Cooperation promotes biodiversity and stability in a model ecosystem

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Abstract

Empirical observations show that natural communities of species with mutualistic interactions such as plant and pollinators, can have a number of coexisting species of the order of hundreds. However the standard modeling of population dynamics would predict that these systems become less stable than communities with competitive or prey-predator interactions as the number of species increases. We propose a stochastic model which is appropriate for species communities with mutualistic/commensalistic interactions and find that, in the large system size limit, any number of species can coexist for a very general class of interaction networks and that the stationary state is globally stable. The stochastic dynamics can be exactly solved at the leading order in the system size. We obtain results for species abundance distributions, correlation functions and classification of network topologies of stable interacting communities.

Keywords: Voter Model, Population Dynamics, Ecological Networks, Cooperation, Stability-Complexity

Research in population dynamics has a long history dating back to almost one thousand year ago with Fibonacci modeling of rabbits population. Nevertheless there are still several open issues of paramount importance in the research of ecological population dynamics [30, 21, ?], and the current loss of earth biodiversity [31, 11] makes this research field of great relevance today more than ever. Many fundamental and long-standing questions in biology concerning ecosystem dynamics are, for example, how does simplicity result from apparently complex interactions? How does diversity emerge and what is the role of cooperation? How are these features maintained through robust mechanisms? When several species co-occur in an community there can be a rich set of relationships among them that can be represented as a complex interaction network.

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Historically, the first models defining the dynamics of interacting ecological species were those of Lotka and Volterra, which describe asymmetrical interactions between predator-prey or resource-consumers systems. The Lotka and Volterra (LV) equations have provided much theoretical guidance. While prey-predator and competitive interactions have been extensively studied, mutualistic/commensalistic interactions, which are not disadvantageous to the involved species, have historically received less attention. Nevertheless, in recent years, there have been several studies showing the crucial role of cooperation in ecosystems.

The current approach study to mutualistic/commensalistic population dynamics is the same as in the LV models, but with beneficial interactions among individuals of different species. The limitations of these approaches were identified as more research was carried out. Indeed, a generalization of the May stability-complexity theorem has revealed that mutualism and cooperation in LV models are more detrimental to stability than predator-prey interactions as the product \( SC \) increases, where \( S \) is the number of species and \( C \), the connectivity, is the fraction of non-zero pairwise interactions between species.

From a theoretical point of view, an alternative approach to niche-based multi-species deterministic modeling is the Neutral Theory (NT) of Biodiversity. The NT is an ecological theory within which organisms of a community have identical per-capita probabilities of giving birth, dying, migrating, and speciating, regardless of the species they belong to. In this sense the model is symmetric and it aims to model only species on the same trophic level - species therefore competing for the same pool of resources. For instance, plants and trees in a forest compete for resources like carbon, nitrate and light. An important example of neutral model is the Voter model (VM). The VM is a paradigmatic model to describe competition in many fields going from social sciences to biology. In the ecological context one deals with a community of \( N \) individuals belonging to \( S \) different species. At every time step a randomly selected individual dies and the corresponding resources are freed up for colonization. With probability \( \nu \) the site is taken by an individual of a species not currently present in the system (immigration from surrounding communities or speciation event). With the probability \( 1 - \nu \) the available site is colonized by an individual randomly sampled within the community.

However, an important limitation of this modeling is that it does not consider explicitly species interactions (e.g. mutualism/commensalism). Moreover, adding mutualistic interactions typically places a bound on the diversity of species that can coexist. Two crucial gaps in the current literature are thus: (i) a general framework where species interactions are added on neutral models and can modify the species birth-death rates; and (ii) understand the role of mutualistic/commensalistic interactions in determining species coexistence and how they impact on patterns such as species abundance distribution.

In this Letter we present a theoretical framework, where starting from a VM-like microscopic stochastic modeling, we add mutualistic/commensalistic interactions among species, affecting neutrality and leading to an emergent niche-like multi species-neutralistic model. Reconciling apparently contrasting observations and previous results, we show that in our model ecosystem cooperation promotes biodiversity and diversity increases its stability.

In details, be \( \eta_x \) the species label at spatial position \( x \), where \( \eta_x \in \{1, \ldots, S\} \) and \( x = 1, \ldots, N \). The state at time \( t \) of the system is given by \( \eta(t) = (\eta_1(t), \eta_2(t), \ldots, \eta_N(t)) \). We introduce a
directed graph on the set \{1,\ldots,S\}, where the nodes correspond to species and directed links represent the network of ecological interactions. Given two species \(i\) and \(j\), a directed link of strength \(M_{ij}\) from \(i\) to \(j\) means that the \(i\)-th species interacts with the \(j\)-th species. In our model we focus on mutualistic interactions, \(M_{ij} > 0\), \(M_{ji} > 0\), and commensalistic interactions, \(M_{ij} > 0\), \(M_{ji} = 0\) or \(M_{ij} = 0\), \(M_{ji} > 0\). When \(M_{ij} > 0\), has to be interpreted as “the presence of the \(i\)-th species helps the \(j\)-th species to survive” (i.e. cooperation). In a general setting the matrix entries can be drawn from a given probability distribution [1, 26] and they are decided at time \(t = 0\) and do not change with dynamics. With the matrix \(M\) in hand we can describe the Markovian dynamics for the time evolution of \(\eta(t)\) in terms of the transition rates between states. The rules for the dynamics are given for a system where any individual feels the presence of the others independently of their position and disregarding spatial distance. A situation which is appropriate for a well mixed system. We define \(\eta^k\) the fraction of individuals of the \(k\)-species. In our dynamics a random individual is eliminated and the freed space is colonized by an individual of given species \(j\) with a rate

\[
\omega(j,\eta,M) = \tilde{\eta}^j + \epsilon \sum_{k=1}^{S} \tilde{\eta}^k M_{kj} \theta(\tilde{\eta}^j),
\]

where \(\epsilon\) gives the cooperation intensity, so that we can fix the average of the non-zero \(M_{kj}\)’s to 1, and \(\theta(\cdot)\) is the Heaviside step function, i.e., \(\theta(x) > 0\) when \(x > 0\) and 0 otherwise. The presence of the \(\theta\)-function guarantees that the transition rate is zero if the \(j\)-th species is extinct. For \(\epsilon = 0\) we recover the standard VM. When \(\epsilon > 0\) the species \(j\) is favored by the presence of the other species (\(k\) in the summation) to which it is connected and by their population. It is useful to highlight the differences between the form of the interaction part in our rates (last term of eq. (1)), with the corresponding one in the LV equations. In the LV equation for the time evolution of the population of the \(j\)-th species, the interaction term would read \(\sum_{k=1}^{S} \eta^k B_{kj} \eta^j\). Similarly to \(M\) in (1), the matrix \(B\) describes the interaction among species and \(B_{kj}\) is positive (negative) if \(j\) is the predator (prey) and \(k\) is the prey (predator). The main difference is that this interaction term is quadratic in \(\eta\), while in our setting it is linear. Indeed, rather than conceptualizing this term as the probability that two species interact (which would proportional to the product of the abundance of both the species like it would happen in a chemical reaction between two reactants and in our setting it might be more appropriate for preys and predators), we fix the interactions by expressing a biological links among species, and focus on their impact on the birth rates \(\omega(j,\eta,M)\). To this regard, assuming that all available resources in the community are always saturated [30], then the benefit, which a given species receives, does not depend on its own abundance but only depends on the abundances of the mutualistic partners. Think of the basic example of given bee species mutualistically interacting with a given flowers species. The benefit that bees receive depends on the number of flowers and do not increase with the abundance of their own population, as the amount of nectar provided by the flowers must be shared by all bees of that given species. Thus, we set the interaction term to be linear in eq. (1).

We now want to characterize the large size limit of the dynamics described above. The microscopic dynamics given by rates (1) induce a Markovian evolution on the relative abundance \(\tilde{\eta}^j\) of each species. Standard techniques of convergence of generators [17] can be used to prove that as \(N \rightarrow \infty\), the process \((\tilde{\eta}^1(t),\ldots,\tilde{\eta}^S(t))_{t \geq 0}\) weakly converges to the solution of the system of ordinary differential (mean field) equation:
The stochas-
tic process $(x_N^1(t),\ldots,x_N^S(t))$ converges in distribution to a Gaussian Markov process $X := (X^1(t),\ldots,X^S(t))$ which solves the stochastic differential equation

$$dX = \epsilon AX dt + \Phi dB_t,$$

where $B_t$ is a $S$-dimensional Brownian motion, which corresponds to a $S$-dimensional Ornstein-Uhlenbeck process [17] [22]. The matrices $A$ and $\Phi$ depend on the interaction matrix $M$ and the equilibria of eq. (10), i.e.

$$A_{ij} = M_{ji} - \delta_{ij} \sum_{h,k=1}^{S} m_k M_{hk} - m_i \sum_{k=1}^{S} M_{jk},$$

and $\Phi$ satisfies the following constraint equation

$$(\Phi \Phi^T)_{ij} = -2 \left( m_i m_j + \epsilon m_i \sum_{k=1}^{S} m_k M_{kj} \right) (1 - \delta_{ij}) + 2(1 - m_i) \left( m_i + \epsilon \sum_{k=1}^{S} m_k M_{ki} \right) \delta_{ij}. $$

The covariance matrix can be exactly obtained by solving the following Lyapunov matrix equation

$$\epsilon A V + \epsilon V A^T + \Phi \Phi^T = 0.$$
species \(i\) is non-supported by other species then at stationarity eq. (10) implies that \(\bar{\eta}^i = 0\). The extinction of the \(i\)-th may create new unsupported species that go to zero in the large time limit. Such a cascade of extinctions may eventually end only when all the nodes of interaction network have non-zero in-degree (see Supplementary Material for details). Further we have found sufficient conditions on the topology of the mutualistic interaction matrix \(M\) for the existence of stable stationary states of eq. (10). In fact, if \(M\) is non negative and irreducible, i.e. if for any node \(i\) we can reach any other node \(j\) through a path of oriented links \((k,l)\) such that \(M_{kl} > 0\), then the Perron-Frobenius (PF) theorem holds \cite{48} and a non-trivial stationary state, \((m_k)_{k=1,...,S}\), exists with all positive entries and it is unique. It is proportional to the left eigenvector, \(v\), of \(M\) corresponding to the eigenvalue of \(M\) with the largest modulus, which turns out to be non-degenerate, real and positive, denoted by \(\alpha\) in the following (for brevity we will refer to it as PF eigenvalue in the following). The corresponding right eigenvector will be denoted by \(w\). All components of both \(v\) and \(w\) are strictly positive and so \(m_i = v_i/\sum_k v_k\). An example of irreducible matrix \(M\) occurs when \(M_{ij} > 0\) implies \(M_{ji} > 0\) and the network has a single connected component.

If PF holds and the initial condition \(\bar{\eta}^i(0) > 0\) \(i = 1, \ldots, S\), then the time dependent solution of eq. (10) is

\[
\bar{\eta}(t) = \bar{\eta}(0)^T e^{Mt} T = \sum_i (\bar{\eta}(0)^T e^{Mt})_i.
\]

Since for any eigenvalue, \(\beta \neq \alpha\), of \(M\) we have \(\Re(\beta) < \alpha\) the dominant term in both numerator and denominator in eq. (10) is \(v \ e^{\alpha t} (\bar{\eta}(0) \cdot w)\) leading to \(\lim_{t \to \infty} \bar{\eta}(t) = \frac{v}{\sum_i v_i} = m\). This is an easy computation when \(M\) has a basis of eigenvectors and in general can be derived using the Jordan decomposition. As a corollary of the derivation above we have also that the stationary solution is globally stable in the region \(\bar{\eta}_i(t = 0) > 0\), for all \(i = 1, \ldots, N\). Therefore, within our framework, we can analytically study the impact of the species interaction network architecture on system stability and species extinction. In particular we found that both nested and modular structures observed in real ecological communities \cite{5} satisfy the PF theorem and contribute to the system stability. The results of the mean field predictions and the comparison with the corresponding stochastic dynamics are shown in Figure 1. Two simple examples are shown corresponding to an ecosystem with no extinction (panels A-C) and with extinction (panel D-F). When the mean field predicts the coexistence of all species then the stochastic dynamics leads to the first extinction over exponentially large time with the system size, \(N\) \cite{8, 16}.

To study analytically the stability of the equilibria as a function of ecological complexity, we analyze the eigenvalues of the linearization of eq. (10), i.e. the Jacobian matrix \(A\), around the equilibria, \(m_k\), of the system. Following \cite{37, 1} we set equal to zero the diagonal of \(M\) whereas the the off-diagonal pair \((M_{ij}, M_{ji})\) is equal to \((0,0)\) with probability \(1 - C\) and with probability \(C\) it is drawn from a bivariate gaussian distribution of means \((\mu, \mu)^T\) and covariance matrix \(\Sigma\):

\[
\Sigma = \begin{pmatrix} \sigma^2 & \rho \sigma^2 \\ \rho \sigma^2 & \sigma^2 \end{pmatrix}
\]

This guarantees that, for a connected cluster, coexistence of all species occurs. We define \(\mu_M, \sigma^2_M\) and \(\mu = C\mu, \sigma^2 = C\sigma^2 + C(1 - C)\mu^2, \rho_M = \frac{\sigma^2 + (1 - C)\mu^2}{\sigma^2 + (1 - C)\mu^2}\) as mean, variance and correlation of the elements of matrix \(M\). In the case of \(C = 1\) they reduce to \(\mu, \sigma^2\) and \(\rho\), while in the more general case can be written as functions of the formers \cite{52}. If \(\mu_M \geq \sigma_M \sqrt{(1 + \rho_M)/S}\), the leading eigenvalue \(\lambda_M = S\mu_M = SC\mu\) and the corresponding eigenvector has positive components
Figure 1: Upper panels: (A) Species interaction network for 7 species where each species has one mutualistic partner and all non-zero interaction $M_{ij} = 1$. (B) Time evolution of the populations of the 7 species as predicted by the mean field dynamics eq. (10). (C) Average time for one of the 7 species to get extinct in the full stochastic dynamics eq.(). The average first extinction times grows exponentially with the system size, $N$, i.e. $T_N \sim \exp(N)$. On the contrary if $\epsilon = 0$, the standard voter model, then $T_N \sim N^{13}$. Lower panels: (D) Species interaction network where one species is not helped by any species and the iterative pruning process, as described in the text, leads to no interaction network. (E) This causes a cascade of extinctions as the time evolution of the mean field eq. (10) shows, leading to only one species dominating the community. (F) The corresponding average first extinction times of the microscopic stochastic model at various interaction strength, $\epsilon$ are all compatible with the $\epsilon = 0$ case.
Moreover, the components of the leading eigenvector are approximately constant, i.e. the equilibria of system given by eq. (10) can be written as $m_i = \frac{1}{S}(1 + \xi_i)$ for $i = 1, \ldots, S$ with $\sum_i \xi_i = 0$. Using the fact that $1 = Sm_i - \xi_i$, $\lambda_M = S\mu_M$ and taking into account that all the terms involving $\xi_j$ are sub-leading in $S$, we obtain that the leading term of the system Jacobian is:

$$A_{ij} = -\delta_{ij}S\mu_M + (M_{ij} - \mu_M) = -\delta_{ij}S\mu_M + M'_{ij},$$

(7)

where $M'_{ij} := M_{ij} - \mu_M$ is a random matrix with zero mean variance $\sigma_M^2$ and correlation $\rho_M$. This implies that the eigenvalues are uniformly distributed in an ellipse centered around $-S\mu_M$ with semi-axis $\sqrt{S}\sigma_M(1 + \rho_M)$ and $\sqrt{S}\sigma_M(1 - \rho_M)$ [24] [49]. The largest eigenvalue of the Jacobian is therefore given by $-S\mu_M + \sqrt{S}\sigma_M(1 + \rho_M)$. Thus, for fixed connectivity, $C$, the system stability increases with $S$, whereas becomes independent of $S$ if the connectivity scale as $C \sim 1/S$, that is just above the percolation threshold of a random network [9] (see Fig. 2). Therefore, in the proposed model cooperation promotes ecosystem biodiversity, that in turn increases its stability without any fine tuning of the species interaction strengths or of the self-interactions [52].

An important emergent pattern in ecology, which we can determine within our model, is the relative species abundance (RSA) [30] [39] [43] [44]. It describes commonness and rarity of species, thus characterizing the biodiversity of an ecological community. In our model, the RSA is exactly given by the mean field stationary solution $\mathbf{m}$, that in turn depends on the species interaction matrix $M$. The cumulative RSA is thus defined as the fraction of species with population greater that a certain value, $n$,

$$P_\triangleright[n] = \frac{1}{S} \sum_{k=1}^{S} \theta(n - Nm_k),$$

(8)

where we have fixed $N = 1/\min\{m_1, \ldots, m_S\}$ when all species coexist, i.e. we have made the

\[ \text{Figure 2: Eigenvalues } (\lambda) \text{ spectrum of the Jacobian matrix } A \text{ given by the linearization of eq. (10) around the stationary state for different size (colors) of the networks (from } S = 50 \text{ to } S = 300). \text{ Left panel: (A) the connectivity of } M \text{ is constant } (C = 0.5) \text{ and interaction strengths follow standard half-normal distribution } M_{ij} \sim [\mathcal{N}(0,1)], \text{ i.e. } \mu_M = 0.399, \sigma_M = 0.584, \rho_M = 0.467). \text{ Right panel: (B) the connectivity of } M \text{ scales as } C \sim 20/S \text{ and interaction strengths follow a Gamma distribution with shape parameter } 1 \text{ and scale parameter } 2, \text{ thus } M_{ij} \sim \Gamma(1,2) \text{ and thus for } S = 50/100/200/300, \mu_M = 0.8/0.4/0.2/0.133, \sigma_M = 1.6/1.2/0.872/0.718, \rho_M = 0.375/0.444/0.474/0.483). \text{ Continuous lines represent the analytical approximation for the support of the } A \text{ eigenvalues in the corresponding cases (see eq. (7)).} \]
choice that the rarest species has population equal to 1. We numerically find that the shape of the stationary RSA weakly depends on the specific distribution of the matrix elements $M_{ij}$, and it is mainly determined only on its coefficient of variation, $CV = \sigma_M/\mu_M$, i.e. the variability of the interaction strengths relative to the mean of $M$ (see Figure 3). This allows to constrain the model parameters: In order to parametrize species interactions strengths, that are typically unknown [1, 53], we can make use of a random matrix approach where we fix the mean and the variance according to the desired RSA one needs to fit. We also find that, even for most of the structure of interaction matrix $M$, both $V$ and $V^{-1}$ are not good proxies of the species interactions (see Supplementary Materials) - at least within our framework. This result highlights the importance to properly infer interaction networks from data [18].

Figure 3: Cumulative RSA for 9 different species interaction random networks $M$, where matrix elements $M_{ij}$ have been drawn from three different probability distributions: a Normal distribution $\mathcal{N}(\alpha, \beta)$ (blue lines) ($M_{ij}$'s are the the modulus of normally distributed random numbers), Gamma distribution $\Gamma(\alpha, \beta)$ (green lines) and LogNormal distribution $\ln\mathcal{N}(\alpha, \beta)$ (orange lines lines). We set the distribution parameters $\alpha, \beta$ (see legend) so that in each case we build interaction matrices with three different values of coefficient of variation $CV = \sigma_M/\mu_M = 3, 4, 5$. As we can see, the cumulative RSA is not very sensible to the distribution from which the matrix elements $M_{ij}$ are drawn, but only on the CV. We highlight that in all the above cases $\rho = 0$, but we have non-zero correlation among elements of $M$ as $\rho_M = \frac{\sigma^2 + (1-C)\mu^2}{\sigma^2 + (1-C)\mu^2} \neq 0$. For example, in the first case, the distribution from which the elements are drawn is standard half-normal distribution $|\mathcal{N}(0, 1)|$, the connectivity $C = 0.32$, and the matrix correlation is $\rho_M = 0.543$.

Our framework can be generalized to model population dynamics in meta-communities, i.e. local ecological communities interacting among them [33, 41]. In this case, each node represents a community (see Figure 4), species interact within a community (and from each node of a community one can reach any other node of the same community following links $(i, j)$ such that $M_{ij} > 0$), and communities interact among them. Consider for example the simplest case of two communities A and B, connected by directional mutualism (known also as commensalism), where species in community B benefit from the presence of some species in the other community (e.g. sea turtles in community A and pilot fish, Naucrates ductor, in fish community B). Then species interaction in this ecosystem are described by a matrix of the form

$$M = \begin{pmatrix} M^{AA} & M^{AB} \\ 0 & M^{BB} \end{pmatrix}$$

(9)

where $M^{AA}$ ($M^{BB}$) is a $S_A \times S_A$ ($S_B \times S_B$) matrix, $M_{ij} \geq 0 \forall i, j = 1, .., S$, $S = S_A + S_B$ and the cor-
Figure 4: Meta-community framework. In this example the ecosystem is composed by 8 different communities. The three largest communities (1,2,3) interact among them and correspond to the giant strongly connected component (red dashed line) of the global species interaction network $M$. The other communities composed fewer species are instead isolated. In this case, the PF theorem does not hold, and in fact, if we ran the dynamics we observe extinctions. In particular, as predicted by our model, all isolated communities are going to be extinct (from community 4 to community 8) and only the species involved in the giant strongly connected cluster will survive. Adding a commensalism (green arrow) does not change the situation: again only species in communities 1,2,3 will survive. However, if we add even a small reward for the community 4 by community 3 (dashed orange arrow), then the giant strongly connected cluster will be now composed by communities (1,2,3,4) and a larger number of species can coexist.

responding species abundances are \( m_A \in \mathbb{R}^{S_A^+}, m_B \in \mathbb{R}^{S_B^+} \) where \( (m_A, m_B) = m \) and \( \sum_{i=1}^S m_i = 1 \). The mean-field equilibrium solution of eq. (10) for the \( S \) species is \( (m_A, m_B) M = \alpha (m_A, m_B) \) with \( \alpha > 0 \). Because \( m_A M^{AA} = \alpha m_A \) is independent of \( M^{BB} \) then \( m_A M^{AB} + m_B M^{BB} = \alpha m_B \), and therefore \( m_B = m_A M^{AB} (\alpha I - M^{BB})^{-1} \). Let \( \beta \) be the eigenvalue of \( M^{BB} \) with the largest modulus (for PF, \( \beta > 0 \)). If \( \beta < \alpha \) then \( (\alpha I - M^{BB})^{-1} > 0 \), then \( m_B > 0 \) if at least one entry of \( M^{AB} \) is positive and both communities co-exist (see Supplementary Information). This result can be generalized to three or more communities, \( A, B, \ldots, Z \) connected by directional mutualism, i.e. all blocks below the diagonal are zero and on each of the column blocks there is at least one non-zero interaction. As shown in the Supplementary Information, all species coexist if \( \beta < \alpha, \ldots, \zeta < \alpha \), where \( \alpha \) is the largest real eigenvalue of \( M^{AA}, \beta \) of \( M^{BB}, \ldots, \zeta \) of \( M^{ZZ} \). Beside conditions for meta-communities coexistence, this generalization allows us to understand which species or communities will go extinct based on the topological properties of the species interaction networks. In particular, if \( 0 \neq M_{IZ} \geq 0 \) and \( M_{ZI} = 0 \) for all \( I = A, B, \ldots, Y \) and all other \( M_{K,L} = 0 \) for \( K \neq L \), then the community \( Z \) is helped by all other communities that in
turn are independent to one another. In this case all communities except $A$ and $Z$ are going to be extinct if initially $\bar{\eta}_i(t=0) > 0$ for all $i = 1, \ldots, N$. More generally, within the random matrix approach as described above, isolated species or communities are going to be extinct if they do not belong to the largest cluster, as shown in Figure 4. This simply follows from the fact that the PF eigenvalue of the interaction matrix is proportional to the number of species in a cluster. This result suggests that cooperation play an important role in selecting the coexisting species: species/communities that cooperate (or cooperate more) have competitive advantages with respect to other species/communities that do not cooperate (or cooperate less) and that are thus doomed to extinction.

Our framework thus reconciles, at least for mutualistic/commensalistic communities, long-standing open theoretical question on the relation between stability and complexity and provides a unifying modelling approach between neutral stochastic individual based model, useful to describe emergent patterns in ecology, and niche based, interacting deterministic systems (e.g. Lotka-Volterra).

**Supplementary Material**

0.1 Mean field analysis for the voter model with empty sites

As seen in the main text, the mean field equation without empty site reads

$$\frac{d}{dt} \bar{\eta}^s = \epsilon \sum_{k=1}^{S} \bar{\eta}^k M_{ks} \theta(\bar{\eta}^s) - \epsilon \bar{\eta}^s \sum_{i,j=1}^{S} \bar{\eta}^i M_{ij} \theta(\bar{\eta}^i)$$

(10)

where $s = 1, \ldots, S$ represents different species, $\bar{\eta}^s$ is the average fraction of individuals of the $s$-th species, $M$ is the interaction matrix whose non-zero entries define the network of ecological interactions, $\theta$ is the Heaviside step function ($\theta(x) = 1(0)$ for $x > 0(x \leq 0)$ ) and $\epsilon$ is the cooperation intensity (the average of the non-zero $M_{ij}$ is fixed to 1). For simplicity we have omitted time dependence of $\bar{\eta}$.

We now extend the model presented in the main text introducing the possibility for a site to be empty. In our setting empty sites do not interact with species. Thus the species rates remain unchanged after the introduction of empty sites. Thus the species rates are the same as before whereas non-empty sites become empty with rate $\lambda$. In the case $\epsilon = 0$, the rate $\lambda$ has to be less than 1 otherwise empty sites will cover all the available space. The mean field equations become now:

$$\frac{d}{dt} \bar{\eta}^s = \bar{\eta}^s \bar{\eta}^0 - \bar{\eta}^s \lambda + \epsilon \sum_{k=1}^{S} \bar{\eta}^k M_{ks} \theta(\bar{\eta}^s) - \epsilon \bar{\eta}^s \sum_{i,j=1}^{S} \bar{\eta}^i M_{ij} \theta(\bar{\eta}^i)$$

(11)

$$\frac{d}{dt} \bar{\eta}^0 = (1 - \bar{\eta}^0)(\lambda - \bar{\eta}^0) - \epsilon \bar{\eta}^0 \sum_{i,j=1}^{S} \bar{\eta}^i M_{ij} \theta(\bar{\eta}^i).$$

(12)

Let us analyze the stationary mean-field equations for $\epsilon << 1$. In this case the stable equilibrium for the empty sites is $\bar{\eta}^0 = \lambda - \epsilon \frac{1}{1-\lambda} \sum_{i,j=1}^{S} \bar{\eta}^i M_{ij} \theta(\bar{\eta}^i) + O(\epsilon^2)$. Substituting in the equations for $\bar{\eta}^s$, we obtain

$$\epsilon \sum_{k=1}^{S} \bar{\eta}^k M_{ks} \theta(\bar{\eta}^s) - \epsilon \bar{\eta}^s \sum_{i,j=1}^{S} \bar{\eta}^i M_{ij} \theta(\bar{\eta}^i) + O(\epsilon^2) = 0$$

(13)
where $s = 1, \ldots, S$. After the change of variable $\bar{\eta}' = (1 - \lambda)\bar{\eta}$, the above eq. (13) reduces to the eq. (10) up to a second order perturbation in $\epsilon$. In other words, when $\epsilon$ is small, the introduction of empty sites leads to stationary abundances which are trivially rescaled with respect to the case in absence of empty sites, as a consequence of the reduction of the available space.

### 0.2 Covariance matrix and species interaction

In this section, we consider the normal fluctuations around the deterministic limit of eq. (10). This allows us to calculate the matrix $V$ describing the correlation between pairs of species population abundances [56]. As highlighted in the main text, this quantity, once opportunely thresholded, is used as an empirical proxy of the species interactions network [18, 19, 35]. Other works, applying maximum entropy approach, use $V^{-1}$ as the quantity to describe species interactions [56, 45]. The aim of this section is to test how well $V$ or $V^{-1}$ approximate the true interactions described by $M$ in our model.

For sake of simplicity, we assume that the limiting dynamics start at the equilibrium $m_1, \ldots, m_S$ with $0 < m_i < 1$, $i = 1, \ldots, S$. Thus, we define the fluctuation process as

$$x_i^N(t) = \sqrt{N} \left( \bar{\eta}_i^N(t) - m_i \right) \quad \text{for} \quad i = 1, \ldots, S.$$  \hfill (14)

Again, one can apply standard techniques of convergence of generators to get weak convergence to the thermodynamic limiting evolution [17]. Indeed, the stochastic process $(x_1^N(t), \ldots, x_S^N(t))$ converges in distribution to a Gaussian Markov process $X := (X^1(t), \ldots, X^S(t))$ which solves the stochastic differential equation

$$dX = \epsilon AX \, dt + \Phi dB_t$$  \hfill (15)

where $B_t$ is a $S$-dimensional Brownian motion, and

$$A_{ij} = M_{ij}^T - \delta_{ij} \sum_{h,k=1}^S m_h M_{hk} - m_i \sum_{k=1}^S M_{jk}$$  \quad \text{for} \quad j = 1, \ldots, S$$

$$(\Phi \Phi^T)_{ij} = -2 \left( m_i m_j + \epsilon m_i \sum_{k=1}^S m_k M_{kj} \right) (1 - \delta_{ij})$$

$$+ 2(1 - m_i) \left( m_i + \epsilon \sum_{k=1}^S m_k M_{ki} \right) \delta_{ij} \quad \text{for} \quad j = 1, \ldots, S,$$

where $\delta_{ij}$ is the Kronecker delta.

From eq. (15), it is then possible to derive the dynamics of the covariance matrix $V_{ij}(t) = \langle X^i(t), X^j(t) \rangle$ (see [20] for details). Therefore, we have

$$\frac{dV(t)}{dt} = \epsilon AV(t) + \epsilon V(t) A^T + \Phi \Phi^T,$$  \hfill (16)

and at stationarity the covariance matrix resolves the following equation

$$\epsilon AV + \epsilon V A^T + \Phi \Phi^T = 0.$$  \hfill (17)

eq. (17) is a Lyapunov equation, so we could apply standard algorithms to solve it numerically [44].
We have determined $V$ from the solution of eq. (17) and determined $V^{-1}$. If one assume that the population fluctuations around their means are gaussian distributed, then $V^{-1}$ represents the species interaction matrix [34, 56]. Indeed, within a maximum entropy approach, $V^{-1}$ is typically used to infer species interactions based on the available information of the system [45]. In our framework and as shown by eqs. (16) and (17), the relation between the interaction matrix $M$ and the matrix $V$ or $V^{-1}$ is highly non-linear. Moreover, because of the constraint, $\sum_j V_{ij} = 0$, $V$ is not invertible, and thus in order to compute $V^{-1}$ we apply a pseudo-inverse scheme, i.e. we invert $V$ is the subspace of spanned by the eigenvectors corresponding to non-zero eigenvalues. As shown in Figures 5 and 6, even for very simple structure of matrix $M$, $V$ and $V^{-1}$ are not good proxies of the species interactions. The results are shown for the model without empty sites, but there is no qualitatively difference with the model including empty sites. This result highlights the importance to properly infer interaction networks from data.

Figure 5: Histogram with the elements of the covariance Matrix $V$ and its inverse $V^{-1}$ (calculated using pseudo-inverse method) compared to the actual species interaction network $M$ for a small ($S=7$) and sparse ($C=1/(S-1)$) species interaction network. We see that both $V$ and $V^{-1}$, if used as a proxy of $M$, overestimate the real interactions in the ecological community.

0.3 Topology of the interaction network and stationary states

In this section, we discuss some features of the topology of the mutualistic interaction matrix $M$ and how they relate to stationary states of the system. The main concept in this section is the one of pruned graph and the operation of pruning a network. A node with in-degree equals to zero and out-degree different from zero is called a dead leaf of the network. The operation of pruning consists in eliminating one by one the dead leaves of a given network together with their outbound links. After a first pruning, we will obtain a new network (that is a subnetwork of the starting one) that may still have dead leaves - the elimination of dead leaves may create new dead leaves. The pruning process end when the resulting network has no more dead leaves. The latter network is called stable or pruned. It is easy to see that the minimal pruned network (i.e. with the smallest
Figure 6: Elements of the covariance matrix $V$ and its inverse $V^{-1}$ (calculated using pseudo-inverse method) compared to the actual species interaction network $M$ for a large ($S=100$) and dense ($C=0.5$) network. We see that, although there is some significant correlations between elements of $V$, $V^{-1}$ and $M$ (see inset), many actual interactions ($M_{ij} \neq 0$) are set close to zero in both $V$ and $V^{-1}$. On the other hand, matrix elements of both $V$ and $V^{-1}$ wrongly indicate relatively strong interactions even though the corresponding elements in $M$ are zero.

number of links) that can be constructed with $S$ nodes is the cyclic graph. More in general, we have:

**Proposition:** The pruned network is a union of isolated nodes and graphs that contain at least one cycle each.

Indeed, pruning stops when the obtained graph is a union of isolated nodes and graphs where all nodes have at least an ancestor (i.e. the in-degree of each node is positive). Now a finite graph where each node has a least one incoming link contains at least a cycle. In fact, starting from one node it is possible to walk through the ancestors and never stop. Since the graph is finite, soon or later, the walker will visit twice the same node - so the walk contains a cycle - at most after a number of steps that equals the size of the graph.

The pruned network has at least one cycle but when not simply union of isolated cycles it can be very complex. Fig. 7 shows an example of the pruning procedure and of a non-trivial pruned network.

As we anticipated at the beginning of this section, the dynamics of species sitting on dead leaves of the interaction network is trivial as their relative abundance goes to zero. This is a simple consequence of the fact that a dead leaf has no incoming bond. Thus, when $s$ is a dead leaf, the first term on the right of (10) is zero and simple estimate gives $d\bar{\eta}^s/dt = -\epsilon \bar{\eta}^s \sum_{i,j} \bar{\eta}^i M_{ij} \theta(\bar{\eta}^j) \leq 0$. The previous simple remark leads to the following:

**Limiting dynamics of dead leaves:** Start the dynamics from a point with $\bar{\eta}^i \neq 0$ for all $i = 1, \ldots, S$. If $k$ is a dead leaf then $\lim_{t\to\infty} \bar{\eta}^k(t) = 0$.

Thus the presence of a dead leaf inhibits coexistence equilibria on the whole graph. More precisely, if $i = 1, \ldots, \gamma$ are dead leaves (at some step of the pruning), the stable equilibria must have $\bar{\eta}^1 = \ldots = \bar{\eta}^\gamma = 0$. 

Figure 7: The diagram of how to prune network. (a) An example of how the operation of pruning works. First the 0-node is eliminated with its outbound link. After that, the node 1 becomes a dead leaf and has to be pruned. The cycle shown by the red links is the resulting pruned network. (b) An example of a pruned network that is not made by cycles.

### 0.4 Stability of the equilibria of networks with $M$ irreducible

Let $m_i$ with $i = 1, \ldots, S$ the stationary solution of equation (10). If all the components are positive, they are solutions of

$$
\sum_k m_k M_{ki} = m_i \sum_{jk} m_k M_{kj} .
$$

(18)

We consider now the case where the interaction matrix, $M$, is irreducible. This means to require that a path of oriented links (a link is present from $i$ to $j$ is $M_{ij} > 0$) exists joining each pairs of nodes, say $k$ and $l$. In this case the interaction network is pruned. Furthermore the Perron-Frobenius theorem holds (see Theorem 1.5 in [48]) implying that a positive solution, i.e. $m_k > 0$ for all $k$, exists. This solution is unique and it is proportional to the left eigenvector, $v$, of $M$ corresponding to the eigenvalue of $M$ with the largest real part (see Theorem 1.7 in [48]), which turns out to be non-degenerate, positive and will be denoted $\alpha$ in the following. All components of $v$ are strictly positive and so $m_i = v_i / \sum_k v_k$. Notice that when an irreducible matrix $M$ is also aperiodic (i.e. returns to any state $i$ can occur in any number of steps) then it is primitive (see Theorem 1.4 in [48]), that is there exists a positive integer $k$ such that $(M^k)_{ij} > 0$ for all pairs of nodes $i$ and $j$. This condition allows for a stronger version of the Perron-Frobenius theorem (compare Theorem 1.1 with Theorem 1.5 [48]).

We now show that the stationary solution is reached at infinite time as far as the initial condition $\eta^i > 0$, $i = 1, \ldots, S$. It is immediate to see that the time dependent solution of eq. (10) is given by

$$
\hat{\eta}(t) = \frac{\eta(0)^T e^{Mt}}{\sum_i (\eta(0)^T e^{Mt})_i} .
$$

(19)

If $M$ has a basis of eigenvectors then one can expand $\hat{\eta}(0)$ using the left eigenvectors. Since for any eigenvalue, $\lambda \neq \alpha$, of $M$ we have $\Re(\lambda) \leq |\lambda| < \alpha$ the dominant term in both numerator and denominator in eq. (19) is $v e^{\alpha t} (\hat{\eta}(0) \cdot w)$, where $w$ is the right eigenvector of $M$ corresponding to $v$, leading to

$$
\lim_{t \to \infty} \hat{\eta}(t) = \frac{v}{\sum_i v_i} = m .
$$

(20)

As a byproduct of the derivation above we have also that the stationary solution is stable in the whole domain where initial abundances are strictly positive.
Now we want to quantify the degree of stability of the stationary solution, \( m \), for the case of random matrices \( M \). This is done by analyzing the eigenvalues of the Jacobian matrix resulting from the linearization of eq. (11) around \( m_i \). Standard theory of dynamical systems assures that when the real parts of the eigenvalues are all negative then equilibria are stable. The Jacobian of (10), evaluated at the fixed point, reads

\[
A_{ij} = M_{ji} - m_i \sum_{k=1}^{S} M_{jk} - \delta_{ij} \sum_{kl} M_{ik} m_l
\]

\[
= M_{ji} - m_i \sum_{k=1}^{S} M_{jk} - \delta_{ij} \alpha .
\]  

(21)

We set equal to zero the diagonal of \( M \) whereas the the off-diagonal pair \((M_{ij}, M_{ji})\) is equal to \((0, 0)\) with probability \(1 - C\) and with probability \(C\) it is drawn from a bivariate gaussian distribution of means \((\mu, \mu)^T\) and covariance matrix \(\Sigma\):

\[
\Sigma = \begin{pmatrix}
\sigma^2 & \rho \sigma^2 \\
\rho \sigma^2 & \sigma^2
\end{pmatrix}
\]

The global mean, standard deviation and correlation coefficient are [52]

\[
\mu_M = C \mu,
\]

\[
\sigma_M = \sqrt{C (\sigma^2 + (1 - C) \mu^2)}
\]

and

\[
\rho_M = \frac{\rho \sigma^2 + (1 - C) \mu^2}{\sigma^2 + (1 - C) \mu^2} .
\]

We want to prove the following result. The average eigenvalue distribution of the matrix \((A + S \mu_M m) / S\), in the large \( S \) limit, is uniform in an ellipse, in the complex plane, centered at \((0, 0)\), with real semi-axis \(\sigma_M (1 + \rho_M)\) and imaginary semi-axis \(\sigma_M (1 - \rho_M))\). The last part of the proof is heuristic. First we show that if \(\lambda\) is an eigenvalue of \(M\) with \(\lambda \neq \alpha\), then \(\lambda - \alpha\) is an eigenvalue of \(A\), where, as in the main text, \(m^T M = \alpha m^T\), i.e. \(m\) is the left eigenvalue of \(M\) with eigenvalue \(\alpha > 0\), whose existence is assumed (guaranteed if \(M\) is irreducible as seen above). Indeed if \(v\) is a right eigenvector of \(M\) corresponding to the eigenvalue \(\lambda \neq \alpha\) of \(M\) (i.e. \(M v = \lambda v\)) then \(v^T m = 0\) and \(v^T A = (\lambda - \alpha) v^T\). Thus the spectrum of \(A\) is simply the one of \(M\) shifted by \(-\alpha\) apart from the eigenvalue \(\alpha\) itself, which is transformed in \(-\alpha\) since \(A m = -\alpha m\).

Let us now define the new matrix \(M'_{ij} = M_{ij} - S \mu_M m_{ij}\). All the eigenvalues \(\lambda \neq \alpha\) are also eigenvalues of \(M'\) whereas the eigenvalue \(\alpha\) itself is transformed in \(\alpha - S \mu_M\). In fact, with the same notation as above, it is trivial to see that \(M' v = \lambda v\) and \(m^T M' = (\alpha - S \mu_M) m^T\). Furthermore the ensemble average of matrix elements \((M'_{ij})_0 = 0\). In summary, apart for the eigenvalue \(-\alpha\), the other eigenvalues of \(A\) are those of \(M'\) translated by \((-\alpha, 0)\). Thus we have reduced the problem of calculating the spectrum of \(M'\). For large \(S\) the law of large number implies that \(\sum_{j} M_{ji} = S \mu_M\) apart from corrections that are gaussian distributed of zero average and variance of order \(\sqrt{S}\). This implies that \(m_{ij} \approx 1 / S, \alpha \approx S \mu_M\) and \(M'_{ij} = M_{ij} - \mu_M\), which is a random matrix of the same kind as \(M\) itself with zero mean and covariance matrix \(\Sigma\) given above. Thus
we can apply the results of references (see also [1, 24, 49, 47]) to $M'/\sqrt{S}$ to deduce that its average eigenvalue distribution, in the large $S$ limit, is uniform in an ellipse, in the complex plane, centered at $(0, 0)$, with real (imaginary) semi-axis $\sigma_M(1 + \rho_M)(\sigma_M(1 - \rho_M))$, which leads to the claimed results about the spectrum of $A$.

Substituting the formulas given above for $\mu_M$, $\sigma_M$ and $\rho_M$ we get that the eigenvalues of the Jacobian matrix $A$ are uniformly distributed inside the following ellipse:

center = $(-CS\mu, 0)$
horizontal semiaxis = $\frac{\sqrt{CS} \left( (\rho + 1) \sigma^2 + 2(1-C)\mu^2 \right)}{\sqrt{(\sigma^2 + (1-C)\mu^2)}}$
vertical semiaxis = $\frac{\sqrt{CS} (1 - \rho) \sigma^2}{\sqrt{(\sigma^2 + (1-C)\mu^2)}}$
eigenvalue with the largest real part = $-CS\mu + \frac{\sqrt{CS} \left( (\rho + 1) \sigma^2 + 2(1-C)\mu^2 \right)}{\sqrt{(\sigma^2 + (1-C)\mu^2)}}$.

Thus if $S$ is large enough ($S > \left( \frac{\sigma_M(1+\rho_M)}{\mu_M} \right)^2$), the system is always stable (see Figure 2 in the main text).

### 0.5 Extension of our framework to meta-community population dynamics

In the main text we have shown that result presented on one single ecological communities can be generalised to a meta-community framework, where different communities are connected among them. In this section we give some details on the calculations underlying the presented results.

Let us start from the case of two communities, in which the first one benefit of the presence of the second one (see Fig. 8 (a) for a simple visualisation). Then the meta-community interaction matrix, of size $S = S_A + S_B$, is described by $M = \begin{pmatrix} A & X \\ 0 & B \end{pmatrix}$, where $A, B$ describe the mutualistic interactions within each community, and the corresponding species abundances are $m_A \in \mathbb{R}^{S_A}$, $m_B \in \mathbb{R}^{S_B}$. Both $A$ and $B$ are irreducible and $0 \neq X \geq 0$. For simplicity we denote the vector describing the abundance of all the specie is the meta-community as $m = (m_A, m_B)$ and remember that $\sum_{i=1}^{S_i} m_i = 1$. Using this notation we can write the new mean-field equation as an eigenvalue equation $(m_A, m_B)^T \cdot M = \alpha (m_A, m_B)$. Because $m_A A = \alpha m_A$ is independent of $B$, we could apply the previous presented method based on the Perron-Frobenius theorem [38] to calculate $m_A$ (with $\alpha > 0$ and $m_A > 0$). Then $m_A X + m_B B = \alpha m_B$, and therefore $m_B = m_A X (\alpha I_{S_B} - B)^{-1}$. Finally, let $\beta$ be the eigenvalue of $B$ with the largest modulus (for Perron-Frobenius theorem it is real and positive). If $\beta < \alpha$, $(\alpha I_{S_B} - B)^{-1} = \frac{1}{\alpha} \sum_{k=0}^{\infty} \left( \frac{B}{\alpha} \right)^k > 0$ since $B$ is irriducible. Thus it follows that $m_B > 0$.

We can generalize the same approach to three communities (see Fig. 8 (b)). Let

$$M = \begin{pmatrix} A & X_1 & Y \\ 0 & B & X_2 \\ 0 & 0 & C \end{pmatrix}$$
be the meta-community interaction matrix of size $S = S_A + S_B + S_C$ and $m_A \in \mathbb{R}^{S_A}$, $m_B \in \mathbb{R}^{S_B}$ and let $m_C \in \mathbb{R}^{S_C}$ be the corresponding species abundances. Assume $A$, $B$ and $C$ to be irreducible, $0 \neq X_1 \geq 0$ and $0 \neq Y \geq 0$ and/or $0 \neq X_2 \geq 0$. As before we can set $(m_A, m_B, m_C) = m$ and $\sum_{i=1}^{S} m_i = 1$. Therefore, the mean field equation for this system is $(m_A, m_B, m_C) M = \alpha (m_A, m_B, m_C)$. As before, $m_A A = \alpha m_A$ is independent of $B$ and $C$, and thus, again, by Perron-Frobenius theorem $m_A (\alpha > 0$ and $m_A > 0)$. Accordingly, as before, $m_B = m_A X_1 (\alpha I_{S_B} - B)^{-1} > 0$ if $\beta < \alpha$ and $m_C = (m_A Y + m_B X_2) (\alpha I_{S_C} - C)^{-1} > 0$ if $\gamma < \alpha$.

Notice that if $X_1 = 0$ (i.e. $C$ is helped both by $A$ and $B$, but $A$ and $B$ are independent) then the community $B$ gets extinct, $A$ survives and so $C$ if $0 \neq Y \geq 0$.

The generalization to the case (see Fig. 8 (c))

$$M = \begin{pmatrix} A & X_{12} & \cdots & X_{1n} \\ 0 & B & \cdots & X_{2n} \\ 0 & 0 & \ddots & : \\ 0 & 0 & \cdots & Z \end{pmatrix}$$

where the matrices $A, \ldots, Z$ are irreducible and their eigenvalues, $\alpha, \ldots, \zeta$, with the largest modulus are such that $\alpha > \beta, \ldots, \zeta$ then all species in the meta-community co-exist, i.e. there are no extinction in the system if $0 \neq X_{12} \geq 0$, $0 \neq X_{13} \geq 0$ and/or $0 \neq X_{23} \geq 0$, etc.

![Figure 8](image_url)

**Figure 8:** Mutualistic meta-community diagram. (a) two meta-communities; (b) three meta-communities; (c) many meta-communities

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