Evading tipping points in socio-mutualistic networks via structure mediated optimal strategy☆

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ABSTRACT

The threat of large-scale pollinator decline is increasing globally under stress from multiple anthropogenic pressures. Traditional approaches have focused on managing endangered species at an individual level, in which the effect of complex interactions such as mutualism and competition are amiss. Here, we develop a coupled socio-mutualistic network model that captures the change in pollinator dynamics with human conservation opinion in a deteriorating environment. We show that the application of social norm (or conservation) at the pollinator nodes is fit to prevent sudden community collapse in representative networks of varied topology. Whilst primitive strategies have focused on regulating abundance as a mitigation strategy, the role of network structure has been largely overlooked. Here, we develop a novel network structure-mediated conservation strategy to find the optimal set of nodes on which norm implementation successfully prevents community collapse. We find that networks of intermediate nestedness require conservation at a minimum number of nodes to prevent a community collapse. We claim the robustness of the optimal conservation strategy (OCS) after validation on several simulated and empirical networks of varied complexity against a broad range of system parameters. Dynamical analysis of the reduced model shows that incorporating social norms allows the pollinator abundance to grow that would have otherwise crossed a tipping point and undergo extinction. Together, this novel means OCS provides a potential plan of action for conserving plant–pollinator networks bridging the gap between research in mutualistic networks and conservation ecology.

1. Introduction

Pollinators serve as an integral component of our ecosystem affecting the growth of nearly 75% of important crops (Garibaldi et al., 2013; Potts et al., 2016c) and global food production worth $235–$577 billion (Aizen et al., 2009; Potts et al., 2016b). From yielding sustainable crops, aiding in reproduction of wide range of flowering plants (Rodger et al., 2021; Wei et al., 2021), insect pollination nurtures biodiversity and ecosystem functioning (Altieri and Nicholls, 1998), and economic welfare (Hanley et al., 2015). Among the leading pollinators are bees (*Apis mellifera*) that have been found to pollinate 90% of the 107 globally essential crops (Klein et al., 2007). Yet bee and other pollinator species worldwide undergo massive extinction each year (Rhodes, 2018). Threats to pollinators include factors such as intense land use, climate change, habitat fragmentation, pests, pathogens, etc (Vanbergen and Initiative tIP, 2013; Potts et al., 2016a). Despite widespread importance, survival rates of managed pollinators across different regions of the globe are estimated at around 45% or less

over the years (Kulhanek et al., 2017; Potts et al., 2010b). Pollinator decline at such a rapid rate incites cessation of pollinator services which shall further disorder balanced human diet causing nutrient deficiencies. Statistics estimate additional 1.4 million human deaths owing to pollinator loss, which contributes to deprivation of 29 million years of healthy living (Smith et al., 2015). From the accumulated evidence, concerns of global pollinator decline are genuine and require focused and timely management to prevent dire consequences (Burkle et al., 2013; Vanbergen and Initiative tIP, 2013).

Traditional conservation policies devoted to managing and rehabilitating individual pollinator species (Soulé et al., 2005). This often misses the indirect influence of interacting species within ecosystems and is held at fault for managed bees that are still at risk. Insect pollinators are individuals that belong to a complex community and may be better managed by the conservation of the interactive components whilst also considering the impact of anthropogenic activities (Borchardt et al., 2021; Faith, 1996). Pollinators are majorly in mutualistic

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interaction with plants and constitute complex higher dimensional networks (Bascompte and Jordano, 2007). Mutualism is attributed to positive interaction amongst species, species gain growth benefits in a community from such interactions and are also predicted to contribute to community productivity. Mutualistic plant–pollinator networks (Bascompte and Jordano, 2013) exhibit characteristic structural properties such as nestedness (Bascompte et al., 2003) and modularity (Olesen et al., 2007), combinations of which are responsible for the stability and persistence of networks (Song et al., 2017; Rohr et al., 2014). The dynamics of plant–pollinator networks are well explained by a set of non-linear mathematical equations and exhibit sudden community collapse or critical transitions from one stable state to a contrasting state in a degrading environment (Scheffer et al., 2001; Lever et al., 2014; Dakos and Bascompte, 2014).

Although conservation of pollinators within the multitude of ecological networks remains largely unexplored, Jiang et al. (2019) have framed strategies such as fixing the abundance and mortality of generalists to a fixed non-zero value and zero, respectively, to delay tippings. While they aid in delaying tippings, implementing these may not always be feasible. Complementing the classical approaches with a modern conservation program coupled with human conservation opinion, i.e., refraining from malpractices (Kearns et al., 1998) will provide a practical strategy for evading tippings in plant–pollinator networks. Studying complex systems as coupled human–environment system (Lade et al., 2013; Levin et al., 2013) and prescribing norms have proven effective at conserving various natural systems such as forest (Bauch et al., 2016), fisheries (Sarkar et al., 2021), Caribbean coral reefs (Thampi et al., 2018), preventing the spread of epidemics (Bauch, 2005; Wang et al., 2015), and many more. With rapid urbanization, human impact on natural systems is rising further. In many complex systems, humans influence them, which in turn impacts human opinion. Nonetheless, this feedback is non-linear and modeled using dynamical equations rather than treated as a constant. The evolution of human behavior towards natural systems changes with their needs and is well described by imitation dynamics from evolutionary game theory (whereby individuals adopt either of two opinions based on their utility) (Sigmund and Nowak, 1999; Weibull, 1997). As stated earlier, pollinators are at constant threat of extinction from factors, some of which are purely anthropogenic such as land use, habitat fragmentation, and overuse of pesticides (Vanbergen and Initiative tIP, 2013; Van der Sluijs et al., 2015; Kennedy et al., 2013). In this context, mathematical models of plant–pollinator networks portraying the dynamics of interacting species include a constant term representing the death of pollinators due to external factors (Lever et al., 2014; Jiang et al., 2019). Whilst this provides some insight into the effects of external stress on pollinators, their modulation by human opinion on conservation may result in a clearer understanding of the anthropogenic influence on the external death rate.

Studies at individual levels to conserve pollinators have provided management strategies that have shown mixed success (Borchardt et al., 2021; Soulé et al., 2005). Some studies on empirical plant–pollinator networks have shown that sustainable management of the agricultural environment, restoration of botanical gardens, removing invasive species and other awareness programs (Bosch et al., 2009; Vilella-Arnizaut et al., 2022) have appeared beneficial in preventing pollinator extinction. To the best of our knowledge, no studies have yet considered a modeling approach incorporating the human dimension within plant–pollinator networks to conserve pollinators amid the risk of sudden extinctions. Under this backdrop, we formulate a socio-mutualistic network model that incorporates human opinion (conservation or non-conservation) at the pollinator nodes (see Fig. 1(a)), intending to alter the fate of the mutualistic community on the verge of extinction. We hypothesize that the complex dynamics of the coupled socio-mutualistic system and network structure play role in preventing collapse as it interplays with the acceptance of conservation opinion. Our results support our hypothesis and show

that applying social norm prevents a community collapse. Significantly, conservationists need to optimize their policies to minimize the cost, i.e., as public opinion alleviates the dire consequences, finding the minimality criteria to achieve the same is also important. Conservation applied at a minimum number of nodes will reduce the cost borne by the governing body, increasing the feasibility and urge for conservation while ensuring the system's recovery from being perturbed. We design a novel optimal conservation strategy majorly deploying network structural properties that can prevent or delay tippings. Further, we validate the strength and generality of our algorithm on both simulated and empirical networks of varied structural properties.

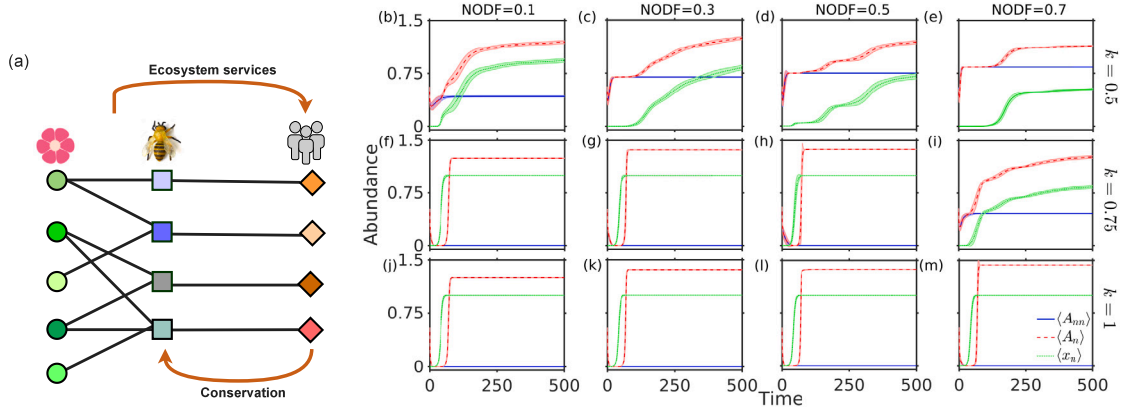## 2. A coupled socio-mutualistic network model

We consider a generic model that describes plant–pollinator interaction (Okuyama and Holl, 2008; Bastolla et al., 2009) and can be tuned to exhibit first order (discontinuous and catastrophic) and second order (continuous and non-catastrophic) transitions in a deteriorating environment replicating real scenarios. The model considers Holling's type-II dynamics and incorporates processes such as intrinsic growth rate, mutualistic interaction between plants and pollinators, inter and intra-specific competition among species, and external death rate of pollinators. We model the dynamics of plant–pollinator networks in the presence of human feedback following the imitation dynamics from game theory (Sigmund and Nowak, 1999; Weibull, 1997). Humans adopt either of two opinions – conservation or non-conservation – depending upon the utility of a particular opinion to them at a level of environmental deterioration. Interestingly, one influences the other, i.e., individuals adopting a particular opinion obtaining more profit influence others to adopt a similar opinion with an associated rate. In our notation, x_j represents the proportion of population at the jth node adopting an opinion C (conservationist) and $(1 - x_j)$ is the part of the population adopting an opinion NC (non-conservationist). The density of x_j and $(1-x_j)$ change as individuals switch between opinions as the pollinator density changes due to variation in external death rate, thus affecting their associated profit. The pressure created due to anthropogenic activities that affect pollinators can be modeled by defining payoff (utility) functions. The rate of change of x_j is given by $\sigma_j x_j (1 - x_j) \triangle U$; with $\triangle U = U_C - U_{NC}$, where $U_C = \hat{d}_j x_j + \frac{1}{A_j + c} - l_j$ and $U_{NC} = \hat{d}_j (1 - x_j)$ are the payoffs associated with conservation and non-conservation opinion, respectively (Levin et al., 2013; Bauch et al., 2016). The parameter $\hat{d}_j$ represents the strength of the social norm, σ_j represents the learning rate, l_j is the cost associated with conservation, $\frac{1}{A_j + c}$ controls the influence of pollinator abundance in accepting the conservationist's opinion, and c is the rarity parameter. Taking into account the above factors, a coupled socio-mutualistic network is modeled by a system of differential equations and is given as follows:

$$\frac{dP_i}{dt} = P_i \left(\alpha_i^{(P)} - \sum_{k'=1}^{S_P} \beta_{ik'}^{(P)} P_{k'} + \frac{\sum_{k=1}^{S_A} \gamma_{ik} A_k}{1 + h \sum_{k=1}^{S_A} \gamma_{ik} A_k} \right) + \mu_P, \tag{1a}$$

$$\frac{dA_j}{dt} = A_j \left(\alpha_j^{(A)} - k_j(1 - x_j) - \sum_{k'=1}^{S_A} \beta_{jk'}^{(A)} A_{k'} + \frac{\sum_{k=1}^{S_P} \gamma_{jk} P_k}{1 + h \sum_{k=1}^{S_P} \gamma_{jk} P_k} \right) + \mu_A, \tag{1b}$$

$$\frac{dx_j}{dt} = \sigma_j x_j (1 - x_j) \left(\hat{d}_j (2x_j - 1) + \frac{1}{A_j + c} - l_j \right), \tag{1c}$$

where $\alpha_i^{(P)}$ and $\alpha_j^{(A)}$ represent the intrinsic growth rate of ith plant and jth pollinator, respectively. k_j denotes the rate of pollinator decline due to external factors, h is the handling time, and $\beta_{ik'}^{(P)}$ and $\beta_{jk'}^{(A)}$ represent the competition strength between plant and pollinator species, respectively. μ_P and μ_A represent the immigration factor of plants and pollinators, respectively, and are incorporated in order to prevent underflow errors or allow the re-establishment of otherwise extinct species. However, these terms do not influence the qualitative

Fig. 1. Socio-mutualistic plant–pollinator networks and their time series evolution: (a) Schematic representation of a socio-mutualistic network comprising a bipartite plant–pollinator network coupled with human conservation opinion. (b)–(m) Average abundances of pollinators for different levels of external death rate k without norm (blue) and with norm (orange) for the four hundred representative simulated networks of varying nestedness (see *SI Appendix*, Section S2, Figs. S2.1(a)–(d)). The evolution of human conservation opinion with time is shown in green. $\langle A_{mn} \rangle$, $\langle A_n \rangle$ and $\langle x_n \rangle$ denote the pollinator abundances averaged over all nodes in absence of social norm, on applying social norm, and the evolution of human conservation opinion (social norm), respectively. The parameter values are: $\alpha_i \in U[0.05, 0.15]$, $h = 0.4$, $\gamma_0 = 1$, $\beta_{jj}^A = \beta_{ii}^P = 1$, $\beta_{jk'}^A (j \neq k') = \beta_{ik'}^P (i \neq k') = 0$, $\delta = 0.5$, $\mu_A = \mu_P = 10^{-4}$, $\sigma_j = \sigma = 0.18$, $l_j = l = 0.14$, $\hat{d}_j = \hat{d} = 0.5$, and $c = 0.5$.

dynamics of the system (Jiang et al., 2018, 2019; Lever et al., 2014). d_i is the nodal degree, γ_{ik} is the interaction strength coefficient and takes the following form:

$$\gamma_{ik} = \epsilon_{ik} \frac{\gamma_0}{(d_i)^\delta}, \tag{2}$$

where ϵ_{ik} denotes the entries of the network interaction matrix (obtained from 144 real-world networks from "http://www.web-of-life.es/" or simulated networks of varied topology); $\epsilon_{ik} = 0$ if a link is absent between the ith plant and kth pollinator species, and is 1 for an active link. A similar expression holds for the pollinator species. γ_0 is the average mutualistic strength, δ modulates the trade-off between the interaction strength and the number of interactions. Zero trade-off (i.e., $\delta = 0$) corresponds to the case of mutualistic interaction strengths not influenced by the network structure. In contrast, a full trade-off ($\delta = 1$) represents a scenario where benefits attained by species from mutualism depend on the network topology. In reality, one often assumes a moderate δ value, and here we consider $\delta = 0.5$ for simplicity. We consider the intraspecific competitions $\beta_{ii}^P = 1$, $\beta_{jj}^A = 1$ and interspecific competitions for plants and pollinators $\beta_{ik'}^P (i \neq k') = \beta_{jk'}^A (j \neq k') = 0$, unless mentioned (however $\beta_{ik'}$ can take any value in $(0,1)$, i.e., intraspecific competition higher than inter-specific competition). In the coupled system (see Eq. (1)(a)–(c)), the external death rate is modulated by human conservation opinion forcing a change in the parameter k_j by $(1 - x_j)$, thus reducing the decline in pollinators by prohibiting undesirable practices. This is an improvement over the traditional approaches that have either considered constant payoffs or framed strategies that conserve only individual pollinator species leading to an expensive affair often preventing social acceptance of conservation opinion. This can be illustrated as saying — the utility of conserving pollinators increases with reduced pollinator abundance, and humans begin to adopt conservation.

Moreover, previous studies reveal empirical mutualistic plant–pollinator networks exhibit non-trivial (non-zero values ranging in the interval $(0,1)$) nestedness and modularity values (Song et al., 2017; Bastolla et al., 2009; Olesen et al., 2007). Whilst nestedness is a celebrated property of plant–pollinator networks (Bascompte et al., 2003), the prevalence of modularity in mutualistic networks is less emphasized. The critical species may vary depending on the context such as some species may be more important for ecosystem functioning while others may be more important in controlling the abundance of other species in the network. However, recent studies reveal that only a proportion

of species in a network are important for ecosystem management and biodiversity preservation (Domínguez-García and Munoz, 2015; Sazima et al., 2010). To determine the structurally important species for network resilience, the aspect modularity is principal too (Olesen et al., 2007; Cagua et al., 2019; Guimera and Amaral, 2005). Naturally, species are selective and may prefer interacting in small groups or modules while only interacting weakly outside modules. Hubs and connector species are some of the key species that, when extinct, can lead to the extinction of the entire community. Motivated by the abovementioned studies, we aim at designing a novel optimal conservation strategy (OCS) to delay or prevent tipping in socio-mutualistic plant–pollinator networks. Within the framework of a coupled socio-mutualistic network, we deploy network structural attributes (Olesen et al., 2007; Bascompte and Jordano, 2013; Fortuna et al., 2019) to frame optimal strategies that evolve with environmental deterioration. In determining the OCS, we start with the most generalist species – the more functionally important species and specialists – species which are more likely to go extinct in individual iterations. While these did not aid in preventing a community collapse, we ponder that large mutualistic networks which are structurally asymmetric and show some degrees of nestedness, species prefer to interact more in small groups forming highly interconnected nodes being less connected to the rest of the network. We explore how both modularity and nestedness can be exploited to find the optimal set of species to prevent a community collapse, which play equivalent roles in the functionality of complex networks.

Further, species comprising ecological networks are constantly influenced by their surrounding environment. Stochasticity or random disturbances omnipresent in natural ecosystems — perpetually affect the species dynamics, abundance, and its response to perturbations (Bjørnstad, 2015). Owing to the above concerns, we investigate the variation in the length of the optimal species to prevent collapse with a change in the intensity of the Gaussian white noise (see *SI Appendix*, Section S4, Eqn. 2(a)–(c)), which acts as an environmental perturbation on the socio-mutualistic network. All parameters, including the mutualistic system and the coupled model, are chosen from the previous studies (Lever et al., 2014; Bauch et al., 2016). We solve both the uncoupled and coupled system using the fourth-order Runge–Kutta method with adaptive step size, and the model is run till a stationary state is reached. In generating nested networks and determining the OCS, we require measuring nestedness and modularity

of the networks. Nestedness is calculated using the NODF (Nestedness metric based on Overlap and Decreasing Fill) measure (Almeida-Neto et al., 2008) and modularity is calculated following the Adaptive Brim algorithm (Barber, 2007) using the BiMat package in Matlab (Flores et al., 2016).

3. Results

We develop a coupled socio-mutualistic network model to prevent a sudden community collapse in mutualistic plant–pollinator networks. We determine the mean change in species abundances (via time series) across 100 networks of varied topology and compare their dynamics in the absence and presence of norm. Next, we observe the change in steady-state abundances of pollinators in 4 networks of distinct nestedness values in the uncoupled system and the coupled socio-mutualistic system. Further, we aim at minimizing the application of norm at the pollinator nodes using an optimal conservation algorithm utilizing the structural properties of the system. We validate the OCS on both the simulated and real networks across a broad spectrum of the parameter space to account for its significance. Finally, in a semi-analytical approach and bifurcation theory, we show how the application of norm transforms a saddle–node bifurcation in the uncoupled system to a transcritical bifurcation in the coupled system allowing an increase in abundance in the latter.

3.1. Evading collapse in the socio-mutualistic network model

We study the dynamics of the socio-mutualistic network model (see Eq. (1)) aimed at preventing community collapse for a gradual increase in the external death rate (k - driver parameter). We generate simulated network interaction matrices (see *SI Appendix*, Section S2) by varying a network structural property- nestedness (Fortuna et al., 2019; Bascompte et al., 2003) keeping the size and connectance of the network fixed. We show the time series evolution of pollinators in both the uncoupled system (*SI Appendix*, Section S1, Eqn. S1) and the coupled socio-mutualistic network model (Eq. (1)) for 100 networks of 4 different nestedness of fixed dimension (25×25) and connectance ($C = 0.15$) (see *SI Appendix*, Section S2, Fig. S2.1(a)–(d)) across a range of values of the driver ($k_j = k$). In the absence of conservation activities driven by social norm, the mean pollinator abundance (A_{nn}), in all the networks remains constant at a non-zero value at $k = 0.5$ or reaches a zero state for $k = 1$. For $k = 0.75$, whilst the pollinator population maintains a non-zero abundance for the network with high nestedness (NODF = 0.7), in the rest of the 3 cases, networks with lower nestedness values remain at the extinction state. Time series well depict the increase in pollinator abundance in the presence of norm (A_n) as the human conservation opinion (x_n) evolves showing an increasing trend (Fig. 1(b)–(p)). One can observe that at $k = 0.5$ (low pollinator decline due to external factors), human conservation opinion gradually increases pollinator abundance. With further increase in k, the pollinators undergo extinction (the pollinator abundance in the absence of norm (A_{nn}) drops below the threshold value of 10^{-3}), and the practicality of conservationist opinion befalls. Notably, applying conservation opinion at the pollinator nodes prevents extinction and increases pollinator abundance A_n in all instances. In Fig. 1, we also show that for small variation in the intrinsic growth rate around the mean, the results remain qualitatively similar.

Moreover, at a low k value ($k = 0.5$) the social norm is less required, also evident from the slow evolution of the conservation opinion. Nonetheless, conservation sentiments, always improve the steady state abundances. With further increase in k value at $k = 0.75, 1$, the urge for conservation increases as pollinators go extinct without conservation. Overall, conservation is always beneficial, improving abundance in situations of no extinction at low k value and preventing extinction at high k value. As observed, the time at which the pollinator abundance

reaches a steady state can be dependent on the network structure (nestedness value) at a fixed k value.

Further, we demonstrate critical transitions in mutualistic plant–pollinator networks in absence of any mitigation (Fig. 2(a)–(d)). For our purpose, we consider the external death rate parameter (k) as the driver parameter since environmental deterioration directly affects its value, further reducing pollinator abundance (Lever et al., 2014). As observed in Fig. 1, small variation in the growth rate about the mean do not affect the system, for the rest of the study for the sake of simplicity we consider fixed parameter values across nodes unless mentioned. In the absence of social norm, with a gradual change in the driver parameter k, the network undergoes a sudden transition from one stable state to an alternate state (Fig. 2(a)–(d)). Applying social norm (human conservation opinion and its evolution modeled by leaning to imitation dynamics model of human behavior) at all the pollinator nodes prevents sudden collapse in the 4 representative mutualistic networks (Fig. 2(e)–(h)). As k increases, pollinator abundance decreases further and stimulates a human response to protect and safeguard pollinators. This act reduces the death of pollinators due to external factors (k value) by regulating their activities. Alongside, implementation of a social norm also prevents sudden decline of plants (if any), and in the absence of tipping, it increases the abundance at the plant nodes (see *SI Appendix*, Section S2, Fig. S2.5). Thus, implementing social norm prevents a critical transition in the plant–pollinator community, which were otherwise inevitable in the absence of a norm.

3.2. Network structure aided optimal conservation strategy (OCS) to prevent community collapse
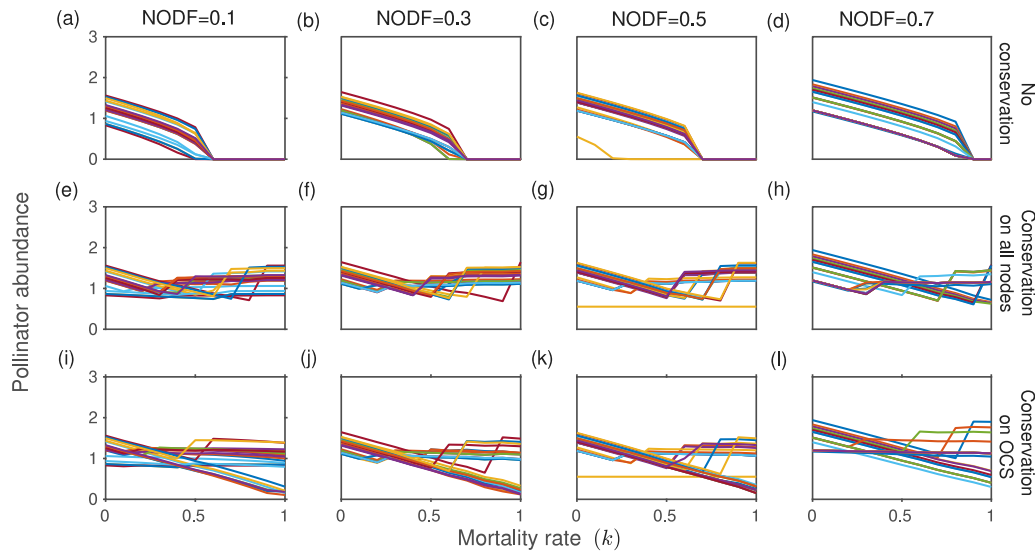
We investigate the structural properties of mutualistic networks to derive an optimal conservation strategy that applies social norms at a minimum number of nodes to prevent community collapse.

Algorithm 1 Algorithm for finding optimal conservation strategy

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1: Calculate total degree (D_j) of all pollinator species within the network, $D = \{D_j | D_j = deg(A_j)\}; j = 1, \ldots, S_A$; S_A is the number of pollinator species.

2: Select all pollinators that have total degree 1 irrespective of their module; $S = \{D_j | D_j = 1\}$; $j = 1, \ldots, S_A$

3: Calculate the number of modules (N) in a network and find the in-module degree of j'-th pollinator in k-th module ($M_{j'}^k$); $j' = 1, \ldots, i^k$; where i^k is the number of pollinator species in k-th module; $k = 1, \ldots, N$.

4: Select the pollinator with the maximum degree in each module and sample them in the set $T_{max} = \{M^k | M^k = max(M_{j'}^k)\}$, for $j' = 1, \ldots, i^k$, $k = 1, \ldots, N$. If two or more pollinators have same in-module degree i.e., $M_{j'}^k = M_l^k$ for any pollinator j', l within k-th module, we find the total degree $D_{j'}$ and D_l of j'-th and l-th species. Choose the species with higher total degree. If $D_{j'} = D_l$, we randomly sample any of the two species.

5: Apply norm on $OS = T_{max} \cup S$ and find pollinator species that go extinct (i.e., abundance $A_j \leq 10^{-3}$, where $j = 1, \ldots, S_A$)

6: If not—stop here else from the set of pollinator species that go extinct $S_E = \{A_j | A_j \leq 10^{-3}\}$ find the module of each pollinator in S_E and their in module degree

7: Select the species with highest in-module degree of pollinator species in S_E $T_n = \{A | A \in S_E; M_A^k > M_y^k \forall y \in S_E\}$ one at a time. Now go to step 5 and update the optimal set $OS1 = OS \cup T_n$. After updating, if $A_j \geq 10^{-3}$ for all $j = 1, \ldots, S_A$, stop here else repeat the process (step 6) and update the optimal set until extinction is prevented for all nodes.

This greedy algorithm means OCS (see Algorithm 1) is built on finding in-module generalists and the uni-degree species in the network

Fig. 2. Conservation opinion at pollinator nodes evade sudden collapse in mutualistic networks: (a)–(d) Sudden collapse of pollinator abundance as derived from the mutualistic plant–pollinator network model not coupled with social norm (see *SI Appendix*, Section S1, Eqn. S1 for the model) for a gradual increase in the external death rate ($k_i = k$). (e)–(h) Pollinator abundance after applying social norm in the socio-mutualistic plant–pollinator network model. Social norm implemented at each node prevents community collapse in all the considered networks. (i)–(l) Applying norm obtained using OCS only at 72% (NODF=0.1), 56% (NODF=0.3), 52% (NODF=0.5), and 64% (NODF=0.7) of pollinator nodes of the 4 representative networks sufficiently prevent community collapse. The different lines in each subfigure correspond to each species in the network. The parameter values are $\alpha_i = \alpha = 0.1$, $h = 0.4$, $\gamma_0 = 1$, $\beta_{jj}^A = \beta_{ii}^P = 1$, $\beta_{jk'}^A (j \neq k') = \beta_{ik'}^P (i \neq k') = 0$, $\delta = 0.5$, $\mu_A = \mu_P = 10^{-4}$, $\sigma = 0.18$, $\hat{d} = 0.5$, $l = 0.14$ and $c = 0.5$. The parameters in all other figures are same with above values unless stated.

and applying norm at this set of species in the initial step. In instances where this does not sufficiently prevent tipping, it next finds the in-module degree of the extinct species from model simulations. Further, we apply the norm on an updated set which is the union of the initial set and the pollinator node with the highest in-module degree among the extinct species as obtained by computing pollinator abundance from simulations of the coupled model.

The OCS aids us in optimizing the number of nodes on which we need to apply the social norm to prevent a community collapse. This algorithm achieves the optimal solution early at step 5 for networks with high nestedness (low modularity). At the same time, it may be required to apply to the entire set for networks with low nestedness (close to zero). The results are valid irrespective of the connectance and size of the network and are computationally feasible for networks with dimensions as large as 1044×456 (as estimated for computation of OCS for a real exemplary network).

As observed in Fig. 2(i)–(l), the application of social norm on the optimal set of species obtained from the OCS algorithm prevents collapse in mutualistic plant–pollinator networks. On the contrary, applying the norm to a set of generalists or specialists of the same cardinality in the hierarchy is not able to prevent community collapse in all instances (*SI Appendix*, Section S2, Fig. S2.6). This may lead us to believe that implementing a social norm at an equivalent set of species only based on species degree may prevent collapse for highly nested networks; even then, conservation strategy applied on the optimal set obtained using the OCS results in comparatively higher pollinator abundance. While this is true, it may be noted that the above simple strategies fail to prevent collapse even in the 4th class of networks (NODF = 0.7) at a higher intraspecific competition strength (*SI Appendix*, Section S3, Fig. S3.1-S3.2). On the other hand, the optimal set of species obtained by our approach can evade community collapse in all the 4 networks of varying nestedness at high competition strengths. Thus we may infer that while initial abundance can destine the fate of a community, the topology of the mutualistic network demands equal surveillance.
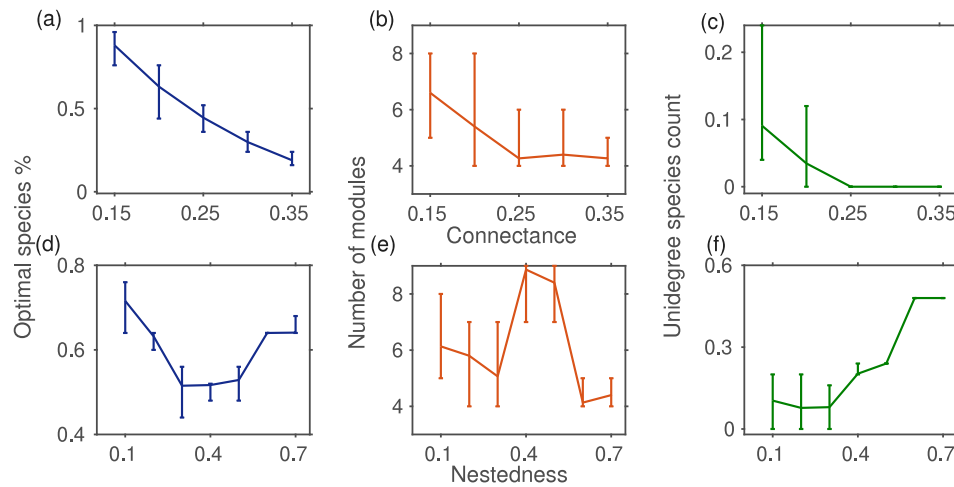
3.3. Generality of the optimal conservation strategy (OCS)

As observed in Fig. 2(i)–(l), adopting conservation opinion at pollinator nodes obtained using the OCS prevents sudden collapse in
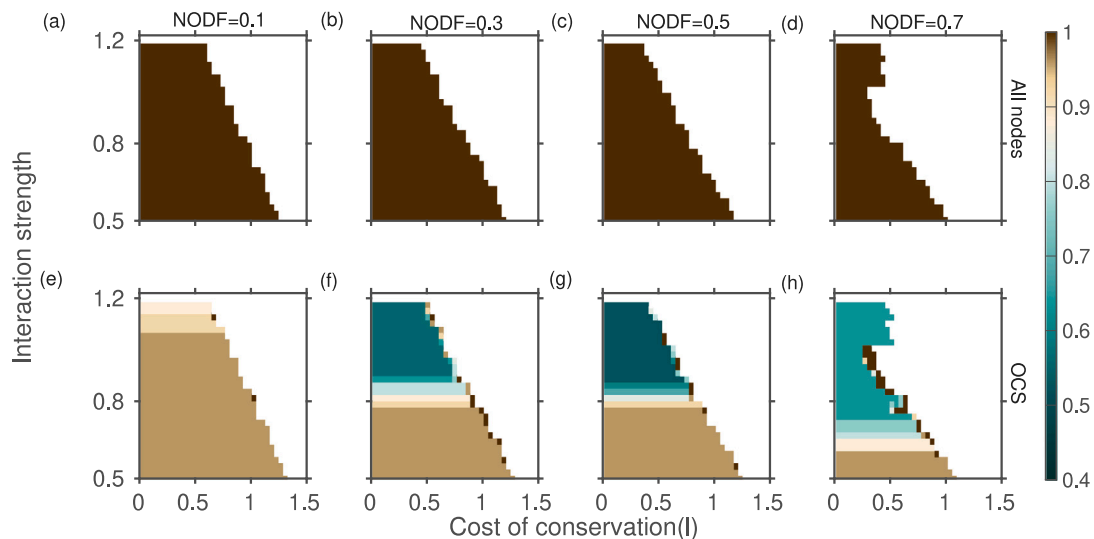
all the 4 networks with different NODF. However, before accepting the OCS as a universal strategy for preventing a collapse in plant–pollinator networks — we analyze the robustness of the OCS to various factors such as connectance, sensitivity to system parameters, and system size. In the process, using an ensemble of 100 networks corresponding to a range of values of connectance (Fig. 3(a)), we show that for an increase in connectance, the % of nodes at which we apply norm using the OCS algorithm decreases, improving the OCS. On the other hand, at a fixed connectance and varying nestedness in a continuous spectrum (Fig. 3(d)), we observe an intriguing result that for intermediate nestedness, the OCS algorithm results in a minimum % of the node to prevent a community collapse. We plot the number of modules (Fig. 3(b)–(e)), and the cardinality of one degree species in each of these networks in Fig. 3(c)–(f). Whilst this is done to envision the factors essential in determining the optimal set, we find that not one factor alone dominates but a combination of species degree and number of modules play a major role.

Next, we investigate the sensitivity of the OCS to other model parameters such as inter-specific competition (β), interaction strength (γ_0), and mutualistic trade-off (δ). While mutualistic interaction strength and competition directly affect community dynamics, mutualistic trade-offs determine whether species interact weakly with many mutualist partners or strongly with fewer species. We plot the % of nodes on which norm if applied, prevents collapse for each of the chosen parameter values (*SI Appendix*, Section S3, Fig. S3.2). We observe that an increase in competition and a decrease in interaction strength leads to an increased number of nodes in the optimal set. Increased trade-offs, which account for the increased effect of asymmetric interaction, also increase the length of the optimal set required to prevent community collapse. Utterly, networks with intermediate nestedness require managing the least number of species to evade a community collapse in mutualistic plant–pollinator networks.

Fig. 4 shows the effects of change in interaction strength (γ_0) and its interplay with the cost of conservation (l) in determining the optimal % of nodes to prevent tipping. The upper and lower panel in Fig. 4 presents the results for applying norm at all the pollinator nodes (Fig. 4(a)–(d)) and on the optimal set obtained using the OCS (Fig. 4(e)–(h)), respectively. The parameter regime for which implementation of a

Fig. 3. Variation in the size of optimal set requisite to prevent sudden collapse for networks of different connectance and nestedness: % of nodes on which successful application of social norm prevents tipping in structured communities with different levels of (a) connectance, and (d) nestedness. Network properties, viz, the number of modules ((b), (e)), and ((c), (f)) the number of uni-degree species for chosen networks are plotted against their level of connectance and nestedness, respectively. The error bars in each subplot correspond to the range for 100 simulated networks corresponding to each structural property.

Fig. 4. Phase diagrams showing the relationship between interaction strength (γ_0) and cost of conservation (l) in determining the size of an optimal set: (a)–(d) Figures show parameter regimes for which tipping can be prevented by applying a social norm on all the pollinator nodes, and (e)–(h) on an optimal set of pollinator nodes, for different values of NODF. The color bar corresponds to the % of nodes that are optimal to prevent tipping. Each sub-figures also shows the region on the parameter space for which conservation opinion fails to prevent tipping (white region).
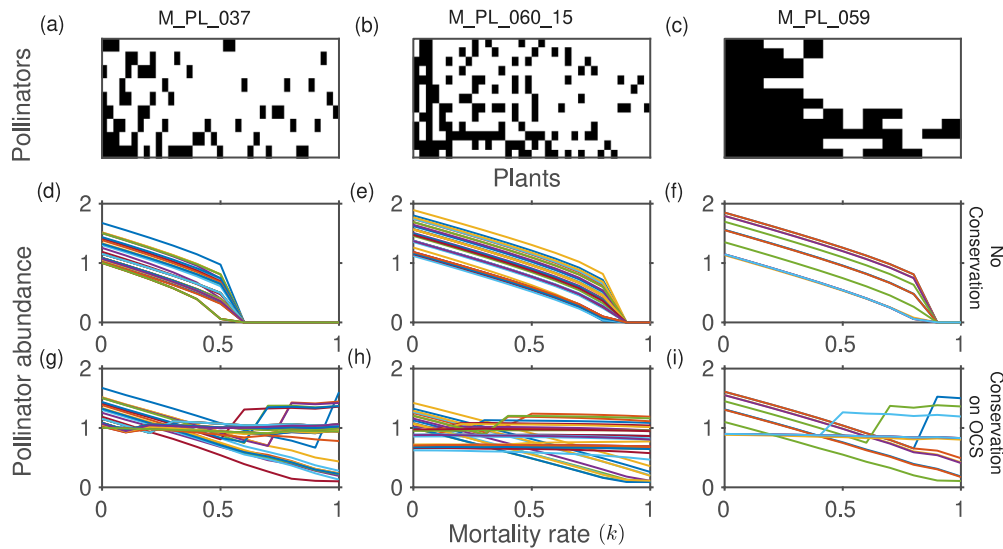
social norm prevents tipping is the same for both the panels, confirming the utility of the OCS. However, for extreme values, the OCS converges at 1. As observed in Fig. 4(e)–(h), model dynamics and further the size of the optimal set depend on the magnitude of the interplaying parameters - γ_0 and l. As γ_0 increases, the size of the optimal set decreases, along with the cost that the system can bear to implement conservation also narrows down. Instinctively at low γ_0, mutualism is weak, and species undergo an early critical transition (the threshold value of k drops) and reduced pollinator abundance, which motivates conservation bearing higher threshold cost. In contrast, at high γ_0, pollinator abundance is larger at a fixed k value, thereby reducing the impulse for conservation at a high cost. Altogether we present the robustness of the OCS while also projecting the change in length of the optimal set with varying network structures by depicting results for the 4 representative networks of varied structures. The interplay of γ_0 with other parameters of the coupled system (see Eq. (1)) show similar changes in the OCS with change in the structure of the network (see *SI*

Appendix, Section S3, Fig. S3.3). Albeit the magnitude of interplaying parameters influences the length of the optimal set, we can court the OCS to evade tippings in socio-mutualistic networks of varied structures as well as dimension (see *SI Appendix*, Section S3, Fig. S3.4).

We observe little to no effect on the optimal set length for increasing the noise intensity to 0.1. Further, an increase in noise intensity beyond 0.1 leads to an increase in the number of species required to prevent collapse, alh fith the amount of increase in the length of the optimal species set is subject to network properties (see *SI Appendix*, Section S4, Fig. S4.1).

3.4. Validation on empirical plant–pollinator networks

We calculate the optimal % of nodes for the 144 real plant–pollinator networks (from the Web of Life: Ecological Networks Database "http://www.web-of-life.es/") of diverse taxonomic precision. In Fig. 5, we

Fig. 5. Validation of the OCS on three distinct empirical plant–pollinator networks: (a)–(c) Matrix representation of empirical networks of varied structural properties. The presence of an interaction in the networks is denoted by black, and white is for no interaction between the respective plant and pollinator. (d)–(f) Critical transitions in the corresponding plant–pollinator networks for gradual change in the external death rate (k). (g)–(i) Application of norm at 75%, 72%, and 54% nodes using OCS prevents tipping in structured communities of different sizes, connectance, and nestedness.

present the structure and dynamics of three empirical plant–pollinator networks. The details of the networks are presented in *SI Appendix*, Section S3, Table. S3.1. A critical transition is evident in all the 3 networks. Application of norm at 75%, 72%, and 54% of the pollinator nodes, respectively, using the OCS (see Fig. 5(g)–(i)) is capable of preventing an upcoming sudden shift to the extinction state. In *SI Appendix*, Section S3, Fig. S3.5, we present trends in the optimal % of nodes for all the 144 networks plotted against their nestedness. The results show that the OCS converges to a number of nodes lesser than the total number of pollinators in most networks despite the diversity in the taxonomy of the empirical networks. The size of the optimal set is heterogeneous across the interaction networks. It converges to the total length of the pollinator node (or 100% only for 6% of the considered networks elsewhere, the size varies from 20–90%). The above result can be explained by the high disparity in the dimension of plants and pollinators and widely varying connectance. We can claim from our results that by using the OCS, we can evade a community collapse by applying norm at fewer pollinator nodes.
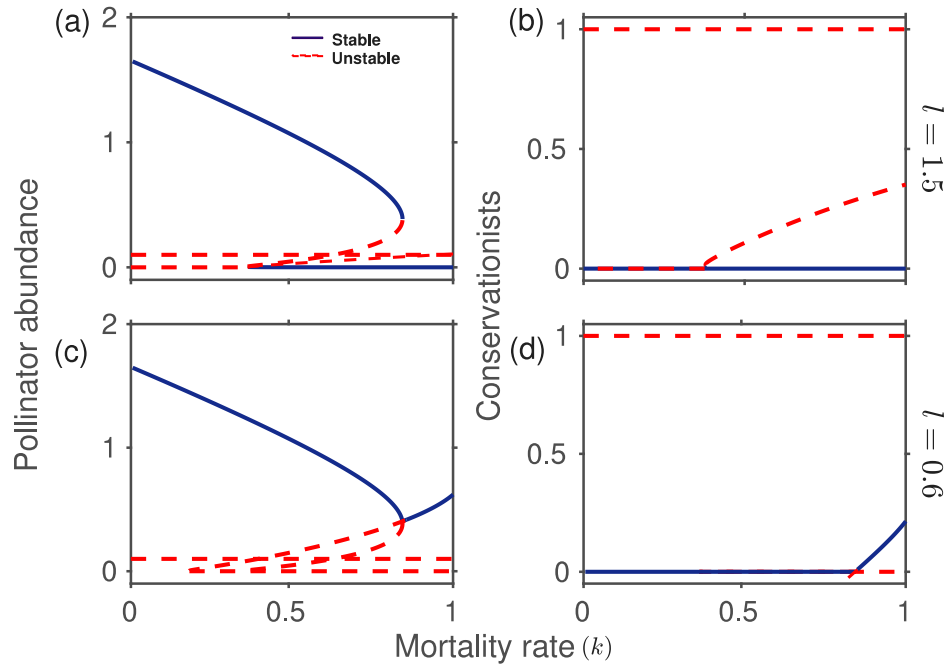
3.5. Dynamics of the reduced model

The higher dimensional mutualistic network model manifests rich dynamics; deriving the equilibrium points and performing stability analysis is cumbersome. To mathematically investigate the dynamics of the above model, we perform dimension reduction by considering the averaged value of mutualistic interaction strength of plants and pollinators as in Jiang et al. (2018). This allows us to carry out bifurcation analysis and find the stability regions. For the dimension-reduced socio-mutualistic network model (*SI Appendix*, Section S5, Eqn. S3), we plot the abundance for both state variables — pollinator (A) and human conservation opinion (x) at high and low cost of conservation (l) (Fig. 6). We observe that at high cost ($l = 1.5$) the system undergoes a fold bifurcation (Fig. 6(a)) while the system experiences a transcritical bifurcation at low cost ($l = 0.6$) (Fig. 6(c)). Thus, bifurcation analysis of the reduced model supports our results for the higher dimensional system and guarantees that the application of a social norm can debilitate the occurrence of a catastrophic transition and the system undergoes a gradual increase in abundance via a transcritical bifurcation. The fixed points and stability analysis of the reduced model are presented in (*SI Appendix*, Section S5, Fig. S5.1).

4. Discussion

Recognizing the dependence on pollinator services (Novais et al., 2016; Kevan and Phillips, 2001) and the significant rate of decline in pollinator abundance (Potts et al., 2010a), pragmatic management strategies are the need of the hour. While the major threats to pollinators have been identified, policies formulated in favor of indigenous practices to prevent pollinator loss, such management strategies of individual species (Soulé et al., 2005) fall short of providing success at a collective level. Some initiatives at protecting habitats of plant–pollinator communities, restoring grasslands patches in botanical gardens (Vilella-Arnizaut et al., 2022), preventing invasion by alien species, and preserving plant–pollinator interactions (Borchardt et al., 2021) have shown promising impacts on pollinator communities. Amidst the rising concerns and demand for efficient and cost-effective mitigation strategies, our proposed socio-mutualistic network model provides with a theoretical framework for integrating human conservation practices and estimating parameter bounds for preventing tippings in plant–pollinator networks. Guided by the reduced socio-mutualistic model (that well depicts the dynamics of the higher dimensional system), the coupled model is analyzed further to achieve an optimal strategy to prevent a collapse of plant–pollinator networks. Human conservation opinion at the pollinator nodes prevents a critical transition in the system while allowing a gradual transition followed by an increase in abundance of both the mutualist partners irrespective of the network topology. We step forward to achieve an optimal strategy that prevents community collapse by applying social norm at a minimal number of nodes. While this is being done, obvious directions include deploying degree distribution of species and conserving generalists. As observed from obtained results, they do not always appear productive under harsh conditions and diverse structures. Species with functional dissimilarity are less likely to influence each other. In light of the fact, exclusively the generalists or specialists in the network may not prevent the extinction of other species in reality.

With regard to the above concerns, we develop the OCS that applies norm on more functionally dissimilar species with a higher degree as well as the uni-degree species in the first attempt to prevent collapse. We observe that the OCS algorithm converges at this step for highly nested networks. In contrast, for networks with moderate to low nestedness, the algorithm converges only after a few repeated iterations

Fig. 6. Bifurcation diagrams depicting dynamics of the reduced socio-ecological mutualistic network model: Change in the dynamics of ((a),(c)) pollinator abundance, and ((b),(d)) social norm for a gradual increase in the mortality rate (k) at cost of conservation $l = 1.5$ (a–b) and $l = 0.6$ (c–d), obtained for the reduced socio-mutualistic network model (see *SI Appendix*, Section S5, Eqn. S3). At a lower cost of conservation (i.e., $l = 0.6$), catastrophic collapse of pollinator community can be prevented and the system undergoes a non-catastrophic transition via a transcritical bifurcation. Other parameter values are $\alpha = 0.1$, $h = 0.4$, $\gamma_0 = 1$, $\beta_{jj}^A = \beta_{ii}^P = 1$, $\delta = 0.5$, $\mu_A = \mu_P = 10^{-4}$, $\sigma = 0.18$, $\hat{d} = 0.5$, and $c = 0.5$.

of step 6 of Algorithm 1. However, for all the networks, the OCS is achieved in finite time, although harsh conditions such as high competition, high mutualistic trade-off, or low mutualistic strength increase the length of the optimal set of species. High nestedness in plant–pollinator networks has been previously associated with increased stability and delayed critical transition (Tylianakis and Coux, 2014). While this is so, management of plant–pollinator networks with intermediate nestedness requires conservation opinion at a minimum number of nodes to prevent collapse when compared across networks of fixed size and connectance. Key to the applicability of the OCS — is its potential to enhance the abundance of the plants within the network alongside preventing pollinator collapse while implementing social norms only at the pollinator nodes. However, this is forbidden at a high k value, when improving pollinator abundance is more difficult, although extinction is prevented with the OCS algorithm. The OCS is likely to provide a minimal set of nodes in the face of disturbances in the system expressed in terms of environmental noise (see *SI Appendix*, Section S4, Fig. S4.1).

Though, fitting empirical data to the coupled model and obtaining the norm parameters would strengthen our study, we are limited by the availability of empirical data on the benefits of conservation on the abundance of plant–pollinator networks in the required form. The rationale behind coupling the plant–pollinator system to the parameters of the norm system of a very different natural system (Bauch et al., 2016) is that the differential equation governing the social norm dynamics constitutes a non-dimensionalized system. Further to account for the generality of the coupled socio-mutualistic system and our proposed algorithm we perform sensitivity analysis against variation in the norm parameters (see Fig. 4, *SI Appendix*, Section S3, Fig. S3.3). The effect of social norm holds good over a large region in the norm parameter space except for variation in strength of the norm ($\hat{d}_j = \hat{d}$) results in different outcomes on the coupled system. Interestingly starting with a low initial abundance of conservationists, the effect of $\hat{d}$ is surpassed at a low to intermediate cost of conservation. At a high cost of conservation, for a low $\hat{d}$ value the system oscillates in a vicious cycle, where the

system evolves from no conservation thus conserving pollinators. With an increase in the strength of the norm $\hat{d}$, conservation is repressed and at a very high value of $\hat{d}$, the system remains at the extinction state (see *SI Appendix*, Section S2, Fig. S2.3–S2.4).

Our study takes a novel approach to develop a structure-mediated optimal strategy within a modeling framework opening up prospects of preventing community-wide collapse of the plant–pollinator system with cost-effective conservation practices. While it achieves its primary goals, there are some limitations and trade-offs of the current study which may be improved or reduced with further investigation along this direction in future projects. Firstly, the cost savings of conserving fewer species (i.e. the OCS set rather than all pollinators) is offset by a decline in pollination and plant biomass at high k value, when improving pollinator abundance with conservation is more difficult, nonetheless, conservation prevents extinction. Another important concern prevalent in a socio-coupled system of highly interconnected networks is free-riding where some groups may enjoy the reward of conservation without sharing the cost borne by the latter. This creates an imbalance in the community leading to a lack of faith and reduced conservation practice by the community in the long term. In context, determining the distribution of conservation nodes or finding the degree of randomness of the optimal species across networks is crucial. For instance, if the optimal species share some degree of autocorrelation with other species across networks, this shall promote conservation sentiment at the other nodes contributing to the conservation of the optimal set of nodes, and reducing the free-riding of non-conservationists. Intuitively, the formation of a checkerboard-like pattern in the socio-mutualistic network is likely to be correlated with the nestedness of the network, networks at very high nestedness with an increased number of specialists are less likely to form such a pattern compared to others. Computing an equivalent C-score (Novak et al., 2011) for mutualistic networks can answer the question and is a potentially important aspect pertaining to the conservation of mutualistic networks.

The current study is focused on OCS in mutualistic plant–pollinator networks, the utility of the above algorithm can be verified in the class

of mutualistic networks across interdisciplinary fields exhibiting similar characteristic properties. Apart from mutualistic networks, modular structures have been associated with increased persistence in multi-trophic food webs such as bipartite plant–herbivore food webs (Stouffer and Bascompte, 2011; Garay-Narváez et al., 2014). Another future avenue of research includes applying the algorithm to another complex two-layered food web network or modifying the same for conserving endangered species in food webs with higher trophic level interactions with analogous structures (Garay-Narváez et al., 2014; Kortsch et al., 2019). Acknowledging the numerous merits despite limitations, the OCS is a first pass management strategy to prevent community extinction requiring further expending upon and application to higher dimensional systems at risk. In our approach, we present a novel restoration policy using evolutionary mechanisms reinstating ecological plant–pollinator networks with ample scope of execution for the conservation of other ecological networks in future endeavors. Currently, our modeling approach deals with human opinion to conserve pollinators locally, a far more simplified set up. However, humans can influence such networks globally as well as at different scales. This, may be incorporated within the model with further modifications. For instance, the influence of human social learning on sustainable management of agriculture, restoring gardens and orchids and other initiatives toward improving the habitats for plant–pollinator networks can occur at-a-distances, e.g. through travel, telephone, and social media. Modeling a coupled socio-mutualistic system incorporating these factors can further reduce the size of the optimal set of species of conservation.

CRediT authorship contribution statement

Smita Deb: Performed the simulations, Analyzed the results, Discussed the results, Writing – original draft. **Subhendu Bhandary:** Performed the simulations, Analyzed the results, Discussed the results, Writing – original draft. **Partha Sharathi Dutta:** Conceived the study, Discussed the results, Writing – original draft.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Codes and data are available in a Zenodo repository (http://dx.doi.org/10.5281/zenodo.7327476).

Appendix A. Supplementary data

Supplementary material related to this article can be found online at https://doi.org/10.1016/j.jtbi.2023.111494.

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