = 0$ otherwise; γ is the normalized mutualistic strength and d_i is the degree if the ith plant or pollinators. Here the parameter ρ determines the trade-off between mutualistic strength and the degree of the species and hence is associates mutualism with the network topology. $\rho = 0$ means the mutualistic strengths are independent of the network structure. In contrast, $\rho = 1$ means there is a full trade-off; gain from the mutualism of a species from the interacting species is split by the number of interactions and weakened the mutualism between each interacting species. Between the two extreme cases, we took $\rho = 0.5$ following previous studies [8,13,48]. h is the half saturation constant, as the mutualistic benefit will saturate with the abundance of the interactive partners, and the Holling type response was first introduced in Ref. [73] in mutualistic network model. κ_i^A is the decline rate of the pollinators due to the external effects, and we took $\kappa_i^A = \kappa^A$ for simplicity. Finally, u^P (u^A) are the constant immigration rates of plant (pollinators), which takes typically small value and thus have a little effect on the dynamics.

We finally incorporate the effect of pesticide through species body burden in order to construct our plant-pollinator-pesticide (PPP) model [see Supplemental Material (SM) (SM Note 1) [74] for details]. The pesticide body burden of plants is directly related to the applied pesticide amount, while that of pollinators depends on their per-capita interaction with the plants and the pesticide burden of those plants (see Fig. 1). The decay rate of pollinators, the strengths of plant-pollinator mutualistic interactions, and the plant growth rate are all functions of their respective pesticide body burdens [Supplemental Material [74] (SM Note 2)]. With all

these considerations, our final PPP model becomes

$$
\frac{dP_i}{dt} = P_i\left(\hat{\alpha}_i^P - \sum_{j=1}^{SP}\beta_{ij}^P P_j + \frac{\sum_{j=1}^{SA}\hat{\gamma}_{ij}^P A_j}{1 + h\sum_{j=1}^{SA}\hat{\gamma}_{ij}^P A_j}\right) + u^P
$$

$$
\frac{dA_i}{dt} = A_i\left(\alpha_i^A - \sum_{j=1}^{SA}\beta_{ij}^A A_j + \frac{\sum_{j=1}^{SP}\hat{\gamma}_{ij}^A P_j}{1 + h\sum_{j=1}^{SP}\hat{\gamma}_{ij}^A P_j}\right)
$$
$$
- \hat{\kappa}^A A_i + u^A. \tag{2}
$$

Two-dimensional reduced model

Our two-dimensional (2D) reduced model, following the approach in Ref. [11], is given by

$$
\frac{d\bar{P}}{dt} = \bar{P}\left(\hat{\alpha}^P - \beta\bar{P} + \frac{\hat{\gamma}^P\bar{A}}{1 + h\hat{\gamma}^P\bar{A}}\right) + u^P
$$

$$
\frac{d\bar{A}}{dt} = \bar{A}\left(\alpha^A - \beta\bar{A} + \frac{\hat{\gamma}^A\bar{P}}{1 + h\hat{\gamma}^A P}\right) - \hat{\kappa}^A\bar{A} + u^A, \tag{3}
$$

where $\bar{P}$ and $\bar{A}$ are the average plant and pollinator abundance, respectively. The derivation and the description of the other terms are detailed in the Supplemental Material [74] [Eqs. (S7)–(S12) and Supplementary Note 3].

The steady-state solution can be obtained by equating the derivatives to zero [Eq. (S14) and Supplementary Note 3 [74]]. Initially we obtained a quadratic equation in A [Eq. (S15), Supplementary Note 3 [74]] by assuming P as a constant and got the pollinator equilibrium as a function of P, with certain restrictions [Eq. (S18) and Supplementary Note 3 [74]]. Using this pollinator equilibrium in plant steady-state equation, we obtain a quadratic in P [Eq. (S20) and Supplementary Note 3 [74]]. Note that both the quadratic equations are inter-related. In the subsequent section, we explore whether the tipping point estimates derived from the reduced 2D model align closely with the tipping behavior of the exact high-dimensional model across 123 real networks.

III. RESULTS

A. Tipping of the PPP model: Full and reduced 2D setup

The proposed model reduces to the existing mutualistic plant-pollinator framework used in previous studies [7,9,11,13,24] in the absence of the pesticide (notationally, $C = 0$). Trivially, the prediction of tipping points under zero pesticide level (hereafter PL) coincides with those obtained in previous studies when we demonstrate the figure based on the one parameter bifurcation diagram with respect to mutualistic strength (γ), for the four prototype networks Ⓐ–Ⓓ as mentioned in Sec. II A. For example, see Fig. 1 as depicted in Ref. [13] and the first panel of Fig. 2 in the present study are pretty similar. We refer to the threshold γ below which the system collapses as minimum gamma for coexistence (MGC). The magnitude of the tipping points changing under the application of pesticide in three different levels viz., none ($C = 0$), medium ($C = 0.5$), and high ($C = 1$). This phenomenon is presented in three
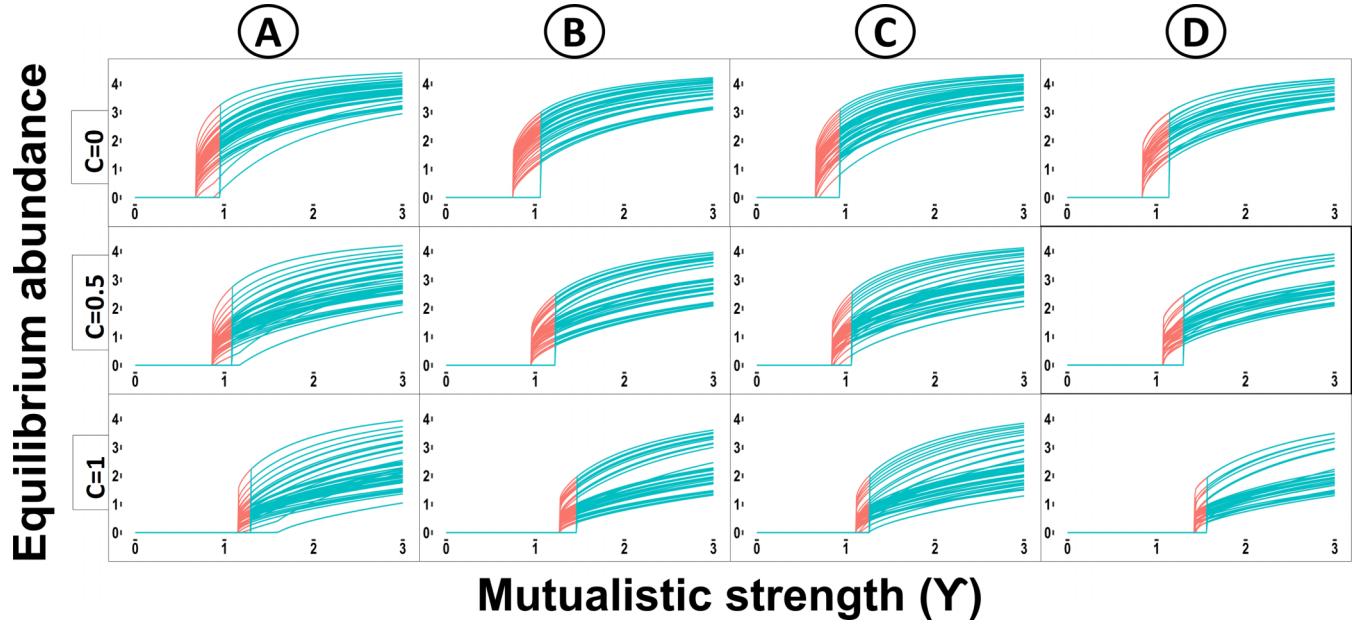
FIG. 2. Equilibrium abundance of both plants and pollinators within a network in relation to mutualistic strength. The three rows correspond to different levels of pesticide exposure: none ($C = 0$), moderate ($C = 0.5$), and high ($C = 1$), while each column represents one of the four specific networks mentioned in Sec. II A. The orange line signifies a collapse, while the blue line represents recovery. The community's abundance gradually decreases with decreasing γ, eventually reaching a tipping point where the community collapses. Notably, the threshold level of γ at which the community collapses (MGC) increases with pesticide levels (C). Here $\alpha_A = \alpha_P = -0.3$, $\mu_A = \mu_B = 0.0001$, $h = 0.2$, $\kappa_A = 0.1$, $\rho = 0.5$, $\sigma^\kappa = 0.1$, $\sigma^{\gamma A} = 0.5$, $\sigma^{\gamma P} = 0.1$, $\zeta = 0.1$, and $\sigma^{\alpha_P} = 1$.

different panels of Fig. 2. The figure clearly articulates that the networks need more mutualistic strength (γ) to delay the tipping. For example, in the absence of pesticide ($C = 0$), MGCs are approximately around $\gamma = 0.75$ for the four networks. For $C = 0.5$ and 1, MGC rises to 1 and 1.5, respectively.

This phenomenon motivates us to understand the intricate dynamics of the system on a deeper level. It is not sufficient to study the system equilibrium for only zero, moderate, and high levels of pesticide. To overcome this, we study the behavior of the equilibrium density with pesticide level as a potential driver for a wide range of values of C (Fig. 3). Initially, the equilibrium abundance of all plant and pollinator species in each community decreases gradually with the pesticide level (C). Further, with a gradual increase of C, the system experiences a catastrophic transition from the stable coexistence state to community collapse, which is denoted by the orange lines in Fig. 3. The pesticide tipping threshold (MPT) significantly reduces when γ decreases. This implies that networks with low γ are more vulnerable to pesticide application.

A natural question arises as to whether the system recovery starts when pesticide level reaches just below the critical threshold. To answer this query, we developed blue lines in each panel of Fig. 3. A small reduction of C can lead the system to a recovery state when γ is high. However, the system recovery threshold is significantly lesser than the tipping threshold of community collapse when γ decreases, for all 123 networks. The system cannot exhibit a recovery state unless we push to reduce C to a substantial amount in comparison to the threshold C level of collapse. This phenomenon is known as hysteresis.

We ultimately computed the MPTs for all 123 real networks, employing both the full network model and the simplified 2D model [as described in Eq. (3)]. The MPT values derived from the 2D reduced model exhibit a remarkably strong alignment with those obtained from the full network system. This association is readily apparent in the scatter plot comparing the two datasets (refer to Fig. S1, SM Note 3 [74]). This finding provides compelling evidence that our intricate, high-dimensional plant-pollinator-pesticide system can be accurately approximated using a 2D mean-field model, based on network topological properties.

In the aforementioned section, we identified that MPT largely varies across 123 networks with varying γ (see Fig. 4). The mean and variances for low, moderate, and high γs are depicted in the figure. Variances are substantially large under all three levels of γ but the magnitude remains almost invariant.

B. Forging a connection: Network architecture attributes and pesticide-induced tipping points

In the crude and simplest way of understanding the relationship between MPTs and network properties, we must assume the linear association assessed using the Pearson correlation coefficient, whose significance level needs to be tested through a standard statistical hypothesis tool. Let us assume the MPT values of 123 networks as the dependent variable (say, y). We have four independent variables, namely network richness (x_1), connectance (x_2), nestedness (x_3), and modularity (x_4). We consider four sets of 123 paired observations, viz., (y, x_1), (y, x_2), (y, x_3), (y, x_4), and evaluate the Pearson
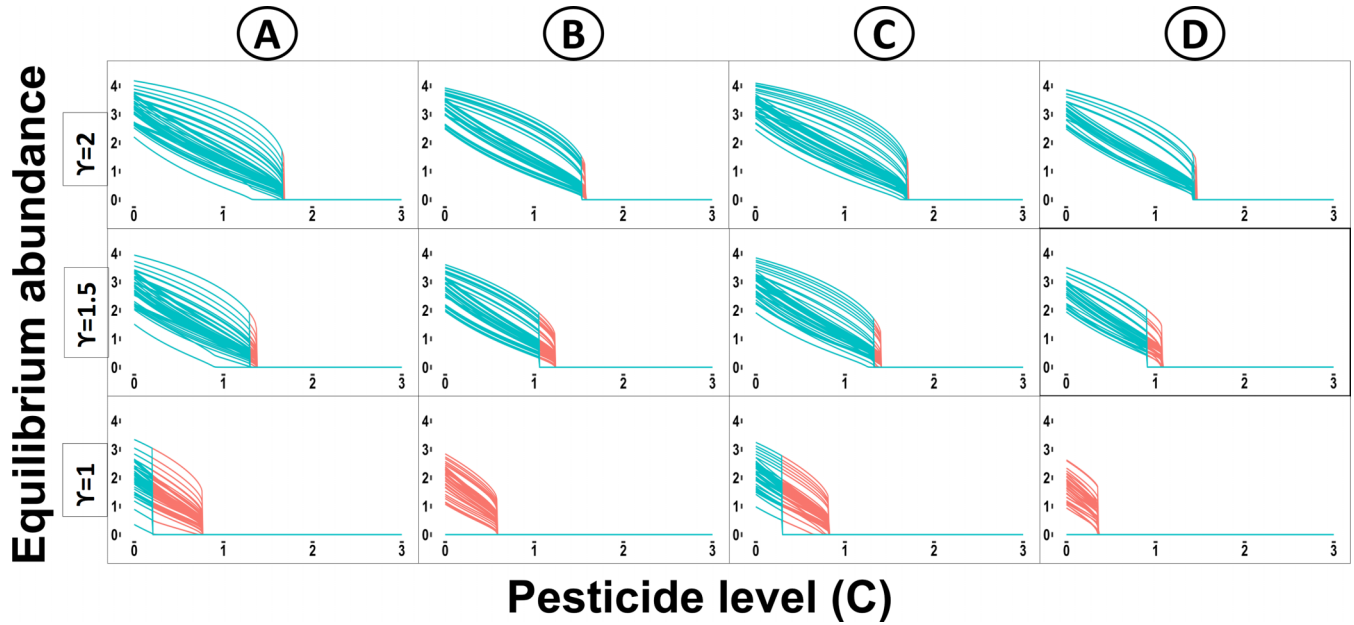
FIG. 3. Equilibrium abundance of both plants and pollinators within a network as it relates to varying pesticide levels (C). The three rows correspond to different levels of mutualistic strength (γ), and each column represents one of the four specific networks mentioned in Sec. II A. The orange line signifies a collapse, while the blue line represents recovery. The community's abundance gradually decreases with increasing C, eventually reaching a tipping point where the community collapses. Notably, the threshold level of pesticide (C) at which the community collapses, referred to as MPT, diminishes and size of the hysteresis loop increases as mutualistic strength (γ) weakens. Parameter values are same as in Fig. 2.

correlation coefficients based on the four sets of paired observations. The correlation coefficients are, respectively, 0.73, -0.38, 0.03, and -0.57, for high mutualistic strength ($\gamma = 2$). Both correlation and regression coefficients are significant for the three pairs (MTP, richness), (MPT, connectance), and (MPT, modularity) but insignificant for the pair (MTP, nestedness). Note that for the other two level of MS, the correlation and their significance is almost same. The estimated regression coefficients and the associated p values for the statistical test are explicitly displayed in Fig. 5.

Climate is a pivotal factor influencing the structure of plant-pollinator networks, mediating the roles of various pollinator species [75–77]. While it is commonly understood that climatic variations are primarily regulated in temperate zones, there is ample evidence suggesting substantial climatic diversity within the same temperate zones. For instance, the climatic conditions in Africa and South America, both situated within temperate zones, exhibit significant differences. It is prudent to visually analyze the initial impression of the global distribution of MPT, as depicted in Fig. 6. On visual inspection, the prevalence of green shading in the upper hemisphere appears more pronounced compared to the lower hemisphere. On closer examination, significant variations between continents become apparent. The African continent is distinguished by its abundance of blueish circles, whereas Europe exhibits a prevalence of green-shaded circles. This suggests that African networks face a higher risk of tipping, while European networks are at a lower risk. Conversely, North and South America are characterized by a mixture of blue and green circles, indicating a moderate MPT risk level. However, to ensure robust analysis, these visual observations warrant statistical validation.

Initially, we assess the normality of each of the four network variables (richness, connectance, nestedness, and modularity), as well as MPTs, employing the Shapiro-Wilk test (SM Note 4A [74]). The null hypothesis for the Shapiro-Wilk test posits that the sample originates from a normal distribution, while the alternative hypothesis suggests otherwise. When the p values from this test fall below the threshold of 0.05, it signifies that the sample does not conform to a normal distribution with a 95% confidence level. Our examination of four network properties and the MPTs reveals multiple instances of non-normality, with specific p values provided in the Supplemental Material [74] (see Table S1, SM Note 4A). Consequently, we deduce that our data do
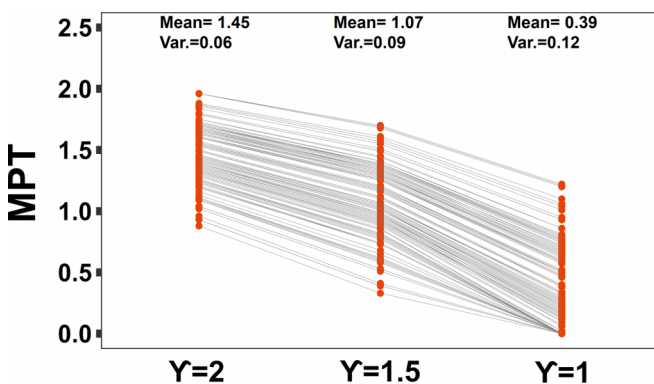

FIG. 4. MPT for all 123 empirical networks for three levels of mutualistic strength (γ). The mean and variance of the MPTs are mentioned on the above of each dataset. MPT decreases with decreasing γ, as evidenced by a significant decrease in the mean.
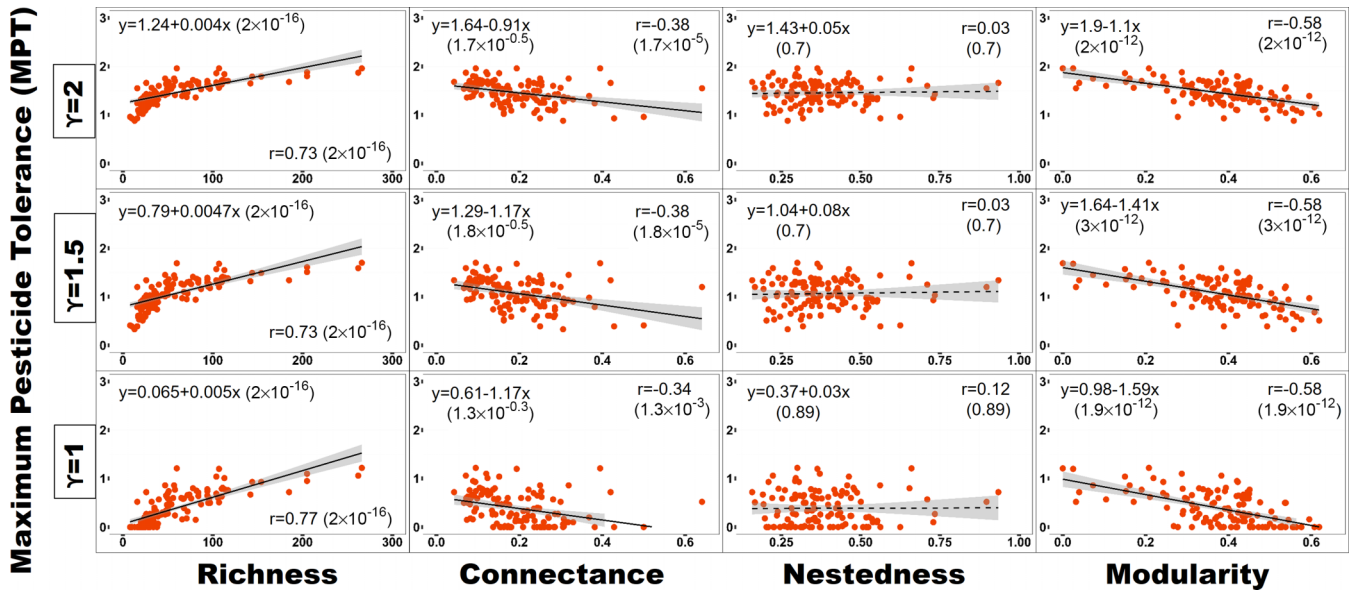
FIG. 5. Pearson correlation coefficients of the MPT across all 123 networks. Each row represents a different level of γ. Four columns correspond to various network properties, and each column illustrates the correlation between MPT and a specific network topological characteristic. Each subfigure contains both the correlation value and the regression equation, including their respective p values (values less than 0.05 implies statistical significance). Importantly, richness exhibits a positive association with MPT, while connectance and modularity demonstrate an opposite trend, supported by statistically significant correlations. In contrast, nestedness displays an insignificant correlation with the MPT. The regression is also statistically insignificant and represented by dotted lines.

not adhere to a normal distribution, leading us to employ nonparametric tests for comparing means.

In the subsequent step, we employ the Kruskal-Wallis test to examine whether there are statistically significant differences in the means of the five variables across the four continents. The results indicate that for all five variables, the p values are less than 0.05 (details provided in SM Note 4B, Table S2 [74]), signifying a notable distinction in means among the continents. Following this, we conduct pairwise comparisons between the continents using the nonparametric Wilcoxon's rank-sum test, yielding a ranking of means for the five variables across the four continents (refer to the Table S3, in SM Note 4C [74]).

Specifically, we observe that network richness is significantly lower in Africa and notably higher in South America, while Europe and North America fall in
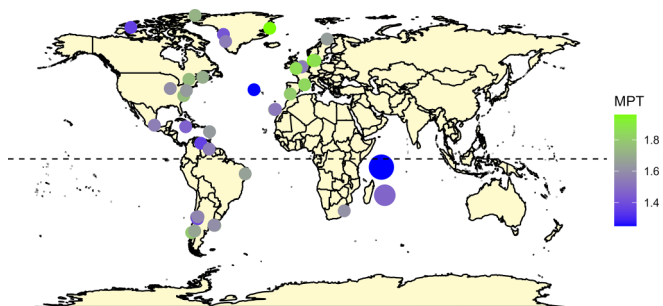

FIG. 6. The MPT values for 123 networks are mapped across different geographical locations. Circle size represents the number of overlapping networks at each location, while color indicates the average MPT value for that specific location.

intermediate positions. Conversely, when considering network connectance, the order is reversed, with South America showing lower values and North America exhibiting higher ones, while Europe and Africa occupy intermediate positions. As for network nestedness, South American networks exhibit lower values, whereas North American networks display higher values; Europe and Africa maintain intermediate standings. In terms of modularity, networks in North America and Europe have significantly lower values compared to those in Africa and South America. Furthermore, we find that African continental networks exhibit a lower tolerance to pesticides, as indicated by a lower tipping threshold. In contrast, European continental networks demonstrate a substantially higher threshold for pesticide tolerance. North and South America occupy intermediate positions in this regard.

The analysis aimed at assessing the proximity among continents can be effectively visualized through the application of linear discriminant analysis, as detailed in Ref. [78]. The biplot representing the first and second linear discriminant is provided below (refer to Fig. 7). On examination of the figure, it becomes evident that the four continents exhibit distinct separations attributed to substantial disparities in MPTs and network richness, which is denoted by T and R, respectively, in the figure. Notably, a pronounced differentiation between Africa and Europe is readily apparent, aligning with our research findings. Therefore, it becomes relevant to examine the interplay of MPTs and network characteristics across different continents.

We have categorized a total of 123 networks across four continents, as outlined in Sec. II A. For each continent, we have computed the Pearson correlation coefficient between MPTs and each of the network properties. Additionally, we have fitted regression lines for all the paired variables. The
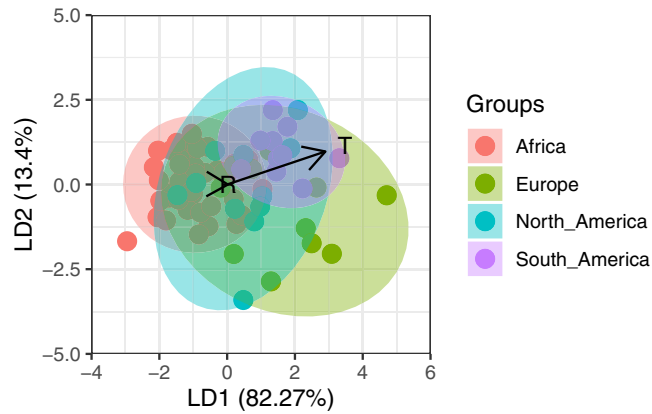
FIG. 7. Biplot of the discriminant analysis of the data set consisting of the tipping threshold with the network properties.

detailed results, including p values, can be found in the Supplemental Material [74] (Note 4D). In summary, we can conclude that, surprisingly, the association of tipping point and connectance is weak for all the continents except Africa, with insignificant p values. Modularity has a strong negative correlation with MPTs, with significant p values. In contrast, the correlation of MPTs and nestedness is insignificant for all the continents, which remains invariant under continent-wise classification. Last, richness demonstrates a strong positive correlation with MPTs, substantiated by significant p values, although the correlation is positive but insignificant in the case of South America (see Table S4, SM Note 4D [74]). We will discuss the explanation of these summary in Sec. IV.

Furthermore, we have conducted a linear regression analysis to formulate a statistical model for predicting tipping thresholds across all continents, except South America, where we used nonparametric regression, since normality does not holds for MPT values. The regression coefficients, along with their corresponding p values, are provided in the Table S5 displayed in SM Note 4D [74]. It is noteworthy that despite an insignificant correlation between richness and tipping thresholds in South America, richness emerges as a significant covariate in regression equation. Additionally, the correlation between nestedness and MPTs is insignificant across the continents, but surprisingly, nestedness appears as a significant contributory variable in the final regression equation under the stepwise scheme for all the continents except North America. Some possible reasons behind these anomalies are the irregularity and scarcity of data points across the continents.

Hence, we are confronted with the dilemma of whether to persist with our data analysis at the continent level or, alternatively, shift our research focus to the hemisphere level in order to mitigate the data sparsity issue. We contend that the scarcity of data is a more pressing concern when compared to the endeavor of evaluating the performance of the regression setup across distinct climatic zones associated with the four continents. In the subsequent phase of our analysis, we will pivot our attention to the hemisphere level by aggregating data from individual continents.

C. Connection revisit: At hemisphere level

We conduct comparison tests for the mean network properties and tipping thresholds across hemispheres (Table S6, SM Note 4E [74]). Similarly to our earlier findings (Table S1, SM Note 4A [74]), we once again identify non-normality in the data. Consequently, we employ the nonparametric Wilcoxon rank-sum test for these comparisons (Table S7, SM Note 4E [74]). The results from these tests indicate that networks situated in the upper hemisphere are characterized by higher species richness, sparser connections, and lower modularity compared to their counterparts in the lower hemisphere. However, nestedness did not differ between groups. Notably, the threshold pesticide level for networks in the lower hemisphere is lower in comparison to those in the upper hemisphere.

We have conducted multiple linear regression analyses for both hemispheres, and the results are presented in the supplementary material (Table S9, SM Note 4E [74]). These regression analyses reveal that each of the four network characteristics significantly influences the pesticide threshold in both hemispheres, with the exception of nestedness in the upper hemisphere. Of particular importance is the finding that modularity emerges as the most influential factor in both hemispheres. This underscores its pivotal role in shaping the response of plant-pollinator communities to pesticide exposure. Our regression models offer a valuable tool for predicting the tipping threshold values for new networks based on their specific structural properties. It is crucial to highlight that the regression formula varies depending on the hemisphere to which the network belongs. This enables us to estimate the tipping threshold for each network by applying the appropriate regression formula, facilitating a ranking of networks based on their predicted threshold values. This ranking allows us to prioritize interventions for plant-pollinator communities, focusing our attention on those in most urgent need.

IV. SIGNIFICANCE OF RESULTS

A. Do species-rich plant-pollinator networks have greater tolerance to pesticides?

Species richness exhibits a strong positive correlation with the MPT (first column in Fig. 5, Table S4 in SM Note 4D, Table S8 in SM Note 4E [74]). In simpler terms, within a more diverse network, both plants and pollinators demonstrate greater resilience when exposed to pesticides. In species-rich communities, both pollinators and plants benefit from greater food source diversity and increased pollination opportunities, respectively. So in such mutualistic plant-pollinator communities, higher species richness is more likely to enhance the positive interactions between plant and pollinator species, potentially disrupting the chain of cascading extinctions and thus increasing the community's ability to withstand pesticide exposure. These findings align with previous research [73,79,80], which have consistently shown that diversity is positively associated with the persistence and resilience of mutualistic communities.

B. Modularity and MPT association: A negative alliance

Modularity demonstrates a significant negative correlation with the system's persistence under pesticide (fourth column

in Fig. 5, Table S4 in SM Note 4D, Table S8 in SM Note 4E [74]). Interactions between plants and pollinators become confined within modules which hinders the stabilizing mechanism of mutualistic communities: specialists to generalists interaction. In a highly modular network, the connections are primarily facilitated by a few crucial pollinator species, which function as either hubs (highly interconnected species within their respective modules) or connectors (species bridging different modules). These highly connected pollinator species tend to accumulate higher pesticide body burdens. Consequently, as the abundance of these key pollinators declines, the interconnections between modules begin to deteriorate, thus triggering the extinction cascade [81]. Our findings align with prior research that consistently reports a negative correlation between modularity and the persistence and resilience of mutualistic communities [79]. However, it is worth noting that modularity may have a beneficial effect on the stability of a food web network, especially in contaminated environments [82], which contrasts with the trends we observed in mutualistic communities.

C. Why connectance and MPTs are negatively correlated?

Local stability and degree of localization (metrices of stability; ability of a system to absorb perturbations) negatively depends on the connectence of a mutualistic community [83,84]. Also extinction cascades, the tendency of secondary extinction of a mutualistic network increases with connectence [85]. Overall connectence has negative impact on the stability of a mutualistic community (but see Refs. [73,79,80]). Our results is synergistic with the previous findings, as the MPT has negative correlation with the connectence (second column in Fig. 5). Specifically, when pollinators are connected to more plants in a densely interconnected community, their pesticide body burden increases. Consequently, this leads to an elevation in pollinator decay and a reduction in mutualistic strength, ultimately pushing the community closer to a tipping point.

D. Higher nestedness may not be beneficial: Offering a nontrivial conclusion

Nestedness, the anomalous property of a mutualistic network [4], can generally boost the ability of the system to persists, especially in extreme circumstances [79]. Species in a nested networks are cohesively connected to a central core of interaction, where generalists and specialists both interacts with generalists and specialist-specialist interactions are rare. Nestedness creates a positive feedback loop between the interacting species and increase the diversity by reducing the interspecific competition [55]. Community response to cascading extinction of pollinators is minimized for nested structure [54]. Nestedness has a positive effect on community persistence, resilience and structural stability (Refs. [8,73,79], but see Refs. [83,86]). However, results from our study indicates that nestedness has no effect in pesticide tolerance of a plant-pollinator network (third column in Fig. 5, Table S4 in SM Note 4D, Table S8 in SM Note 4E [74]). Within a highly nested network, the generalist pollinator, serving as the linchpin of the community, accumulates a substantial pesticide body burden. Consequently, the detrimental impact of nestedness, manifesting as increased pesticide body burdens of such crucial generalist pollinators, counteracts the positive effects associated with nestedness, which are typically characterized by a central core of interactions. Results from our study agrees with the recent findings of Ref. [80] where nestedness is shown to have no statistically significant effect on the resilience of a plant-pollinator community in the presence of external disturbances.

E. MPT is low for Africa and high for Europe

The threshold pesticide level is low for African networks, while it is high for European networks (Table S3, SM Note 4C [74], also see Fig. 6). This difference arises from the fact that African continental networks have lower richness but higher connectance and modularity. As the threshold pesticide level is positively correlated with richness and negatively correlated with connectance and modularity, the pesticide threshold becomes low for this continent. In contrast, European networks display moderate richness and connectance, but low modularity, resulting in a higher tolerance level to pesticides. In our data set, mutualistic networks from the temperate and Mediterranean regions (Europe and North America) tend to be species-rich, while networks from the African and South American continents mainly belong to the tropical zone, resulting in lower species richness [87]. These regional differences in species richness and connectance contribute to significant variations in pesticide threshold within these regions.

F. MPT is low in lower hemisphere

The pesticide threshold significantly differs between the two hemispheres (Table S7, SM Note 4E [74]). Networks in the lower hemispheres possess low richness but high connectance and modularity, leading to a lower pesticide threshold compared to the upper hemisphere.

V. INTERVENTION STRATEGY FOR DELAYING TIPPING POINT

In this section, we developed an ecologically viable strategy for effectively managing critical transitions within a mutualistic community. The management of critical transitions or tipping points generally means strategies aimed at delaying global extinction or transforming it into a more gradual process. A biologically feasible intervention strategy by selecting an influential pollinator species and then controlling its abundance or fixing its decay rate was proposed [13]. Implementing this straightforward yet efficient intervention strategy can effectively alleviate the sudden collapse of a plant-pollinator community. Nevertheless, providing a feasible practical implementation framework for this strategy in real-world contexts poses a significant challenge. In our case, community tipping is primarily triggered by pesticide usage. Therefore, we put forth an intervention strategy focused on the prudent management of pesticides in plant cultivation. A recent field study conducted [88], which underscores the substantial positive impact of reducing pesticide usage on crop production. We have developed our intervention strategy, which involves systematically selecting a "targeted plant"
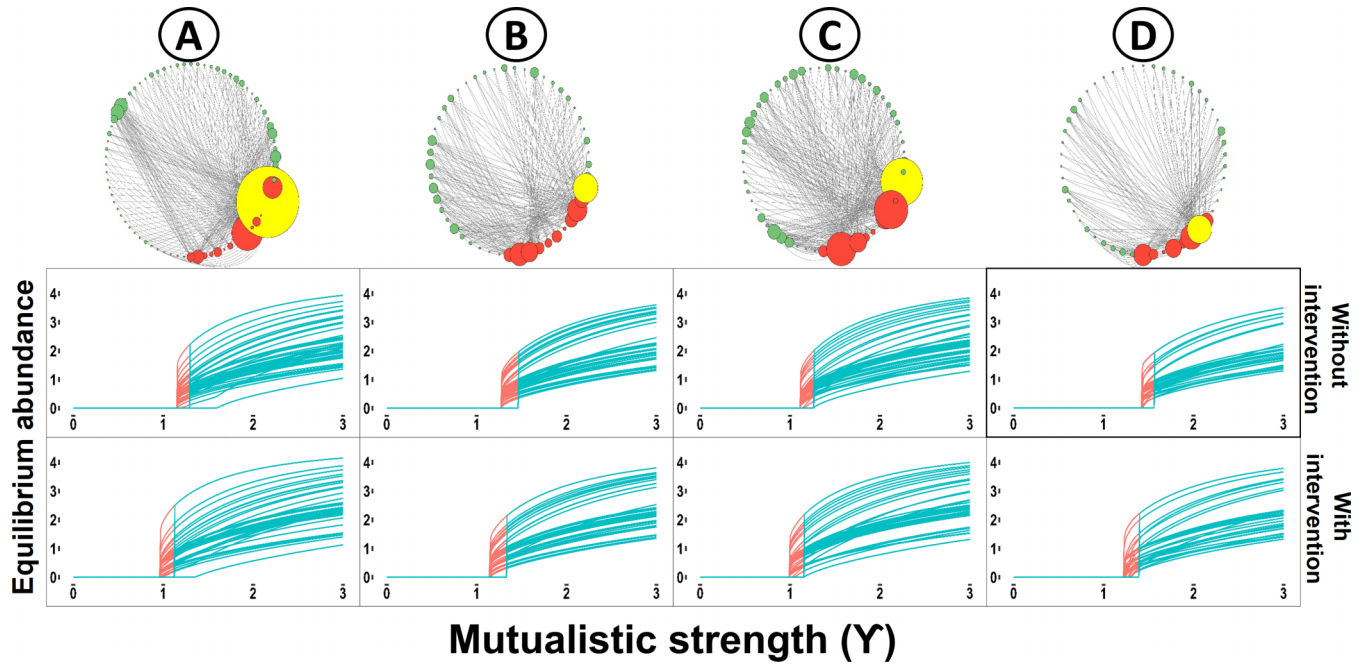
FIG. 8. Four network representations denoted as Ⓐ to Ⓓ, with red nodes representing plants and green nodes representing pollinators. The circle sizes of each node correspond to their degrees. The plant highlighted by a yellow circle is the highest degree plant, designated as the target plant. In the second and third columns, the equilibrium abundance of these four specific networks at varying mutualistic strengths (γ), both without and with intervention, are illustrated. Intervening with the targeted plant has the potential to reduce the minimum mutualistic strength for coexistence (MGC). Here $C = 1$; other parameters are same as in Fig. 2.

from the community and implementing measures to regulate its pesticide levels. The subsequent steps of our strategy are detailed below.

A. Selection of the target plant species

In our study, we designate the target plant species based on its centrality, a extensively explored concept employed to quantify the significance of nodes within a network. Although various centrality measures exist, our attention is directed toward centrality metrics tailored for bipartite networks, as a plant-pollinator mutualistic community can be represented as a bipartite network. Two frequently employed centrality metrics for bipartite networks encompass degree centrality [89,90], which tallies the number of connections associated with a node, and eigenvector centrality, computed using the elements of the eigenvectors corresponding to the largest eigenvalue [91], where a node's centrality is elevated if it is linked to other nodes exhibiting high centrality. We opt for degree centrality due to its straightforward yet potent concept. In the context of plant-pollinator networks, it quantifies the number of interactions a species (either plant or pollinator) has with other species. Degree centrality is straightforward to compute, requiring only the count of connections for each node. A higher degree indicates a species that interacts with many others, suggesting its potential significance in the network. Plants with high degree centrality can be considered as hubs that play crucial roles in maintaining network persistence. Since community tipping in our case is primarily triggered by pesticide use, maintaining pesticide levels in the hub plant (the plant with the highest degree centrality) should significantly influence community

tipping. This is because the hub plant, being connected to the highest number of pollinators, can increase the pesticide body burden across a larger portion of the pollinator community. However, it is worth noting that the alternative centrality measure consistently identifies the same nodes (plants) in the majority of the empirical networks we examined.

Once the target plant has been identified, reduction in pesticide application in this particular plant species serves as a highly effective intervention strategy. The extent of pesticide load reduction is contingent on the specific pests and crop production of the communities. To showcased the efficacy of this approach, we provide an example by considering a specific reduction level, such as a 50% decrease. First we illustrate the results for the networks Ⓐ–Ⓓ. We plot the equilibrium abundance with respect to average mutualistic strength (γ) without and with intervention strategy (see Fig. 8). Our results indicates that intervention strategy significantly decreases the extinction threshold of the community (i.e., MGC) with decreasing mutualistic strength. For instance, the network Ⓐ, Ⓒ cannot survive with average mutualistic strength $\gamma = 1.1$. But when intervention acts, the coexistence is restored, though some of the species may go to extinction before the whole community collapse, but the global extinction is delayed (see Fig. S2 in SM Note 5 [74], for the time series plots). Similar results holds for networks Ⓑ and Ⓓ, for $\gamma = 1.2$ and 1.3, respectively. However extinction of few species may be regarded as a precursor of the critical transition in this case. Recovery threshold from the extinction state with increasing γ is also shifted due to the intervention, which means that community recovers from the extinction state for a slight increase in mutualistic strength when intervention is used. In order to
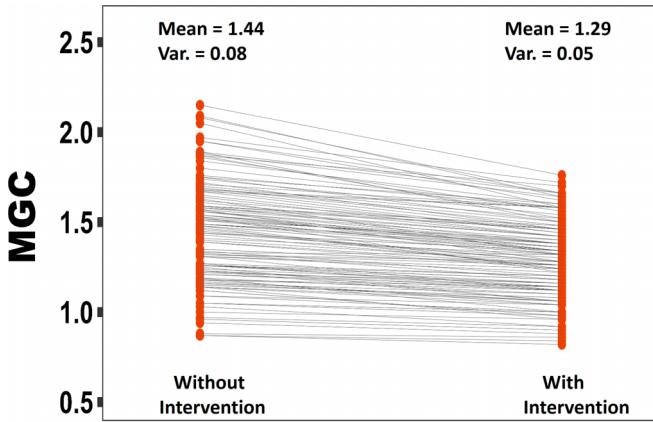
FIG. 9. Tipping thresholds of mutualistic strength (γ) below which community collapses (referred to as MGCs) for all 123 networks both with and without intervention. The mean and variances for both data sets are shown. Remarkably, implementing the suggested intervention on the targeted plant effectively reduces the MGC, as evidenced by a significantly lower mean MGC in the intervention scenario compared to the nonintervention case.

provide a comprehensive view of our findings, we generate a plot of the MGC for all 123 empirical networks, comparing the results without and with intervention (see Fig. 9). It is evident that the intervention significantly reduces the MGC across all real networks, demonstrating the substantial potential of our proposed strategy to delay the tipping point.

VI. DISCUSSION

Plant-pollinator interactions are crucial for biodiversity and crop productivity [92,93], but excessive pesticide use in intensive agriculture threatens pollinators, surpassing the long-term factors like climate change and habitat loss in the current era of anthropogenic changes [59,60]. Pollinators can accumulate pesticides through multiple pathways during their interactions with flowers [63]. This exposure to toxic substances can lead to various lethal and sublethal effects, such as a weakening of the strength of mutualistic interactions and an elevation in mortality rates [62,64–66,68,94]. These consequences can trigger a rapid and irreversible transition from a stable state of coexistence to the extinction, commonly referred to as a tipping point [7,9,29,31,36]. By formulating a PPP model and using 123 real empirical plant-pollinator networks collected from a database as prototype networks, we investigated the effect of pesticide on the tipping phenomenon of a pollination network.

Our study reveals a clear decrease in the abundance of both plants and pollinators as pesticide levels increase, leading to a tipping point where the community experiences a sudden collapse. Importantly, the system cannot recover unless pesticide levels are substantially reduced compared to the threshold at which the collapse occurred, leading to a hysteresis loop [95–97]. The collapse thresholds predicted by our 2D reduced model closely matched those obtained from the full network simulations for all 123 real-world networks, validating its effectiveness in approximating the complex dynamics

of high-dimensional plant-pollinator-pesticide systems. This aligns with numerous previous studies [98–101] that have successfully used dimensional reduction techniques to analyze complex network dynamics. As our real networks were collected from diverse geographical regions across various continents and climatic zones, there are notable differences in their size and structure [87]. These variations directly contribute to the variability in MPTs, which serves as a representation of the threshold pesticide level at which a community undergoes collapses. We observed that a species-rich plant-pollinator network, characterized by low modularity and connectance, exhibits higher tolerance to pesticides. It is worth noting that, in the presence of pesticides, nestedness does not have any statistically significant impact on system persistence and tipping.

We have observed that networks from the African continent tend to have lower species richness but higher connectance and modularity. Consequently, they exhibit a lower MPT. It is also worth noting that pesticide use in Africa is comparatively lower than in other continents [102]. In contrast, European networks display a higher MPT due to their lower modularity and greater species richness. North and South America occupy an intermediate position in terms of MPT rankings. However, pesticide use is high in all the three continents, according to the aforementioned database, suggesting they face a similar risk of tipping as Africa. Furthermore, the MPTs are generally low for regions in the southern hemisphere, primarily due to their lower species richness and higher modularity.

We finally proposed an ecologically viable intervention strategy aimed at sustaining plant-pollinator communities amid global collapse, involving the management of pesticide levels in a single pivotal plant species from the community, as an effective intervention. The targeted plant is, specifically, the highest degree plant, meaning the one with the most interacting pollinators. Pollinators, from most specialist to generalist status, are likely to interact with the highest degree plant of the network. So reducing the pesticide level of the most connected plant or hub of the community can effectively decrease the pesticide body burden of the pollinators. This in turn helps the community to sustain by delaying the tipping. Furthermore, when intervention applies, extinction of some species is seen before the system reaches to its tipping threshold, which may be pointed out as the precursor of the whole community collapse.

The limitations of our study are as follows. First, the pesticides are applied to the crops and managed plants. However, we considered mainly wild plant-pollinator networks (some of our considered networks contains managed plants, as example, the networks with ID: M_PL_032 [103] and M_PL_073 [104]) as prototype, due to the lack of availability of the data. Nonetheless, our PPP model framework is adaptable to various bipartite mutualistic networks, including crop-pollination networks. We believe our findings can be extrapolated to real crop-pollination networks, a hypothesis that field ecologists can potentially verify. Additionally, we did not incorporate pests as state variables into our PPP model. The structure of plant-pest (herbivore) bipartite networks can significantly influence plant-pollinator communities, as demonstrated in Ref. [105], suggesting that a more realistic

approach would involve considering the pesticide effect on a tripartite plant-pollinator-herbivore network. However, we simplified our assumptions by omitting pests. This decision was primarily influenced by the high complexity of our system and the scarcity of real plant-pollinator-pesticide tripartite network data. Nevertheless, it is important to note that we indirectly accounted for the pesticide-induced pest mortality through its observable impact on increased plant growth. Moreover, within mutualistic ecological systems, it is feasible to identify species that can anticipate critical transitions early, and these are referred to as sensor species. This identification can be achieved solely by analyzing the network topology of plant-animal interactions, as demonstrated in Ref. [106]. However, in the presence of pesticides, it becomes particularly intriguing to ascertain the set of sensor species involved in pesticide-mediated critical transitions. Addressing these limitations and exploring future directions will enable us to enhance the monitoring and understanding of plant-pollinator systems under pesticide influence.

Data sets are available in the websites. All computer codes are available from the authors on request.

A.C.: conceptualization, model formulation, method, writing first draft; A.S.: conceptualization, model formulation, manuscript editing; S.M.: method; S.B.: manuscript writing and editing, supervision; Y.C.L.: formulating objectives, manuscript writing and editing.

The authors declare that they have no competing interests.

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