

The architecture of mutualistic networks minimizes competition and increases biodiversity

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1 The main theories of biodiversity either neglect species interactions^{1,2} or
2 assume that species interact randomly with each other^{3,4}. In contrast, recent
3 empirical work has revealed that ecological networks are highly structured⁵⁻⁷.
4 Yet, the lack of a theory that takes into account the structure of interac-
5 tions precludes further assessment of the implications of such network pat-
6 terns for biodiversity. Here, we use a combination of analytical and empirical
7 approaches to quantify the influence of network architecture on the number
8 of coexisting species. As a case study we consider mutualistic networks be-
9 tween plants and their animal pollinators or seed dispersers^{5,8-11}. These net-
10 works have been found to be highly nested⁵, with specialists interacting with
11 proper subsets of the species generalists interact with. We show that nest-
12 edness reduces effective interspecific competition and enhances the number
13 of coexisting species. Further, we show that a nested network will naturally
14 emerge if new species are more likely to enter the community where they have
15 minimal competitive load. Nested networks seem to occur in many biologi-
16 cal and social contexts¹²⁻¹⁴, suggesting that our results are relevant in a wide
17 range of fields.

18 A long-held tenet in ecology is that the structure of ecological networks can largely
19 affect its dynamics^{3,6,7,15,16}. Recent work has unravelled the structure of plant-animal
20 mutualistic networks^{5,8-11}, but little is known about the implications of these network
21 patterns for the persistence of biodiversity. Previous theory has analyzed the dynamics of
22 mutualistic communities without considering their structure^{3,17-20}. More recently, ecol-
23 ogists have started to explore numerically the robustness of mutualistic networks^{10,21-25},
24 but no study so far has determined how the size of the network depends on its structure.

1 Yet, understanding the factors determining the number of coexisting species is possibly
2 the most fundamental question in ecology and conservation biology. Here we analytically
3 quantify whether and to what extent the architecture of mutualistic networks enhances
4 the number of species that can stably coexist in a community (Fig. 1). Second, we explore
5 the emergence of this network architecture through the assembly process. Our analytical
6 approach provides general, insightful, results about the equilibrium behaviour instead of
7 simulating the dynamics of our system prior to such an equilibrium (Supplementary Fig.
8 1).

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

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

18 where $\tilde{\rho}^{(P)}$ is the normalized effective interspecific competition parameter that can be
19 computed from the main eigenvalue λ_1 of the normalized competition matrix (see Sup-
20 plementary Methods) as

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

1 $S^{(P)}$ being the observed number of plant species which gives the dimensions of the inter-
 2 action matrices. Qualitatively, the larger is $\tilde{\rho}^{(P)}$, the smaller is the number of species that
 3 can stably coexist in a purely competitive system. To obtain explicit analytical formulas,
 4 we will consider hereafter direct competition of mean field type assuming that all species
 5 within a set compete with each other with identical intensities (this can be relaxed in
 6 numerical simulations, Supplementary Methods). In this case the quantity $\tilde{\rho}^{(P)}$ computed
 7 through Eq. (2) is equal to the direct competition parameter $\rho^{(P)}$.

8 Now that we have set up the baseline limit to the number of coexisting species defined
 9 by Eq. (1), we can incorporate mutualism between plants and animals and quantify the
 10 new limit to biodiversity. We can then estimate the relative effect in biodiversity due to
 11 mutualism as the ratio between these two values. It is still possible to derive an effective
 12 competition matrix that includes the effect of mutualism. The maximum eigenvalue of
 13 this matrix limits biodiversity through Eqs. (1) and (2). We first consider the fully
 14 connected mutualistic network where all plants interact with all animals (Fig. 1a). The
 15 normalized effective interspecific competition ($\tilde{\rho}_{\text{mut}}^{(P)}$) is related to the direct competition
 16 without mutualism as follows

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

17 where $a^{(P)}$ is a parameter defined in Supplementary Eq. (7) that is proportional to the
 18 strength of mutualistic interactions. Stable solutions exist for $a^{(P)} < \rho^{(P)}$. We can see
 19 from Eq. (3) that $\tilde{\rho}_{\text{mut}}^{(P)}$ is smaller than $\rho^{(P)}$. This means that mutualism always reduces
 20 the effective interspecific competition in a fully connected plant-animal network. The
 21 predicted maximum number of plant species in the presence of mutualism ($\bar{S}_{\text{mut}}^{(P)}$) becomes
 22 (Supplementary Methods):

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

1 which is strictly greater than $\overline{S}^{(\text{P})}$, proving that fully connected mutualistic interactions
 2 increase the number of coexisting species by reducing the effective interspecific competi-
 3 tion.

4 Having quantified the increase in biodiversity due to mutualism in the fully connected
 5 case, we proceed by assessing how this mutualistic effect is shaped by the structure of
 6 mutualistic networks (Fig. 1b-c). We will repeat the above arguments relaxing the as-
 7 sumption that plant and animal species interact with all species in the other group. While
 8 the effective competition matrix in the case of mean field mutualism contained terms de-
 9 scribing an average identical effect of one species on another, now the elements of the
 10 effective competition matrix $C_{ij}^{(\text{P})}$ are different and have to be written explicitly as (Sup-
 11 plementary Methods):

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

12 where δ_{ij} is the Kronecker's Delta (1 if $i = j$, 0 otherwise), R is the mutualism-to-
 13 competition ratio (Supplementary Eq. 22), and $n_i^{(\text{P})}$, $n_j^{(\text{P})}$, and $n_{ij}^{(\text{P})}$ are the number of
 14 interactions of plant species i , of plant species j , and the shared interactions between
 15 both species, respectively. Importantly, the right-hand side of Eq. (5) decreases with
 16 the nestedness of the mutualistic network (as defined in Methods). As a consequence,
 17 under visual inspection nestedness reduces the effective interspecific competition for a
 18 given distribution of number of interactions across plant species and fixed parameters.
 19 Since the predicted maximum number of plant species (Eq. 4) increases with decreasing
 20 effective competition, the model predicts that the more nested the matrix is, the higher

1 the maximum biodiversity.

2 To explicitly quantify the increase in biodiversity (from the baseline of an exclusively
 3 competitive system) due to the nested architecture of mutualistic networks, we computed
 4 the derivative of the predicted maximum number of plant species (Eq. 4) with respect to
 5 the mutualism-to-competition ratio, which is equal to

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

6 where $\langle n^{(P)} \rangle = \sum_i n_i^{(P)} / S^{(P)}$ and $\langle (n^{(P)})^2 \rangle = \sum_i (n_i^{(P)})^2 / S^{(P)}$ are the mean and mean
 7 square number of mutualistic interactions per plant species, respectively. This derivative
 8 increases with the parameter $\hat{\eta}^{(P)} = \sum_{i \neq j} n_{ij}^{(P)} / \left((S^{(P)} - 1) \sum_i n_i^{(P)} \right)$ which is highly cor-
 9 related with the measure of nestedness defined in Methods. As seen before, mutualism
 10 of the fully connected type always increases the number of coexisting species, setting up
 11 the maximum limit to biodiversity (fully connected networks have the maximum number
 12 of mutualistic interactions and are maximally nested; Fig. 1a). Structured networks,
 13 however, may increase the effective competition and reduce biodiversity if there are not
 14 enough shared interactions (i.e., for low nestedness; Fig. 1c), or if direct competition is
 15 strong so that the predicted maximum number of species in the absence of mutualism,
 16 $\bar{S}^{(A)}$ and $\bar{S}^{(P)}$, are small. Therefore, the architecture of mutualistic networks highly con-
 17 ditions the sign and magnitude of the effect of mutualism on the number of coexisting
 18 species. Nestedness provides the maximum number of species given a certain number of
 19 interactions (Fig. 1b). But how do nested mutualistic networks arise in the first place?
 20 In Supplementary Methods, we analytically show that a new species entering the com-

1 munity will experience the lowest competitive load, and will therefore be most likely to
2 be incorporated into the community, if it interacts with the most generalist species. This
3 naturally leads towards a nested network.

4 To test the predicted effect of network architecture on biodiversity, we incorporate the
5 structure of each one of 56 real mutualistic networks (Supplementary Table 1) in our ana-
6 lytical expression (Eq. 5). Fig. 2a represents the increase in biodiversity in relation to the
7 baseline limit without mutualism (Eq. 6) versus the level of nestedness. As can be seen,
8 more nested real communities show higher increases in biodiversity. One could adduce,
9 however, that this increase is mediated by any covariant variable such as the number of
10 species or interactions. To rule this possibility out, we use an alternative way to explore
11 the role of network structure that maintains constant all variables but nestedness. Fig.
12 2b shows the comparative increase in biodiversity for both real and randomized networks
13 (Methods). In the bulk of communities (45 out of 56, $P = 2.0 \times 10^{-6}$, binomial test),
14 the real architecture induces a higher increase in biodiversity than the randomization.
15 More importantly, all networks that are significantly nested (Methods; solid symbols in
16 Fig. 2b) have a higher increase in biodiversity than their randomizations. Nestedness
17 may be correlated with other properties of network structure such as degree distribution
18 or disassortativity, and therefore the overall contribution to biodiversity increase may be
19 a composite of all these properties that shape the architecture of mutualistic networks.

20 Our analytical framework can complement previous non-interacting or mean field ap-
21 proaches to ecology^{1,2} by quantifying the importance of network structure for biodiversity.
22 Ideally, this could provide an assessment of the relative contribution of different mecha-
23 nisms to biodiversity maintenance, a critical task at present in the face of global change.
24 A variety of systems can be described as similar cooperative networks¹²⁻¹⁴. The dynamics
25 of such systems can be captured by appropriate versions of the mutualistic model here

1 studied. Therefore, our analysis can be extended to address questions such as to what
2 extent systemic risk depends on the structure of the financial systems¹³, how the opti-
3 mum number of companies is determined by the architecture of contractor-manufacturer
4 networks¹⁴, or to what degree the structure of social networks favors the evolution of
5 cooperation²⁸.

METHODS SUMMARY

We used a mutualistic model describing 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 non-linear, saturating functional responses. We controlled the structure of the plant-animal mutualistic network and were able to solve analytically 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 number 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, besides probabilistically maintaining the total number of plant species, animal species, and interactions.

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8 **Supplementary Information** is linked to the online version of the paper at www.nature.com/nature.
9

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20 the simulations. J.B. compiled the real data, and jointly with U.B. designed the study
21 and wrote a first version of the manuscript.

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¹ ture.com/reprints. The authors declare no competing financial interests. Correspondence
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1 Figure Legends

2 **Figure 1 | The structure of mutualistic networks determines the number of**
3 **coexisting species.** Each panel represents a plant-animal network with different struc-
4 tures: **(a)** all plants interact with all animals; **(b)** a nested structure; **(c)** a compartmen-
5 talized structure. Animals and plants are represented in rows and columns, respectively,
6 and interactions are indicated by a square. Two plants and their respective interactions
7 are highlighted. They compete for resources such as nutrients (red arrow), but also have
8 indirect interactions mediated by their common pollinators (blue arrow), that may change
9 in sign and magnitude. As the number of shared pollinators is higher, positive effects out-
10 weigh the negative ones, and the theory predicts a higher number of coexisting species as
11 indicated by the size of the matrices.

12 **Figure 2. | The nested architecture of real mutualistic networks increases**
13 **their biodiversity.** **(a)** The increase in the predicted maximum biodiversity (sum of
14 plant and animal species) of a mutualistic network as a function of its value of nestedness.
15 Each dot represents a real network. **(b)** Relationship between the increase in the pre-
16 dicted maximum biodiversity for real networks versus randomizations. All significantly
17 nested networks (solid symbols) show a higher increase in biodiversity. The increase in
18 biodiversity is calculated as a numerical approximation to Eq. (6). The observed number
19 of species ($S^{(P)}$ and $S^{(A)}$) are given in Supplementary Table 1. Other parameters are
20 $\bar{S}^{(P)} = \bar{S}^{(A)} = 50$ and $R = 0.005$.

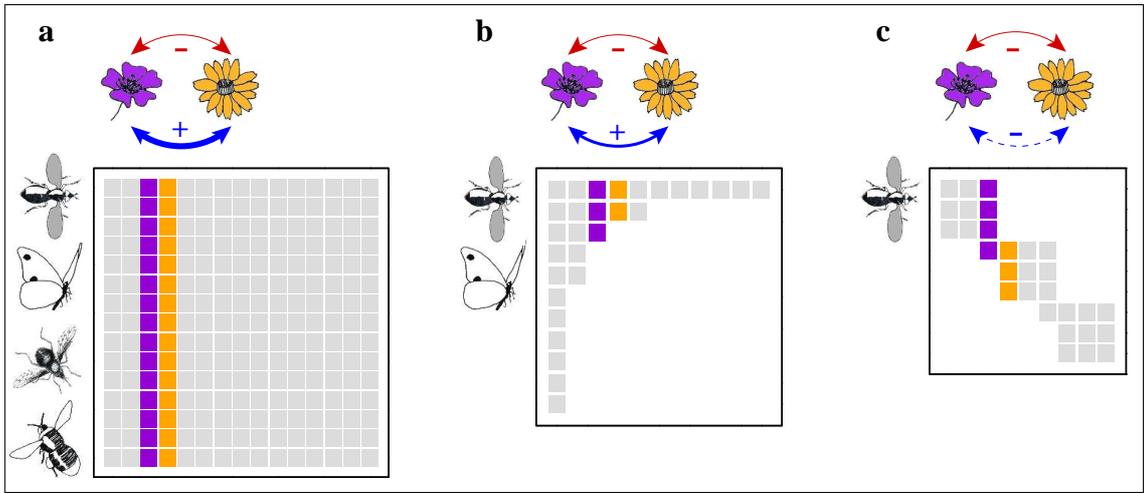


Figure 1: *Bastolla et al.*

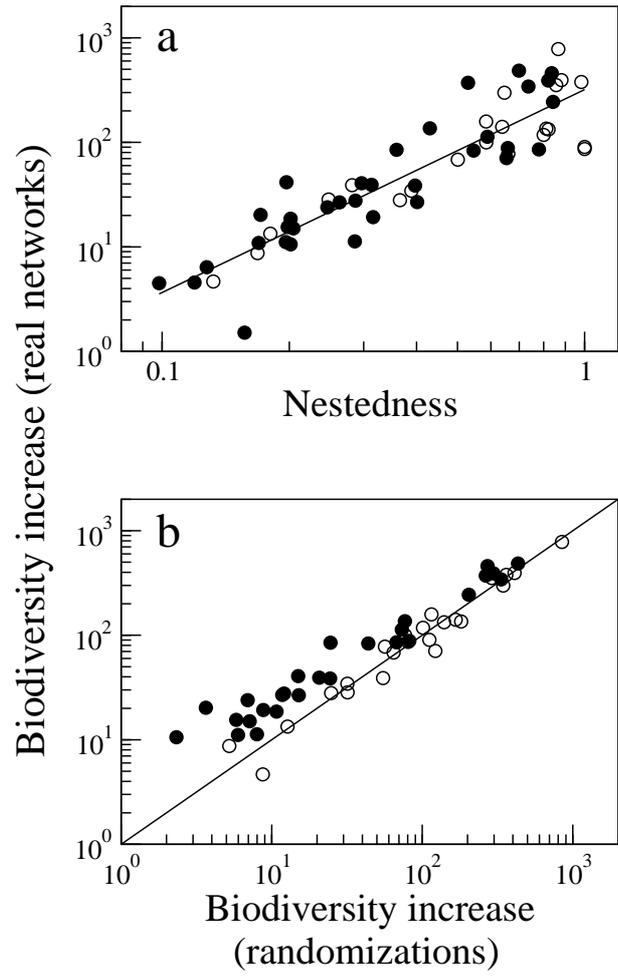


Figure 2: *Bastolla et al.*

METHODS

The mutualistic model. The dynamical equations 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 superindices (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 set 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 (e.g., light and nutrients in the case of plants; breeding sites in the case of animals). The last term describes the mutualistic interaction, through non-linear 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 interchanging superindices A and P. Eq. (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 one is characterized by small equilibrium biomasses, $h\gamma N \ll 1$. Because the mutualistic

1 strength γ has to remain small for this to be stable, we call this regime *weak mutualism*.
2 A second type of fixed point, hereafter referred to as *strong mutualism*, corresponds to
3 equilibrium biomasses N of order $1/(h\gamma)$. As soon as the weak mutualism fixed point
4 becomes unstable, the strong mutualism fixed point becomes stable. Because mutualistic
5 networks are built upon weak dependences¹⁰, the weak mutualism solution seems the most
6 plausible, and the one we considered in the main text, whereas the strong mutualism
7 regime is described in Supplementary Methods.

8 The weak fixed point equations can be written in the form of a linear system $\sum_j C_{ij}^{(P)} N_j^{(P)} =$
9 $p_i^{(P)}$, where $p_i^{(P)}$ is the effective productivity vector defined in Supplementary Methods and
10 $C^{(P)}$ is the effective competition matrix, and the foundation of our analysis. We show in
11 Supplementary Methods that the necessary and sufficient condition for dynamic stability
12 in the weak mutualism regime is that all equilibrium biomasses are positive and the ef-
13 fective competition matrix is positive definite (i.e., all eigenvalues are real and positive).

14

15 **Measuring nestedness.** The level of nestedness of the mutualistic matrix is usually
16 estimated by means of an appropriate software^{5,12,30}. Here, we introduced an explicit
17 definition of nestedness that makes the calculation more straightforward and had the
18 advantage of being related to the form of the effective competition matrix. From the
19 point of view of the plants, it reads:

$$\eta^{(P)} = \frac{\sum_{i<j} n_{ij}^{(P)}}{\sum_{i<j} \min(n_i^{(P)}, n_j^{(P)})}, \quad (8)$$

20 where $n_i^{(P)}$ and $n_j^{(P)}$ are the number of interactions of plants i and j , respectively, and
21 $n_{ij}^{(P)}$ is the number of interactions common to both plants i and j . Here $\min(n_i^{(P)}, n_j^{(P)})$
22 refers to the minimum value between $n_i^{(P)}$ and $n_j^{(P)}$. The symmetric definition holds from

1 the point of view of animals. This index goes from zero to one, and is highly correlated
2 with previous measures of nestedness.

3 In order to assess the significance of nestedness in a real community, we used a popula-
4 tion of randomizations of the real community. Our null model randomized the interaction
5 matrix maintaining the generalization level of both the plant and the animal. Specifi-
6 cally, the probability of an interaction between plant i and animal j (ρ_{ij}) is given by the
7 following expression⁵:

$$\rho_{ij} = \frac{p_i + q_j}{2}, \quad (9)$$

8 where p_i and q_j are the fraction of occupied cells in row i and column j , respectively.

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