

LETTERS

The architecture of mutualistic networks minimizes competition and increases biodiversity

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The main theories of biodiversity either neglect species interactions^{1,2} or assume that species interact randomly with each other^{3,4}. However, recent empirical work has revealed that ecological networks are highly structured^{5–7}, and the lack of a theory that takes into account the structure of interactions precludes further assessment of the implications of such network patterns for biodiversity. Here we use a combination of analytical and empirical approaches to quantify the influence of network architecture on the number of coexisting species. As a case study we consider mutualistic networks between plants and their animal pollinators or seed dispersers^{5,8–11}. These networks have been found to be highly nested⁵, with the more specialist species interacting only with proper subsets of the species that interact with the more generalist. We show that nestedness reduces effective interspecific competition and enhances the number of coexisting species. Furthermore, we show that a nested network will naturally emerge if new species are more likely to enter the community where they have minimal competitive load. Nested networks seem to occur in many biological and social contexts^{12–14}, suggesting that our results are relevant in a wide range of fields.

A long-held tenet in ecology is that the structure of an ecological network can largely affect its dynamics^{3,6,7,15,16}. Recent work has unravelled the structure of plant–animal mutualistic networks^{5,8–11}, but little is known about the implications of these network patterns for the persistence of biodiversity. Previous theory has analysed the dynamics of mutualistic communities without considering their structure^{3,17–20}. More recently, ecologists have started numerically to explore the robustness of mutualistic networks^{10,21–25}, but no study

has yet determined how the size of the network depends on its structure. However, understanding the factors determining the number of coexisting species is possibly the most fundamental problem in ecology and conservation biology. Here we analytically quantify whether and to what extent the architecture of mutualistic networks enhances the number of species that can stably coexist in a community (Fig. 1). Also, we explore the emergence of this network architecture through the assembly process. Our analytical approach provides general, insightful results about the equilibrium behaviour instead of simulating the dynamics of our system before such an equilibrium (Supplementary Fig. 1).

We must first derive a baseline biodiversity that will occur in the absence of mutualistic interactions. We therefore begin by considering previous theory that predicts the number of coexisting species when there are only competitive interactions^{26,27}. Next we build a generalized model of mutualisms in which species in the same group compete with each other and interact mutualistically with species in the other group (Methods). For direct competition for resources without mutualism, previous work has shown that the largest eigenvalue of the competition matrix limits the maximum biodiversity that the system can attain^{26,27}. This predicted maximum number of plant species (similar for animals) can be expressed as

$$\bar{S}^{(P)} = \frac{1 - \tilde{\rho}^{(P)}}{\tilde{\rho}^{(P)}} \quad (1)$$

where $\tilde{\rho}^{(P)}$ is the normalized effective interspecific competition parameter, which can be computed from the main eigenvalue, λ_1 , of the normalized competition matrix (Supplementary Methods) as

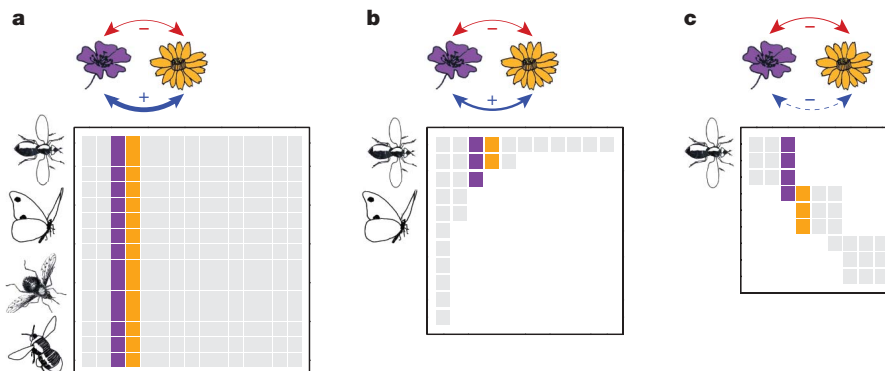


Figure 1 | The structure of mutualistic networks determines the number of coexisting species. Each panel represents a plant–animal network with different structures: **a**, fully connected; **b**, nested; **c**, compartmentalized. Two plants and their respective interactions are highlighted. They compete for resources such as nutrients (red arrow), but also have indirect

interactions mediated by their common pollinators (blue arrow), which may change in sign and magnitude (indicated by arrow line style). As the number of shared pollinators is higher, positive effects outweigh negative ones, and the theory predicts a higher number of coexisting species as indicated by the size of the matrices.

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$$\tilde{\rho}^{(P)} = \frac{\lambda_1 - 1}{S^{(P)} - 1} \quad (2)$$

Here $S^{(P)}$ is the observed number of plant species, which gives the dimensions of the interaction matrices. Qualitatively, the larger is $\tilde{\rho}^{(P)}$, the smaller is the number of species that can stably coexist in a purely competitive system. To obtain explicit analytical formulae, we will henceforth consider direct competition of mean-field type assuming that all species within a set compete with each other with identical intensities (this can be relaxed in numerical simulations; Supplementary Methods). In this case, the quantity computed using equation (2) is equal to the direct competition parameter, $\rho^{(P)}$.

Now that we have set up the baseline limit to the number of coexisting species defined by equation (1), we can incorporate mutualism between plants and animals and quantify the new limit to biodiversity. It is still possible to derive an effective competition matrix that includes the effect of mutualism. The maximum eigenvalue of this matrix limits biodiversity through equations (1) and (2). We first consider the fully connected mutualistic network in which all plants interact with all animals (Fig. 1a). The normalized effective interspecific competition, $\tilde{\rho}_{\text{mut}}^{(P)}$, is related to the direct competition without mutualism as follows, where $a^{(P)}$ is a parameter (Supplementary Information equation (7)) that is proportional to the strength of mutualistic interactions:

$$\tilde{\rho}_{\text{mut}}^{(P)} = \frac{\rho^{(P)} - a^{(P)}}{1 - a^{(P)}} \quad (3)$$

Stable solutions exist for $a^{(P)} < \rho^{(P)}$. We can see from equation (3) that $\tilde{\rho}_{\text{mut}}^{(P)}$ is smaller than $\rho^{(P)}$. This means that mutualism always reduces the effective interspecific competition in a fully connected plant–animal network. The predicted maximum number of plant species in the presence of mutualism, $\bar{S}_{\text{mut}}^{(P)}$, becomes (Supplementary Methods)

$$\bar{S}_{\text{mut}}^{(P)} = \frac{1 - \tilde{\rho}_{\text{mut}}^{(P)}}{\tilde{\rho}_{\text{mut}}^{(P)}} = \frac{\bar{S}^{(P)}}{1 - a^{(P)}/\rho^{(P)}} \quad (4)$$

which is strictly greater than $\bar{S}^{(P)}$, proving that fully connected mutualistic networks increase the number of coexisting species by reducing the effective interspecific competition.

Having quantified the increase in biodiversity due to mutualism in the fully connected case, we proceed by assessing how this mutualistic effect is shaped by the structure of mutualistic networks (Fig. 1b, c). We will repeat the above arguments relaxing the assumption that plant and animal species interact with all species in the other group. Whereas the effective competition matrix in the case of mean-field mutualism contained terms describing an average identical effect of one species on another, now the elements of the effective competition matrix, $C_{ij}^{(P)}$, are different and have to be written explicitly as (Supplementary Methods)

$$C_{ij}^{(P)} = \delta_{ij} + \frac{1}{\bar{S}^{(P)}} + R \left(\frac{1}{S^{(A)} + \bar{S}^{(A)}} n_i^{(P)} n_j^{(P)} - n_{ij}^{(P)} \right) \quad (5)$$

where δ_{ij} is the Kronecker delta function (1 if $i = j$, 0 otherwise), R is the mutualism-to-competition ratio (Supplementary Information equation (23)), $n_i^{(P)}$ is the number of interactions of plant species i and $n_{ij}^{(P)}$ is the number of shared interactions between species i and j . Importantly, the right-hand side of equation (5) decreases with the nestedness of the mutualistic network (as defined in Methods). As a consequence, by inspection nestedness reduces the effective interspecific competition for a given distribution of number of interactions across plant species and fixed parameters. Because the predicted maximum number of plant species (equation (4)) increases with decreasing effective competition, the model predicts that the more nested is the matrix, the higher is the maximum biodiversity.

To explicitly quantify the increase in biodiversity (from the baseline of an exclusively competitive system) due to the nested architecture of mutualistic networks, we computed the derivative of the predicted maximum number of plant species (equation (4)) with respect to the mutualism-to-competition ratio:

$$\left. \frac{1}{\bar{S}_{\text{mut}}^{(P)}} \frac{\partial \bar{S}_{\text{mut}}^{(P)}}{\partial R} \right|_{R=0} = \left(1 + \frac{1}{\bar{S}^{(P)}} \right) \langle n^{(P)} \rangle \left[\bar{S}^{(P)} \left(\hat{\eta}^{(P)} - \frac{\langle n^{(P)} \rangle}{S^{(A)} + \bar{S}^{(A)}} \right) - (1 - \hat{\eta}^{(P)}) + \frac{\langle (n^{(P)})^2 \rangle - \langle n^{(P)} \rangle^2}{\langle n^{(P)} \rangle (S^{(A)} + \bar{S}^{(A)})} \frac{S^{(P)} + \bar{S}^{(P)}}{S^{(P)} - 1} \right] \quad (6)$$

Here $\langle n^{(P)} \rangle = \sum_i n_i^{(P)} / S^{(P)}$ and $\langle (n^{(P)})^2 \rangle = \sum_i (n_i^{(P)})^2 / S^{(P)}$ are the mean and mean-square number of mutualistic interactions per plant species, respectively. This derivative increases with the parameter $\hat{\eta}^{(P)} = \sum_{i \neq j} n_{ij}^{(P)} / ((S^{(P)} - 1) \sum_k n_k^{(P)})$, which is highly correlated with the measure of nestedness defined in Methods. As seen above, mutualism of the fully connected type always increases the number of coexisting species, setting a maximum limit to biodiversity (fully connected networks have the maximum numbers of absolute and shared mutualistic interactions; Fig. 1a). Structured networks, however, may increase the effective competition and reduce biodiversity if there are not enough shared interactions (that is, for low nestedness; Fig. 1c), or if direct competition is strong so that the predicted maximum numbers of species in the absence of mutualism, $\bar{S}^{(A)}$ and $\bar{S}^{(P)}$, are small. Therefore, the architecture of mutualistic networks highly conditions the sign and magnitude of the effect of mutualism on the number of coexisting species. Nestedness provides the maximum number of species given a certain number of interactions (Fig. 1b). The next question is to unravel how nested mutualistic networks arise in the first place. In Supplementary Methods, we analytically show that a new species entering the community will experience the lowest competitive load, and will therefore be most likely to be incorporated into the community, if it

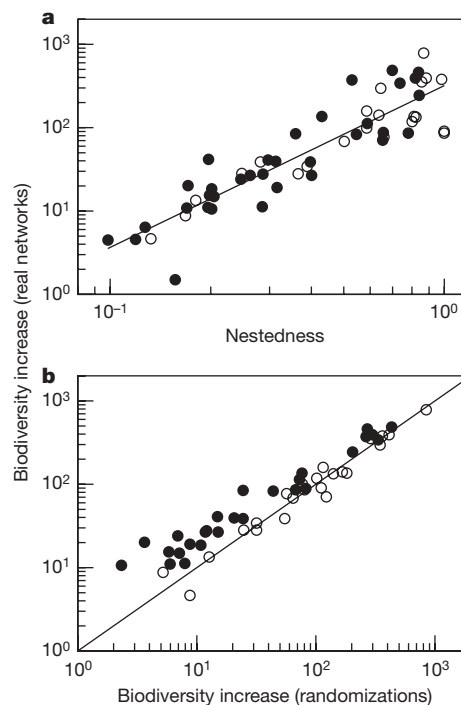


Figure 2 | The nested architecture of real mutualistic networks increases their biodiversity. **a**, The increase in the predicted maximum biodiversity (sum of plant and animal species) of a mutualistic network as a function of its value of nestedness. Each symbol represents a real network. **b**, Relationship between the increase in the predicted maximum biodiversity for real networks versus randomizations. All significantly nested networks (filled symbols) show a higher increase in biodiversity. The increase in biodiversity is calculated as a numerical approximation to equation (6). The observed numbers of species ($S^{(P)}$ and $S^{(A)}$) are given in Supplementary Table 1. Other parameters are $\bar{S}^{(P)} = \bar{S}^{(A)} = 50$ and $R = 0.005$.

interacts with the most generalist species. This naturally leads to a nested network.

To illustrate the predicted effect of network architecture on biodiversity, we incorporate the structure of each one of 56 real mutualistic networks (Supplementary Table 1) into our analytical expression (equation (5)). In Fig. 2a, we plot the increase in biodiversity in relation to the baseline limit without mutualism (equation (6)) against the level of nestedness. As can be seen, real communities that are more nested show higher increases in biodiversity. It is possible, however, that this increase is mediated by a covariant variable such as the number of species or interactions. To rule this out, we use an alternative way of exploring the role of network structure that keeps constant all variables but nestedness. Figure 2b shows the comparative increase in biodiversity for both real and randomized networks (Methods). In the bulk of communities (45 of 56, $P = 2.0 \times 10^{-6}$, binomial test), the real architecture induces a higher increase in biodiversity than the randomization. More importantly, all networks that are significantly nested (Methods; filled symbols in Fig. 2b) have a greater increase in biodiversity than do their randomizations. Nestedness may be correlated with other properties of network structure such as degree distribution or disassortativity, and the overall contribution to biodiversity increase may therefore be a composite of all these properties that shape the architecture of mutualistic networks.

Our analytical framework can complement previous non-interacting or mean-field approaches to ecology^{1,2}, by quantifying the importance of network structure for biodiversity. Ideally, this could provide an assessment of the relative contributions of different mechanisms to biodiversity maintenance, a critical task at present in the face of global change. A variety of systems can be described as similar cooperative networks^{12–14}. The dynamics of such systems can be captured by appropriate versions of the mutualistic model studied here. Therefore, our analysis can be extended to address questions such as to what extent systemic risk depends on the structure of the financial systems¹³, how the optimum number of companies is determined by the architecture of contractor–manufacturer networks¹⁴, and to what degree the structure of social networks favours the evolution of cooperation²⁸.

METHODS SUMMARY

We used a mutualistic model defined as a system of differential equations. It describes the dynamics of a community of n plant species and m animal species as a function of their intrinsic growth rates, interspecific competition, and mutualistic effects represented as nonlinear, saturating functional responses (Holling type II). We controlled the structure of the plant–animal mutualistic network and were able to analytically solve the model for several network architectures.

We analytically estimated nestedness by averaging the number of shared interactions between two given plants relative to their respective numbers of interactions. In a completely nested matrix, the sets of interactions overlap, therefore maximizing the above quantity. This analytical measure of nestedness allowed us to directly relate nestedness to the effective competition matrix, and to write our analytical solutions as a function of nestedness.

We assessed the significance of nestedness by estimating the probability, p , that a randomization of the network is equally or more nested than the real matrix⁵. Our randomizations assumed that the probability of an interaction was proportional to the generalization level of both the plant and the animal species⁵.

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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Author Contributions U.B., jointly with A.P.-G., A.F. and B.L., performed the analytical development. M.A.F. analysed the real data and, jointly with B.L., performed the simulations. J.B. compiled the real data and, jointly with U.B., designed the study and wrote the first version of the manuscript.

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METHODS

The mutualistic model. The dynamical equation for the population of plant species i is

$$\frac{dN_i^{(P)}}{dt} = \alpha_i^{(P)} N_i^{(P)} - \sum_{j \in \mathbf{P}} \beta_{ij}^{(P)} N_i^{(P)} N_j^{(P)} + \sum_{k \in \mathbf{A}} \frac{\gamma_{ik}^{(P)} N_i^{(P)} N_k^{(A)}}{1 + h^{(P)} \sum_{l \in \mathbf{A}} \gamma_{il}^{(P)} N_l^{(A)}} \quad (7)$$

where upper indices (P) and (A) denote 'plant' and 'animal', respectively, N_i represents the number of individuals of species i and \mathbf{P} and \mathbf{A} indicate the sets of plant and animal species, respectively. The parameter α_i represents the intrinsic growth rate in the absence of mutualism, and β_{ij} represents the direct interspecific competition for resources between species i and j (for example light and nutrients in the case of plants, and breeding sites in the case of animals). The last term describes the mutualistic interaction, through nonlinear functional responses representing a saturation of consumers as the resources increase. The parameter γ_{ik} defines the per capita mutualistic strength of animal k on plant i , and h can be interpreted as a handling time. The equations for animal populations can be written in a symmetric form by interchanging the indices (A) and (P). Equation (7) incorporates all elements recently adduced as necessary ingredients for a realistic model of facultative mutualism^{17,29}, plus additional ones such as the explicit interspecific competition term. It generalizes previous mutualistic models and allows the reconciliation of previous results on particular cases (Supplementary Methods).

Fixed points of the model. We can analytically obtain the fixed points of model (7) through some algebraic transformations and Taylor expansions (see Supplementary Methods for the full analytical development). There are two different solutions. The first is characterized by small equilibrium biomasses, $N \ll 1/h\gamma$. Because the mutualistic strength, γ , has to remain small for this to be stable, we call this regime weak mutualism. A second type of fixed point, which we refer to as strong mutualism, corresponds to equilibrium biomasses, N , of order $1/h\gamma$. As soon as the weak-mutualism fixed point becomes unstable, the

strong-mutualism fixed point becomes stable. Because mutualistic networks are built upon weak dependences¹⁰, the weak-mutualism solution seems the most plausible; it is the one considered in the main text, whereas the strong-mutualism regime is described in Supplementary Methods.

The weak-mutualism fixed-point equations can be written in the form of a linear system, $\sum_j C_{ij}^{(P)} N_j^{(P)} = p_i^{(P)}$, where $p_i^{(P)}$ are the entries of the effective productivity vector (Supplementary Methods). We show in Supplementary Methods that the necessary and sufficient condition for dynamic stability in the weak-mutualism regime is that all equilibrium biomasses are positive and the effective competition matrix is positive definite (that is, all eigenvalues are real and positive).

Measuring nestedness. The level of nestedness of the mutualistic matrix is usually estimated by means of appropriate software^{5,12,30}. Here we introduced an explicit definition of nestedness that makes the calculation more straightforward and had the advantage of being related to the form of the effective competition matrix. For plant species, it reads

$$\eta^{(P)} = \frac{\sum_{i < j} n_{ij}^{(P)}}{\sum_{i < j} \min(n_i^{(P)}, n_j^{(P)})}$$

Here $\min(n_i^{(P)}, n_j^{(P)})$ refers to the smaller of the two values $n_i^{(P)}$ and $n_j^{(P)}$. A symmetric definition holds for animal species. This nestedness index ranges from zero to one, and is highly correlated with previous measures of nestedness.

To assess the significance of nestedness in a real community, we used a population of randomizations of the real community. Our null model randomized the interaction matrix probabilistically maintaining the generalization level of both the plant and the animal species. Specifically, the probability of an interaction between plant i and animal j , π_{ij} , is given by the following expression⁵, where p_i and q_j are the fractions of occupied cells in row i and column j , respectively:

$$\pi_{ij} = \frac{p_i + q_j}{2}$$

As a statistic indicating significance, we estimated the probability, p , that a randomization was equally or more nested than the real matrix⁵.