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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 nested[5], 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

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

where $\tilde{\rho}^{(\mathrm{P})}$ 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

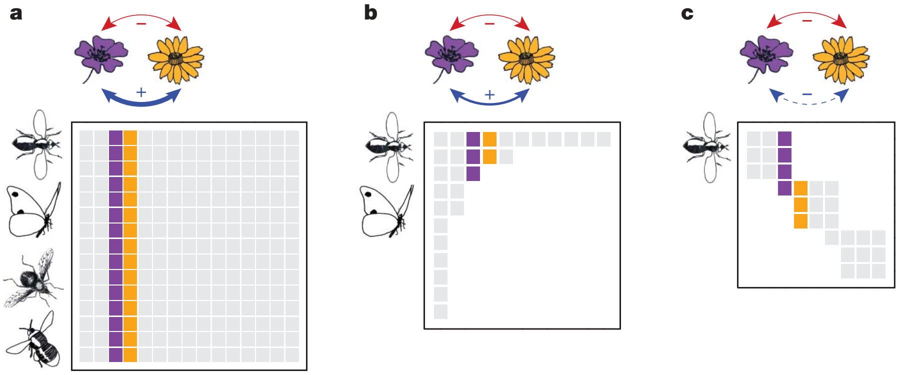

Figure 1 | The structure of mutualistic networks determines the number of coexisting species. Each panel represents a plant–animal network with different structures: **a**, fully connected; **b**, nested; **c**, compartmentalized. Two plants and their respective interactions are highlighted. They compete 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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$$\tilde{\rho}^{(\mathrm{P})} = \frac{\lambda_1 - 1}{S^{(\mathrm{P})} - 1} \qquad (2)$$

Here $S^{(\mathrm{P})}$ is the observed number of plant species, which gives the dimensions of the interaction matrices. Qualitatively, the larger is $\tilde{\rho}^{(\mathrm{P})}$, 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, $\rho^{(\mathrm{P})}$.

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, $\tilde{\rho}^{(\mathrm{P})}_{\mathrm{mut}}$, is related to the direct competition without mutualism as follows, where $a^{(\mathrm{P})}$ is a parameter (Supplementary Information equation (7)) that is proportional to the strength of mutualistic interactions:

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

Stable solutions exist for $a^{(\mathrm{P})} < \rho^{(\mathrm{P})}$. We can see from equation (3) that $\tilde{\rho}^{(\mathrm{P})}_{\mathrm{mut}}$ is smaller than $\rho^{(\mathrm{P})}$. 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, $\bar{S}^{(\mathrm{P})}_{\mathrm{mut}}$, becomes (Supplementary Methods)

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

which is strictly greater than $\bar{S}^{(\mathrm{P})}$, 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, $C^{(\mathrm{P})}_{ij}$, are different and have to be written explicitly as (Supplementary Methods)

$$C^{(\mathrm{P})}_{ij} = \delta_{ij} + \frac{1}{\bar{S}^{(\mathrm{P})}} + R\left(\frac{1}{S^{(\mathrm{A})} + \bar{S}^{(\mathrm{A})}} n^{(\mathrm{P})}_i n^{(\mathrm{P})}_j - n^{(\mathrm{P})}_{ij}\right) \qquad (5)$$

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)), $n^{(\mathrm{P})}_i$ is the number of interactions of plant species i and $n^{(\mathrm{P})}_{ij}$ 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:

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

Here $\langle n^{(\mathrm{P})}\rangle = \sum_i n^{(\mathrm{P})}_i / S^{(\mathrm{P})}$ and $\langle (n^{(\mathrm{P})})^2\rangle = \sum_i (n^{(\mathrm{P})}_i)^2 / S^{(\mathrm{P})}$ are the mean and mean-square number of mutualistic interactions per plant species, respectively. This derivative increases with the parameter $\hat{\eta}^{(\mathrm{P})} = \sum_{i \neq j} n^{(\mathrm{P})}_{ij} \Big/ \left((S^{(\mathrm{P})} - 1)\sum_k n^{(\mathrm{P})}_k\right)$, 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, $\bar{S}^{(\mathrm{A})}$ and $\bar{S}^{(\mathrm{P})}$, 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

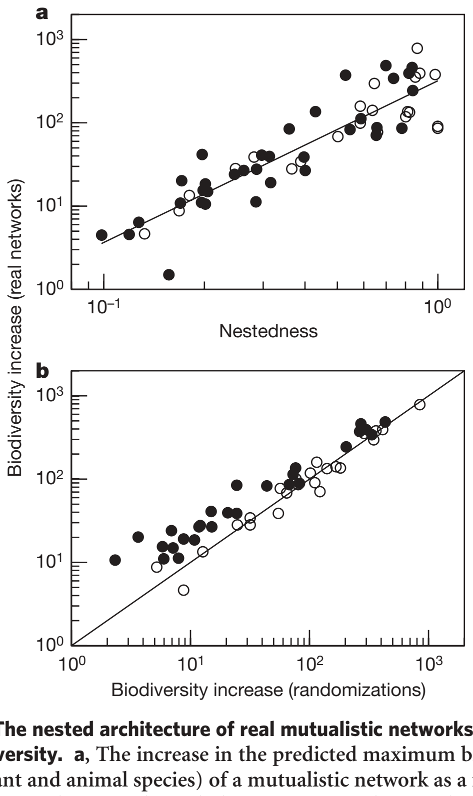

Figure 2 | The nested architecture of real mutualistic networks increases their biodiversity. **a**, The increase in the predicted maximum biodiversity (sum of plant and animal species) of a mutualistic network as a function of its value of nestedness. Each symbol represents a real network. **b**, Relationship 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 ($S^{(\mathrm{P})}$ and $S^{(\mathrm{A})}$) are given in Supplementary Table 1. Other parameters are $\bar{S}^{(\mathrm{P})} = \bar{S}^{(\mathrm{A})} = 50$ 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 systems[13], how the optimum number of companies is determined by the architecture of contractor–manufacturer networks[14], and to what degree the structure of social networks favours the evolution of cooperation[28].

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 matrix[5]. Our randomizations assumed that the probability of an interaction was proportional to the generalization level of both the plant and the animal species[5].

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

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

where upper indices (P) and (A) denote 'plant' and 'animal', respectively, N_i represents the number of individuals of species i and **P** and **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 dependences[10], 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, $\sum_j C_{ij}^{(\mathrm{P})} N_j^{(\mathrm{P})} = p_i^{(\mathrm{P})}$, where $p_i^{(\mathrm{P})}$ 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

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

Here $\min(n_i^{(\mathrm{P})}, n_j^{(\mathrm{P})})$ refers to the smaller of the two values $n_i^{(\mathrm{P})}$ and $n_j^{(\mathrm{P})}$. 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 expression[5], 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 matrix[5].

1 Community model

We consider here model communities of plants and pollinators or seed dispersers where species in the same group are in competition between each other and interact mutualistically with species in the other group. We represent through $N_i^{(\mathrm{P})}$ and $N_k^{(\mathrm{A})}$ the species abundance density of the i-th species of plant and the k-th species of animal respectively, and with $S^{(\mathrm{P})}$ and $S^{(\mathrm{A})}$ the observed number of such species. The intrinsic growth rates in the absence of competition and mutualism are represented as $\alpha_i^{(\mathrm{P})}$ for plants and $\alpha_k^{(\mathrm{A})}$ for animals. In the latter case, they may be either positive or negative, representing the difference between the growth rate in the absence of any plant and the death rate. This choice has no relevant effect on the qualitative results.

For the sake of mathematical simplicity, we represent direct competitive interactions between species i and j through a linear functional response, $-\beta_{ij}^{(\mathrm{P})} N_j^{(\mathrm{P})}$ in the case of plants and $-\beta_{kl}^{(\mathrm{A})} N_l^{(\mathrm{A})}$ for animals. The competition matrices $\beta_{ij}^{(\mathrm{P,A})}$ are assumed to be symmetric and positive, with all positive or zero elements, both for plants and for animals.

The mutualistic interactions between plants and animals are modeled through non-linear functional responses of Holling Type II[1], $f\left(N\right) = \left(\gamma N\right) / \left(1 + h\gamma N\right)$. The denominator of the Holling term slows down the functional response when the densities are large, $N \approx 1/h\gamma$, limiting the maximum growth rate as $1/h$ and preventing it from diverging in the large N limit. The parameter h can be interpreted as a handling time. The mutualistic interactions network is described by a matrix $\gamma_{ij}^{(\mathrm{P})}$ whose non-negative elements represent the increase of the growth rate of the plant species i per unit of animal biomass j, in the limit of very small animal biomass. Similarly, $\gamma_{ji}^{(\mathrm{A})}$ has all non-negative elements that represent the increase of the growth rate of the animal species j per unit of plant biomass i.

The resulting dynamical equations for the plant populations are

$$\frac{1}{N_i^{(\mathrm{P})}}\frac{\mathrm{d}N_i^{(\mathrm{P})}}{\mathrm{d}t} = \alpha_i^{(\mathrm{P})} - \sum_{j\in\mathbf{P}} \beta_{ij}^{(\mathrm{P})} N_j^{(\mathrm{P})} + \sum_{k\in\mathbf{A}} \frac{\gamma_{ik}^{(\mathrm{P})} N_k^{(\mathrm{A})}}{1 + h^{(\mathrm{P})} \sum_{l\in\mathbf{A}} \gamma_{il}^{(\mathrm{P})} N_l^{(\mathrm{A})}} \,. \tag{1}$$

The equations for animal populations can be written in a symmetric form interchanging the indices A and P. When not otherwise stated, we will in the following only write down equations for plants.

In the next section we analyze the fixed points and dynamical stability of the model, leaving for section 3 the interesting problem of how the effective competition limits the structural stability of the model, and correspondingly its maximum biodiversity. Section 4 is a summary of the main results of the stability analysis. This is followed in Section 5 by an analysis of an assembling network, showing that a new species entering the community is favored by interacting with the most generalist species. Section 6 explores the robustness of our analytical results when other interaction types are included (6.1) and when departing from the mean field assumptions using numerical simulations (6.2). We conclude this online material with three appendices, one with the proof of the dynamical stability condition, the second with the numerical calculation of the predicted maximum biodiversity, and the last one presenting the mutualistic networks analyzed in this paper.

2 Fixed points and dynamical stability

We will consider here the fixed points of the dynamical system, defined by the equations $\mathrm{d}N_i^{(\mathrm{A,P})}/\mathrm{d}t = 0$, and analyze their stability. In order to get analytic expressions, we will exploit the fact that the handling time h is small compared with the typical intrinsic time of growth $1/\alpha$. We find two different types of solution. The first one is characterized by small equilibrium biomasses, $N \ll 1/h\gamma$. In this limit, we can expand the functional response in a Taylor series, whose dominant term yields a linear system of fixed point equations. We call this regime *weak mutualism.* A second type of fixed points correspond to equilibrium biomasses N of order $1/h\gamma$. In this case the linear system is not a valid approximation, but it is now possible to get analytic insight by neglecting the terms $h\alpha$ with respect to $h\gamma N$. We call this regime *strong mutualism.*

Furthermore, in order to simplify the analytic expressions, we will consider mainly direct competition matrices $\beta_{ij}^{(\mathrm{P})}$ of mean field type, with $\beta_{ij}^{(\mathrm{P})} = \beta_0^{(\mathrm{P})}\left(\rho^{(\mathrm{P})} + (1-\rho^{(\mathrm{P})})\delta_{ij}\right)$ (see ref. 2), where δ_{ij} is Kronecker's delta (one if $i = j$ and zero otherwise). The dimensionless parameters $\rho^{(\mathrm{P})} < 1$ measure the extent of interspecific competition between different species of the same group.

2.1 Pure competition

For a purely competitive system, i.e., $\gamma_{ik} \equiv 0$, the fixed point densities $\{N_i\}$ satisfy the system of equations

$$\sum_{ij} \beta_{ij}^{(\mathrm{P})} N_j^{(\mathrm{P})} = \alpha_i^{(\mathrm{P})} . \tag{2}$$

The analytical expressions are symmetrical for the case of the animals. The necessary and sufficient conditions for dynamic stability are that (i) all equilibrium biomasses must be positive; and (ii) the direct competition matrix β must be positive definite.

2.2 Weak mutualism: mean field

We now integrate mutualistic interactions into the competitive community. If the equilibrium densities are small, $N \ll 1/h\gamma$, which is a valid approximation within the weak mutualism regime, the fixed point equations for the plant communities at the dominant order in h can be written in the form of a linear system,

$$\sum_j C_{ij}^{(\mathrm{P})} N_j^{(\mathrm{P})} = p_i^{(\mathrm{P})} \, . \tag{3}$$

These equations are mathematically equivalent to the fixed points of a purely competitive system, Eq.(2). We call the vector p_i *effective productivity* and the matrix C_{ij} *effective competition*. We will prove in Appendix A that, in analogy with the purely competitive system, the equilibrium fixed point is stable if and only if the effective competition matrix is positive (i.e., all of its eigenvalues are positive) and all the equilibrium densities are positive.

At zero order in h, the effective productivity and the effective competition are given by the expressions

$$p_i^{(\mathrm{P})} = \alpha_i^{(\mathrm{P})} + \sum_{k,l} \gamma_{ik}^{(\mathrm{P})} \left(\beta^{(\mathrm{A})}\right)_{kl}^{(-1)} \alpha_l^{(\mathrm{A})}, \tag{4}$$

$$C_{ij}^{(\mathrm{P})} = \beta_{ij}^{(\mathrm{P})} - \sum_{k,l} \gamma_{ik}^{(\mathrm{P})} \left(\beta^{(\mathrm{A})}\right)_{kl}^{(-1)} \gamma_{lj}^{(\mathrm{A})}. \tag{5}$$

First order corrections in h are straightforward to compute, and do not change the qualitative picture. They will be omitted in the following.

We first consider mean field mutualist interactions, with all species of plants and animals interacting between each other with equal per capita mutualistic effect, $\gamma_{ik}^{(\mathrm{A,P})} = \gamma_0^{(\mathrm{A,P})}$. We will relax this assumption later on. With this assumption, the effective competition matrix turns out to be of mean field type,

$$C_{ij}^{(\mathrm{P})} = \beta_0^{(\mathrm{P})}(1 - a^{(\mathrm{P})}) \left[\delta_{ij} \left(1 - \rho_{\mathrm{mut}}^{(\mathrm{P})}\right) + \rho_{\mathrm{mut}}^{(\mathrm{P})}\right] \, , \tag{6}$$

$$a^{(\mathrm{P})} = \frac{\gamma_0^{(\mathrm{P})} \gamma_0^{(\mathrm{A})}}{\beta_0^{(\mathrm{A})} \beta_0^{(\mathrm{P})}} \frac{S^{(\mathrm{A})}}{\left(S^{(\mathrm{A})} \rho^{(\mathrm{A})} + (1 - \rho^{(\mathrm{A})})\right)} \, . \tag{7}$$

The effective interspecific competition is given by

$$\rho^{(\mathrm{P})}_{\mathrm{mut}} = \frac{\rho^{(\mathrm{P})} - a^{(\mathrm{P})}}{1 - a^{(\mathrm{P})}} < \rho^{(\mathrm{P})}. \tag{8}$$

We see from the above expression that, for the mean field system and for values of the parameter $a^{(\mathrm{P})} \in [0, \rho^{(\mathrm{P})}]$, the effective interspecies competition $\rho^{(\mathrm{P})}_{\mathrm{mut}}$ is smaller than the bare competition $\rho^{(\mathrm{P})}$, i.e., mutualistic interactions of mean field type reduce the effective interspecies competition. Eq. (8) is valid for $a^{(\mathrm{P})} < \rho^{(\mathrm{P})} + (1 - \rho^{(\mathrm{P})})/S^{(\mathrm{P})}$. At this point, the main eigenvalue λ_1 of the effective competition matrix becomes negative and the community enters into the strong mutualism regime.

Stability of the weak mutualism fixed point requires that the effective competition matrix is positive. The eigenvalues are $\lambda_1 = (1-a)\left(S\rho^{(\mathrm{P})}_{\mathrm{mut}} + (1 - \rho^{(\mathrm{P})}_{\mathrm{mut}})\right) = S(\rho^{(\mathrm{P})} - a) + (1 - \rho^{(\mathrm{P})})$ and $\lambda_k = (1-a)(1 - \rho^{(\mathrm{P})}_{\mathrm{mut}}) = (1 - \rho^{(\mathrm{P})})$ $(k > 1)$. Positivity of the competition matrix requires that $S(\rho^{(\mathrm{P})} - a) + (1 - \rho^{(\mathrm{P})}) > 0$, which in turn yields the condition

$$\gamma_0^{(\mathrm{P})}\gamma_0^{(\mathrm{A})} < \beta_0^{(\mathrm{P})}\beta_0^{(\mathrm{A})}\left(\rho^{(\mathrm{A})} + \frac{1-\rho^{(\mathrm{A})}}{S^{(\mathrm{A})}}\right)\left(\rho^{(\mathrm{P})} + \frac{1-\rho^{(\mathrm{P})}}{S^{(\mathrm{P})}}\right), \tag{9}$$

which generalizes the result presented in ref. 3 to the case where the interspecific competition is not zero. Notice that, if $\rho^{(\mathrm{P})}$ and $\rho^{(\mathrm{A})}$ are not zero, the maximum value of mutualistic interactions in the weak mutualism regime does not vanish for large ecosystems (large $S^{(\mathrm{P})}$ and $S^{(\mathrm{A})}$), but it is limited as $\gamma_0^{(\mathrm{P})}\gamma_0^{(\mathrm{A})} < \beta_0^{(\mathrm{P})}\beta_0^{(\mathrm{A})}\rho^{(\mathrm{A})}\rho^{(\mathrm{P})}$.

2.3 Strong mutualism: mean field

For mutualistic interactions stronger than Eq.(9) the weak mutualism fixed point is not stable, and we have to consider the strong regime in which the equilibrium biomasses are of order $1/h$. In order to get analytic results, we neglect higher order terms in h, such as

$h\alpha$. We consider mean field systems in which all pairs of species interact with the same strength. In this case, positivity of the equilibrium biomasses requires that

$$\gamma_0^{(\mathrm{P})}\gamma_0^{(\mathrm{A})} > \beta_0^{(\mathrm{P})}\beta_0^{(\mathrm{A})}\left(\rho^{(\mathrm{A})}+\frac{1-\rho^{(\mathrm{A})}}{S^{(\mathrm{A})}}\right)\left(\rho^{(\mathrm{P})}+\frac{1-\rho^{(\mathrm{P})}}{S^{(\mathrm{P})}}\right). \tag{10}$$

Therefore, we see from Eq.(9) that, as soon as the weak mutualism fixed point ceases to be stable, the strong mutualism fixed point becomes stable. For the mean field case, the strong mutualism fixed point allows coexistence of an arbitrary number of species, independent of the values of the intrinsic growth rates $\alpha_i^{(\mathrm{P,A})}$.

2.4 Strong and weak mutualism can not coexist

In the general case, stability of the strong mutualism fixed point with positive densities requires that the effective competition matrices $C^{(\mathrm{A})}$ and $C^{(\mathrm{P})}$ are not positive definite, i.e., at least one of their eigenvalues is negative or zero. The proof goes like this. In the strong mutualist regime we can neglect the terms $h\alpha_i$ and the fixed point equations are

$$N^{(\mathrm{P})} = \sum_j \left(\beta^{(\mathrm{P})}\right)^{-1}_{ij} \sum_k \frac{\gamma_{ik}^{(\mathrm{P})} N_k^{(\mathrm{A})}}{1+h^{(\mathrm{P})}\sum_{l\in\mathbf{A}}\gamma_{il}^{(\mathrm{P})}N_l^{(\mathrm{A})}}. \tag{11}$$

Since $\gamma N/(1+h\gamma N) \le \gamma N$, it follows that, in the strong mutualism regime,

$$N_i^{(\mathrm{P})} \le \sum_j \left(\left(\beta^{(\mathrm{P})}\right)^{-1}\gamma^{(\mathrm{P})}\left(\beta^{(\mathrm{A})}\right)^{-1}\gamma^{(\mathrm{A})}\right)_{ij} N_j^{(\mathrm{P})} \equiv \sum_j M_{ij}^{(\mathrm{P})} N_j^{(\mathrm{P})}. \tag{12}$$

We have defined here the mutualistic matrix $M^{(\mathrm{P})} \equiv \left(\beta^{(\mathrm{P})}\right)^{-1}\gamma^{(\mathrm{P})}\left(\beta^{(\mathrm{A})}\right)^{-1}\gamma^{(\mathrm{A})}$. The effective competition matrix $C^{(\mathrm{P})}$ can be written in matrix notation as $C^{(\mathrm{P})} \equiv \beta^{(\mathrm{P})}(I-M)$, where I is the identity matrix. Since the direct competition matrix $\beta^{(\mathrm{P})}$ is positive, if $C^{(\mathrm{P})}$ is positive then all eigenvalues of M must fulfill $\lambda(M) < 1$ (see Appendix A). Together with Eq.(12), this implies that the solutions of the fixed point equation must have $N_i^{(\mathrm{P})} \le 0$

for all i. The same applies to $N^{(\mathrm{A})}$ if $C^{(\mathrm{A})}$ is positive. Therefore, if the weak mutualism fixed point is stable, no stable strong mutualism fixed point can exist.

If we relax the mean field assumption, the behavior of the strong mutualism regime changes dramatically. To get some flavour of this, we examined the simplest possible system, where all species are below the weak mutualism threshold and interact with coefficients $\gamma_0^{(\mathrm{P})}$ and $\gamma_0^{(\mathrm{A})}$ such that $\gamma_0^{(\mathrm{P})}\gamma_0^{(\mathrm{A})} < \beta_0^{(\mathrm{P})}\beta_0^{(\mathrm{A})}\rho^{(\mathrm{P})}\rho^{(\mathrm{A})}$, but one pair of species, animal species 1 and plant species 1, have a strong mutualistic interaction with interaction coefficients $\gamma_1^{(\mathrm{P})}\gamma_1^{(\mathrm{A})} > \beta_0^{(\mathrm{P})}\beta_0^{(\mathrm{A})}$. Solving the fixed point equations and considering all possible cases, it can be shown that in this case there is no possible fixed point where the species below the strong mutualism threshold have positive biomass. It follows from this analysis that, if one pair of species overcomes the strong mutualism threshold, no other species below the threshold can coexist with them at any fixed point. Notice that we have considered the best possible interaction matrices γ_{ij}, since all species below the threshold are assumed to interact with all other species, including the strong interacting ones. To allow coexistence, it would be necessary to relax the hypothesis that all other species are directly competing with the strong interacting species.

Therefore, the model predicts that, when a pair of species overcomes the strong mutualism threshold while the other species remain below it, all species below the threshold become extint, pointing out the interesting possibility of mutualism-induced extinctions. We will analyze this regime in more detail in a forthcoming work.

3 Structural stability and biodiversity

Dynamic stability is an important requirement for the fixed point of a model ecosystem to represent properties of a real ecological community. Despite being neither a necesary, nor a sufficient requirement, local dynamic stability is a simple analytic criterion that has been widely used in theoretical ecology, giving very interesting insights on the properties of real communities. However, we believe that other interesting insights can be gained by considering structural stability, i.e., the stability with respect to modifications in the parameters of the dynamical system. In this section, structural stability is meant as the volume in parameter space compatible with positive densities at the fixed point. Interestingly, for competitive systems structural stability in this meaning is negatively correlated with the number of species in the system, so that, by considering a minimum variance of the parameters compatible with the environmental variability, we can predict the maximum number of species that can coexist in the system[4]. We show here that it is possible to extend this analytic insight also to communities in which competition and mutualism coexist. Notice that the existence of a direct term of interspecific competition, $\rho^{(\mathrm{P})}$, is an essential characteristic of our model with respect to other models in the literature, which alters completely its properties of structural stability.

3.1 Effective competition and structural stability

We consider here a species community in which the fixed point equations can be written in the form $\sum_j C_{ij} N_j = p_i$. We refer to C_{ij} as the effective competition matrix and p_i as the effective productivity vector. This formulation is rather general. It is suitable to represent a purely competitive system, in which $C_{ij} = \beta_{ij}$ and $p_i = \alpha_i$, a system with predation (see ref. 4) or a system with weak mutualism, in which the effective competition matrix and the effective productivity vector are given by equations (5) and (4), respectively.

It is convenient to normalize the effective competition matrix as

$$B_{ij} = \frac{C_{ij}}{\sqrt{C_{ii} C_{jj}}}\,, \tag{13}$$

in such a way that $B_{ii} = 1$. From the main eigenvalue of this matrix, $\lambda_1(B)$, we can derive the effective interspecific competition parameter $\tilde{\rho}$ as

$$\tilde{\rho} \equiv \frac{\lambda_1(B) - 1}{S - 1}. \tag{14}$$

If the effective competition matrix is a direct competition matrix of mean field type, $B_{ij} = \rho + (1 - \rho)\delta_{ij}$, it holds $\lambda_1(B) = S\rho + (1 - \rho)$ and, consequently, $\tilde{\rho} = \rho$. Thus, the quantity $\tilde{\rho}$ measures the effective interspecific competition, generalizing the mean field parameter ρ. Positivity of all equilibrium densities imposes more and more stringent conditions on the effective productivity parameters $\{p_i\}$ for increasing number of species and interspecific competition $\tilde{\rho}$ (see ref. 4). This result generalizes the mean field result in refs. 2, 5 and 6. In other words, the larger is $\tilde{\rho}$, the less structurally stable the system is, in the sense that the productivity vectors must be fine tuned in order to get positive equilibrium densities. Assuming that the fluctuations of the productivity vector are limited from below by the environmental variability Δ, we obtain the following limit to the maximum biodiversity S (ref. 4)

$$S \leq 1 + \left(\frac{1 - \tilde{\rho}}{\tilde{\rho}}\right)\left(\frac{\lambda_2(B)/(1 - \tilde{\rho}) - \Delta}{\Delta}\right). \tag{15}$$

For mean field competition matrices, it holds $\tilde{\rho} = \rho$ and $\lambda_2(B) = 1 - \rho$, whence $S \leq \overline{S}(1 - \Delta)/\Delta$. Therefore, we define the maximum biodiversity parameter

$$\overline{S} \equiv \frac{1 - \tilde{\rho}}{\tilde{\rho}} \tag{16}$$

which sets the scale for the maximum biodiversity that a competitive community can host.

In this work, since we use direct competition matrices of mean field type, we will use the notation $\overline{S} = (1 - \rho)/\rho$ for the maximum biodiversity for the purely competitive system,

ρ_{mut} for the effective interspecific competition in the presence of mutualistic interactions, and $\overline{S}_{\text{mut}} = (1-\rho_{\text{mut}})/\rho_{\text{mut}}$ for the maximum biodiveristy in the presence of mutualistic interactions.

3.2 Weak mutualism: mean field

The above calculations remain valid in the weak mutualist regime. As we have seen, if the mutualistic interactions and the direct competition matrix are of mean field type, the effective competition matrix is also mean field, and the effective interspecific competition parameter can be analytically computed as in Eq.(8). We see from this equation that mean field mutualism reduces the interspecific competition, thereby increasing the number of species that can stably stay in the system, which is now given by

$$\overline{S}^{(\text{P})}_{\text{mut}} \equiv \frac{1-\rho^{(\text{P})}_{\text{mut}}}{\rho^{(\text{P})}_{\text{mut}}} = \frac{\overline{S}^{(\text{P})}}{1-a^{(\text{P})}/\rho^{(\text{P})}} \,. \tag{17}$$

3.3 Weak mutualism beyond the mean field: nestedness

Now we relax the mean field assumption that plant and animal species interact mutualistically with all species in the other group, but for mathematical simplicity, we mantain the assumption that the strength of all existing mutualistic interactions are equal. We will refer to this model as the *soft mean field*. Therefore, we can define a binary matrix g_{ik} whose elements are one if the link is present and zero otherwise, such that $\gamma_{ik} = \gamma_0 g_{ik}$. It holds that $g^{(\text{P})}_{ik} = g^{(\text{A})}_{ki}$. We further denote the number of links of plant i as $n^{(\text{P})}_i = \sum_k g^{(\text{P})}_{ik}$ and the number of common links of plants i and j as

$$n^{(\text{P})}_{ij} \equiv \sum_k g^{(\text{P})}_{ik} g^{(\text{P})}_{jk} \tag{18}$$

which we call the *overlap matrix*.

The elements of the overlap matrix fulfill the inequalities $n_{ij} \leq \min(n_i, n_j)$. We say that the interaction matrix g is maximally nested if all the elements of the overlap matrix take their maximum possible value, namely if $n_{ij} = \min(n_i, n_j)$. This definition coincides with the definition of a maximally nested matrix in terms of the nesting algorithm[7]. This algorithm proceeds by what we will refer to from now on as *nesting steps*. Each nesting step tries to exchange two matrix elements with a common index, either a column or a row, for instance γ_{ik} and γ_{jk}. The move is accepted if the nonzero element is moved to a row (column) whose number of links after the move is larger than the number of links in the original row (column). No row (column) is allowed to be left without any link. A maximally nested matrix is a matrix which can not be changed anymore through this algorithm. This is the case when $n_{ij} = \min(n_i, n_j)$. We therefore define the nestedness of the matrix g with respect to plants as

$$\eta^{(\mathrm{P})} = \frac{\sum_{i<j} n_{ij}^{(\mathrm{P})}}{\sum_{i<j} \min\left(n_i^{(\mathrm{P})}, n_j^{(\mathrm{P})}\right)} . \tag{19}$$

The symmetric definition holds for the nestedness with respect to animals. It is easy to see that the nestedness defined above is zero if $n_{ij}^{(\mathrm{P})} \equiv 0$, which we define as anti-nested interactions, and one for perfect nestedness $n_{ij}^{(\mathrm{P})} \equiv \min\left(n_i^{(\mathrm{P})}, n_j^{(\mathrm{P})}\right)$. For random networks with the same number of independent interactions as in the real network, the average nestedness is $\eta_{\mathrm{rand}}^{(\mathrm{P})} = \sum_i n_i^{(\mathrm{P})} / \left(S^{(\mathrm{P})} S^{(\mathrm{A})}\right)$.

3.4 Weak mutualism beyond the mean field: soft mean field

In order to get a simple analytical formula that explicitates the influence of the network architecture, we introduce here the soft mean field model, in which all parameters are equal but the mutualistic network is not fully connected as in the mean field case. In this model, the direct competition matrix β_{ij} is of mean field type and all non-zero mutualistic interactions are equal, $\gamma_{ij}^{(\mathrm{P})} = \gamma_0^{(\mathrm{P})} g_{ij}^{(\mathrm{P})}$, where the binary matrix $g_{ij}^{(\mathrm{P})}$ is the adjacency matrix of the mutualistic network and $g_{ij}^{(\mathrm{A})}$ is the transpose of $g_{ij}^{(\mathrm{P})}$.

We still have to specify the intrinsic growth rates α_i (or death rates, if they are negative). For this purpose, we explicitate the effective productivity vector from Eq. (4),

$$p_i^{(\mathrm{P})} = \alpha_i^{(\mathrm{P})} + \left(\frac{\gamma_0^{(\mathrm{P})}}{\beta_0^{(\mathrm{A})}(1-\rho^{(\mathrm{A})})} \right) \left[\sum_j g_{ij}^{(\mathrm{P})} \alpha_j^{(\mathrm{A})} - \frac{S^{(\mathrm{A})}}{S^{(\mathrm{A})} + \overline{S}^{(\mathrm{A})}} \overline{\alpha^{(\mathrm{A})}} \right], \tag{20}$$

where $\overline{\alpha^{(\mathrm{A})}}$ is the average growth rate (or death rate, if α is negative) of species of type (A).

As we have seen, a necessary condition for species coexistence under competition is that the effective productivity vector has a narrow distribution. Therefore, we assume that the evolutionary process building the community leads to a narrow distribution of effective productivities, and that its dispersion Δ, which appears in Eq. (15), is the smallest one compatible with the unavoidable environmental variability, and it does not change in the presence or in the absence of mutualism. This assumption, which has to be justified through an explicit model of network assembly, implies that the α_i must be chosen negatively correlated to the number of mutualistic links, and it allows us to concentrate the focus of our analytic computation on the effective competition matrix This depends on the network architecture but it does not depend on the α_i, which will not play any role in the following analytic computation.

Alternatively, we could formulate the soft mean field model in such a way that the more mutualistic links a species has, the weaker these links are, defining the mutualistic parameters as $\gamma_{ij} = \gamma_0 / f(n_i) g_{ij}$, where $f(n_i)$ is a growing function of the number of links. This equation assumes that specialist species are more efficient than generalist species in dealing with their mutualistic partner, which is a quite plausible assumption. In this formulation, the function $f(n)$ should be chosen such that the effective productivity vector given by Eq.(4) is uncorrelated with the number of mutualistic interactions n_i. This formulation of the soft mean field model would lead to different expressions for the effective competitivity matrix from the one that we present below, and we will study this formulation in following work.

In the weak mutualism regime, the normalized competition matrix $B_{ij}^{(\mathrm{P})}$ is defined through

$$\frac{C_{ij}^{(\mathrm{P})}}{\beta_0^{(\mathrm{P})}(1-\rho^{(\mathrm{P})})} = \delta_{ij} + \frac{1}{\overline{S}^{(\mathrm{P})}} + R\left(\frac{n_i^{(\mathrm{P})} n_j^{(\mathrm{P})}}{S^{(\mathrm{A})}+\overline{S}^{(\mathrm{A})}} - n_{ij}^{(\mathrm{P})}\right), \tag{21}$$

$$B_{ij}^{(\mathrm{P})} = \frac{C_{ij}^{(\mathrm{P})}}{\sqrt{C_{ii}^{(\mathrm{P})} C_{jj}^{(\mathrm{P})}}}, \tag{22}$$

where

$$R = \frac{\gamma_0^{(\mathrm{P})}\gamma_0^{(\mathrm{A})}}{\beta_0^{(\mathrm{P})}\beta_0^{(\mathrm{A})}(1-\rho^{(\mathrm{P})})(1-\rho^{(\mathrm{A})})}. \tag{23}$$

Notice that the matrix $B^{(\mathrm{P})}$ depends only on three numerical parameters, R, $\overline{S}^{(\mathrm{P})}$ and $\overline{S}^{(\mathrm{A})}$.

To get more analytic insight on how mutualism influences biodiversity, we computed the derivative of the main eigenvalue of the normalized effective competition matrix, $\lambda_1\left(B^{(\mathrm{P})}\right)$, with respect to the mutualistm-to-competition ratio R at the point $R=0$ (absence of mutualism) This calculation shows that the effective interspecific competition decreases with the nestedness of the mutualist interaction matrix for a given distribution of number of links $\{n_i^{(\mathrm{P})}\}$ and fixed parameters. Since the maximum predicted biodiversity $\overline{S}_{\mathrm{mut}}^{(\mathrm{P})}$ increases with decreasing effective competition, the model predicts that, for perfectly nested mutualist networks, the effective competition is weakest and the maximum biodiversity is largest. Therefore, nested mutualist interactions favor biodiversity.

Specifically, calculating the derivative of $\lambda_1\left(B^{(\mathrm{P})}\right)$, we can easily obtain the derivative of the maximum biodiversity $\overline{S}^{(\mathrm{P})}_{\mathrm{mut}} = \left(1-\rho^{(\mathrm{P})}_{\mathrm{mut}}\right)/\rho^{(\mathrm{P})}_{\mathrm{mut}}$, where $\rho^{(\mathrm{P})}_{\mathrm{mut}} = \left(\lambda_1\left(B^{(\mathrm{P})}\right)-1\right)/(S^{(\mathrm{P})}-1)$ is the effective interspecific competition parameter, with respect to the mutualism-to-competition ratio. This measures the relative increment of the maximum biodiversity due to mutualism, and is equal to

$$\frac{1}{\overline{S}^{(\mathrm{P})}_{\mathrm{mut}}}\frac{\partial \overline{S}^{(\mathrm{P})}_{\mathrm{mut}}}{\partial R}\Bigg|_{R=0} = \left(1+\frac{1}{\overline{S}^{(\mathrm{P})}}\right)\langle n^{(\mathrm{P})}\rangle \quad \Bigg[\overline{S}^{(\mathrm{P})}\left(\hat{\eta}^{(\mathrm{P})}-\tfrac{\langle n^{(\mathrm{P})}\rangle}{S^{(\mathrm{A})}+\overline{S}^{(\mathrm{A})}}\right)-(1-\hat{\eta}^{(\mathrm{P})}) \\ + \tfrac{\langle (n^{(\mathrm{P})})^2\rangle-\langle n^{(\mathrm{P})}\rangle^2}{\langle n^{(\mathrm{P})}\rangle(S^{(\mathrm{A})}+\overline{S}^{(\mathrm{A})})}\left(\tfrac{S^{(\mathrm{P})}+\overline{S}^{(\mathrm{P})}}{S^{(\mathrm{P})}-1}\right)\Bigg], \tag{24}$$

where $\langle n^{(\mathrm{P})}\rangle = \sum_i n_i^{(\mathrm{P})}/S^{(\mathrm{P})}$ and $\langle\left(n^{(\mathrm{P})}\right)^2\rangle = \sum_i\left(n_i^{(\mathrm{P})}\right)^2/S^{(\mathrm{P})}$ are the mean and mean square number of mutualistic interactions per plant species. The parameter $\hat{\eta}^{(\mathrm{P})} = \sum_{i\neq j} n_{ij}^{(\mathrm{P})}/\left((S^{(\mathrm{P})}-1)\sum_i n_i^{(\mathrm{P})}\right)$ is very strongly correlated with the nestedness defined in Eq.(19) (for real networks, the correlation coefficient between nest and the nestedness parameter is 0.97).

The derivative in the above equation is not bound to be positive. In particular, the derivative is typically negative if there are few shared interactions (small $\hat{\eta}$) together with strong direct competition (small $\overline{S}^{(\mathrm{A})}$), so that the term $\hat{\eta}-\langle n^{(\mathrm{P})}\rangle/(S^{(\mathrm{A})}+\overline{S}^{(\mathrm{A})})$ is negative. This result shows that mutualism can also increase the effective competition and hinder biodiversity. Although it looks counter-intuitive, this result can be easily understood by considering that, if plant species i and j do not share any animal species ($n_{ij}^{(\mathrm{P})}=0$), the direct competition between the animals interacting with them has the net effect to increase the effective competition that i and j experience. This illustrates how the direct competition for resources explicitly described by the β_{ij} terms in Eq. (29) is now mediated by the use of a common set of mutualismstic partners.

A second more stringent condition for mutualism to enhance the maximum biodiversity is that the reduction in interspecific effective competition $C_{i\neq j}$ must be larger than tice that, for networks in which $\hat{\eta}$ attains the maximum possible value $\hat{\eta} = 1$, as the fully connected mean field network, the increment of biodiversity Eq.(24) is always positive, independent of the parameters $\overline{S}^{(\mathrm{A})}$ and $\overline{S}^{(\mathrm{P})}$.

4 Summary of the stability analysis

We have shown here that (1) the weak mutualism fixed point is stable if and only if all equilibrium densities are positive and both matrices $C^{(\mathrm{A})}$ and $C^{(\mathrm{P})}$ are positive definite; (2) the strong mutualist fixed point can not have positive densities if the matrices $C^{(\mathrm{A})}$ and $C^{(\mathrm{P})}$ are positive definite; (3) when the system is in the weak mutualism regime, $\lambda_1(B)$ is positive. The limitation to biodiversity imposed by competition becomes less stringent as $\lambda_1(B)$ decreases, and they disappear when $\lambda_1(B) = 1$, implying through Eq.(14) that $\rho_{\mathrm{mut}} = 0$. The maximum biodiversity that each group (plants or animals) can attain is controlled by the main eigenvalue of the normalized effective competition matrix B, and it is larger, the smaller is this eigenvalue, $\lambda_1(B)$. As soon as $\lambda_1(B)$ becomes negative, the weak mutualism fixed point looses its stability, and the strong mutualism fixed point can become stable. However, if only one pair of species overcomes the strong mutualism threshold while the other species still remain below it, the model predicts that only the species above threshold will eventually survive, whereas the other species will go extinct, thus suggesting the interesting possibility of massive extinctions caused by mutualism.

5 Assembly of mutualistic networks

Consider the arrival of a new animal species into a community in the weak mutualism regime (for plants, the mathematical treatment would be exactly symmetric). We will assume that the new species, labelled as 1, is specialist, i.e., it can interact only with one plant species, also labeled as 1. We will show that, if plant species 1 is generalist, the animal species 1 will experience the lowest competitive load, and it will be incorporated most likely in the community.

To prove our thesis, let us consider the effective competition matrix elements for the new animal species 1:

$$C_{1j}^{(\mathrm{A})} = \beta_{1j}^{(\mathrm{A})} - \gamma_{11}^{(\mathrm{A})} \sum_k \left(\beta^{(\mathrm{P})}\right)_{1k}^{(-1)} \gamma_{kj}^{(\mathrm{P})} , \tag{25}$$

where we have explicitly used the fact that the new insect species 1 is specialist. Let us now consider for the sake of simplicity a direct competition matrix $\beta^{(\mathrm{P})}$ of mean field type. The analytic expression for the inverse matrix is $\left(\beta^{(\mathrm{P})}\right)^{-1} = 1/\beta_0^{(\mathrm{P})}(1 - \rho^{(\mathrm{P})}) \left(\delta_{ij} + 1/(S^{(\mathrm{P})} + \overline{S}^{(\mathrm{P})}\right)$, whence

$$C_{1j}^{(\mathrm{A})} = \beta_{1j}^{(\mathrm{A})} - \frac{\gamma_{11}^{(\mathrm{A})}}{\beta_0^{(\mathrm{P})}(1 - \rho^{(\mathrm{P})})} \left(\gamma_{1j}^{(\mathrm{P})} - \frac{1}{S^{(\mathrm{P})} + \overline{S}^{(\mathrm{P})}} \sum_k \gamma_{kj}^{(\mathrm{P})} \right) . \tag{26}$$

Summing over all animal species j, we find

$$\sum_j C_{1j}^{(\mathrm{A})} = \sum_j \beta_{1j}^{(\mathrm{A})} - \frac{\gamma_{11}^{(\mathrm{A})}}{\beta_0^{(\mathrm{P})}(1 - \rho^{(\mathrm{P})})} \left(\sum_j \gamma_{1j}^{(\mathrm{P})} - \frac{1}{S^{(\mathrm{P})} + \overline{S}^{(\mathrm{P})}} \sum_{jk} \gamma_{kj}^{(\mathrm{P})} \right) . \tag{27}$$

The only term that depends on the plant species 1 with which the new animal interacts is $\sum_j \gamma_{1j}^{(\mathrm{P})}$. The larger is this term, the smaller the competition experienced by the new species. Now, although we expect that individual interaction coefficients $\gamma_{1j}^{(\mathrm{P})}$ tend to be larger for specialist species than for generalist species, we also expect that the sum of all interactions $\sum_j \gamma_{1j}^{(\mathrm{P})}$ is largest if plant species 1 is generalist. Therefore, a specialist species is favoured if it interacts with a generalist species, producing nested interaction patterns. This result confirms a recent suggestion that we have to move beyond competition to predict ecosystem invasibility[8], and provides an analytical framework to quantify such an effect of positive interactions.

6 Robustness of our analytic results

Our previous results are based on an analytical solution of our model, i.e., on an analysis of the equilibrium. To obtain such analytic results we have had to make a series of assumptions. To begin with, the model only considers mutualistic and competitive interactions, and therefore one can wonder how robust are our results when other interaction types such as predation are considered. Second, our analyses are based on a mean field assumption whereby the values of competitive coefficients (β), for example, are the same across species. Similarly, we use a soft mean field approach to deal with mutualistic coefficients: while we address the real network of interactions, and therefore some interactions are zero, the observed interactions have the same value of mutualistic strength (γ). Finally, the emphasis on equilibrium precludes an analysis of the transient time before reaching this solution or other dynamic properties. In this section we explore the robustness of our results when these assumptions are relaxed and briefly address these other questions.

6.1 Introducing predation

The formalism of the effective competition matrix allows an analytic treatment of a generalized system including predation. This will allow us to test whether our results are qualitatively unchanged when another interaction type is considered.

We consider four groups of species: plants (P), animal pollinators or seed dispersers (A), herbivores (H) and consumers that predate animal mutualists (e.g., insectivorous birds that predate over pollinator insects) (C). The groups A and P are related through mutualistic interactions, the groups A and C are related through prey-predator interactions, and the same holds for the groups P and H. To simplify the mathematical treatment, we assume that no inteaction occurs between groups C and H (this assumption can be easily relaxed). Species within each group compete between each other. Assuming for simplicity a linear predator functional relationship of Lotka-Volterra type, the dynamic equations for plants and herbivore species are

$$\frac{1}{N_i^{(\mathrm{P})}}\frac{\mathrm{d}N_i^{(\mathrm{P})}}{\mathrm{d}t} = \alpha_i^{(\mathrm{P})} - \sum_{j\in\mathbf{P}} \beta_{ij}^{(\mathrm{P})} N_j^{(\mathrm{P})} + \sum_{k\in\mathbf{A}} \frac{\gamma_{ik}^{(\mathrm{P})} N_k^{(\mathrm{A})}}{1 + h^{(\mathrm{P})} \sum_{l\in\mathbf{A}} \gamma_{il}^{(\mathrm{P})} N_l^{(\mathrm{A})}} - \sum_{k\in\mathbf{H}} \delta_{ik}^{(\mathrm{P})} N_k^{(\mathrm{H})} \tag{28}$$

$$\frac{1}{N_i^{(\mathrm{H})}}\frac{\mathrm{d}N_i^{(\mathrm{H})}}{\mathrm{d}t} = \alpha_i^{(\mathrm{H})} - \sum_{j\in\mathbf{H}} \beta_{ij}^{(\mathrm{H})} N_j^{(\mathrm{H})} + \sum_{k\in\mathbf{P}} \delta_{ik}^{(\mathrm{H})} N_k^{(\mathrm{P})} . \tag{29}$$

The equations for mutualistic insect populations and for insectivorous can be written in a symmetric form interchanging the indices A and P and C and H, respectively. Here we use the same notation as in the paper: superscripts indicate the group of species, α is the vector of intrinsic growth rates, positive for plants and negative for animals, the matrix β represents intra-group competition, the matrix γ represents mutualistic interactions, and the matrix δ represents predator-prey relationships. Notice that in this way all possible kinds of pairwise ecological interactions are represented in the model.

In the weak mutualism regime, and in the small h approximation, the fixed point equations can be written, after some algebra, in the form

$$\sum_{ij} C_{ij}^{(\mathrm{P})} N_j^{(\mathrm{P})} = \pi_i^{(\mathrm{P})} \,, \tag{30}$$

$$\sum_{ij} C_{ij}^{(\mathrm{H})} N_j^{(\mathrm{H})} = \pi_i^{(\mathrm{H})} \,, \tag{31}$$

again, we only show plant and herbivore species since the equations for insects and carnivors can be obtained by permutation of indices. In matrix notation, the effective competition matrices C are given by

$$\widetilde{C}^{(\mathrm{P})} = I^{(\mathrm{P})} + \widetilde{\delta}^{(\mathrm{P})}\widetilde{\delta}^{(\mathrm{H})} - \widetilde{\gamma}^{(\mathrm{P})} \left(I^{(\mathrm{A})} + \widetilde{\delta}^{(\mathrm{A})}\widetilde{\delta}^{(\mathrm{C})} \right)^{-1} \widetilde{\gamma}^{(\mathrm{A})} \tag{32}$$

$$\widetilde{C}^{(\mathrm{H})} = I^{(\mathrm{H})} + \widetilde{\delta}^{(\mathrm{H})} \left[I^{(\mathrm{P})} - \widetilde{\gamma}^{(\mathrm{P})} \left(I^{(\mathrm{A})} + \widetilde{\delta}^{(\mathrm{A})}\widetilde{\delta}^{(\mathrm{C})} \right)^{-1} \widetilde{\gamma}^{(\mathrm{A})} \right]^{-1} \widetilde{\delta}^{(\mathrm{P})} \,, \tag{33}$$

where $\widetilde{C} = \beta^{-1} C$, $\widetilde{\gamma} = \beta^{-1}\gamma$ and $\widetilde{\delta} = \beta^{-1}\delta$ are competition reduced interaction matrices. Through a development similar to the case of mutualism without predation it is possible to show that the equilibrium points are stable if and only if (1) all the equilibrium biomasses are positive, and (2) the effective competition matrices are positive definite for all four groups of species.

Furthermore, the structural stability is related to the effective interspecific competition parameter (which in turn can be obtained from the maximum eigenvalue of the normalized effective competition matrix, as discussed in the paper). This relationship determines that a system with a smaller interspecific competition parameter will be more structurally stable and it will sustain stable equilibrium points for a broader range of productivity parameters π_i. This, in turn, will allow on average a larger number of coexisting species.

Through Taylor expansion, we can compute the effective competition matrix $C^{(\mathrm{P})}$ as follows:

$$\tilde{C}^{(\mathrm{P})} = I^{(\mathrm{P})} + \widetilde{\delta}^{(\mathrm{P})}\widetilde{\delta}^{(\mathrm{H})} - \widetilde{\gamma}^{(\mathrm{P})}\widetilde{\gamma}^{(\mathrm{A})} - \sum_{k=1}^{\infty}(-1)^k\widetilde{\gamma}^{(\mathrm{P})}\left(\widetilde{\delta}^{(\mathrm{A})}\right)^k\left(\widetilde{\delta}^{(\mathrm{C})}\right)^k\widetilde{\gamma}^{(\mathrm{A})}. \tag{34}$$

The terms in the sum are sub-dominant, since stability of the fixed points requires that the matrices $\widetilde{\gamma}^{(\mathrm{P})}\widetilde{\gamma}^{(\mathrm{A})}$, $\widetilde{\delta}^{(\mathrm{P})}\widetilde{\delta}^{(\mathrm{H})}$ and $\widetilde{\delta}^{(\mathrm{A})}\widetilde{\delta}^{(\mathrm{C})}$ have eigenvalues smaller than one. Taking into account only the dominant terms, i.e., omitting the sum, and using the soft mean field approximation in which the elements of the mutualistic interaction matrix γ and the predatory interaction matrix δ are either zero or they are all equal, it is possible to relate structural stability with the architecture of ecological interactions. In particular, by analogy with the case with mutualism and competition, we see that the effective interspecific competition parameter is reduced if mutualistic interactions are nested and predatory interactions are antinested, therefore increasing structural stability and favouring biodiversity. The correlations between the mutualistic network and the predatory network introduces another interesting level at which we can study the architecture of the community.

6.2 Numerical results

We tested our analytic theory through numerical simulations. In particular, we wanted to test the following key aspects: whether the model ecosystems attain fixed points, how rapidly they reach equilibrium and whether some interesting dynamical behavior is observed in the transients. These issues were examined considering fully connected ecosystems. We chose the growth rates α from uniform distributions with variable width, in order to test our predictions that the width of the growth rates distribution limits the maximum possible biodiversity. The competition and mutualistic coefficients β, and γ were also chosen from a uniform distribution, in order to test the robustness of our mean field results with respect to noise in the parameters. Simulations were performed by integrating the system of ordinary diffrential equations using a fourth-order Runge-Kutta method with small integration step.

For purely competitive systems, it can be shown analytically that the stable equilibrium points are also globally stable, in the sense that all initial conditions converge to the equilibrium point. In the presence of mutualistic and predatory interactions global stability can not be proven in general, and interesting dynamical behaviors like limit cycles or even chaos may in principle occurr. Therefore, we tested numerically the convergence to equilibrium. Our numerical results suggest that the direct competition matrix favors fast convergence to the equilibrium points even in the presence of mutualism and predation. In all cases that we simulated, including those with predatory interactions, the system attained a fixed point after a short transient, in which extinction of some species can occurr. Supplementary Fig. 1 below shows an example of the dynamics of this system. These results were robust with respect to fluctuations in the α, β, and γ parameters and confirmed the expected dependence of biodiversity on the width of the distribution of α and the expected increase of species abundance due to mutualism. The simulations not only confirmed our analytic mean field results, but also provided the new observation that the convergence to equilibrium becomes faster for a mutualistic system with respect to a purely competitive one.

Simulating ecosystems that are not fully connected requires further choices of the parameters, which we will explore systematically in future work. As a preliminary observation, we notice that in this case there must be a trade-off between the three types of parameters present in our model, i.e. the growth rates α_i, the direct competition coefficients β_{ij} and the mutualistic interactions γ_{ij}. This can be seen in the following way: The coexistence condition imposes that the main eigenvector c_i of the effective competition matrix, Eq.(5), must be almost parallel to the effective productivity vector, Eq.(4), which

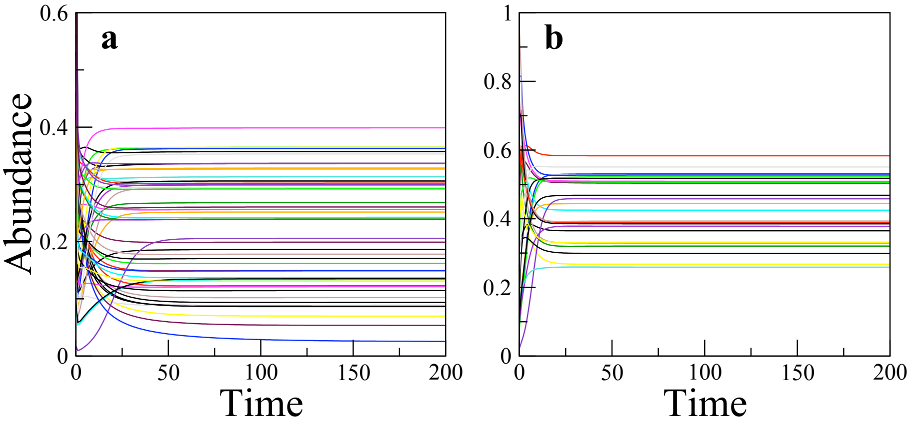

Figure 1: *Temporal dynamics of the abundance of plants (a) and animals (b) in a fully connected mutualistic community with 50 plant species and 25 animal species. The same system without mutualism leads to the extinction of one animal and 17 plant species. Parameter values are as follows:* α_i *are taken from a uniform distribution (0.85, 1.1);* β_{ii} *and* β_{ij} *are taken from a uniform distribution (0.99, 1.01) and (0.22, 0.24), respectively;* γ_{ij} *are taken from a uniform distribution (0.19, 0.21).* $h^{(\mathrm{P})} = h^{(\mathrm{A})} = 0.1$. *Initial population densities are taken from a uniform distribution (0, 1). This parameter combination corresponds to the weak mutualism regime. Qualitatively similar results are obtained for the strong mutualism regime, in which transients are even shorter and abundances higher.*

means that species that effectively compete more should be able to effectively grow faster in the absence of competition in order to survive. We verified through simulations (not shown here) that mutualistic interactions favour biodiversity when such correlations are implemented in the model, even if the number of mutualistic links is broadly distributed, provided that mutualism is weak enough to remain in the weak mutualistic regime.

We can think of these correlations either as the product of some physiological trade-off or as the product of an evolutionary process in which the ecosystem is slowly assembled. They may be achieved in real ecosystems in various ways, for instance through a trade-off between the number and the strength of mutualistic interactions, which decrease the effective competition and at the same time increase the effective productivity. In other words, specialist species must interact more strongly than the generalists. Another way to obtain suitable correlations is a compensation between the growth rates and the mutualistic coefficients, so that species that interact mutualistically with more species have a smaller growth rate

In order to study the effect of mutualism systematically in networks with broad degree distributions, we will adopt in further work the following procedure: (1) Consider direct competition of mean field type, which is more demanding for allowing coexistence; (2) Extract the mutualistic strengths in such a way that there is a trade-off between the number of links and their strength; (3) Compute the effective competition matrix and its main eigenvector c_i; (4) The optimal distribution (i.e. the one that best promotes coexistence) of effective productivities P_i is predicted to be proportional to the eigenvector c_i. (5) From this optimal P_i, we can compute analytically the bare growth rates α_i that best favour coexistence. Our analytic prediction is that weak mutualism makes the system more structurally stable, in the sense that it allows more noise on the parameters α_i with respect to their optimal value. We will test this prediction in future extensive numerical work.

Appendix A: proof of the stability of the weak mutualism fixed point

We prove here that the fixed point in the weak mutualist regime is stable if and only if the effective competition matrices $C^{(\mathrm{P})}$ and $C^{(\mathrm{A})}$ are positive definite and all densities are positive.

If there is a fixed point of Eq. (29), at order zero in h, with all positive densities, it will be stable if and only if its Jacobian matrix J is negative definite, i.e., for any vector z one must have $(z, Jz) < 0$, where the brackets denote scalar product, and (z, Jz) is a generic quadratic form of the matrix J

$$J = \begin{pmatrix} -\beta^{(\mathrm{P})} & \gamma^{(\mathrm{P})} \\ \gamma^{(\mathrm{A})} & -\beta^{(\mathrm{A})} \end{pmatrix} . \tag{35}$$

We use here the matrix notation for the complete community, where the diagonal elements $\beta^{(\mathrm{P})}$ and $\beta^{(\mathrm{A})}$ are matrices acting on plant indices and animal indices, respectively, the upper right element $\gamma^{(\mathrm{P})}$ is a matrix going from plant to animal indices, and the lower left element $\gamma^{(\mathrm{A})}$ is a matrix going from animal to plant indices. With this notation, the notation C will denote the matrix formed with the two matrices $C^{(\mathrm{P})}$ and $C^{(\mathrm{A})}$ as diagonal elements.

We now show that positivity of $C^{(\mathrm{P})}$ and $C^{(\mathrm{A})}$ is necessary for the stability of the fixed point. More precisely, we will show that if J is negative definite then C must be positive definite. In order to do this, let us introduce two column vectors $x = (x^{(\mathrm{P})}, x^{(\mathrm{A})})$ and $y = (y^{(\mathrm{P})}, y^{(\mathrm{A})})$ (here $x^{(\mathrm{P})}$ ($x^{(\mathrm{A})}$) denotes the projection of the vector x on the P (A) subspace respectively), such that $x^{(\mathrm{A})} = \gamma^{(\mathrm{A})} x^{(\mathrm{P})}$, and $y^{(\mathrm{P})} = \gamma^{(\mathrm{P})} y^{(\mathrm{A})}$. These vectors have the property that $(Jx)^{(\mathrm{P})} = -C^{(\mathrm{P})} x^{(\mathrm{P})}$, $(Jx)^{(\mathrm{A})} = 0$, $Jy^{(\mathrm{A})} = -C^{(\mathrm{A})} y^{(\mathrm{A})}$, $(Jy)^{(\mathrm{P})} = 0$. Using these properties, we can see that for a generic vector $z = x + y$, it holds

$$-(z, Jz) = \left(x^{(\mathrm{P})}, C^{(\mathrm{P})} x^{(\mathrm{P})}\right) + \left(y^{(\mathrm{A})}, C^{(\mathrm{A})} y^{(\mathrm{A})}\right) + \left(x^{(\mathrm{A})}, C^{(\mathrm{A})} y^{(\mathrm{A})}\right) + \left(y^{(\mathrm{P})}, C^{(\mathrm{P})} x^{(\mathrm{P})}\right) . \tag{36}$$

From this it is immediate to see that if J is negative definite C must be positive. In fact, if $C^{(\mathrm{P})}$ is not positive, there is a vector such that $\left(x^{(\mathrm{P})}, C^{(\mathrm{P})}x^{(\mathrm{P})}\right) \le 0$. Choosing $y^{(\mathrm{A})} = 0$, we find $(z, Jz) = -\left(x^{(\mathrm{P})}, C^{(\mathrm{P})}x^{(\mathrm{P})}\right) \ge 0$, contrary to the assumption.

We now show that the positivity of C is also a sufficient condition for stability, i.e., if C is positive then J is negative. For this proof it is convenient to rewrite the Jacobian matrix in terms of the competition reduced Jacobian $\widetilde{J}$,

$$J = \begin{pmatrix} \beta^{(\mathrm{P})} & 0 \\ 0 & \beta^{(\mathrm{A})} \end{pmatrix} \begin{pmatrix} -I^{(\mathrm{P})} & \widetilde{\gamma}^{(\mathrm{P})} \\ \widetilde{\gamma}^{(\mathrm{A})} & -I^{(\mathrm{A})} \end{pmatrix} \equiv \beta\, \widetilde{J}. \tag{37}$$

where $I^{(\mathrm{P,A})}$ denotes the identity matrix in the plant (animal) space, respectively, and $\widetilde{\gamma}^{(\mathrm{P})} = (\beta^{(\mathrm{P})})^{-1}\gamma^{(\mathrm{P})}$, $\widetilde{\gamma}^{(\mathrm{A})} = (\beta^{(\mathrm{A})})^{-1}\gamma^{(\mathrm{A})}$. We similarly define the matrix $\widetilde{C}$, satisfying

$$C = \begin{pmatrix} \beta^{(\mathrm{P})} & 0 \\ 0 & \beta^{(\mathrm{A})} \end{pmatrix} \begin{pmatrix} \widetilde{C}^{(\mathrm{P})} & 0 \\ 0 & \widetilde{C}^{(\mathrm{A})} \end{pmatrix} \equiv \beta\, \widetilde{C}\ , \tag{38}$$

where $\widetilde{C}^{(\mathrm{A})} = I^{(\mathrm{A})} - M^{(\mathrm{A})}$, $\widetilde{C}^{(\mathrm{P})} = I^{(\mathrm{P})} - M^{(\mathrm{P})}$, and the mutualistic matrix M can be written as

$$M = \begin{pmatrix} \widetilde{\gamma}^{(\mathrm{P})}\widetilde{\gamma}^{(\mathrm{A})} & 0 \\ 0 & \widetilde{\gamma}^{(\mathrm{A})}\widetilde{\gamma}^{(\mathrm{P})} \end{pmatrix}\ . \tag{39}$$

Since β is positive, J (C) will be positive definite if and only if $\widetilde{J}$ ($\widetilde{C}$) is positive definite. We now proceed to show that the statements

1. The effective competition matrix $\widetilde{C}$ is positive definite.

2. The reduced Jacobian $\widetilde{J}$ is negative definite.

are equivalent. It is crucial to note that M can be written as the square of a matrix, $M = \sqrt{M}\sqrt{M}$, with

$$\sqrt{M} \equiv \begin{pmatrix} 0 & \widetilde{\gamma}^{(\mathrm{P})} \\ \widetilde{\gamma}^{(\mathrm{A})} & 0 \end{pmatrix}\ . \tag{40}$$

Therefore $\sqrt{M}$ and M will have the same basis of eigenvectors and their eigenvalues will be related by $\lambda(M) = \left[\lambda\left(\sqrt{M}\right)\right]^2$. Furthermore note that the competition reduced matrices can be written as

$$\begin{aligned} \widetilde{J} &= \quad -I \quad +\sqrt{M}\ , \qquad (41) \\ \widetilde{C} &= \quad I \quad -M\ . \qquad (42) \end{aligned}$$

Thus $\widetilde{J}$, $\widetilde{C}$, M and $\sqrt{M}$ can be diagonalized in the same basis, and their eigenvalues satisfy

$$\begin{aligned} \lambda(\widetilde{J}) &= \quad -1 \quad +\lambda(\sqrt{M}) \\ \lambda(\widetilde{C}) &= \quad 1 \quad -\lambda(M)\ . \qquad (43) \end{aligned}$$

If $\lambda(\sqrt{M})$ is imaginary then it must be pure imaginary since the $\lambda(\widetilde{C})$ are real and positive by hypothesis. Therefore, in this case it must follow that $\mathrm{Re}(\lambda(\widetilde{J})) < 0$, so that the fixed point is stable. On the other hand, if $\lambda(\sqrt{M})$ is real, it follows that $\lambda(M)$ can not be negative. If we now assume that $\widetilde{C}$ is positive definite, it follows that $0 \leq \lambda(M) < 1$, which implies $-1 < \lambda\left(\sqrt{M}\right) < 1$ and consequently $\lambda(\widetilde{J}) < 0$, i.e., the fixed point is stable.

In this way, we have demonstrated that positivity of the effective competition matrix and the equilibrium biomasses are necesary and sufficient conditions for stability of the weak mutualism fixed points.

As a corollary, we see that if C is positive definite then $\lambda(M) < 1$, a result that was used in a previous section.

Appendix B: numerical calculation

For a given mutualistic interaction network $\{g_{ik}\}$ and given parameters R, $\overline{S}^{(\mathrm{P})}$ and $\overline{S}^{(\mathrm{A})}$, we can compute numerically the effective competition coefficient $\rho^{(\mathrm{P})}_{\mathrm{mut}}$ through Eq.(21), Eq.(22) and Eq.(14), where $\lambda_1(B^{(\mathrm{P})})$ is the main eigenvalue of the normalized competition matrix $B^{(\mathrm{P})}$. The corresponding maximum predicted biodiversity is given by $\overline{S}^{(\mathrm{P})}_{\mathrm{mut}} = (1-\rho^{(\mathrm{P})}_{\mathrm{mut}})/\rho^{(\mathrm{P})}_{\mathrm{mut}}$, and it characterizes the biodiversity of the model ecosystem. For $R=0$ (pure competition) it holds that $\rho^{(\mathrm{P})}_{\mathrm{mut}} = \rho^{(\mathrm{P})}$ and $\overline{S}^{(\mathrm{P})}_{\mathrm{mut}} = \overline{S}^{(\mathrm{P})}$,which can be interpreted as the maximum biodiversity of the system in the absence of mutualism

For this computation, we use the same parameters R, $\overline{S}^{(\mathrm{A})}$, $\overline{S}^{(\mathrm{P})}$ for all systems. The parameters $\overline{S}^{(\mathrm{A})}$, $\overline{S}^{(\mathrm{P})}$ are chosen large enough so that mutualism favors biodiversity in all real networks, i.e., $\rho^{(\mathrm{P})}_{\mathrm{mut}}$ decreases with the mutualism-to-competition ratio R when this is close to zero. The parameter R should be small enough so that all real networks are in the weak mutualism regime (the matrix $B^{(\mathrm{P})}$ is positive for all real networks). To eliminate the dependence on this parameter, we compute numerically the derivative with respect to R of the relative increase in biodiversity due to mutualism, using a very small value of R:

$$r^{(\mathrm{P})} \equiv \frac{1}{\overline{S}^{(\mathrm{P})}} \frac{\partial \overline{S}^{(\mathrm{P})}_{\mathrm{mut}}}{\partial R}\bigg|_{R=0} \approx \frac{\overline{S}^{(\mathrm{P})}_{\mathrm{mut}}\left(R, \overline{S}^{(\mathrm{P})}, \overline{S}^{(\mathrm{A})}, \{g_{ik}\}\right) - \overline{S}^{(\mathrm{P})}}{R\overline{S}^{(\mathrm{P})}} . \tag{44}$$

We verified that this computation agrees within the numerical precision with the analytical calculation reported in Eq.(24).

For each model constructed from a real mutualist network $\{g_{ik}\}$ we considered an ensemble of random networks with the same number of species and the same number of mutualistic links and different overlap matrix n_{ij}, so that their nestedness is different, and we computed $r^{(\mathrm{P})}$ both for the real network and for the ensemble of random networks.

Appendix C: Supplementary Table 1. Real networks

Pollination networks

Network	Plants	Animals	Links	Connectivity	Latitude
Arroyo et al 1982	84	101	361	0.0426	Temperate
Arroyo et al 1982	43	64	196	0.0712	Temperate
Arroyo et al 1982	36	25	81	0.09	Temperate
Elberling & Olesen 1999	24	118	242	0.0855	Arctic
Elberling & Olesen 1999	31	76	456	0.1935	Arctic
Hocking 1968	29	81	179	0.0762	Arctic
Kakutani et al l990	113	315	772	0.0217	Temperate
Kato & Miura 1996	64	187	430	0.0359	Temperate
Kato et al 1990	91	679	1193	0.0193	Temperate
Kato et al 1993	90	356	865	0.027	Temperate
Kevan 1970	20	91	190	0.1044	Arctic
McMullen 1993	10	22	27	0.1227	Tropical
Mosquin & Martin 1967	11	18	38	0.1919	Arctic
Percival 1974	61	36	178	0.0811	Tropical
Primack 1983	49	118	346	0.0598	Temperate
Primack 1983	41	139	374	0.0656	Temperate
Primack 1983	18	60	120	0.1111	Temperate
Petanidou 1991	131	666	2931	0.0336	Mediterranean
Ramirez 1989	47	46	151	0.0698	Tropical
Schemske et al 1978	7	33	65	0.2814	Temperate
Herrera 1988	26	179	412	0.0885	Mediterranean
Olesen unp.	10	12	30	0.25	Tropical
Olesen unp.	10	40	72	0.18	Temperate
Olesen unp.	8	42	79	0.2351	Temperate
Olesen unp.	29	55	145	0.0909	Tropical
Olesen unp.	26	82	248	0.1163	Temperate
Inoue et al 1990	112	840	1872	0.0199	Temperate
Inoue & Pyke 1988	36	81	252	0.0864	Temperate
Eskildsen et al unp.	14	13	52	0.2857	Tropical

Seed dispersal networks

Network	Plants	Animals	Links	Connectivity	Latitude
Baird 1980	21	7	50	0.3401	Temperate
Beeheler 1983	31	9	119	0.4265	Tropical
Jordano unp.	25	33	154	0.1867	Mediterranean
Crome 1975	71	7	142	0.2857	Tropical
Frost 1980	16	10	110	0.6875	Subtropical
Guitian 1983	12	7	40	0.4762	Temperate
Jordano unp.	16	17	121	0.4449	Mediterranean
Kantak 1979	5	27	86	0.637	Tropical
Lambert 1989	25	61	511	0.3351	Tropical
Wheelwright et al. 1984	169	40	666	0.0985	Tropical
Jordano unp.	18	28	129	0.256	Mediterranean
Tutin et al 1997	19	8	75	0.4934	Tropical
Noma 1997	15	8	38	0.31367	Temperate
Sorensen 1981	7	6	22	0.5238	Temperate
Galetti & Pizo 1996	7	18	38	0.3016	Tropical
Galetti & Pizo 1996	35	29	146	0.1438	Tropical
Snow & Snow 1971	50	14	234	0.3343	Tropical
Herrera 1984	14	10	65	0.4643	Mediterranean
Silva et al 2002; unp.	207	110	1120	0.0492	Tropical
Snow & Snow 1988	11	14	47	0.3052	Temperate
Jordano unp.	3	3	6	0.66667	Mediterranean
Jordano unp.	12	4	31	0.64583	Mediterranean
Jordano unp.	8	5	26	0.65	Mediterranean
Jordano unp.	21	6	58	0.4603	Mediterranean
Jordano unp.	11	6	36	0.5455	Mediterranean
Jordano unp.	4	5	10	0.5	Mediterranean
Jordano unp.	5	4	11	0.55	Mediterranean

For the list of references of Table S1 see ref. 9.

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COMPLEX SYSTEMS

Cooperative network dynamics

George Sugihara and Hao Ye

Nested, or hierarchically arranged, mutualisms allow ecosystems to support more species than they otherwise would. But in this and other contexts, the growth of such networks could carry a heavy price.

On page 1018 of this issue, Bascompte and colleagues (Bastolla *et al.*)[1] describe how they have followed up earlier studies[2] of the mutualistic networks of plants and their animal pollinators. This new investigation is an intriguing enquiry into whether the particular topology of cooperative interactions accommodates greater biodiversity (network size), and it has potential applications beyond ecology to the dynamics of social and financial systems.

In the ecological networks under consideration, plants and animals compete for resources within their respective groups. But they may obtain mutual pay-offs across groups, in the form of pollination services and nectar rewards, that can offset the dynamic limits to system size determined by competition. These 'dual category', or bipartite, cooperative networks exhibit a common architecture called nestedness[2], in which relative specialists — those species with few cooperative links — interact only with subsets of species having greater numbers of cooperative links. This somewhat abstract hierarchical feature gives rise to network 'disassortativity'[2,3], in which nodes with few connections (specialists) tend to be connected to nodes with many connections (generalists), and vice versa. (Strictly speaking, nestedness is restricted to bipartite networks, and disassortativity is a more general property of node connectivity.) Either way, this gives the network an overall appearance similar to that of the Fedwire network operated by the US Federal Reserve System for interbank payment transfers[3]. This network has a dense core of well-connected large institutions (generalists) fringed by a periphery of smaller banks (specialists).

How does nested mutualism affect the way systems operate? In a fully connected network in which all plants cooperate with all animals, mutualism reduces the effective competition within each bipartite class: within plants and within animals. However, in situations in which not all mutualistic interactions are present, some cooperative links will serve to decrease competition (Fig. 1a), whereas others can actually increase it (Fig. 1b). To clarify the role of nestedness in reducing the effects of competition, Bastolla and colleagues[1] apply a 'soft mean field' approximation to the plant–animal interaction matrix to derive an analytical expression for competitive load. They clearly show that nested mutualism reduces overall competition for a given number of cooperative interactions, and so has a potential stabilizing effect.

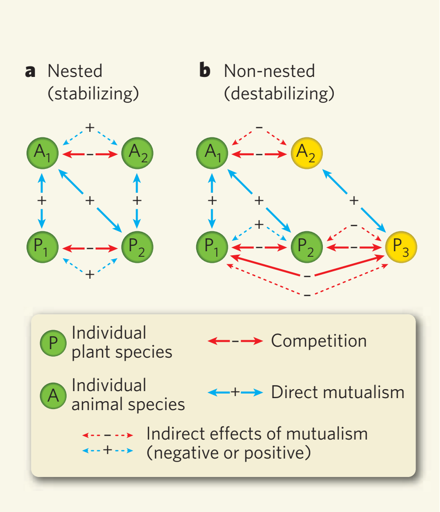

Figure 1 | Nested mutualism reduces competition. a, A nested cooperative network[1], in which both the specialist plant P_1 and the generalist plant P_2 interact with the generalist animal A_1. Because both plants share a mutualism with the generalist animal A_1, the competition between them is reduced. Similarly, competition between both animals is decreased by mutualism with generalist plant P_2. **b,** In a non-nested network, the specialist animal A_2 does not interact cooperatively with a subset of the species with which the generalist animal A_1 interacts. So competition between animals A_1 and A_2 is exacerbated by mutualism with competing plants. The same principles apply to competition between P_1 and P_3 and between P_2 and P_3 (amplified by their mutualism with competing animals).

Thus, whereas competition normally limits the number of species that can coexist (as tough competitive markets often tend towards monopoly), the nested cooperative models studied here reduce competition and allow the system to support more species, or higher biodiversity. This model prediction is supported by data from 56 plant–animal mutualistic networks, providing evidence that real cooperative networks with this structure attain a larger size than those that are relatively less nested.

Nestedness is not an isolated property of plant–animal communities, however, but appears in various social contexts, including the organization of the New York garment industry[4] and as disassortativity in the topology of the Fedwire network[3]. Indeed, it is possible that the appearance of similar topology among diverse cooperative networks may be a result of simple shared assembly rules[5].

A common theme among various network assembly rules[5–7] in ecology (for food webs, for instance) is the idea of growing the network along paths of least resistance, with simple constraints that minimize competition. This is the situation in which species join the network in order of increasing specialization with minimal competitive resistance[7] (Fig. 2). As described by Bastolla *et al.*[1], when a specialist species joins the community by interacting with a generalist species, overall competitive load is decreased. This results in a self-reinforcing nested network, in which existing generalist species gain more connections as specialist species enter the system: reduced competition, in turn, attracts more specialists.

In the case of the New York garment industry[4], where cooperation occurs between two classes of companies — contractors and manufacturers — the establishment of a new small contractor (that is, a specialist animal) is facilitated if that company cooperates with a large, well-established manufacturer (a generalist plant). An analogous case may hold for the payment networks of banks[3], where the network topology is disassortative. Here, disassortativity may arise naturally when banks seek relationships with each other that are the most mutually beneficial: for example, small banks may interact with large banks for security, lower liquidity risk and lower servicing costs, and large banks may interact preferentially with small banks in part because they can extract a higher premium for services and can in principle accommodate more risk. Simple incentive rules can give rise to self-reinforcing disassortativity.

However, the same hierarchical structure that promotes biodiversity in plant–animal mutualistic networks may also increase the risk

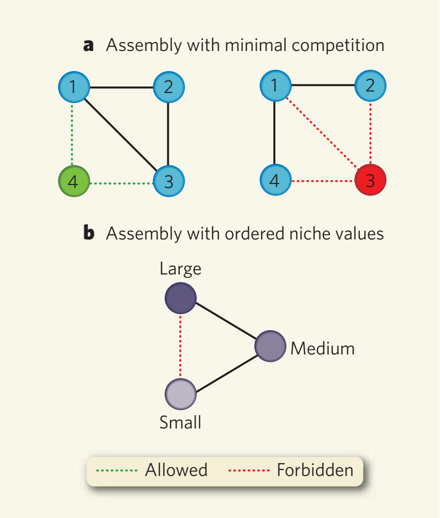

Figure 2 | Minimal assembly rules can explain structure. **a**, An assembly rule that minimizes competition by adding specialists along paths of least resistance[1]; solid lines denote existing connections. The left-hand sequence minimizes competition by adding species 4 to a single guild of competing species (1 and 3). Because it is easier for species 4 to join the network as a specialist, this is a path of least resistance. In the right-hand 'forbidden' sequence, the new species (3) must compete with two guilds of species — (4 and 1), (2 and 1) — and is not entering as a specialist. **b**, Another common minimal assembly constraint is a natural ordering in the resource set[7], as might result from evolution[6]. The nodes are resources used by each species (here, seed sizes), and each species is represented as a line joining two resource classes. Adding a species that eats small and large seeds, but ignores middle-sized ones, violates the niche ordering (a common minimal assembly constraint)[1,5–7]. (Graphic modified from ref. 7.)

of large-scale failures in cooperative networks[8]. Mutualism facilitates greater biodiversity. But it also creates the potential for many contingent species to go extinct, particularly if large, well-connected generalists (for example, certain large banks) disappear.

Moreover, as reported by Bastolla *et al.*[1], a strong mutualistic interaction between two species (excessively favourable selective terms) can move the system into a strong mutualistic regime; this will destabilize other weakly mutualistic species groups whose interaction strength falls below some threshold. Over time, only the strong cooperators survive, and the weakly cooperating species groups go extinct. This stylized behaviour of simple mutualistic networks possibly applies to other domains, in which strong cooperation between two agents may cause the demise of all other agents — or where, in less-stylized cases, uneven cooperative subsidy or advantage in global networks can be dangerous unless the mutually beneficial effects propagate more or less evenly throughout the network.

As a specific speculative example, consider the interdependence of the Internet auction site eBay and the payment system PayPal. PayPal was the dominant method of payment for eBay auctions when it was bought by eBay in 2002, strengthening cooperative links between the two companies. Insofar as this simplified model applies, this duopolistic partnership would have encouraged the demise of alternative competing payment systems, such as eBay's Billpoint (phased out after the purchase of PayPal), Citibank's c2it (closed in 2003) and Yahoo!'s PayDirect (closed in 2004).

Whether Bastolla and colleagues' model[1] of structured cooperation performs the same role in other domains is intriguing but unclear. In particular, the extent to which the topology of cooperative linkages in payment networks — or more importantly, in networks of balance sheets — may increase systemic risk in the financial sector remains an open question[9]. Tackling such questions will no doubt require mutualistic cooperation between researchers linking different competitive fields. ■

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NEUROSCIENCE

Optical control of reward

David E. Moorman and Gary Aston-Jones

Is it wishful thinking that the behaviour of an organism as complex as a mouse might be controlled by modulating its intracellular signalling with light? No: this is just what researchers have achieved with an elegant technique.

Ever since the Italian physician Luigi Galvani discovered that frogs' muscles twitch when stimulated electrically, the integral role of electricity in the functioning of the nervous system has seemed clear. But there is also a growing appreciation that intracellular signalling pathways — which can interact with the extracellular environment through G proteins and G-protein-coupled receptors (GPCRs) — play an essential part in the processing of information by neurons. Deisseroth and colleagues[1] (Airan *et al.*, page 1025 of this issue) now describe a powerful technique that allows intracellular signalling pathways to be controlled through the activation of GPCRs by light. Intriguingly, by modulating specific signalling cascades in this way, the authors can control behaviour in mice.

Deisseroth and colleagues[2] had previously shown that naturally occurring light-activated ion channels, such as channelrhodopsin-2 (ChR2) and halorhodopsin, could be integrated into neuronal cell membranes to drive the respective activation or inhibition of electrical impulses using light. By means of this and other similar techniques[3,4], neuronal impulses can be regulated with unprecedented temporal, spatial and cell-type specificity. In the latest development, Airan *et al.*[1] have created chimaeric GPCR molecules that they call optoXRs. The extracellular and transmembrane portions of optoXRs (opsin) consist of the light-activated rhodopsin protein, but their intracellular components are those of specific GPCRs. The authors focused on two main receptors for the neurotransmitters adrenaline and noradrenaline: the β_2 receptor, which couples to G_s proteins, and the α_{1a} receptor, which couples to G_q proteins. As these two classes of G protein activate signalling pathways that are mediated by different effector molecules[5], the authors could control a wide range of intracellular signalling pathways.

Airan *et al.* first expressed optoXRs in cell lines to test the molecules' basic functionality. Depending on the optoXR expressed, they observed a robust light-driven increase in the levels of the cellular signalling molecules calcium, cAMP and $Ins(1,4,5)P_3$ — effects that are associated with activation of the corresponding native GPCRs. What's more, the levels of increase were similar to those that occurred after activation of the native receptors, demonstrating that optoXRs can potentially regulate intracellular signalling in a physiologically relevant yet precise manner via specific G proteins.

The authors next investigated light activation of optoXRs in brain slices containing neurons from the nucleus accumbens region. They report an increase in the levels of phosphorylated CREB, a protein that functions downstream of G_s- and G_q-mediated pathways. So it seems that even downstream components of these pathways can be activated by light without the need for additional cofactors, a requirement that would have limited this technology's applicability