The architecture of mutualistic networks minimizes competition and increases biodiversity

Ugo Bastolla,¹ Miguel A. Fortuna,² Alberto Pascual-García¹
Antonio Ferrera,³ Bartolo Luque,³ and Jordi Bascompte²∗

¹Centro de Biología Molecular
Universidad Autónoma de Madrid - CSIC
Cantoblanco 28049, Madrid, Spain

²Integrative Ecology Group
Estación Biológica de Doñana, CSIC
Apdo. 1056, E-41080 Sevilla, Spain

³Departamento de Matemática Aplicada y Estadística
E.T.S.I. Aeronáuticos
Universidad Politécnica de Madrid
Plaza Cardenal Cisneros 3, Madrid 28040, Spain

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∗Corresponding author: bascompte@ebd.csic.es
The main theories of biodiversity either neglect species interactions\textsuperscript{1,2} or assume that species interact randomly with each other\textsuperscript{3,4}. In contrast, recent empirical work has revealed that ecological networks are highly structured\textsuperscript{5−7}. Yet, 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\textsuperscript{5,8−11}. These networks have been found to be highly nested\textsuperscript{5}, with specialists interacting with proper subsets of the species generalists interact with. We show that nestedness reduces effective interspecific competition and enhances the number of coexisting species. Further, 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\textsuperscript{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 ecological networks can largely affect its dynamics\textsuperscript{3,6,7,15,16}. Recent work has unravelled the structure of plant-animal mutualistic networks\textsuperscript{5,8−11}, but little is known about the implications of these network patterns for the persistence of biodiversity. Previous theory has analyzed the dynamics of mutualistic communities without considering their structure\textsuperscript{3,17−20}. More recently, ecologists have started to explore numerically the robustness of mutualistic networks\textsuperscript{10,21−25}, but no study so far has determined how the size of the network depends on its structure.
Yet, understanding the factors determining the number of coexisting species is possibly the most fundamental question 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). Second, 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 prior to 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 which predict the number of coexisting species when there are only competitive interactions\textsuperscript{26,27}. Next, we build a generalized model of mutualisms where 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\textsuperscript{26,27}. This predicted maximum number of plant species (similar for animals) can be expressed as

\[
\frac{S(P)}{\rho(P)} = 1 - \frac{\tilde{\rho}(P)}{\rho(P)},
\]

where \(\tilde{\rho}(P)\) is the normalized effective interspecific competition parameter that can be computed from the main eigenvalue \(\lambda_1\) of the normalized competition matrix (see Supplementary Methods) as

\[
\tilde{\rho}(P) = \frac{\lambda_1 - 1}{S(P) - 1},
\]

(2)
$S^{(P)}$ being 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 formulas, we will consider hereafter 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 $\tilde{\rho}^{(P)}$ computed through Eq. (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 Eq. (1), we can incorporate mutualism between plants and animals and quantify the new limit to biodiversity. We can then estimate the relative effect in biodiversity due to mutualism as the ratio between these two values. 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 Eqs. (1) and (2). We first consider the fully connected mutualistic network where 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

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

where $a^{(P)}$ is a parameter defined in Supplementary Eq. (7) that is proportional to the strength of mutualistic interactions. Stable solutions exist for $a^{(P)} < \rho^{(P)}$. We can see from Eq. (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 ($S_{\text{mut}}^{(P)}$) becomes

(Supplementary Methods):
\[
\overline{S}^{(P)}_{\text{mut}} = \overline{S}^{(P)} - \overline{\rho}^{(P)}_{\text{mut}} = \frac{\overline{\rho}^{(P)}}{1 - a^{(P)} / \rho^{(P)}},
\] (4)

which is strictly greater than \(\overline{S}^{(P)}\), proving that fully connected mutualistic interactions 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. While 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):

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

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

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

\[
+ \left( \frac{(\langle n^{(P)} \rangle)^2 - \langle n^{(P)} \rangle^2}{\langle n^{(P)} \rangle (S_{(A)} + S_{(A)^2})} \left( \frac{S_{(P)} + S_{(P)}}{S_{(P)} - 1} \right) \right) \right],
\] (6)

where \( \langle n^{(P)} \rangle = \sum_i n_{i}^{(P)}/S_{i}^{(P)} \) and \( \langle (n^{(P)})^2 \rangle = \sum_i (n_{i}^{(P)})^2 / S_{i}^{(P)} \) are the mean and mean square number of mutualistic interactions per plant species, respectively. This derivative increases with the parameter \( \hat{\eta}^{(P)} = \sum_{i \neq j} n_{ij}^{(P)}/(S_{(P)} - 1) \sum_i n_i^{(P)} \) which is highly correlated with the measure of nestedness defined in Methods. As seen before, mutualism of the fully connected type always increases the number of coexisting species, setting up the maximum limit to biodiversity (fully connected networks have the maximum number of mutualistic interactions and are maximally nested; Fig. 1a). Structured networks, however, may increase the effective competition and reduce biodiversity if there are not enough shared interactions (i.e., for low nestedness; Fig. 1c), or if direct competition is strong so that the predicted maximum number of species in the absence of mutualism, \( S_{(A)} \) and \( S_{(P)} \), 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). But how do nested mutualistic networks arise in the first place? In Supplementary Methods, we analytically show that a new species entering the com-
munity will experience the lowest competitive load, and will therefore be most likely to
be incorporated into the community, if it interacts with the most generalist species. This
naturally leads towards a nested network.

To test the predicted effect of network architecture on biodiversity, we incorporate the
structure of each one of 56 real mutualistic networks (Supplementary Table 1) in our ana-
lytical expression (Eq. 5). Fig. 2a represents the increase in biodiversity in relation to the
baseline limit without mutualism (Eq. 6) versus the level of nestedness. As can be seen,
more nested real communities show higher increases in biodiversity. One could adduce,
however, that this increase is mediated by any covariant variable such as the number of
species or interactions. To rule this possibility out, we use an alternative way to explore
the role of network structure that maintains constant all variables but nestedness. Fig.
2b shows the comparative increase in biodiversity for both real and randomized networks
(Methods). In the bulk of communities (45 out 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; solid symbols in
Fig. 2b) have a higher increase in biodiversity than their randomizations. Nestedness
may be correlated with other properties of network structure such as degree distribution
or disassortativity, and therefore the overall contribution to biodiversity increase may 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 ap-
proaches to ecology$^{1,2}$ by quantifying the importance of network structure for biodiversity.
Ideally, this could provide an assessment of the relative contribution of different mecha-
isms 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 here
studied. Therefore, our analysis can be extended to address questions such as to what extent systemic risk depends on the structure of the financial systems\textsuperscript{13}, how the optimum number of companies is determined by the architecture of contractor-manufacturer networks\textsuperscript{14}, or to what degree the structure of social networks favors the evolution of cooperation\textsuperscript{28}. 
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 matrix. Our randomizations assumed that the probability of an interaction was proportional to the generalization level of both the plant and the animal species, besides probabilistically maintaining the total number of plant species, animal species, and interactions.
References


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. analyzed 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 a first version of the manuscript.

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ture.com/reprints. The authors declare no competing financial interests. Correspondence and request for materials should be addressed to J.B. (bascompte@ebd.csic.es).
Figure 1 | The structure of mutualistic networks determines the number of coexisting species. Each panel represents a plant-animal network with different structures: (a) all plants interact with all animals; (b) a nested structure; (c) a compartmentalized structure. Animals and plants are represented in rows and columns, respectively, and interactions are indicated by a square. 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), that may change in sign and magnitude. As the number of shared pollinators is higher, positive effects outweigh the negative ones, and the theory predicts a higher number of coexisting species as indicated by the size of the matrices.

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 dot represents a real network. (b) Relationship between the increase in the predicted maximum biodiversity for real networks versus randomizations. All significantly nested networks (solid symbols) show a higher increase in biodiversity. The increase in biodiversity is calculated as a numerical approximation to Eq. (6). The observed number of species ($S^{(P)}$ and $S^{(A)}$) are given in Supplementary Table 1. Other parameters are $\overline{S^{(P)}} = \overline{S^{(A)}} = 50$ 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:

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

where superindices (P) and (A) denote plant and animal, respectively, $N_i$ represents the number of individuals of species $i$, and $P$ and $A$ indicate the set of plant and animal species, respectively. The parameter $\alpha_i$ represents the intrinsic growth rate in the absence of mutualism, and $\beta_{ij}$ 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 $\gamma_{ik}$ 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\textsuperscript{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
strength $\gamma$ has to remain small for this to be stable, we call this regime weak mutualism. A second type of fixed point, hereafter referred 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 dependences, the weak mutualism solution seems the most plausible, and the one we considered in the main text, whereas the strong mutualism regime is described in Supplementary Methods.

The weak fixed point equations can be written in the form of a linear system $\sum_j C^{(P)}_{ij} N^{(P)}_j = p^{(P)}_i$, where $p^{(P)}_i$ is the effective productivity vector defined in Supplementary Methods and $C^{(P)}$ is the effective competition matrix, and the foundation of our analysis. 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 (i.e., all eigenvalues are real and positive).

**Measuring nestedness.** The level of nestedness of the mutualistic matrix is usually estimated by means of an appropriate software. 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. From the point of view of the plants, it reads:

$$\eta^{(P)} = \frac{\sum_{i<j} n^{(P)}_{ij}}{\sum_{i<j} \min(n^{(P)}_i, n^{(P)}_j)}, \tag{8}$$

where $n^{(P)}_i$ and $n^{(P)}_j$ are the number of interactions of plants $i$ and $j$, respectively, and $n^{(P)}_{ij}$ is the number of interactions common to both plants $i$ and $j$. Here $\min(n^{(P)}_i, n^{(P)}_j)$ refers to the minimum value between $n^{(P)}_i$ and $n^{(P)}_j$. The symmetric definition holds from...
the point of view of animals. This index goes from zero to one, and is highly correlated
with previous measures of nestedness.

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

\[
\rho_{ij} = \frac{p_i + q_j}{2},
\]  

(9)

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

As a statistic for significance, we estimated the probability \( p \) that a randomization
was equally or more nested than the real matrix\(^5\).