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RESEARCH ARTICLE

Network Ecology in the Anthropocene

Complexity promotes stability in mutualistic networks through weaker mutualistic dependencies: Insights from Generalized Modelling

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Abstract

1. Mutualistic networks provide essential contributions to long-term ecosystem functioning and food security, but Anthropocene stressors continue to alter their structure and size. Previous theoretical approaches produce conflicting predictions for how network features influence dynamical stability, which is the ability to return to the original state after a disturbance. The main methods, which are random matrix models and conventional differential equation models, face certain limitations, including difficulties in incorporating some biological details or explicit parameterization. An alternative approach is given by Generalized Modelling, which combines both high efficiency with high biological realism, but has not been applied to plant-animal mutualistic networks prior to this study.
2. Here, we develop a Generalized Model for mutualism that allows the mathematically rigorous and highly efficient analysis of dynamical stability for many network replicates ($\sim 10^5$ per data point). The model incorporates important biological mechanisms that are known to influence stability behaviour, such as animal competition for limited plant resources and saturating mutualistic benefits, without the need for explicit parameterization.
3. Using simulated network structures we find increasing dynamical stability with increasing complexity as measured by the product of species richness and connectance. We are able to explain this effect mechanistically: While mutualistic interactions do represent destabilizing positive feedbacks, the strengths of those feedbacks weaken with increasing complexity because mutualistic dependencies as given by the Jacobian matrix elements in the off-diagonal blocks decrease. We further show that the effect of nestedness on the dynamical stability of simulated

Timo Metz and Jan Timo Bachmann contributed equally to this work.

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networks is negligible compared to the effect of connectance and species richness. Additionally, we find similar relationships between network features and dynamical stability for 160 empirical networks as an input for our model, highlighting the robustness of our findings.

4. As Anthropocene stressors lead to species and interaction loss, our model results predict a corresponding loss in dynamical stability if network complexity is decreased, highlighting the urgency of conservation strategies that preserve network complexity.

KEYWORDS

complexity, dynamical stability, feedbacks, Generalized Modelling, mutualistic networks, Nestedness, plant–pollinator networks

1 | INTRODUCTION

Mutualistic networks, such as seed-dispersal or pollination, are globally under pressure (Dicks et al., 2021; Ghisbain et al., 2024; Hallmann et al., 2017; Williams & Hemberger, 2023). Increasing stressors in the Anthropocene such as land-use change, invasive species, pesticide use and global warming drive losses of species and interactions and accordingly cause changes in network structure and size (Potts et al., 2010; Tylianakis et al., 2008; Valiente-Banuet et al., 2015). This poses the question of when networks reach tipping points at which their ability to recover from disturbances is lost (Bascompte & Scheffer, 2023; Huang et al., 2021; Scheffer et al., 2001). Mutualistic networks provide essential services to plant reproduction, with 88% of flowering plants depending on animal pollination (Ollerton et al., 2011) and animal-mediated pollination supporting 35% of global crop production (Klein et al., 2007). Therefore, preventing their collapse is of high importance to long-term ecosystem functioning and food security.

While many different stability metrics exist (Kéfi et al., 2019), dynamical stability provides a simple and intuitive measure of stability by analysing whether a system will return to its original state after a perturbation. Knowledge of the main drivers that confer dynamical stability in networks is crucial to stopping and potentially reversing mutualistic network collapse.

Studying the stabilizing effect of network complexity (defined here as the product of species richness and connectance in accordance with May (1972) and Gross et al. (2009)) compared to the effect of network structural patterns is especially relevant in that regard, as it is important to know whether conservation efforts should be targeted specifically to preserve certain network features to avoid network destabilization. However, despite much research in this field in recent years, the impact of varying structural features on dynamical stability of mutualistic networks remains debated (Valdovinos, 2019).

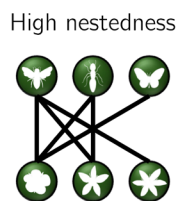
Complexity was initially believed to increase the stability of ecological systems (McCann, 2000). May (1972), however, showed that dynamical stability is negatively related to complexity in random

communities using random matrix theory. This negative relationship was also confirmed for purely mutualistic interactions (Allesina & Tang, 2012). On the contrary, studies using conventional dynamical models based on differential equations showed positive relationships of complexity with other stability metrics such as resilience (Huang et al., 2021; Okuyama & Holland, 2008; Thébault & Fontaine, 2010) and persistence (Thébault & Fontaine, 2010) for mutualistic networks.

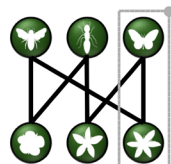
Empirical mutualistic networks are often found to exhibit a non-random nested pattern, where species with few links tend to interact more with species with more links (Figure 1a) (Bascompte et al., 2003). An interaction matrix is maximally nested when there is a strict hierarchy where partners of specialists are subsets of partners of generalists. A nested pattern thereby maximizes niche overlap of interacting species and thereby leads to functional redundancy, but also an increased competition for mutualistic resources. This observation sparked interest in the potentially stabilizing properties of nestedness. However, there is also evidence that nestedness in empirical networks may arise as a sampling artefact or by the co-occurrence of common and rare species alone (Blüthgen et al., 2008; Blüthgen & Staab, 2024; Valdovinos, 2019). Random matrix models showed nestedness to decrease dynamical stability in mutualistic networks (Allesina & Tang, 2012). Some studies based on conventional dynamical models based on explicit differential equations found nestedness to have a stabilizing role (Bastolla et al., 2009; Okuyama & Holland, 2008; Rohr et al., 2014; Thébault & Fontaine, 2010), but others challenge these findings (Benadi et al., 2013; Chattopadhyay et al., 2025; James et al., 2012; Pascual-García & Bastolla, 2017; Saavedra et al., 2016).

While conventional dynamical models allow easy biological interpretation, results are heavily dependent on model assumptions and parameter choice, which could explain diverging results. Since it is computationally expensive to perform linear stability analyses for large and complex systems using such conventional models, strong simplifications are necessary to obtain analytically solvable equations to calculate dynamical stability. Random matrix theory, on the other hand, is a powerful tool that allows highly rigorous mathematical and efficient numerical investigation, but it is a fairly abstract approach that is not designed to accommodate a detailed description

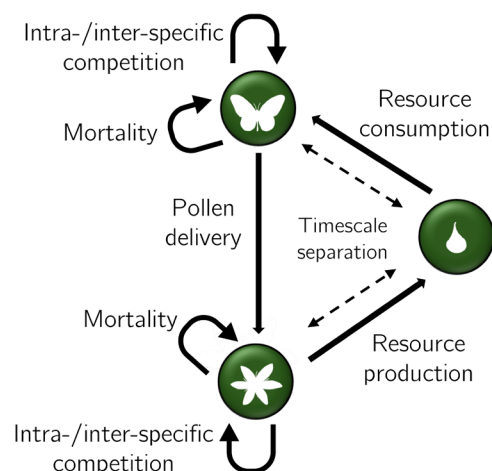
(a) Mutualistic interaction network structure



Low nestedness



(b) Dynamical model



(c) Generalized Modeling procedure and simulation structure

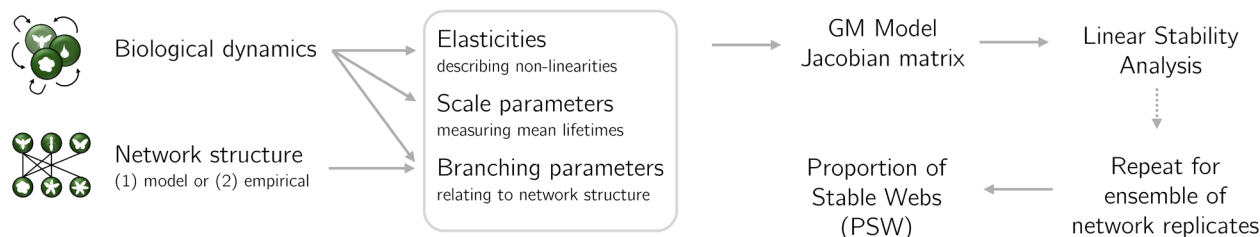


FIGURE 1 Illustration of the Generalized Modelling approach. (a) We generated mutualistic interaction networks with a given species richness and connectance, and a varying degree of nestedness. (b) We developed a Generalized Model for the plant–pollinator dynamics, which contains self-regulation and the service-for-resource mutualism. (c) The details of the dynamical model and the network structure determine the dynamical behaviour in the form of three different types of parameters which emerge naturally during the Generalized Modelling procedure: Elasticities measure the non-linearity of the different processes capturing different dynamical regimes, scale parameters measure the strength of the biomass turnover at the steady state and are thus related to the mean lifetimes, and branching parameters describe the relative contribution of species to processes and are related to the network structure. Those three types of parameters constitute the Jacobian matrices which are used for performing the linear stability analyses. We used both simulated model networks and empirical networks, and evaluated for each network whether it is stable or not. Repeating the simulation procedure for a whole ensemble of networks while varying network structures and parameter values within biologically realistic intervals allows calculation of the proportion of stable webs (PSW) as an indicator for stability as a function of species richness and network structure.

of underlying biological processes and can be hard to interpret. For instance, random matrix models draw interaction strengths randomly from statistical distributions without connecting them to biological mechanisms such as resource competition or saturating benefits.

Generalized Modelling (Gross & Feudel, 2006) combines the advantages of random matrix models and conventional dynamical models: the approach allows the direct and highly efficient computation of the Jacobian matrix (which captures how small changes in one species' abundance affect other species and thereby governs local stability dynamics), while including multiple relevant biological features known to influence stability, such as dynamical properties of resource dynamics and animal competition for finite resources. The effect of species relative abundances, network structure and the sensitivity of biological processes can all be investigated independently, allowing a mathematically rigorous stability analysis that admits meaningful biological interpretation. A key strength of

Generalized Models is that parameters are typically taken from intervals constrained by biological mechanisms rather than being set to specific values. Dynamical stability is then reported as the proportion of stable webs (PSW), thereby showing insights applicable to a large class of realistic mutualistic models instead of representing particular parameter choices. Generalized Models have already seen wide usage across disciplines (Massing & Gross, 2022), for example, to identify a negative complexity–stability relationship for food webs (Gross et al., 2009).

Here, we develop a novel Generalized Model for bipartite plant–animal mutualistic networks to investigate the influence of network structure, in terms of connectance and nestedness, and species richness on dynamical stability. While we use the language of plant–pollinator networks, the model is also applicable to other mutualisms such as plant–frugivore mutualisms or plant–ant mutualisms and the results thus transferrable (see Supporting Information Material S2).

2 | MATERIALS AND METHODS

2.1 | Developing a Generalized Model for mutualistic networks

We consider a system where the number of plant species is S^p and the number of pollinator species is S^a . We denote the population density of a plant species i as P_i and that of a pollinator species j as A_j . Each plant species i produces a resource, whose density per individual is denoted as N_i . P_i , A_j and N_i change over time according to the balance of strictly positive gain processes G and loss processes L , which can be described by differential equations of the form

$$\dot{P}_i = G_i^p(P_i, H_i^p, T^p) - L_i^p(P_i, T^p) \quad (1)$$

$$\dot{A}_j = G_j^a(A_j, H_j^a) - L_j^a(A_j, T^a) \quad (2)$$

$$\dot{N}_i = G_i^n(T^p) - L_i^n(H_i^n, P_i) \quad (3)$$

where the dot denotes the rate of change, $T^{p,a}$ denote the cumulative plant or pollinator population densities, H_i^p denotes the total pollen transfer of plant species i , H_j^a the total nectar consumption by pollinator species j and H_i^n the total nectar extraction from plant species i .

As the specific kinetics of processes are often not known, Generalized Models do not restrict process functions such as G_i^p to specific functional forms. Biological mechanisms are modelled through the dependence of the gain and loss processes on generalized variables and their inter-dependencies (see [Figure 1b](#); [Figure S1](#)). These dependencies are captured in three types of parameters that emerge during derivation of the Generalized Model (see [Figure 1c](#) and Supporting Information [Text S1](#)): First, scale parameters measure population density turnover. At the steady state, gains and losses must balance, but the strength of gains and losses per time can be larger or smaller. This is related to the average lifetimes. A ratio of plant and pollinator scale parameters of, for example, 100 reflects conditions in a forest with trees with average lifetimes much longer than those of their pollinators (100 years compared to 1 year). Second, branching parameters capture how processes, such as visitation and successful pollen transfer, are distributed among partner species, as shaped by the network structure. Third, elasticities describe how (e.g. linearly, sublinearly or superlinearly) processes or sub-processes (such as successful pollen transfer) depend on other sub-processes (such as number of visits) or population densities. These three types of parameters constitute the Jacobian matrix of each network (see [Figure 1c](#)), which captures its dynamical stability. While the branching parameters are determined by the network structure, scale parameters and elasticities can be set or varied in reasonable ranges based on biologically plausible mechanisms (Supporting Information [Text S1](#)).

Plant and pollinator species' growth depends on the total amount of the provided service or resource ([Figure 1b](#)), but also on their own population densities, such that both obligate and facultative mutualisms can be described by the model. Plant species are (self-)regulated

by intra-specific and interspecific competition and mortality through the dependence of the growth and loss processes on their own population density and the cumulative population density of all plant species. Pollinator species are (self-)regulated similarly with the difference that interspecific competition is dominated by competition for finite resources, which is included explicitly through the resource dynamics. Resource production may depend on the cumulative plant densities due to plant competition for abiotic resources. Resources are lost through extraction by pollinators. We use a timescale separation between consumer and resource dynamics so that resource levels are always at equilibrium with respect to the consumption rates. The limited production rate of resources leads to competition between consumers, and we therefore need not include an explicit interspecific competition term.

Performing the Generalized Model procedure for a large ensemble of network replicates allows us to calculate the fraction of stable networks as a stability metric, which we call the PSW similar to previous Generalized Model studies (Gross et al., 2009; Gross & Feudel, 2006; Massing & Gross, 2022). The efficiency of the Generalized Modelling method allows performing simulations for ensemble sizes of the order of $\sim 10^5$ networks per data point for our study.

2.2 | Simulations using model networks

All calculations were done in Julia v1.9.1. R packages were used inside Julia-Scripts using the package *RCall* v0.13.17. Visualization of the data was done in Python v3.10.9.

We generated networks with varying connectance and nestedness using the algorithm from Thébaud and Fontaine (2010): We first drew for each species a measure of generalization, which we call *degree* in the following, although this measure is not equal to the resulting actual number of links. We drew the degrees from a scale-free distribution for all plant and pollinator species, where the probability of a species to have degree k follows a power law $P(k) \sim k^{-\gamma}$ with the degree exponent $\gamma = 2$. For each link, we picked one plant and one pollinator species. With probability p_{nest} , we picked both species with probabilities proportional to their assigned *degree*. With probability $1 - p_{\text{nest}}$, we picked both species randomly using a uniform distribution. This was repeated until the desired connectance was reached. Unless otherwise stated, the parameter p_{nest} was drawn from a uniform distribution between 0 and 0.5. For high p_{nest} , this algorithm has been shown to generate nested matrices (Thébaud & Fontaine, 2010), where species with few links tend to interact more with species with more links. The above description is valid for all networks shown in [Figures 3, 4 and 6](#). For the networks shown in [Figure 5](#), we also systematically varied the modularity alongside the connectance and nestedness according to the algorithm from Thébaud and Fontaine (2010). For this, two rules were applied that lead to the modularity and the nestedness patterns, respectively. The first rule (the nestedness pattern) follows exactly the procedure described above. For the second rule (the modularity pattern), each network was split in four modules of similar sizes and each species assigned to one module. Then, a plant

or pollinator was randomly picked from all species in the network. With a probability p_{comp} , the interaction partner of that species was picked randomly among pollinators or plants of the same module as the initial plant or pollinator. With a probability p_{comp} , the interaction partner was picked randomly among all other animals or plants in the network. To construct networks with varying modularity and nestedness, the first interacting partner was selected according to rule 1 and hence depended on p_{nest} . The range of interacting partners that could be selected for that species was defined by rule 2, depending on p_{comp} . The specific partner within that range was then again selected with rule 1, hence depending on p_{nest} . The nestedness of the interaction matrix was then quantified via the *nestedness metric based on overlap and decreasing fill* (NODF) using the *nestednodf* function from the R package *vegan* v2.6.4. The modularity was calculated using the *computeModules* function from the R package *bipartite* v2.20. We used a connectance range of $[0.1, 0.7]$ and a total species richness range of $[20, 150]$. The connectances were drawn from a uniform distribution within the given interval. We used a minimum species richness of 10 plant and 10 animal species, with a corresponding minimum possible connectance of $C_{\text{min}} = 0.1$. We used this connectance value therefore as a minimum for all our simulations, while we chose a maximum value of $C = 0.7$ according to the maximum connectance value of empirical mutualistic networks, as reported in the web of life database (see Figure 2). We used a maximum species richness of 90 plants plus the same number of animal species, as this leads to a total species richness that is rather large compared to most empirical networks found (see Figure 2). Larger species richnesses were not studied as these were computationally expensive to investigate and no further insights were expected to be drawn from the analysis.

During the simulation procedure, we deal with two different types of matrices: the (binary) mutualistic interaction matrices with their associated connectance and nestedness, which are generated via the procedure described in the previous subsection, and the Jacobian matrices which carry the information about the dynamical

stability of the networks. The Jacobian matrix of a network is obtained from the interaction matrix and the Generalized Model parameters according to Equation (56–63) in Supporting Information Text S1. We calculated the eigenvalues of the Jacobian matrix using Julia's *eigvals* function from the *LinearAlgebra* package. If all real parts of the eigenvalues of the Jacobian matrix were negative, the network was considered dynamically stable, otherwise it was considered unstable. We repeated this procedure for a set of network replicates to obtain the fraction of stable networks, which we call the PSW. Throughout the study, we used ensemble sizes of the order of 10^5 for calculating ensemble-averaged quantities such as the PSW. The fits were performed with the function *curve_fit* from the package *scipy.optimize* v1.10.0.

2.3 | Simulations using empirical networks

We downloaded 165 interaction networks from the web of life (<https://www.web-of-life.es/>, last access: 9 October 2023). Ethical approval was not required for data analysis in this study as no new data was collected. We inserted the respective interaction matrix into the expression for the Jacobian matrix given in Equation (56–63) in Supporting Information Text S1. For each empirical interaction network, we performed 10^4 simulations, for each simulation drawing elasticities randomly from suitable distributions as given in Table S2. In each simulation, we performed a linear stability analysis as described in the previous subsection, to obtain the proportion of stable webs PSW for each empirical network. For five networks (M_PL_006, M_PL_026, M_PL_044, M_PL_062, M_PL_063), it was not possible to create random networks with the same nestedness as the empirical networks with sufficient numbers.

To compare the networks based on empirical topologies with randomized reference networks, we generated for each empirical structure 10^4 (i) networks with the same species richness, connectance

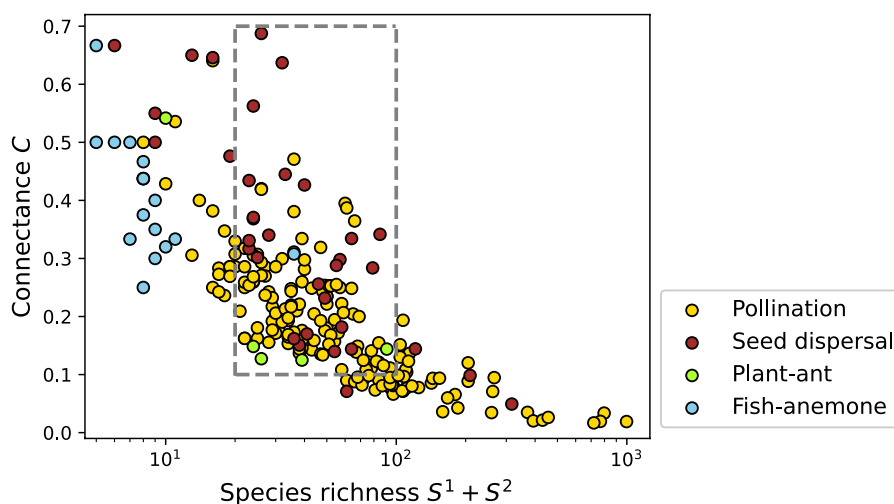


FIGURE 2 Connectances and species richnesses of empirical mutualistic networks. Networks taken from the web of life database (<https://www.web-of-life.es/>). The grey dashed lines show the connectance and species richness of the model networks used in this study, which contains 58% of all mutualistic networks and 60% of all pollination networks of the database.

and nestedness, and (ii) networks with the same species richness and connectance but a randomized link distribution, with the algorithm by Thébault and Fontaine (2010). For case (i), we generated networks with varying p_{nest} using the condition that the nestedness in terms of the NODF has to be within ± 5 of the nestedness of the respective empirical structure. In case (ii), we used $p_{\text{nest}} = 0$. Therefore, each link is drawn with equal probability between any plant and pollinator species.

We again performed a linear stability analysis for each of the reference networks and calculated their nestedness, in order to compare the PSW and nestedness of the networks based on empirical topologies and those based on randomized reference topologies.

2.4 | Statistical analyses

We used a Generalized Linear model (GLM) in R with binomial error distribution and logit link function to investigate the effects of connectance, nestedness and modularity on the PSW of model networks with fixed species richness (see Figure 5). All predictors were scaled (mean=0, standard deviation=1) prior to analysis. The response variable (PSW) was modelled as a Bernoulli experiment with stable and unstable as an outcome for each replicate. Each simulation served as a replicate in the model. The model included the main effects and their interaction term. The following equation was used:

$$\text{PSW} \sim \text{Connectance} \times \text{NODF} + \text{Connectance} \times Q \quad (4)$$

When the p -value was below 0.05, the effect was considered significant.

3 | RESULTS

3.1 | Complexity increases dynamical stability

We varied the species richness and connectance in realistic ranges (see Section 2) to investigate the relationship of complexity (defined here as species richness multiplied with connectance) and dynamical stability. The PSW increases with increasing complexity, while we approximate the shape of the positive relationship using a power law function of the form $\log_{10}(\text{PSW}) + a = bx^c$ (see Figure 3). The fit parameters allow direct comparison with the complexity–stability relationship for food webs using an analogous Generalized Model for food webs: the power law exponent c in the fit function for mutualistic webs shows a different sign than the parameter in the food web case (Gross et al., 2009), which is reflected in the positive complexity–stability relationship for mutualistic webs while the relationship is negative for the food webs. Comparing the data points for different connectances in Figure 3 shows that the slope, that is, the increase in stability, is stronger at low connectances. The individual relationships of species richness and connectance with the PSW are also positive (see Figure 3b,c).

3.2 | Complexity weakens mutualistic dependencies

To understand drivers of the observed positive correlation between complexity and stability, we evaluated properties of the Jacobian matrix elements that govern the local stability dynamics. We investigated the mean magnitude M of the Jacobian matrix elements in

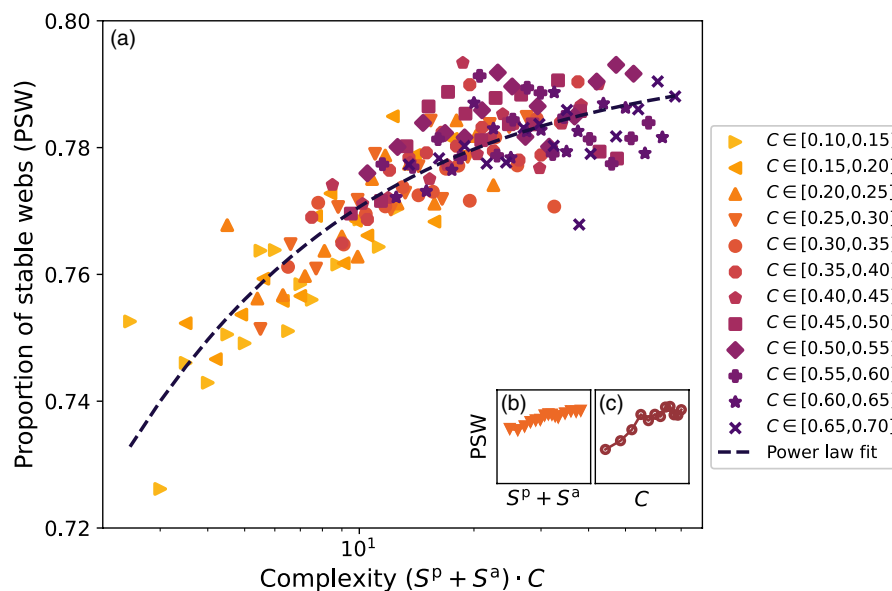


FIGURE 3 Positive complexity–stability relationship. PSW as a function of complexity, as given by the product of species richness and connectance (a). The dashed curve shows a fit with the power law function $\log_{10}(\text{PSW}) + a = bx^c$, analogous to the fit function for the complexity–stability relationship in generalized food webs in Gross et al. (2009). The fit parameters were $a = 0.010$, $b = -0.067$ and $c = -0.705$. In Figure 3b,c, we varied the species richness (b) and the connectance (c) separately using the same rules, while keeping the other quantity constant (or within a small interval). In Figure 3b, we used a narrow connectance interval of $C \in [0.25, 0.3]$, while in Figure 3c, we used a species richness of $S^p = S^a = 20$.

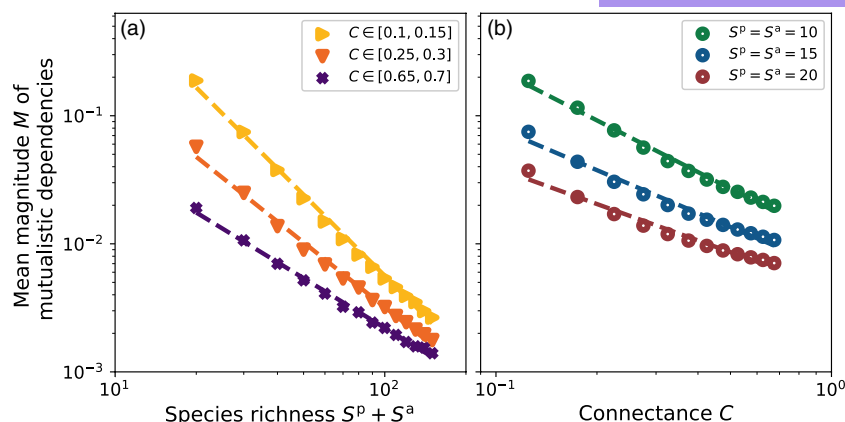


FIGURE 4 Complexity weakens mutualistic dependencies. Influence of species richness (a) and the connectance (b) on the mean magnitude M of the Jacobian elements in the off-diagonal blocks, which we call the *mutualistic dependencies*. They represent the dependencies of plant (pollinator) species on their pollinator (plant) species and thus provide a measure for the mutualistic feedback strength. The orange curve in a ($C \in [0.25, 0.30]$) and the red curve in b ($S^P = S^A = 20$) correspond to the curves shown in Figure 3b,c, respectively. The dashed curves are fits with the power law $M \propto x^\gamma$ where the exponent γ determines the slope in the log-log visualization. The fitted exponents in Figure 4a are (from top to bottom) $\gamma = -2.104$, $\gamma = -1.679$ and $\gamma = -1.289$. The fitted exponents in Figure 4b are (from top to bottom) $\gamma = -1.339$, $\gamma = -1.115$ and $\gamma = -0.944$. As for each network, we have not just one but many values in the off-diagonal blocks, we could reduce the ensemble size to 10^3 for each species richness in Figure 4a and 10^4 in Figure 4b and use a larger range of species richness values up to 150 in Figure 4a.

the off-diagonal blocks that describe the effect of a plant (pollinator) population density on the growth and loss of a pollinator (plant) population density per unit time and hence describe how mutualistic dependencies drive the behaviour of the system around the equilibrium point after a disturbance. In the following, we call the Jacobian matrix elements only *mutualistic dependencies* for simplicity.

The mutualistic dependencies M decrease with increasing species richness (Figure 4a) and connectance (Figure 4b), according to a power law $M \propto x^\gamma$ where the exponent γ determines the slope in the log-log visualization. The fitted exponents for the relationship between species richness and the mutualistic dependencies for different connectance intervals (see Figure 4a) are $\gamma = -2.104$ ($C \in [0.1, 0.15]$), $\gamma = -1.679$ ($C \in [0.25, 0.30]$) and $\gamma = -1.289$ ($C \in [0.65, 0.7]$). The fitted exponents for the relationship between connectance and the mutualistic dependencies for different species richnesses (see Figure 4b) are: $\gamma = -1.339$ ($S^P = S^A = 10$), $\gamma = -1.115$ ($S^P = S^A = 15$) and $\gamma = -0.944$ ($S^P = S^A = 20$). Hence, the decrease is stronger, that is, the fitted exponents are more negative, for lower connectances (Figure 4a) and smaller species richnesses (Figure 4b). This is consistent with the larger slope in the PSW for smaller values of the complexity visible in Figure 3. While Figure 4 shows the ensemble average over both off-diagonal blocks, calculating the mean separately for the two off-diagonal blocks reveals that this power law behaviour with negative exponent is driven more strongly by the dependencies of the pollinators on the plants than the other way around (see Figure S3). While a decomposition of the effects of competition for limited resources and the effects of the elasticities (including sublinear growth) is not possible in a strict sense, we show that pollinators competition for limited plant resources is a key ingredient for generating the positive complexity–stability relationship (see Supporting Information Text S7). This

is in line with the observation that the weakening of the mutualistic feedbacks is stronger when considering the dependencies of the pollinators on the plants.

3.3 | Nestedness does not stabilize model or empirical networks

We investigated the influence of nestedness and modularity on dynamical stability of simulated and in the case of nestedness also on empirical network topologies using the Generalized Modelling approach. We use the nestedness metric NODF (Almeida-Neto et al., 2008), which ranges from 0 to 100, with small values corresponding to low-nested matrices and high values representing highly nested matrices. Modularity ranges from 0 to 1. We generated model networks with different degrees of nestedness and modularity according to the algorithm by Thébaud and Fontaine (2010).

A positive correlation between nestedness and the PSW as well as a negative correlation between modularity and PSW is observed when the connectance is also varied (see Figure 5a,c). However, connectance, nestedness and modularity are all correlated. This is visible from the horizontal colour gradient in Figure 5a,c that indicates varying connectances as well as the strong relationship between connectance, nestedness and modularity in Figure 5d. Low values of nestedness are correlated with low values of connectance and high values of modularity and vice versa. Hence, we used a GLM to disentangle the effects of connectance, nestedness and modularity on PSW. This analysis revealed that connectance has a significant and positive influence on PSW ($z = 6.470$, $p < 0.0001$), while the effects of nestedness ($z = -0.676$, $p = 0.4989$) and modularity ($z = 1.146$, $p = 0.2519$) are not significant. While also the interaction

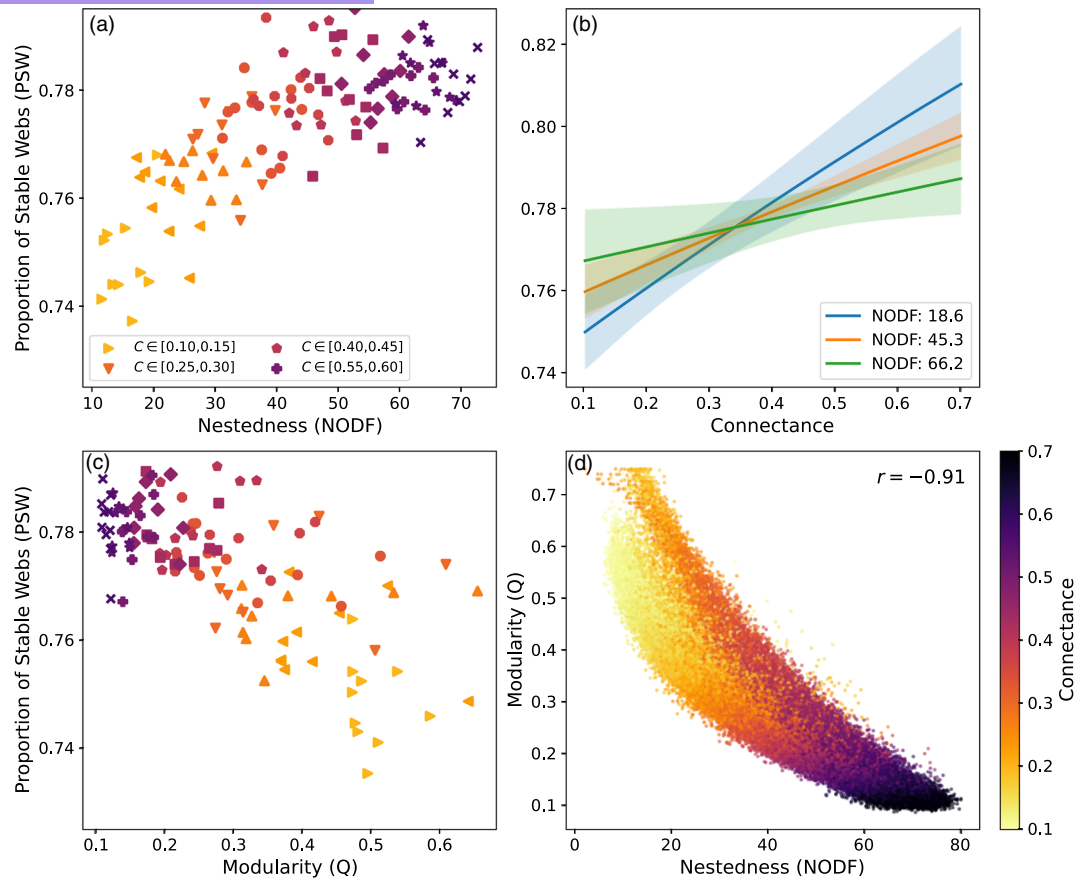


FIGURE 5 Nestedness and modularity do not increase PSW at fixed connectance. While nestedness as measured by the metric NODF and modularity are correlated with the PSW, the horizontal colour gradient in a and c indicates that this correlation is mainly driven by the connectance. In (a) and (c), the same colour scheme is used to indicate different connectances as in Figure 3a,b, while the legend only defines a subset of colours for easier interpretation. In (b), the relationship between connectance and PSW is shown at three different fixed NODF values that represent the 10%, 50% and 90% percentiles of NODF model network values. Shaded areas indicate 95% confidence intervals. (d) It shows the anticorrelation between modularity and nestedness, with a Pearson correlation coefficient of -0.91 . A species richness of $S^p = S^a = 20$ was used, corresponding to the red curves in Figure 3b,c.

between modularity and connectance was not significant ($z=0.893$, $p=0.3721$), the analysis showed that the interaction of connectance and nestedness was significant as well ($z=-2.481$, $p=0.0131$). Connectance has a stronger positive impact on PSW when nestedness is low, but a lower positive impact when nestedness is high (see Figure 5b). These results hold true when increasing species richness (see Figures S5 and S6). This analysis revealed that nestedness and modularity have no effect on PSW in model networks independent of connectance.

Since empirical mutualistic networks have been reported to be more nested than random networks (Bascompte et al., 2003), we used 160 empirical network topologies as input for the Generalized Model to investigate whether nestedness drives stability in empirical networks. While until now we always used the same species richness for plant and animal species for investigating the model networks, we now use the empirical species richness for plant and animal species of the respective empirical networks, which are in general not equal. We compared the PSW using the empirical networks with the PSW of randomly generated reference networks that (i) had the same species richness, connectance and nestedness as the empirical

networks, and (ii) had the same species richness and connectance but a randomized link distribution and thus a lower nestedness (see Figure S4) when compared to the empirical networks (see Section 2).

Model networks with empirical species richness and connectance but randomized links and hence lower nestedness have a similar PSW to model networks with empirical species richness, connectance and nestedness (see Figure 6a). This indicates that varying nestedness, while leaving species richness and connectance constant, has no significant effect on stability. This is consistent with the results of Figure 5 showing that nestedness has no systematic effect on the PSW in model networks but extending this observation to empirical networks and their specific features, most importantly with varying plant and animal species numbers. We found the PSW of empirical network topologies to be approximately equal to that of model networks with the same species richness, connectance and nestedness (see Figure 6b). This indicates that empirical networks have no substantial features (such as different degree distributions) influencing their stability, which are not captured by the simulated model networks. This supports the robustness of the results obtained with the model networks in the previous subsections.

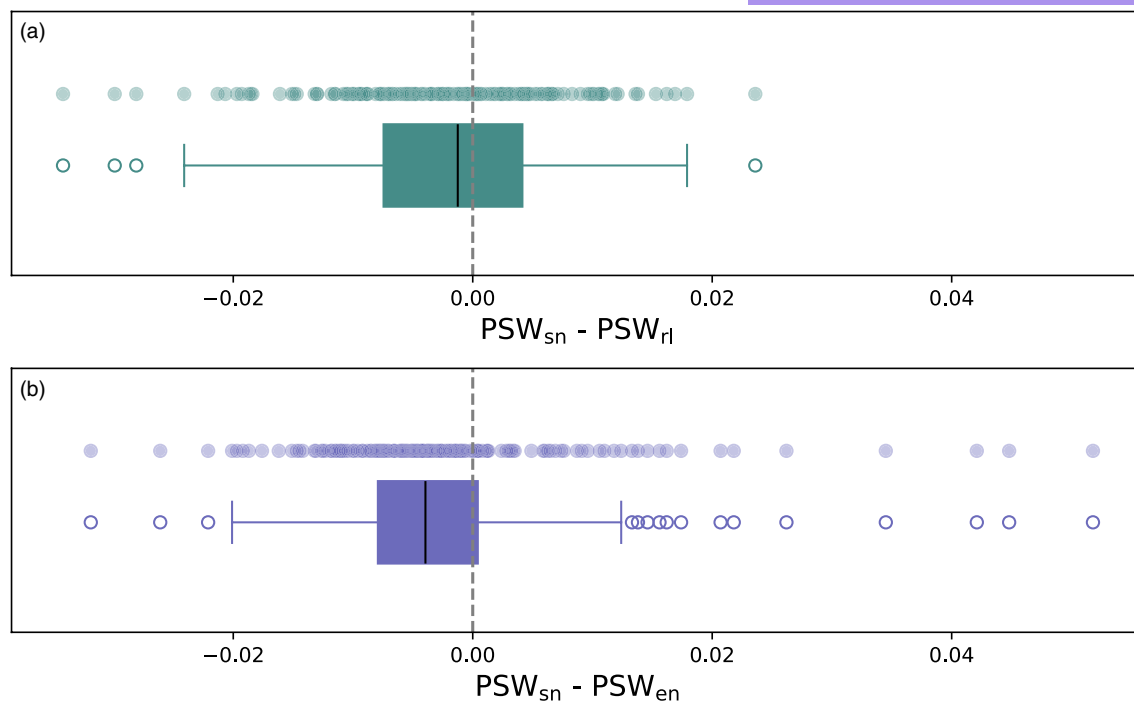


FIGURE 6 The PSW of model networks with similar species richness, connectance and nestedness as empirical networks (sn) is similar to model networks with similar species richness and connectance as empirical networks but randomized link distributions and hence lower nestedness (rl) in (a). It is also similar to that of empirical networks (en) themselves (i.e. using the exact same network structure) (b). The black line shows median, boxes show data in 25th and 75th quartile and whiskers indicate 1.5x the interquartile range.

4 | DISCUSSION

Anthropogenic disturbances put increasing pressures on ecological networks, raising the question which features are most relevant for preserving or restoring their dynamical stability (i.e. their ability to recover from disturbances). We developed a novel Generalized Model for mutualistic networks to show that (i) complexity (i.e. species richness multiplied by connectance) increases their dynamical stability, (ii) complexity weakens mutualistic dependencies explaining the positive complexity–stability relationship and (iii) nestedness has negligible effects on the dynamical stability of model or empirical networks.

Our results are consistent with previous relationships of complexity with the stability metrics resilience (Huang et al., 2021; Okuyama & Holland, 2008; Thébault & Fontaine, 2010) and persistence (Thébault & Fontaine, 2010) found for mutualistic systems. They disagree, however, with results for dynamical stability from random matrix models (Allesina & Tang, 2012) both in terms of the effect of complexity and nestedness. Mutualistic interactions represent a positive feedback loop, which is inherently destabilizing, explaining previous results from random matrix models (Allesina & Tang, 2012). We attribute the differences in our model results mainly to two biological mechanisms that are absent from random matrix models: competition for finite mutualistic resources and non-linear dynamical processes. Biologically realistic non-linearities such as saturating functional responses have already been proposed to resolve the tendency for instability

for other stability metrics in conventional models (Okuyama & Holland, 2008). The Generalized Model used here shows that this effect is more generic by taking into account non-linearities of various biological processes and showing that stabilization of complexity happens for a large class of possible mutualistic models. Our model specifically also includes sublinear elasticities in many processes, that have been shown to lead to positive diversity–stability relationships (Hatton et al., 2024). We relate the observed weakening of the mutualistic feedback to the branching parameters (that capture biomass flows and are connected to the network structure). While the scale parameters and elasticities are independent of species richness and connectance, the branching parameters depend on both species richness and connectance (see Equations 56–63 in the Supporting Information) as they measure relative contributions of individual species. Their dependence on complexity is associated with the weakening of the mutualistic feedback with increasing complexity. While elasticities represent non-linearities, the non-linearity of the Jacobian matrix elements is a function of both elasticities and branching parameters. We can interpret our results in such a way that the positive complexity–stability relationship is a result of non-linearities changing with increasing complexity. We furthermore show that this positive relationship only arises if competition for limited resources is included in our model. This means that competition for limited resources leads to a weakening of the mutualistic feedbacks through the complexity-dependent branching parameters in the off-diagonal Jacobian matrix elements.

May (1972) showed that, in random communities, the standard deviation of the off-diagonal Jacobian matrix elements is negatively related to dynamical stability. More specifically, he showed that with increasing species richness S or connectance C , the standard deviation must decrease $\propto (S \cdot C)^{-1/2}$ to avoid decreasing the dynamical stability. This means that increasingly complex systems can only be stable when interspecies dependencies become weaker. In May's study, the standard deviation of the off-diagonal elements was varied while the mean of the distribution was kept zero. Since the off-diagonal elements in our model are generated by our model and not drawn from specified distributions, their mean will not be equal to zero. We therefore chose to evaluate the mean magnitude of the off-diagonal elements, since this includes influences from the standard deviation as well as the mean and at the same time can be intuitively interpreted as the magnitude of the feedback strength between mutualistic species. While the mutualistic dependencies decline with increasing complexity in our model, they increase in May's model, explaining the divergence between ours and May's results with respect to the relationship between complexity and stability (see [Supporting Information S6](#)). The weakening of mutualistic feedbacks in mutualistic networks therefore allows increasingly complex communities to not only remain stable, but also increase in their probability to be stable.

Other recent studies have found mixed results for complexity–stability relationships in other network types. Jacquet et al. (2016) report no significant relationship in empirical food webs. We argue that the absence of a positive complexity–stability relationship in these systems is related to the lack of the positive mutualistic feedback that is dampened through competition for limited mutualistic resources. Wang et al. (2025) found positive, negative and peaked patterns in mutualist-exploiter-predator communities with adaptive foraging. Adaptive foraging leads to a restructuring of networks that may explain variable complexity–stability relationships, but which is a feature that is currently absent from our Generalized Model. Future developments of the Generalized Model that include other interaction types than mutualism and also adaptive foraging may test how Generalized Model results relate to these observations from empirical systems and conventional models with mixed interaction types.

These model results may be connected to empirical observations through functional redundancy and the insurance hypothesis: in a species-rich and highly connected network, the reciprocal dependence of mutualistic partners on each other is weak and loss of species or interactions may have a less severe effect (Winfree et al., 2018; Yachi & Loreau, 1999). Empirical support of the theory that complexity enhances stability is given by biodiversity experiments that confirmed an almost unequivocal positive effect of biodiversity on the stability of ecosystem functions due to underlying mechanisms such as functional complementarity, response diversity, portfolio effects and insurance hypothesis (Loreau & De Mazancourt, 2013; Schnabel et al., 2021; Tilman & Downing, 1994). Stability of ecosystem functions is often mirrored by a concomitant stability of species communities, and indeed the species richness

of plants or animals also improved community stability via an increased asynchrony of species in real-world ecosystems (Blüthgen et al., 2016; Ma et al., 2017).

Effects of species richness and connectance on dynamical stability are dominating in our model and outweigh the effects due to nestedness and modularity. Both nestedness and modularity were found to have no effect on PSW independent of connectance. Furthermore, modularity and nestedness are strongly negatively correlated for the species richness and connectance combinations we studied, reflecting previously observed redundancies between both network descriptors (Fortuna et al., 2010). This is in contrast with Thébault and Fontaine (2010), who found a decrease of persistence and resilience in mutualistic networks with increasing modularity and a decrease in persistence and an increase in resilience with nestedness. We attribute these differences to our use of dynamical stability and the explicit modelling of competition for limited resources.

We also found empirical networks to have higher nestedness than networks with randomized link distributions (see [Figure S4c](#)), but nestedness is not the feature conferring this increase in stability, as empirical and random networks do not differ in stability even when the nestedness is drastically different. These results are in contrast to research showing nestedness to have a positive effect on structural stability (Rohr et al., 2014) or a negative effect on dynamical stability (Allesina & Tang, 2012). However, a direct comparison between results obtained for dynamical stability and structural stability is not permitted, as dynamical stability assumes a feasible equilibrium, whereas structural stability investigates under which circumstances an equilibrium may be feasible. Our findings suggest that nestedness patterns may not be as relevant in conferring stability as previous research indicates, especially not with regard to dynamical stability. In our model, we explicitly consider the dynamics of finite resources. As nestedness maximizes niche overlap, our results suggest that the potentially stabilizing effect of nestedness through a higher redundancy of interacting partners is offset by the destabilizing effect through a higher competition for mutualistic resources. The question then remains why empirical networks are more nested than expected by chance. A potential explanation is given by null model simulations which suggest that incomplete sampling of the interactions of rare species may lead to empirical networks appearing more nested and less connected than they actually are (Blüthgen et al., 2008; Blüthgen & Staab, 2024). If such sampling artefacts are present, actual empirical networks may be less nested and more connected than empirical data suggests. If we assume empirical networks to have structures that maximize their stability, our findings of a neutral nestedness–stability relationship combined with a positive connectance–stability relationship would be consistent with this scenario, since connectance increases the dynamical stability while nestedness does not. However, our model results are based on averaging over a large class of mutualistic models. While we argue this leads to the most robust and most generalizable results, it may be possible that nestedness has stabilizing features

in specific scenarios, that is, for certain parameterizations in combination with certain values of species richness or connectance. Further research would be necessary to confirm this hypothesis.

The range of PSW variation due to changes in species richness or connectance is modest ($\sim 5\%$) compared to Generalized Model studies on food webs where PSW varied from 0 to 1 (see Gross et al. (2009)). This reflects our decision to sample elasticities broadly from biologically realistic ranges rather than fixing them at specific values. We thereby investigated the effect of species richness and structural network features for a large class of mutualistic models rather than considering a specific case. We argue that this causes higher robustness and generality of the results across a large variety of mutualistic systems. As it is difficult to exactly parameterize models based on empirical data, we refrained from selecting specific values which may cause larger PSW variations but would only allow insights into special cases rather than obtaining generic insights as is the case here.

A limitation of our model is that it only considers local stability. While local stability by definition allows long-term persistence of communities, real-world ecosystems may also persist through complex dynamical trajectories. Therefore, networks found to be dynamically unstable may still allow long-term coexistence of most or all species. Furthermore, we only look at single networks. As mutualistic networks mostly exist in a matrix of habitats, a meta-network approach to the Generalized Model could reveal further insights into ecosystem-scale stability patterns.

The results shown here nevertheless allow profound ecosystem-scale interpretations: the negative complexity–stability relationship found for food webs (Gross et al., 2009) could be counteracted by a stabilizing role of mutualism in large ecosystems with mixed types of interactions. Further research should dive deeper into the potentially positive effect of mutualism in multipartite interaction networks including various types of interactions. For example, studies investigating multiplex networks with mutualistic and antagonistic interactions show that the presence of mutualists increases the persistence and temporal stability of both mutualist and non-mutualist species (Hale et al., 2020). Extending our Generalized Model to networks with multiple interactions could be used to confirm this positive effect of mutualists on the dynamical stability of multiplex networks.

Our results furthermore have interesting implications for conservation. While the model setup currently does not admit the specific simulation of Anthropocene stressors, it has repeatedly been reported that land-use change, pesticides and global warming lead to species and interaction loss (Potts et al., 2010; Tylianakis et al., 2008; Valiente-Banuet et al., 2015), thereby decreasing complexity. Our model results suggest that complexity loss is more severe than network structure change in leading to a loss in dynamical stability, implying a potential feedback loop in which destabilization may lead to further species loss. However, species loss is not random: specialized and rare species are often lost first (Aizen et al., 2012). At the same time, species have the potential to rewire interactions (CaraDonna et al., 2017). Our

model results indicate that if rewiring maintains connectance, stability could be preserved despite species loss to some extent, as connectance was a key driver of stability. However, if species loss becomes too severe, rewiring is insufficient or generalized species (hubs) are lost, our model results predict networks to be pushed towards the point at which they lose their dynamical stability and hence the ability to recover. Solutions to this problem may be given through restoration of plant communities that have been shown to successfully restore pollination network function and resilience, providing a way to reverse network degradation (Kaiser-Bunbury et al., 2017). Our results support the idea that conservation strategies should prioritize conservation and restoration of network complexity, rather than the exact distribution of links or network patterns.

AUTHOR CONTRIBUTIONS

Timo Metz and Jan Timo Bachmann conceptualized the study. Timo Metz, Jan Timo Bachmann and Thilo Gross developed the model. Timo Metz and Jan Timo Bachmann wrote the simulation code, performed the simulations and the data analysis, and wrote the initial manuscript. All authors interpreted the results, revised the manuscript and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors have no relevant financial or non-financial interests to disclose.

DATA AVAILABILITY STATEMENT

Data and code are available in the Figshare Digital Repository <https://doi.org/10.6084/m9.figshare.31683988>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Visualization of the interdependencies of the generalized functions and variables used to model the service-for-resource mutualism.

Table S1. Scale and branching parameters with definitions, interpretations and values.

Table S2. Elasticities with definitions, interpretations and value ranges.

Figure S2. Correlation of GM parameters with stability.

Figure S3. Influence of complexity on mutualistic dependencies.

Figure S4. Difference in nestedness (NODF) between empirical networks (en) and randomized networks with different (rl) or the same (sn) nestedness, species richness and connectance.

Figure S5. Nestedness and modularity do not increase PSW at fixed connectance ($S^p = S^a = 30$).

Figure S6. Nestedness and modularity do not increase PSW at fixed connectance ($S^p = S^a = 40$).

Figure S7. Comparison of scaling behaviour of mean magnitudes of off-diagonal elements between May's and our model.

Figure S8. Complexity-stability relationships for different model scenarios.

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