

Stability of Ecosystems Enhanced by Biological Constraint.

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Ecosystem stability is a central question both in theoretical and applied biology. Dynamical systems theory can be used to analyse how growth rates, carrying capacities and patterns of species interactions affect the stability of an ecosystem. The response to increasing complexity has been extensively studied and the general conclusion is that there is a limit. In this paper we show that while there is a limit to stability at which global destabilisation occurs, the collapse typically does not happen suddenly if a system is fully viable (no species is extinct). In fact, the generic system response is to go through multiple single species extinctions before a global collapse. We support this observation with both numerical simulations and theoretical predictions, for different interaction patterns. In addition, we find constrained interaction structures that can prevent extinctions from occurring. This makes an ecosystem more robust in terms of accepted complexity but without single species extinction events signalling an imminent global collapse, a drastically different behaviour compared to the generic case. We argue that the constrained interaction structures, that limits the total interactions affecting each specific species, could be biologically plausible. It is clearly important to know if such constraints are present when trying to determine the robustness of a given ecosystem.

In theoretical studies of ecosystem stability, dynamical systems are often used. These models were initially extended from a few species [1, 2] to whole ecosystems by using random matrices to represent the interaction network among species. In particular, May found increased complexity in terms of number of species and interactions typically leads to instability— a surprising result at the time [3]. Since then, more powerful numerical methods have opened additional approaches for insights into ecosystem stability including dynamical modelling [4–6] and topological studies [7–10]. Although features such as adaptive foraging have been shown in some circumstances to reverse the generic conclusion that increased complexity leads to system wide instabilities [11, 12], many studies confirm it [4–6].

The most widely used dynamical model capturing the interaction complexity, and the closest related to May’s result, is the Generalized-Lotka Volterra model

$$\begin{aligned} \frac{dx_i}{dt} &= x_i f_i(\mathbf{x}) \\ &= r_i x_i \left(1 - \frac{x_i}{K_i}\right) + \sigma x_i \sum_{j=1}^N A_{ij} x_j, \end{aligned} \quad (1)$$

where the x_i are the relative species abundances for species $i = 1, 2, \dots, N$, and the r_i and K_i are intrinsic growth rates and carrying capacities for each species respectively. A is the $N \times N$ interaction matrix and σ a parameter that regulates the standard deviation of the interaction strengths. The diagonal of A is set to zero ($A_{ii} = 0$), because the first term on the right hand side of Eq. 1 already captures the

self interactions.

The fixed-points of Eq. 1 are

$$x_i^* = K_i/r_i \left(r_i + \sigma \sum_{j=1}^N A_{ij} x_j^* \right) \quad \text{or} \quad x_i^* = 0 \quad (2)$$

and the Jacobian evaluated at a fixed-point (J^*) is used to assess the stability of the system

$$J^* = J^> + J^0. \quad (3)$$

Where $J^>$ includes non-extinct ($x_i^* > 0$) and J^0 includes extinct species ($x_i^* = 0$), with

$$J^> = X^*(\sigma A - RK) \quad \text{and} \quad J^0 = E(R + \sigma D). \quad (4)$$

Here X^* , K , R and, D are diagonal matrices with x_i^* , r_i , $1/K_i$ and $(A\mathbf{x}^*)_i$ on the diagonal respectively. E is a diagonal matrix with ones corresponding to extinct species, $E_{ii} = 1$ when $x_i^* = 0$ and zero otherwise. Note that rows corresponding to extinct species in $J^>$ are zero, and equivalently rows for non-extinct species in J^0 . This means the spectrum of J^* has two separate parts $\{\lambda_1, \dots, \lambda_n, \gamma_1, \dots, \gamma_m\}$ where n and m are the number of non-extinct and extinct species respectively.

The Jacobian used in May, $J_M = (I - \sigma A)$, is similar to $J^>$ or the entire Jacobian under the assumption that all species are non-extinct (called feasible fixed-point), when $r_i = K_i = 1$. By assuming feasibility, drawing entries of A from a random normal distribution $\mathcal{N}(\mu = 0, 1)$ with probability c (connectance), and using Wigner’s semi-circle law

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[13], May derived a limit for fixed-point stability in terms of σ , N and c ,

$$\sigma_M = 1/\sqrt{cN}, \quad (5)$$

i.e the point when we expect the Jacobian to have an eigenvalue with positive real part. This result has ever since been extensively discussed/debated [14], applied [15, 16] and extended [17].

The Jacobian introduced by May and its extensions do not include fixed-point abundances. The Jacobian's sign structure (hence the stability) can in some cases be affected by the X^* -scaling [18]. However, the main qualitative difference is the possibility of extinctions in the dynamical model. If extinctions occur for smaller values of σ than for destabilisation, $\sigma_M = 1/\sqrt{cN}$, it will shift the stability boundary to larger σ . Not only does the boundary shift, a system's approach to the stability boundary significantly changes, with strong impact on the predictions of collapse. We therefore investigate two main questions in this paper: are extinctions generic in these models, especially in more realistic interaction patterns expected in real ecosystems? If extinctions are generic, are there any examples of biologically relevant conditions for when extinctions will not occur before the global collapse?

Fig. 1 demonstrates the general behaviour of the GLV model with random interactions. When σ is increased, the dynamical system can respond in two qualitatively different ways, either a single species goes extinct or the system loses stability. Interestingly both of these occur when an eigenvalue hits zero from below.

In Fig. 1 species extinctions occur for smaller σ than May's stability boundary. To determine if this behaviour is generic we need to calculate the expected value of σ at the first extinction, to compare with the stability boundary in Eq. 5.

Assuming no extinction has occurred, the fixed-point equation is linear

$$\mathbf{x}^* = (I - \sigma A)^{-1} \mathbf{1}. \quad (6)$$

where we set $r_i = K_i = 1$ for simplicity (derivation with $r_i \neq 1$ and $K_i \neq 1$ in SI). Re-expressing the inverse $(I - \sigma A)^{-1}$ as a von Neumann series expansion gives

$$\mathbf{x}^* = \left(\sum_{p=0}^{\infty} \sigma^p A^p \right) \mathbf{1}. \quad (7)$$

For guaranteed convergence of the von Neumann expansion $\|\sigma A\|_{\infty} < 1$ (or any equivalent norm). This strict condition does not hold for σA in the σ -ranges of interest here, although there are less strict criteria of convergence and rigorous numerical investigations that confirm the sum converges until in the vicinity of the stability boundary, σ_M .

From Eq. 7 it follows that x_i^* are sums of products of the random variables A_{ij} , and from now on we treat them as

stochastic variables, X_i^* . For simplicity we start by assuming that the mean of interaction strengths, μ , is zero. The general case with $\mu \neq 0$ is treated below.

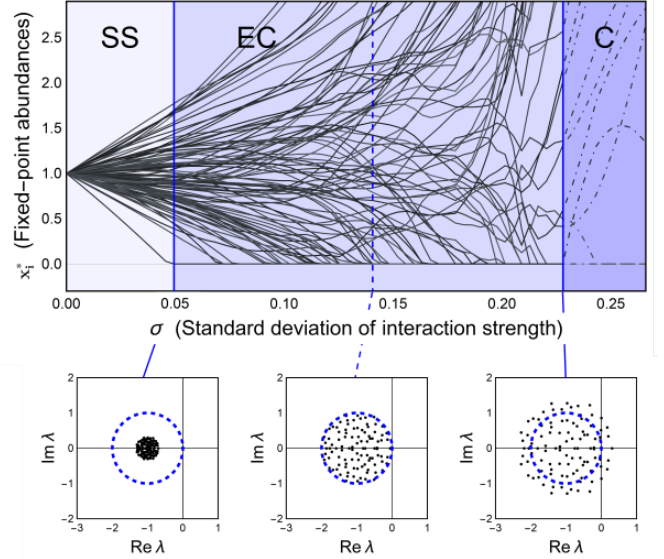


Figure 1 | Effects on stability of increasing interaction strength in a complex system. Example simulation of a system with initial biodiversity, $N = 100$, connectance (fraction of realised species interactions), $c = 0.5$, $r_i = K_i = 1$, and $\mu = 0$ for the mean of the distribution of inter-specific interaction. The plot shows the species abundances (top) and the spectrum (bottom panels) at locally stable fixed-points for increasing values of the standard deviation of interaction strength, σ . The first extinction event and collapse are indicated by the blue lines, and the dashed blue line indicates σ_M . Up to the first extinction, the system is in a feasible fixed point where all $N = 100$ species are non-extinct, $x_i^* > 0$. The collapse, where no similar stable fixed point exists, occurs for larger σ and the stability limit introduced by May is seen to be in between. The bottom panels show the spectrum of the general Jacobian used by May J_M at three point of interest first extinction event, σ_M and loss of stability, with the circle indicating the radius of stability. Note how the σ_M both overestimates the first extinction event and underestimates global collapse.

Assuming independence between the terms in the outer sum (scalar product with the vector $\mathbf{1}$) in Eq. 7, the X_i^* will converge to the normal distribution for sufficiently large cN in accordance with the central limit theorem. Then the variance of the X_i^* can be found using the rules for mean and variance of product and sum distributions for independent stochastic variables, for example $\text{Var} \left[\prod_{i=1}^N Y_i \right] = \prod_{i=1}^N \left(\text{Var} [Y_i] + E [Y_i]^2 \right) - E \left[\prod_{i=1}^N Y_i \right]^2$. Especially, we use that $E \left[\prod_{i=1}^N Y_i \right] = 0$ and $\text{Var} \left[\prod_{i=1}^N Y_i \right] = \prod_{i=1}^N \text{Var} [Y_i]$ when $E[Y_i] = \mu = 0$. An element of A^2 will be a sum of approximately $c^2 N$ random variables with mean zero

($E[A_{ij}]E[A_{jk}]$) and variance one ($Var[A_{ij}]Var[A_{jk}]$), therefore we have $E[(A^2)_{ij}] = 0$ and $Var[(A^2)_{ij}] = c^2N$. Similarly for A^3 , $E[(A^3)_{ij}] = 0$ and $Var[(A^3)_{ij}] = c^3N^2$, etc. Finally the outer sum in Eq. 7 gives the total variance of X_i^*

$$\sigma_+^2 = \sum_{p=1}^{\infty} (cN\sigma^2)^p = \frac{cN\sigma^2}{1 - cN\sigma^2}, \quad (8)$$

i.e. $X_i^* \sim \mathcal{N}(\mu_+ = 1, \sigma_+ = \sqrt{\frac{cN\sigma^2}{1 - cN\sigma^2}})$.

It follows that for $\mu = 0$ the species abundances have a Normal distribution with mean 1, variance zero at $\sigma = 0$, and diverging variance at May's stability limit Eq. 5. The divergence is however artificial since when increasing σ one of the x_i^* will become zero, breaking the assumptions in Eq. 6, marking the first extinction event. Statistically we can express this event in terms of order statistics where the distribution of the q th smallest species abundance of X_i^* (with distributions $f(x)$) can be expressed as

$$f_{Z_q}(x) = \frac{N!}{(q-1)!(N-q)!} (1 - F(x))^{N-q} F(x)^{q-1} f(x), \quad (9)$$

where $F(x)$ is the cumulative distribution function of $f(x)$.

The explicit minimum distribution $f_{Z_{q=1}}(x)$ is then

$$f_{Z_1}(x) = N(1 - F(x))^{N-1} f(x) = \frac{Ne^{-(x-\mu_+)^2/2\sigma_+^2}}{\sigma_+\sqrt{2\pi}} \left(\frac{1}{2} - \frac{1}{\sqrt{\pi}} \int_0^{\frac{x-\mu_+}{\sigma_+\sqrt{2}}} e^{-t^2} dt \right)^{N-1}. \quad (10)$$

The first extinction boundary is located at the σ for which Eq. 10 has mean zero.

To account for systems with non-zero mean interaction strengths, $\mu \neq 0$, the interaction matrix can be written as $A = A_{\mu=0} + M$ where $A_{\mu=0} \sim \mathcal{N}(0, 1)$, $A \sim \mathcal{N}(\mu, 1)$, and M is a matrix with μ at the same positions as the non-zero entries of A . Then for $(I - \sigma A_{\mu=0} + \sigma M)\mathbf{x}^* = \mathbf{1}$ and $c = 1$, $M\mathbf{x}^*$ is approximately a constant vector $x_{TOT}\mathbf{1}$. Each of these sums exclude the diagonal element but is approximately correct when the variance of the species abundances is small. Therefore

$$\mathbf{x}^* = (\sigma\mu x_{TOT} + 1)(I - \sigma A_{\mu=0})^{-1}\mathbf{1}, \quad (11)$$

and we conclude that $\mu \neq 0$ only adds to a multiplicative scaling factor, that does not affect the first extinction event. This result is verified in Fig. 2.

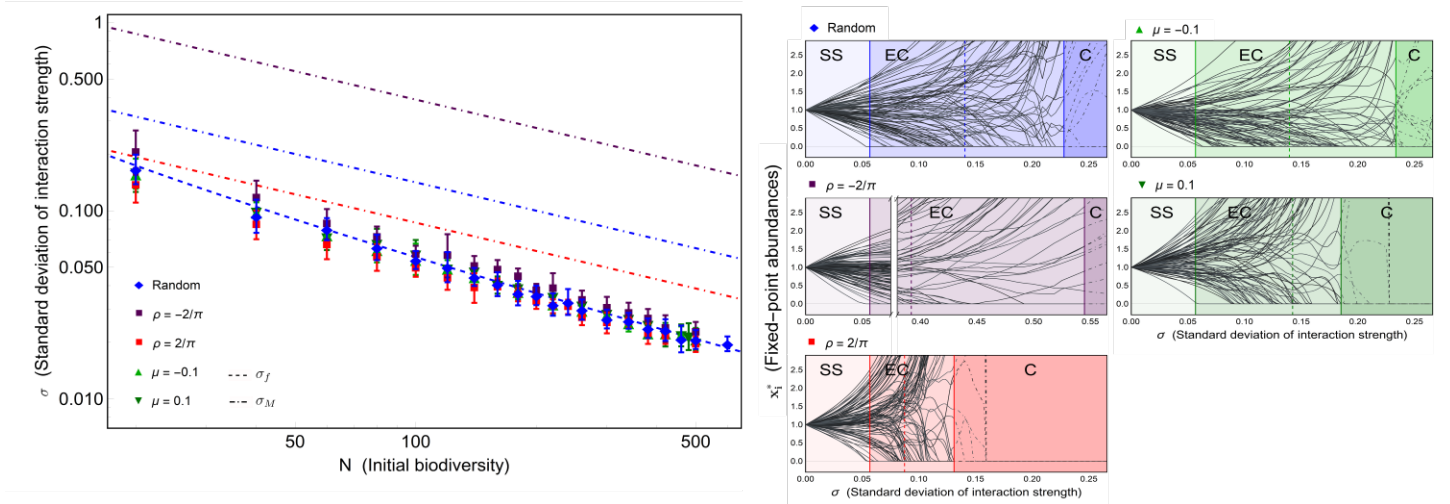


Figure 2 | Extinctions or destabilisation first? The left plot shows averages from simulations of standard deviation of interaction strengths for first extinction σ_f with one standard deviation errorbars. Random systems $A_{ij} \sim \mathcal{N}(0, 1)$, predator/prey systems $\text{sign}(A_{ij}) = -\text{sign}(A_{ji})$, mutualistic/competitive systems $\text{sign}(A_{ij}) = \text{sign}(A_{ji})$, random $A_{ij} \sim \mathcal{N}(-0.1, 1)$ and random $A_{ij} \sim \mathcal{N}(0.1, 1)$. All with $r_i = k_i = 1$. The dotted lines are theoretical first extinction and stability boundary colour coded according to legend. The stability boundary is given by $\sigma_{M;\mu,\rho} = 1/(\sqrt{cN}(1 + (1 - c)\mu^2)(1 + \rho) - c\mu)$, where $\rho = \pm 2/\pi$ for predator/prey and mutualistic/competitive respectively [9]. Note the spread in stability boundary in structured systems compared to the first extinction which is equal for all systems. The right panels show an example simulation of each type, with same color-coding. The vertical lines indicate first extinction boundary σ_f , May's stability limit σ_M and the actual loss of stability σ_c , in order of increasing σ . Three phases are marked by the different shades: Strict Stability (SS) before the first extinction boundary, Extinction Continuum (EC) a phase of single species extinctions and, Collapse (C) where no stable nearby fixed-point exists. Note that the classical stability boundary σ_M always falls in the Extinction Continuum for every variation.

The above analysis can be extended to interaction-webs capturing biological interaction structures found in the literature, for example predator-prey, $\text{sign}(A_{ij}) = -\text{sign}(A_{ji})$ [17] and mutualistic/competitive, $\text{sign}(A_{ij}) = \text{sign}(A_{ji})$ [9]. Even for these structures, entries generally do not match when producing elements of A^p in Eq. 7. Thus the outer sum can be assumed a sum of independent variables. This implies no significant change in the species abundance distributions, and we expect the first extinction event, as in the case with $\mu \neq 0$, to be little affected by these structures. A comparison between first extinction and the stability boundary shown in Fig. 2, confirms this and our assumption of independence.

From our analysis and Fig. 2 we conclude that extinctions are generic in the GLV with random interactions, as well as for more biologically inspired systems. How this splits the parameter space of ecological systems into three stability phases Strict Stability (SS), Extinction Continuum (EC) and, Collapse (C) as seen in Fig. 1, is analysed in detail in [19]. The Extinction Continuum is a phase between the first extinction event and actual collapse, σ_c , (containing σ_M), where a system can remain stable through single species extinctions. In contrast to [19], here we derive an exact expression for the variance of species abundances (Eq. 8).

The second main question of this paper is if there are biologically relevant structures that significantly shift the boundaries, possibly in such a way that $\sigma_M < \sigma_f$, eliminating extinctions before collapse. As seen in Fig. 2, sign symmetry shifts σ_M to smaller values of σ although σ_f is almost unchanged. The smallest value of σ_M is obtained for symmetric matrices. Symmetry also violates the assumption of independence in the outer sum in Eq. 7 shifting σ_f . However, this shift of σ_f is in the same direction as σ_M thus keeping a distance between the boundaries. A shift of boundaries in the same direction also occurs for large values of $|\mu|$, both these cases are discussed in SI Sec 2.

From our discussion so far we can glean two interesting features. First, different aspects of the interaction matrix are involved in the two boundaries. The first extinction boundary is dependent on sums and multiplications of the entries of A , while the stability boundary on its spectrum. These aspects can affect each other but need not. Second, the way to significantly shift the first extinction boundary is to some degree correlate the entries of the outer sum in Eq. 7, thereby decreasing the variance in Eq. 8 of the minimum distribution Eq. 10. To answer the second question, if there are biologically relevant structures that significantly change the EC, we should search for features that correlate the entries of the sum in Eq. 7 but leave the spectrum unaffected or inversely affected.

From Eq. 7 the most obvious departure from independence is to constrain the row-sums of the interaction matrix to some constant. Such a constraint will leave the spectrum unaffected. A global constraint of this kind, akin to

energy or momentum constraints in physics, is indeed biologically reasonable. Physical resources, energy, time, space are all degrees of freedom that constrain biological system and affect the interaction patterns of species. Any one of these may result in a row-sum constraint, the representation of species balancing negative and positive interactions with their ecosystem neighbours. This connection is discussed further later on.

To investigate row-sum constraints and their dynamical consequences, we use an interaction matrix constructed as $A = (1 - \xi)A_c + \xi A_0$. With A_c a random matrix with rows shifted as to make the sums constant $\sum_j A_{c;ij} = B$ according to

$$A_{c;ij} = A_{ij} - \frac{1}{n_i} \left(B - \sum_{j=1}^N A_{ij} \right). \quad (12)$$

Here $A_{c;ij}$ is an entry of the matrix A_c and n_i the number of nonzero entries in row i . A_0 is a random matrix $A_0 \sim \mathcal{N}(0, 1)$ with entries at the same positions as A_c (thus only disturbing the existing interactions), and we set $B = 0$ for simplicity. The parameter ξ regulates the row-sum variance of A . Written in this form the row-sum constraint can be enforced to different degrees by varying ξ .

The distribution of the non-zero entries of A will slightly change with this construction $\mathcal{N}(0, 1) \rightarrow \mathcal{N}\left(0, \sqrt{(1 - \xi)^2 + \xi^2}\right)$. This in turn shifts the the stability boundary to

$$\sigma_M = \frac{1}{\sqrt{cN(1 - \xi)^2 + cN\xi^2}}. \quad (13)$$

This construction of the interaction matrix together with the conclusion that $\mu \neq 0$ does not affect the first extinction boundary, allows us to handle these types of global constraints in a straight-forward manner. For systems with constrained row-sums according to, $A = (1 - \xi)A_c + \xi A_0$, powers of ξ , $(1 - \xi)$ and, mixed terms ($A_c A_0 A_0$ etc.) are introduced in the von Neumann series of in Eq. 7. The terms with A_c in the rightmost position disappear in the outer sum due to the row-sums being zero. This leads to X_i^* normally distributed (due to central limit theorem) with mean 1 but with variance according to

$$\begin{aligned} \sigma_+(c, N, \sigma, \xi)^2 &= \sum_{p=1}^{\infty} \left[(cN\sigma^2)^p \sum_{q=0}^{p-1} (1 - \xi)^{2q} \xi^{2(p-q)} \binom{p-1}{q} \right] \\ &= \frac{cN\sigma^2\xi^2}{1 - cN\sigma^2 \left((1 - \xi)^2 + \xi^2 \right)}. \end{aligned} \quad (14)$$

This can be seen to reduce to the solution without constraint when $\xi = 1$.

Averages of the first extinction event from dynamics with row-sum constrained interaction matrices are shown in Fig. 3 together with example simulations. As expected, the first

extinction boundary occurs at larger σ the stricter the constraint is enforced. For sufficiently constrained systems the first extinction boundary converges to the stability boundary. This is seen in Eq. 14. A small ξ will reduce the variance of the species abundances unless the denominator compensates by approaching zero, which is exactly when $\sigma \rightarrow \sigma_M = 1/\sqrt{cn(1-\xi)^2 + cn\xi^2}$.

For weakly constrained systems the variance of species abundances, σ_+ , is large enough for extinctions to occur before it diverges at σ_M , meaning collapse is always preceded by an Extinction Continuum. For significantly constrained systems, when the first extinction boundary converges to the

stability boundary, the approach to collapse is highly variable.

We notice two types of collapses in these cases. Either the system collapses at σ_M before any extinction occurs, or some species abundances suffer a sharp decrease as the variance diverges at σ_M , leading to an Extinction Continuum and eventual collapse as for less constrained systems. These two collapse types are shown in Fig. 3. For the type-two collapse, the drop in abundance is sharp enough (and not predicted by $|\text{Re}(\lambda)_{max}|$ as in [20]) to merit being called collapse in and of itself.

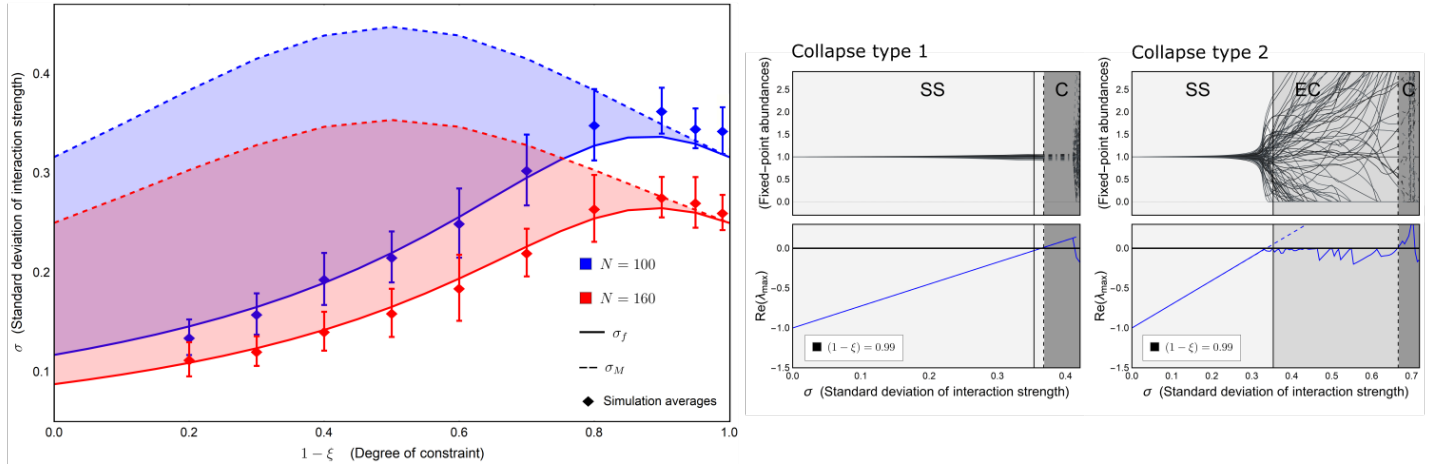


Figure 3 | Decreasing the Extinction Continuum. The left plot shows averages from simulations of standard deviation of interaction strengths for first extinction σ_f , with one standard deviation errorbars, for increasing row sum constraint $(1 - \xi)$. Theoretical predictions of first extinction are shown as full lines and σ_M as striped lines for systems of size $N = 100$ and $N = 160$. The decreasing width for small ξ and convergence to σ_M is clearly seen for both system sizes. The Left panels show example simulations of the two collapse types for highly constrained systems ($\xi = 0.01$). The behavioural phases are marked by different shades of grey: Strict Stability (SS) before the first extinction boundary, Extinction Continuum (EC) and, Collapse (C) where no stable nearby fixed-point exists. Note that Collapse type 1 does not have an Extinction Continuum. Collapse type 2 abruptly enters the Extinction Continuum at σ_M and can uphold stability by single species extinctions until eventual collapse.

In contrast to the extinction boundary, the new collapse boundary— after the succession of extinctions— cannot be obtained directly from order statistics. Although, a combination of the prediction of extinct species (from q th order statistics distribution) and σ_M , which is accurate when all species are assumed non-extinct [21], can be used, outlined in [19]. For both systems with or without the row-sum constraint an estimation for actual collapse is at the σ where the amount of non-extinct species n reaches $\sigma = 1/\sqrt{cn}$. Simulation averages and prediction are shown in SI Sec 3.

In summary, the behaviour of Lotka-Volterra dynamics including extinctions is generic but can be altered with certain types of constraints on the interaction matrix that break the assumption of independence of the random entries without affecting the spectrum. For such systems the approach to collapse is highly variable and can be without extinctions such that the collapse is located approximately at the classi-

cal stability boundary. Or the system can have a phase of single species extinctions that locates the actual collapse at larger values of σ . It is therefore vital to know what type of constraints are obtained for a system because it qualitatively changes its response to species abundance perturbations or change in its structure, represented here by the interaction strength standard deviation σ .

In ecosystem interaction webs, there are many constraints in terms of energy, space, time, and other resources. That some such constraints might translate into a restriction of total interaction strength— in effect row-sum constraints— is biologically plausible and needs further research. Row-sum restrictions might for example connect to Damuth’s law [10, 22], stating that the energy consumption for each species is rather constant over all species. Species with small body sizes tend to consume less per individual but compensate with more numbers. If this connection or some analogue

holds, then the work in this paper to derive its repercussions and develop theory is of high relevance. This connection has not been studied in depth, as the matrices used have not been specified or otherwise fashioned to energy constraints. Fully exploring this connection is left for future work.

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