

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 $N_i^{(P)}$ and $N_k^{(A)}$ the species abundance density of the i -th species of plant and the k -th species of animal respectively, and with $S^{(P)}$ and $S^{(A)}$ the observed number of such species. The intrinsic growth rates in the absence of competition and mutualism are represented as $\alpha_i^{(P)}$ for plants and $\alpha_k^{(A)}$ 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, $-\beta_{ij}^{(P)} N_j^{(P)}$ in the case of plants and $-\beta_{kl}^{(A)} N_l^{(A)}$ for animals. The competition matrices $\beta_{ij}^{(P,A)}$ 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 II¹, $f(N) = (\gamma N) / (1 + h\gamma N)$. 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 $\gamma_{ij}^{(P)}$ 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, $\gamma_{ji}^{(A)}$ 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

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

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 $dN_i^{(A,P)}/dt = 0$, 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 $\beta_{ij}^{(P)}$ of mean field type, with $\beta_{ij}^{(P)} = \beta_0^{(P)} (\rho^{(P)} + (1 - \rho^{(P)})\delta_{ij})$ (see ref. 2), where δ_{ij} is Kronecker's delta (one if $i = j$ and zero otherwise). The dimensionless parameters $\rho^{(P)} < 1$ 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

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

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,

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

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

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

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

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, $\gamma_{ik}^{(A,P)} = \gamma_0^{(A,P)}$. We will relax this assumption later on. With this assumption, the effective competition matrix turns out to be of mean field type,

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

$$a^{(P)} = \frac{\gamma_0^{(P)} \gamma_0^{(A)}}{\beta_0^{(A)} \beta_0^{(P)}} \frac{S^{(A)}}{(S^{(A)} \rho^{(A)} + (1 - \rho^{(A)}))}. \quad (7)$$

The effective interspecific competition is given by

$$\rho_{\text{mut}}^{(P)} = \frac{\rho^{(P)} - a^{(P)}}{1 - a^{(P)}} < \rho^{(P)}. \quad (8)$$

We see from the above expression that, for the mean field system and for values of the parameter $a^{(P)} \in [0, \rho^{(P)}]$, the effective interspecies competition $\rho_{\text{mut}}^{(P)}$ is smaller than the bare competition $\rho^{(P)}$, i.e., mutualistic interactions of mean field type reduce the effective interspecies competition. Eq. (8) is valid for $a^{(P)} < \rho^{(P)} + (1 - \rho^{(P)})/S^{(P)}$. 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 $\lambda_1 = (1 - a) \left(S\rho_{\text{mut}}^{(P)} + (1 - \rho_{\text{mut}}^{(P)}) \right) = S(\rho^{(P)} - a) + (1 - \rho^{(P)})$ and $\lambda_k = (1 - a)(1 - \rho_{\text{mut}}^{(P)}) = (1 - \rho^{(P)})$ ($k > 1$). Positivity of the competition matrix requires that $S(\rho^{(P)} - a) + (1 - \rho^{(P)}) > 0$, which in turn yields the condition

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

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

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

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

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 $\alpha_i^{(P,A)}$.

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 $C^{(A)}$ and $C^{(P)}$ 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

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

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

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

We have defined here the mutualistic matrix $M^{(P)} \equiv (\beta^{(P)})^{-1} \gamma^{(P)} (\beta^{(A)})^{-1} \gamma^{(A)}$. The effective competition matrix $C^{(P)}$ can be written in matrix notation as $C^{(P)} \equiv \beta^{(P)} (I - M)$, where I is the identity matrix. Since the direct competition matrix $\beta^{(P)}$ is positive, if $C^{(P)}$ 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 $N_i^{(P)} \leq 0$

for all i . The same applies to $N^{(A)}$ if $C^{(A)}$ 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 $\gamma_0^{(P)}$ and $\gamma_0^{(A)}$ such that $\gamma_0^{(P)}\gamma_0^{(A)} < \beta_0^{(P)}\beta_0^{(A)}\rho^{(P)}\rho^{(A)}$, but one pair of species, animal species 1 and plant species 1, have a strong mutualistic interaction with interaction coefficients $\gamma_1^{(P)}\gamma_1^{(A)} > \beta_0^{(P)}\beta_0^{(A)}$. 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 extinct, 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 necessary, 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 system⁴. 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, $\rho^{(P)}$, 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

$$B_{ij} = \frac{C_{ij}}{\sqrt{C_{ii}C_{jj}}}, \quad (13)$$

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

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

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)

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

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

$$\bar{S} \equiv \frac{1 - \tilde{\rho}}{\tilde{\rho}} \quad (16)$$

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 $\bar{S} = (1 - \rho)/\rho$ for the maximum biodiversity for the purely competitive system,

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

$$\bar{S}_{\text{mut}}^{(\text{P})} \equiv \frac{1 - \rho_{\text{mut}}^{(\text{P})}}{\rho_{\text{mut}}^{(\text{P})}} = \frac{\bar{S}^{(\text{P})}}{1 - a^{(\text{P})}/\rho^{(\text{P})}}. \quad (17)$$

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 maintain 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 $g_{ik}^{(\text{P})} = g_{ki}^{(\text{A})}$. We further denote the number of links of plant i as $n_i^{(\text{P})} = \sum_k g_{ik}^{(\text{P})}$ and the number of common links of plants i and j as

$$n_{ij}^{(\text{P})} \equiv \sum_k g_{ik}^{(\text{P})} g_{jk}^{(\text{P})} \quad (18)$$

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 algorithm⁷. 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

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

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

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, $\gamma_{ij}^{(P)} = \gamma_0^{(P)} g_{ij}^{(P)}$, where the binary matrix $g_{ij}^{(P)}$ is the adjacency matrix of the mutualistic network and $g_{ij}^{(A)}$ is the transpose of $g_{ij}^{(P)}$.

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),

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

where $\overline{\alpha^{(A)}}$ 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 competitiveness 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 $B_{ij}^{(P)}$ is defined through

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

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

where

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

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

To get more analytic insight on how mutualism influences biodiversity, we computed the derivative of the main eigenvalue of the normalized effective competition matrix, $\lambda_1(B^{(P)})$, with respect to the mutualism-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 $\{n_i^{(P)}\}$ and fixed parameters. Since the maximum predicted biodiversity $\bar{S}_{\text{mut}}^{(P)}$ 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 $\lambda_1(B^{(P)})$, we can easily obtain the derivative of the maximum biodiversity $\bar{S}_{\text{mut}}^{(P)} = (1 - \rho_{\text{mut}}^{(P)}) / \rho_{\text{mut}}^{(P)}$, where $\rho_{\text{mut}}^{(P)} = (\lambda_1(B^{(P)}) - 1) / (S^{(P)} - 1)$ 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

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

where $\langle n^{(P)} \rangle = \sum_i n_i^{(P)} / S^{(P)}$ and $\langle (n^{(P)})^2 \rangle = \sum_i (n_i^{(P)})^2 / S^{(P)}$ are the mean and mean square number of mutualistic interactions per plant species. The parameter $\hat{\eta}^{(P)} = \sum_{i \neq j} n_{ij}^{(P)} / ((S^{(P)} - 1) \sum_i n_i^{(P)})$ 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 $\bar{S}^{(A)}$), so that the term $\hat{\eta} - \langle n^{(P)} \rangle / (S^{(A)} + \bar{S}^{(A)})$ 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 ($n_{ij}^{(P)} = 0$), 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 $\overline{S}^{(A)}$ and $\overline{S}^{(P)}$.

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 $C^{(A)}$ and $C^{(P)}$ are positive definite; (2) the strong mutualist fixed point can not have positive densities if the matrices $C^{(A)}$ and $C^{(P)}$ 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 $\rho_{\text{mut}} = 0$. 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 loses 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:

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

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 $\beta^{(P)}$ of mean field type. The analytic expression for the inverse matrix is $(\beta^{(P)})^{-1} = 1/\beta_0^{(P)}(1 - \rho^{(P)}) \left(\delta_{ij} + 1/(S^{(P)} + \bar{S}^{(P)}) \right)$, whence

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

Summing over all animal species j , we find

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

The only term that depends on the plant species 1 with which the new animal interacts is $\sum_j \gamma_{1j}^{(P)}$. The larger is this term, the smaller the competition experienced by the new species. Now, although we expect that individual interaction coefficients $\gamma_{1j}^{(P)}$ tend to be larger for specialist species than for generalist species, we also expect that the sum of all

interactions $\sum_j \gamma_{1j}^{(P)}$ 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 invasibility⁸, 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 interaction 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

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

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

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

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

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

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

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

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

where $\tilde{C} = \beta^{-1}C$, $\tilde{\gamma} = \beta^{-1}\gamma$ and $\tilde{\delta} = \beta^{-1}\delta$ 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 $C^{(P)}$ as follows:

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

The terms in the sum are sub-dominant, since stability of the fixed points requires that the matrices $\tilde{\gamma}^{(P)}\tilde{\gamma}^{(A)}$, $\tilde{\delta}^{(P)}\tilde{\delta}^{(H)}$ and $\tilde{\delta}^{(A)}\tilde{\delta}^{(C)}$ 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 differential 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 occur. 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 occur. 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

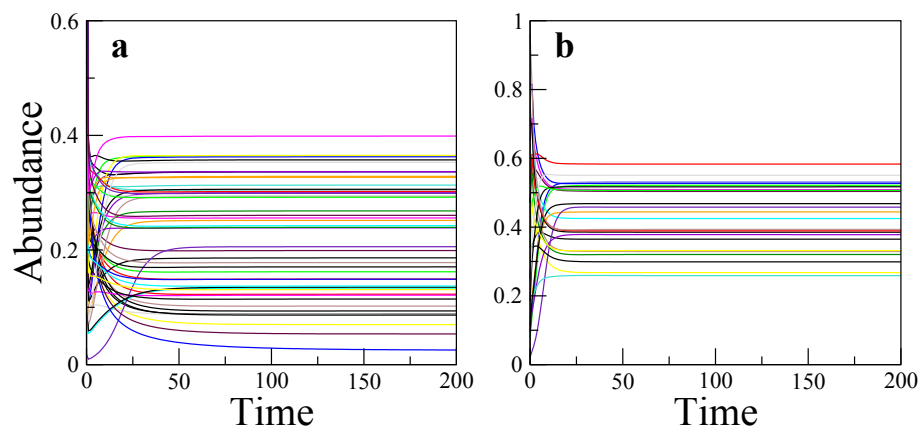


Figure 1: Temporal dynamics of the abundance of plants (a) and animals (b) in a fully connected mutualistic community with 50 plant species and 25 animal species. The same system without mutualism leads to the extinction of one animal and 17 plant species. Parameter values are as follows: α_i are taken 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). $h^{(P)} = h^{(A)} = 0.1$. 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 $C^{(P)}$ and $C^{(A)}$ 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

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

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

We now show that positivity of $C^{(P)}$ and $C^{(A)}$ 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 $x = (x^{(P)}, x^{(A)})$ and $y = (y^{(P)}, y^{(A)})$ (here $x^{(P)}$ ($x^{(A)}$) denotes the projection of the vector x on the P (A) subspace respectively), such that $x^{(A)} = \gamma^{(A)}x^{(P)}$, and $y^{(P)} = \gamma^{(P)}y^{(A)}$. These vectors have the property that $(Jx)^{(P)} = -C^{(P)}x^{(P)}$, $(Jx)^{(A)} = 0$, $Jy^{(A)} = -C^{(A)}y^{(A)}$, $(Jy)^{(P)} = 0$. Using these properties, we can see that for a generic vector $z = x + y$, it holds

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

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

$$J = \begin{pmatrix} \beta^{(P)} & 0 \\ 0 & \beta^{(A)} \end{pmatrix} \begin{pmatrix} -I^{(P)} & \tilde{\gamma}^{(P)} \\ \tilde{\gamma}^{(A)} & -I^{(A)} \end{pmatrix} \equiv \beta \tilde{J}. \quad (37)$$

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

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

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

$$M = \begin{pmatrix} \tilde{\gamma}^{(P)}\tilde{\gamma}^{(A)} & 0 \\ 0 & \tilde{\gamma}^{(A)}\tilde{\gamma}^{(P)} \end{pmatrix}. \quad (39)$$

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

1. The effective competition matrix \tilde{C} is positive definite.
2. The reduced Jacobian \tilde{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

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

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

$$\tilde{J} = \begin{pmatrix} -I & +\sqrt{M} \end{pmatrix}, \quad (41)$$

$$\tilde{C} = \begin{pmatrix} I & -M \end{pmatrix}. \quad (42)$$

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

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

If $\lambda(\sqrt{M})$ is imaginary then it must be pure imaginary since the $\lambda(\tilde{C})$ are real and positive by hypothesis. Therefore, in this case it must follow that $\text{Re}(\lambda(\tilde{J})) < 0$, 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 \tilde{C} is positive definite, it follows that $0 \leq \lambda(M) < 1$, which implies $-1 < \lambda(\sqrt{M}) < 1$ and consequently $\lambda(\tilde{J}) < 0$, 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 necessary 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 , $\bar{S}^{(P)}$ and $\bar{S}^{(A)}$, we can compute numerically the effective competition coefficient $\rho_{\text{mut}}^{(P)}$ through Eq.(21), Eq.(22) and Eq.(14), where $\lambda_1(B^{(P)})$ is the main eigenvalue of the normalized competition matrix $B^{(P)}$. The corresponding maximum predicted biodiversity is given by $\bar{S}_{\text{mut}}^{(P)} = (1 - \rho_{\text{mut}}^{(P)})/\rho_{\text{mut}}^{(P)}$, and it characterizes the biodiversity of the model ecosystem. For $R = 0$ (pure competition) it holds that $\rho_{\text{mut}}^{(P)} = \rho^{(P)}$ and $\bar{S}_{\text{mut}}^{(P)} = \bar{S}^{(P)}$, 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 , $\bar{S}^{(A)}$, $\bar{S}^{(P)}$ for all systems. The parameters $\bar{S}^{(A)}$, $\bar{S}^{(P)}$ are chosen large enough so that mutualism favors biodiversity in all real networks, i.e., $\rho_{\text{mut}}^{(P)}$ 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 $B^{(P)}$ 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 :

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

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

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

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

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