

Strong contributors to network persistence are the most vulnerable to extinction

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The architecture of mutualistic networks facilitates coexistence of individual participants by minimizing competition relative to facilitation^{1,2}. However, it is not known whether this benefit is received by each participant node in proportion to its overall contribution to network persistence. This issue is critical to understanding the trade-offs faced by individual nodes in a network^{3–5}. We address this question by applying a suite of structural and dynamic methods to an ensemble of flowering plant/insect pollinator networks. Here we report two main results. First, nodes contribute heterogeneously to the overall nested architecture of the network. From simulations, we confirm that the removal of a strong contributor tends to decrease overall network persistence more than the removal of a weak contributor. Second, strong contributors to collective persistence do not gain individual survival benefits but are in fact the nodes most vulnerable to extinction. We explore the generality of these results to other cooperative networks by analysing a 15-year time series of the interactions between designer and contractor firms in the New York City garment industry. As with the ecological networks, a firm's survival probability decreases as its individual nestedness contribution increases. Our results, therefore, introduce a new paradox into the study of the persistence of cooperative networks, and potentially address questions about the impact of invasive species in ecological systems and new competitors in economic systems.

Mutualistic interactions form the basis of many biological and human systems of cooperation and competition^{2,6–14}. Mutualistic networks are composed of mutually beneficial interactions between individual participants or nodes of two distinct sets, such as plant species and their pollinators¹⁵ or designers and their contractors¹¹. One pattern in particular—nestedness—appears ubiquitous in mutualistic networks from a variety of contexts^{1,2,16}. In a nested network, the interactions are organized such that specialists (for example, plants with few pollinators) interact with proper subsets of the nodes with whom generalists (for example, plants with many pollinators) interact¹⁶. This nested architecture has been shown to minimize competition between species and therefore allows the network to support greater biodiversity¹.

Although greater nestedness allows for the successful coexistence of more species, it is unclear how the decreased risk of extinction is distributed among the nodes in the network. Here we quantify whether node-level survival benefits are related to each node's 'contribution' to the nested architecture, defined as the degree to which the organization of their interactions increases overall nestedness. A positive relationship could create a positive feedback of benefits to those that most support nestedness and the community; a negative relationship, in contrast, could imply that some nodes stand to benefit from the contributions of others.

To answer these questions, we integrate structural and dynamic analyses of 20 ecological networks that describe mutually beneficial interactions between flowering plants and their insect pollinators across

diverse environmental and biotic conditions¹⁷. In these bipartite networks, nodes correspond to individual plant or pollinator species and links between nodes indicate that a pollinator species has been found empirically to pollinate a given plant species (Methods).

To measure the individual contribution to nestedness for each species or node, we develop a novel, node-level metric that quantifies how an individual's contribution to network nestedness compares to that expected at random (Fig. 1). The measure quantifies the degree to which the overall nestedness of the network compares with the value obtained when randomizing just the interactions of that particular node.

Mathematically, this is defined as $c_i = (N - \langle N_i^* \rangle) / \sigma_{N_i^*}$, where N is the observed nestedness of the network and $\langle N_i^* \rangle$ and $\sigma_{N_i^*}$ are the average and standard deviation of nestedness across an ensemble of random replicates within which the interactions of node i have been randomized (Methods). The greater the degree to which the interactions of node i are consistent with the network's overall nestedness, the stronger is this node's contribution c_i , and vice versa.

We calculate this measure for each species in each of the networks and observe that node contributions to the network architecture are

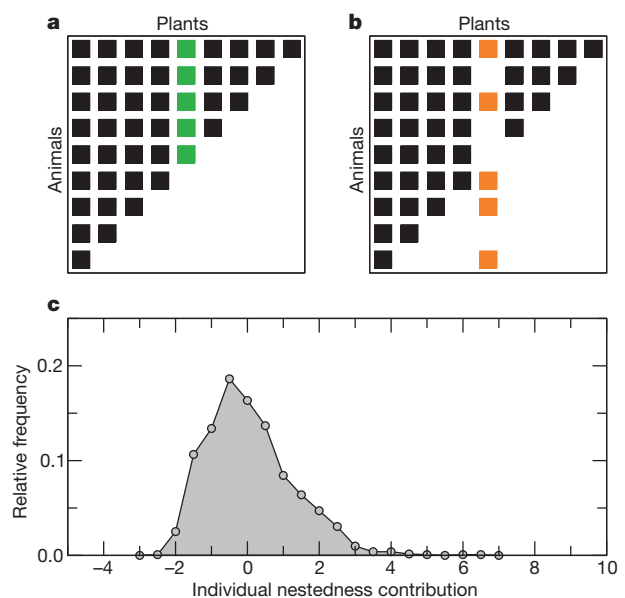


Figure 1 | Nodes contribute to the nested architecture of the network in distinct proportions. **a, b,** The individual nestedness contribution of a node (for example, the plant species whose interactions are highlighted in green in **a**) is defined as the degree to which the observed network nestedness compares to the value obtained when randomizing just the interactions of that particular node, highlighted in orange in **b**. **c,** The empirical distribution of individual nestedness contribution for all species in the 20 pollination networks studied here.

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heterogeneously distributed across our empirical data set (Fig. 1c). Importantly, some species contribute comparatively little to the nested structure of the network whereas others contribute considerably more.

Having shown that species contribute to the overall network architecture in distinct proportions, we next explore the systemic consequences of species extinctions across the spectrum of contributions. This allows us to test whether or not a node's contribution in topological terms translates to a dynamic contribution in terms of network persistence. As there are no dynamic, empirical data with which to quantify network persistence in our ecological networks, we simulate species dynamics with a recently published model that is appropriate for mutualistic systems¹ (Methods). To measure the dynamic impact of a node on overall network persistence, we calculate the difference between the persistence of the network with and without removal of the focal node. Network persistence is measured as the fraction of initial species remaining at the end of the simulation. Here, we consider plant and pollinator species pooled together, while in Supplementary Information we calculate the persistence for each set independently.

We find that the more a node contributes to nestedness, the more likely it is that its loss is detrimental to the network's persistence (Fig. 2). Nestedness contribution therefore represents a key measure of the degree to which each node's interactions work for or against the long-term persistence of species in the mutualistic network.

Because the extinction of strong contributors has significant repercussions on network persistence, we proceed by estimating the vulnerability of these strong contributors to extinction. Specifically, we compare each node's nestedness contribution to its survival probability, where survival is determined by whether or not the node goes extinct before the dynamic simulations reach equilibrium.

Surprisingly, we find that nodes that contribute the most to the nestedness of the network—and its persistence—are the most likely to go extinct (Fig. 3). Indeed, individual nestedness contribution has a significant, negative correlation with survival probability (Methods). This conclusion is independent of whether all networks are analysed together ($P < 10^{-8}$ and $P < 10^{-15}$ for plants and pollinators, respectively) or each network is analysed separately. Specifically, the negative relationship between contribution and survival probability is significant for pollinators in 17 out of 20 networks and for plants in 20 out of 20 networks ($P < 10^{-4}$). Furthermore, our results capture the importance of nestedness contribution above and beyond the effect of the number of interactions per node (Methods). In general, the more a node contributes to the architecture of its network, the greater its

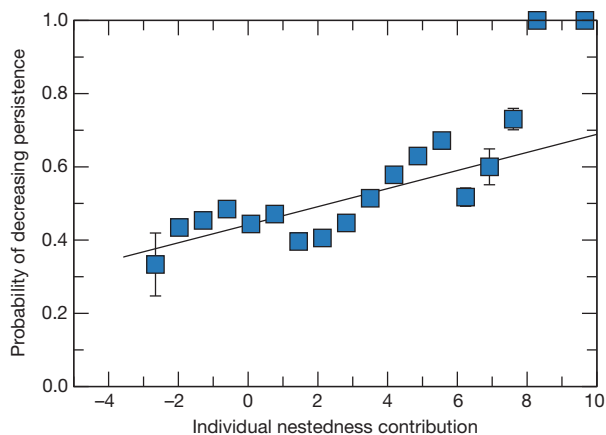


Figure 2 | The extinction of stronger contributors leads to a decrease in network persistence. We plot the probability that a node's removal causes a decrease in network persistence in the dynamic simulations as a function of that node's contribution to nestedness. All species in the 20 pollination networks are plotted together. Error bars, standard errors of the reported averages; in some cases they are smaller than the plotting symbols. Solid line, best-fit linear regression ($P < 0.005$).

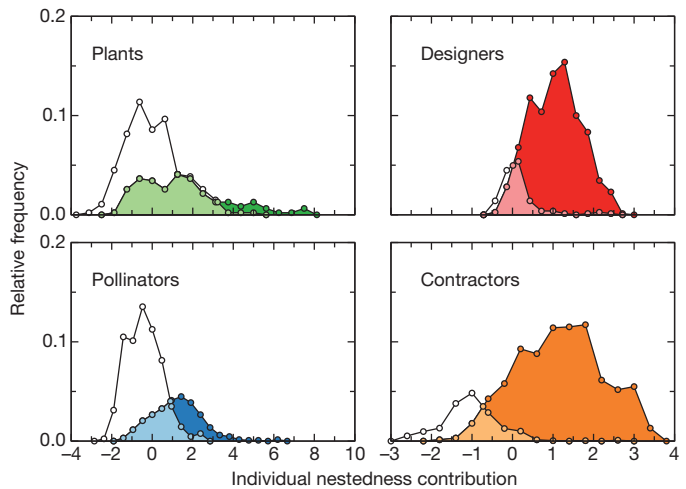


Figure 3 | Strong contributors to nestedness are the most vulnerable to extinction. We plot histograms of individual nestedness contribution for nodes that survive, with the area under the curve shaded in white, and for those that do not, with the area under the curve shaded in colour. In each case, the lighter colour indicates overlap between the two distributions. Nodes from all networks are pooled together for each class of node studied.

probability of extinction. These results imply that some species can benefit from others by participating in mutualistic interactions that differ from those that would maximize network persistence.

To explore the generality of these results to other types of cooperative networks, we build on previous work that illustrates commonalities between ecological and human systems^{2,9,11}. Specifically, we apply our node-contribution measure to the network formed by the cooperative interactions between designers and their contractors in the New York City garment industry across a 15-year observation period¹⁸. This industry is characterized by a competitive and dynamic environment where resource exchanges among firms and survival depends on collaborative links between firms^{11,18}. Though earlier studies have attributed the failure of firms to their lack of adaptation to new business networks^{19–21}, none have unambiguously linked firm survival to the network architecture. Here, nodes correspond to an individual designer or contractor firm, and links between nodes indicate that a designer exchanged money for the contractor's production services. We quantify a firm's survival by comparing whether or not the company was still operating at the end of the observation period.

Importantly, the negative relationship that we observed in ecological networks—between a node's contribution and its survival—also holds for the firms in this socio-economic network. This conclusion is obtained both when looking at the companies that went out of business by the end of the 15-year period ($P < 10^{-11}$ and $P < 10^{-12}$ for designers and contractors, respectively) and when tracking the yearly dynamics across the data set. In 14 out of 15 year-to-year intervals, the relationship between individual nestedness contribution and node survival is significant and negative for both contractors and designers ($P < 10^{-4}$). Just as for nodes in the ecological networks, the nodes that contribute the most to the nestedness of the network are the most likely to have failed (Fig. 3). This analysis suggests that our results may apply generally across different types of cooperative networks, whether they are shaped as a consequence of evolution or conscious decisions.

The individual nestedness contribution that we define here provides a means to estimate the expected survival of participants in cooperative systems solely from knowledge of the network structure. Moreover, we have revealed a paradox of nestedness: although strong contributors to nestedness are more important for the persistence of the entire network, they are also more prone to extinction compared to those nodes that contribute proportionally less. Although there is no clear explanation for this result, one could speculate that nodes that conform to the

architectural expectation of a nested network are subject to greater constraints than nodes that interact freely. If these linkage constraints have a cost in terms of fitness (for example, they lead to a pollinator species interacting with a less rewarding plant species), they could ultimately translate to a higher probability of extinction. Our study therefore raises new questions about the origins of nodes that make strong contributions to the collective good and nodes that appear to improve their own survival at the expense of others^{4,5,14}. In ecology, our results could inform a quantitative assessment of the likely persistence of an invasive species in the network and its effects on the overall welfare of the community. In socio-economic systems, our results could be used to identify those companies and economic sectors that undermine stable, long-term economic prosperity, as well as to develop interventions that take into account collective interests.

METHODS SUMMARY

Our ecological data set contains the 20 largest plant–pollinator mutualistic networks provided in the Supplementary Information of ref. 17; details about the networks and original sources can be found therein. Additionally, we analyse the network between designer and contractor firms in the New York City garment industry¹¹. Details about this temporal network can be found in the Supplementary Information of ref. 11.

Nestedness N is quantified using the measure proposed in ref. 22. In calculating nestedness contributions, the interactions of a node were randomized according to the null model specified in ref. 16; we used 1,000 random replicates. Note that all results presented in the present Letter hold both for alternative measures of nestedness and alternative null models (Supplementary Methods; Supplementary Figs 1–6).

To explore network dynamics, we employed the mutualistic model defined in ref. 1. This model is based on a system of differential equations describing the dynamics of P plant species and A animal species as a function of their intrinsic growth rates, interspecific competition, and mutualistic effects of one set on another.

We quantified the relationship between nestedness contribution c_i and node's survival probability s_i via a logistic regression. To ensure that our analysis is capturing a significant pattern over and above a node's degree (that is, its number of interactions), two additional terms in the regression controlled for the degree of the node and the potential interaction between degree and contribution to nestedness.

Full Methods and any associated references are available in the online version of the paper at www.nature.com/nature.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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METHODS

Data sets. Here we analyse two types of empirical data. First, we analyse a data set containing the 20 largest plant–pollinator mutualistic networks provided in the Supplementary Information of ref. 17. Further details about the network size, species composition and geographic location can be found in ref. 17, together with the actual network and original source. Additionally, we analyse the socio-economic network first described in ref. 11. This network contains approximately 700,000 commercial interactions between manufacturer and contractor firms in the New York City garment industry between January 1985 and December 2003. From this data set, we can generate yearly snapshots of the bipartite network. Additional details can be found in the Supplementary Information of ref. 11.

Nestedness measure. We quantify nestedness using NODF, the measure recently introduced in ref. 22. This measure reduces potential bias introduced by network size and shape compared with alternative measures. The overall nestedness of the network N is defined mathematically as:

$$N = \frac{\sum_{i < j}^P M_{ij} + \sum_{i < j}^A M_{ij}}{\left[\frac{P(P-1)}{2} \right] + \left[\frac{A(A-1)}{2} \right]}$$

where the first sum is across all pairs of plant species, the second sum is across all pairs of animal species, and P and A are the total number of plant species and animal species, respectively. For every pair of nodes i and j , $M_{ij} = 0$ if $k_i = k_j$, and $M_{ij} = n_{ij}/\min(k_i, k_j)$ otherwise. Here, k is a node's number of interactions; n_{ij} is the number of interactions in common between nodes i and j ; and $\min(k_i, k_j)$ refers to the minimum of the two values k_i and k_j .

This nestedness metric takes values in the interval $N \in [0, 1]$, where 1 designates a perfectly nested network and 0 indicates a network with no nestedness. Alternative measures of nestedness are highly and significantly correlated to this one (Supplementary Methods; Supplementary Fig. 1). Furthermore, all results presented in this Letter hold for such alternative measures of nestedness (Supplementary Figs 2 and 3).

Null model. To randomize interactions, we use the null model outlined in ref. 16. Under the specifications of this null model, the interactions are assigned according to the rule:

$$p_{ij} = \frac{1}{2} \left(\frac{k_i}{P} + \frac{k_j}{A} \right)$$

where p_{ij} is the probability of an interaction between node i (of set A) and node j (of set P) and A and P are the total number of animal and plant species in sets A and P ,

respectively. In the socio-economic networks, the model is specified in the same fashion except with designers and contractors in the place of animals and plants. We use 1,000 replicates. Note that all results presented in this Letter hold for alternative null models (Supplementary Methods; Supplementary Figs 4, 5, and 6).

Dynamic model for ecological mutualistic networks. To simulate interspecies dynamics in the ecological networks, we run the dynamic model of ref. 1 using each of the real networks as the skeleton of the model. The real networks specify the number of plant species, the number of animal species, and who interacts with whom. In the dynamic model, the change in abundance over time for a plant species i follows:

$$\frac{dS_i^{(P)}}{dt} = \alpha_i^{(P)} S_i^{(P)} - \sum_{j \in P} \beta_{ij}^{(P)} S_i^{(P)} S_j^{(P)} + \sum_{k \in A} \frac{\gamma_{ik}^{(P)} S_i^{(P)} S_k^{(A)}}{1 + h^{(P)} \sum_{l \in A} \gamma_{il}^{(P)} S_l^{(A)}}$$

The same equations for animal species can be written in a symmetric form interchanging the indices (P) and (A).

To fully specify the remainder of the dynamic model, we use the following parameter values for all plant species (P) and animal species (A): intrinsic growth rates α_i are drawn uniformly from the interval [0.85, 1.1]; the competitive interactions β_{ii} and β_{ij} are drawn uniformly from the intervals [0.99, 1.01] and [0.22, 0.24], respectively; the mutualistic interactions γ_{ij} , encapsulating the *per capita* effect of animal j on plant i , are drawn uniformly from the interval [0.19, 0.21]; the handling time h is set to 0.1.

Simulations are performed by integrating the system of ordinary differential equations using a fourth-order Runge-Kutta method with small integration steps. All initial abundance densities S_i are drawn uniformly from the interval (0, 1]. Species are considered to have gone extinct when their abundance density S_i is lower than 10^{-30} . All results are robust to changes in parameter values (growth rates $\alpha_i \in [0, 2]$, competitive interactions $\beta_{ij} \in [0, 1]$, and mutualistic interactions $\gamma_{ij} \in [0, 1]$) as well as changing the functional responses of the above model from Holling type II to Holling type III.

Relationship between nestedness contribution and node survival. We quantify the relationship between nestedness contribution c_i and node's survival probability s_i by using a logistic regression with the form $\text{logit}(s_i) = \alpha + \beta c_i$. Survival was coded as 0 and 1 for non-surviving and surviving nodes, respectively. To ensure that our analysis is capturing a significant pattern above and beyond other network attributes, we perform the same analysis but also include terms for node degree k (that is, number of interactions) and the potential interaction term for degree and contribution. This extended model takes the form $\text{logit}(s_i) = \alpha + \beta c_i + \gamma k_i + \delta c_i k_i$.