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Author for correspondence:

M. N. Mooij

e-mail: m.n.mooij@uu.nl

Stable coexistence in indefinitely large systems of competing species

M. N. Mooij^{1,2}, M. Baudena^{2,3,4,5}, A. S. von der Heydt^{2,6} and I. Kryven^{1,2}

¹Mathematical Institute, Utrecht University, Utrecht, The Netherlands

²Centre for Complex Systems Studies (CCSS), Utrecht University, Utrecht, The Netherlands

³National Research Council of Italy, Institute of Atmospheric Sciences and Climate (CNR-ISAC), Torino 10133, Italy

⁴National Biodiversity Future Center (NBFC), Palermo 90133, Italy

⁵Copernicus Institute of Sustainable Development, Utrecht University, Utrecht, The Netherlands

⁶Institute for Marine and Atmospheric Research (IMAU), Utrecht University, Utrecht, The Netherlands

MNM, 0009-0000-3042-4363; MB, 0000-0002-6873-6466; ASvdH, 0000-0002-5557-3282; IK, 0000-0002-3964-2196

The Lotka–Volterra system is a set of ordinary differential equations describing growth of interacting ecological species. One of the debated questions is understanding how the number of species in the system influences the stability of the model. Robert May studied how large systems may become unstable when species–species interactions do not vanish. This outcome has frequently been interpreted as a universal phenomenon and summarized as ‘large systems are unstable’. By exploring general interaction networks, we show that the competitive Lotka–Volterra system may maintain stability even for large networks, despite non-vanishing interaction strength. We establish sufficient conditions for stability as a threshold on the interspecific interaction strength, formulated in terms of the maximum and minimum degrees (or weights) rather than the network’s size. For values below this threshold, coexistence of all species is attained, regardless of the system size. Our finding generalizes May’s result by showing that it is the outlier nodes with large degree that cause instability rather than the large number of species in the system.

1. Introduction

Robert May exposed the role of random network structures in the description of large ecological systems in his seminal work [1]. A key conclusion drawn from his work is the diversity–stability paradox, which states that the likelihood of stable coexistence—defined as the convergence to a state where all species are present with positive density—is negatively affected by the size of the system n . Thus, large networks tend to be less stable than smaller ones. This is a paradox since empirical observations indicate that large ecological networks are ubiquitous and stable [2]. May studied the Erdős–Rényi model with edge weights and established that for random interaction matrices with sufficiently small average interaction, decaying at least as $n^{-1/2}$, coexistence is guaranteed with probability equal to one. Consequently, large systems are less favourable to stable coexistence compared with small systems. However, since it is unclear whether this conclusion is universally applicable, a host of research followed to verify May's principle on networks with other connectivity assumptions, searching for structural patterns that stabilize large networks.

Allesina & Tang [3] and Allesina *et al.* [4] generalized May's model to include exclusively competitive, exclusively mutualistic and predator–prey interaction types. Mutualistic interactions occur when two species mutually benefit each other, whereas competitive interactions arise when two species adversely affect each other. Predator–prey interactions entail an asymmetric interaction, as observed, for instance, when a predator consumes its prey. The inverse relationship between system complexity (size) and stability has been demonstrated under all these interaction types. Recently, researchers have moved beyond the concept of species coexistence to examine the number of surviving species in large Lotka–Volterra models [5].

Due to the observed diversity–stability paradox in numerous systems, a substantial body of work has aimed to explain the presence of large systems in nature, using a variety of techniques and ideas. Serván *et al.* [6] developed an evolutionary model that produces large stable networks by selectively removing 'weak' species. Bairey *et al.* [7] argued that while stability of networks governed solely by pairwise interactions is hampered by a large number of species, the inclusion of higher order interactions may yield opposite effects, when mutualistic interactions are considered. Grilli *et al.* [8] and Eppinga *et al.* [9] considered higher order interactions in competitive network models, leading to similar conclusions. Grilli *et al.* [10] studied the impact of network compartmentalization on stability. Barabás *et al.* [11] showed that negative self-regulation has a favourable effect on stability. Furthermore, cyclical interactions may serve as a mechanism for stable coexistence in directed networks [12]. Recently, Hatton *et al.* [13] have shown that using sublinear growth instead of logistic growth can account for diversity in ecosystems. For an exhaustive review on complexity (number of species) and stability, we refer the reader to Landi *et al.* [14].

In this study, we explore a bounded degree network topology, wherein the maximum degree of the network is constrained by a function independent of the number of species. This contrasts May's assumptions, which allowed nodes of arbitrary large degrees. Our assumption of bounded degree, often referred to as network sparseness, is ecologically reasonable and also motivated by physical considerations. For instance, ecological networks inherently possess an underlying spatial domain with locally finite carrying capacity, possibly limiting the number of interactions in each location. Moreover, ecological networks are likely to be sparse for structural reasons, as detailed for mutualistic networks [15,16]. In fact, many interactions might be forbidden by different natural historical reasons (e.g. asynchronicities connected to phenology, especially in highly seasonal environments). Sparseness in recorded ecosystem data may also be overestimated due to the inability to measure all interactions. This limitation is particularly pronounced in the case of competitive interactions, as they are an indirect effect exerted by a third party, such as a shared food resource or limited habitat space. Nonetheless, undersampling of interactions is not believed to be the major reason behind unobserved links

[15]. In tropical forests, plant–plant heterospecific interactions have been observed to be very often close to zero [17,18], pointing at the fact that the interaction matrix might be sparse in these very relevant and extremely diverse systems. Moreover, sparse species interactions have been identified as a distinctive structural property in microbial communities [19].

We will use the generalized Lotka–Volterra equations (well known in ecology but also celebrated in for example economics [20,21]), which characterize the system in terms of the growth rates \mathbf{r} and the symmetric interaction matrix M and are expressed as follows:

$$\frac{d\mathbf{x}(t)}{dt} = \mathbf{x}(t) \circ (\mathbf{r} + M\mathbf{x}(t)), \quad (1.1)$$

where $\mathbf{x}(t)$ represents the species abundances at time $t \geq 0$ and \circ denotes the Hadamard (component-wise) product. Without loss of generality, we impose the initial condition $\mathbf{x}(0) = \mathbf{x}_0 \in [0, \infty)^n$.

Different types of ecological interactions are modelled by choosing appropriate pair-wise interaction matrix M . Positive values for the elements M_{ij} and M_{ji} indicate mutualism between species i and species j . Negative values of M_{ij} and M_{ji} indicate a competitive relationship, whereas positive M_{ij} and negative M_{ji} imply a predator–prey dynamic.

In the rest of the paper, we consider two types of competitive interactions on a network with bounded degrees. In §2a, we consider a competitive system wherein each species has unit growth rate and the same (negative) interaction with every other species in its neighbourhood. This is achieved by setting the growth rates as $\mathbf{r} = \mathbf{1}$ and the interaction matrix as $M = -\tau A - \mathbb{1}$, where $\tau > 0$ is a parameter representing the competition strength and A represents the binary adjacency matrix of an undirected network. Then, in §2b, we examine an arbitrary competitive system, with growth rates defined by a positive vector \mathbf{r} , and an interaction matrix M represented as $M = -T - D$, shown in figure 1. The matrix T contains only non-negative entries, while the diagonal self-regulation matrix D exclusively contains positive elements. Note that the choice $\mathbf{r} = \mathbf{1}$, $T = \tau A$ and $D = \mathbb{1}$ yields the constant interaction competitive system, studied in the first case. In both scenarios, we show the existence of a subset within the parameter space (specified in terms of \mathbf{r} , T and D) where stable coexistence of the dynamics is achieved in the asymptotic limit. This contradicts previous findings where the size of the subset of the parameter space facilitating stable coexistence was observed to shrink as $n^{-1/2}$.

2. Results

We define the coexistence of species as stable when, for certain interaction types (represented by M) and growth rates \mathbf{r} , and every initial condition with positive components, system (1.1) converges to a steady-state solution with only positive components. Generally speaking, system (1.1) can have up to 2^n steady-state solutions. However, among these solutions, only those that solve the condition $M\mathbf{x}^* = -\mathbf{r}$ can be component-wise positive. To demonstrate stable coexistence, we will verify two conditions: (i) feasibility, ensuring that \mathbf{x}^* is indeed component-wise positive and (ii) stability, which requires that the latter steady-state solution is globally stable. Goh [22] demonstrated that the former condition (feasibility) implies the latter condition (stability) if symmetric M is negative definite. For assessing local stability, it is sufficient to study the Jacobian evaluated at \mathbf{x}^* , which is given by

$$J(\mathbf{x}^*)_{ij} = x_i^* M_{ij}. \quad (2.1)$$

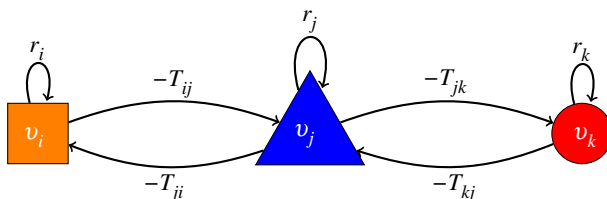


Figure 1. The conceptual structure of a three-species network (v_i , v_j and v_k) within a competitive ecological system. The interactions T (black arrows between species) are symmetric and have negative sign, while the growth rates \mathbf{r} (black arrows within one species) are all strictly positive.

(a) Case 1: constant competition

In this scenario, the interaction matrix M is solely determined by the interaction strength parameter τ , with stability ensured when $\tau = 0$ and resulting in $\mathbf{x}^* = \mathbf{1}$. Investigating $\mathbf{x}^*(\tau)$ reveals that there are two pathways, illustrated in figure 2, where a discontinuity emerges upon incrementally increasing τ , leading to a transition to a distinct steady state:

- (1) A transcritical bifurcation when \mathbf{x}^* moves outside of the unit hypercube $[0,1]^n$ and therefore becomes unfeasible. This bifurcation is induced by the \mathbf{x}^* term in equation (2.1).
- (2) A pitchfork bifurcation when $\mathbf{x}^* \in (0,1)^n$ becomes locally unstable. This bifurcation is induced by the M term in equation (2.1).

Note that the transcritical bifurcation entails a continuously declining coexistence point, whereas a pitchfork bifurcation occurs abruptly and non-continuously. For both types of bifurcation, we will show a lower bound for parameter τ at which the bifurcation occurs; first for the transcritical bifurcation and then for the pitchfork bifurcation.

Rewriting the k th component of the stable coexistence point $\mathbf{x}^* = -M^{-1}\mathbf{r}$ as a Neumann series yields (assuming $\tau < d_{\max}^{-1}$):

$$x_k^* = \sum_{i=0}^{\infty} (-1)^i \tau^i (A^i \mathbf{1})_k \geq \sum_{l=0}^{\infty} \tau^{2l} d_{\min}^{2l} - \sum_{l=1}^{\infty} \tau^{2l-1} d_{\max}^{2l-1} = \frac{1 - d_{\max} \tau - d_{\max}^2 \tau^2 + d_{\min}^2 d_{\max} \tau^3}{(d_{\min}^2 \tau^2 - 1)(d_{\max}^2 \tau^2 - 1)}. \quad (2.2)$$

For the inequality, we utilized the powers of the adjacency matrix enumerate the number of distinct walks, which can be bounded using the minimum and maximum degrees, d_{\min} and d_{\max} , of the network. Let $\alpha = d_{\min}/d_{\max}$ and consider the expression

$$P(\tau) := d_{\max}^3 \alpha^2 \tau^3 - d_{\max}^2 \tau^2 - d_{\max} \tau + 1. \quad (2.3)$$

The transcritical bifurcation does not occur as long as $P(\tau) > 0$; an analysis of the third-order polynomial equation $P(\tau) = 0$ reveals that this equation has three real roots, with the smallest one being:

$$\Omega := \frac{1 - 2\sqrt{1 + 3\alpha^2}}{3\alpha^2} \sin \left[\frac{1}{3} \arcsin(\theta) \right] \frac{1}{d_{\max}} \geq \frac{\sqrt{5} - 1}{2} \frac{1}{d_{\max}},$$

$$\theta = \frac{2 + 9\alpha^2 - 27\alpha^4}{2(1 + 3\alpha^2)^{3/2}}. \quad (2.4)$$

This expression provides an upper bound, $\tau < \Omega$, for which we can ensure that no transcritical bifurcation occurs.

It remains to show that also the pitchfork bifurcation will not occur for $\tau < \Omega$. By Gershgorin's Circle Theorem, we know that all eigenvalues of the matrix M are contained in the union of

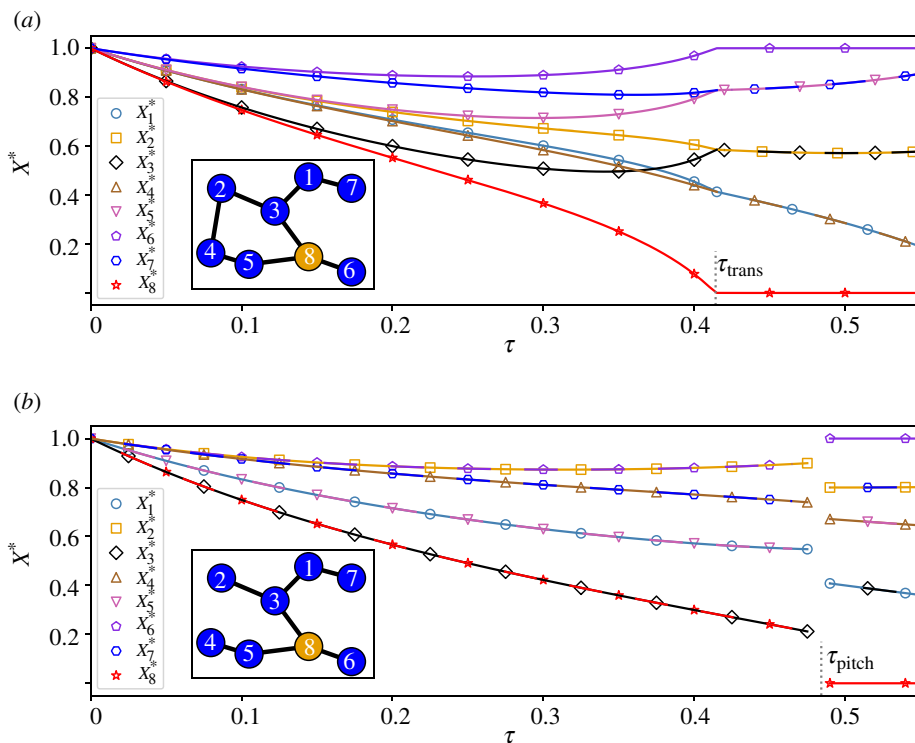


Figure 2. Two possible bifurcation types for constant interaction competitive Lotka–Volterra systems with different underlying interaction networks. In the networks, we highlighted the vertex corresponding to the variable going to zero, identified as vertex 8. Note that the lower network is derived from the upper one by simply removing the edge (2, 4). (a) In this network, a transcritical bifurcation occurs where the bifurcation value of the interaction parameter is denoted by τ_{trans} . (b) In this (only slightly modified) network, a pitchfork bifurcation takes place, demonstrating a non-continuous phase transition at the bifurcation value τ_{pitch} . Different variables are represented by different colours, with dashed lines featuring multiple colours to denote equal variable values.

the disks $\mathcal{D}_{-1}(\sum_{j \neq i} |A_{ij}|)$, where $\mathcal{D}_p(r)$ is the disk centred around the (possibly complex) point p , with radius $r > 0$. In our case, this simplifies to

$$\mathcal{D}_i = \mathcal{D}_{-1}(\tau d_i), \quad (2.5)$$

where d_i denotes the degree of vertex v_i . Hence, if the condition $\tau d_i < 1$ holds true for all $i = 1, 2, \dots, n$, we can ascertain that the coexistence point is stable whenever it is feasible. This condition is indeed fulfilled for

$$\tau < \Omega \leq d_{\text{max}}^{-1}.$$

In conclusion, we have established that any interaction strength $\tau \in [0, \Omega)$ ensures stable species coexistence. Note that this condition is sufficient but not necessary, as there may exist networks with $\tau > \Omega$ that still permit stable coexistence. Remarkably, this interval is independent of the size of the network, indicating that coexistence is not contingent upon the network size when the maximum degree d_{max} is fixed. If the maximum degree of the network is bounded, the probability of stable coexistence does not diminish to zero even as the system size grows indefinitely. Our bound is tight across the entire spectrum of possible networks, as it aligns with the bifurcation point for complete bipartite graphs [23]. However, by restricting attention to a particular subclass of graphs, it is possible to determine the bifurcation value more precisely. We demonstrate this with the following two examples.

(i) Example 1: regular graphs

In regular graphs, all degrees are the same and the maximum eigenvalue of the adjacency matrix is given by the constant degree d , corresponding to the eigenvector $\mathbf{1}$. Therefore, we know

$$\mathbf{x}^* := -M^{-1}\mathbf{1} = (\tau A + \mathbb{1})^{-1}\mathbf{1} = (\tau d + 1)^{-1}\mathbf{1}. \quad (2.6)$$

Let $\mathbf{v} \in \mathbb{R}^n$ be an eigenvector of A corresponding to eigenvalue λ then there exists an eigenvalue of the Jacobian evaluated at \mathbf{x}^* , given by

$$J(\mathbf{x}^*)\mathbf{v} = \text{diag}(-M^{-1}\mathbf{1})M\mathbf{v} = -\frac{\tau\lambda + 1}{\tau d + 1}\mathbf{v}. \quad (2.7)$$

Note that the stability of the interior fixed point relies on the topology of the regular network. In equation (2.7), we observe a monotonically increasing eigenvalue with respect to τ . Hence, by using the Alon–Boppana bound, we can infer that almost surely (with probability one) every eigenvalue of the Jacobian adheres to the bound:

$$-1 \leq \lambda \leq -\frac{-2\tau\sqrt{d-1} + 1}{\tau d + 1} \quad \text{for } d \geq 2. \quad (2.8)$$

Consequently, we obtain stable coexistence for almost all d -regular network configurations when $\tau < \frac{1}{2\sqrt{d-1}}$. Note the scaling of order $d^{-1/2}$ compared with the d^{-1} scaling for general graphs, suggesting that regular networks enhance coexistence.

(ii) Example 2: configuration model

To illustrate our findings, we have generated multiple networks with binomially distributed degrees using the configuration model. We use a binomial degree distribution to control the maximum degree of the networks, which we set to be 30. For various network sizes, we generated 500 such networks and computed the average ratio of the actual bifurcation value τ_c to our bound Ω (2.4), as depicted in figure 3. This ratio indicates the deviation of the true bifurcation point from our bound. We conducted different simulations for various connectivity values $0 < p < 1$ where large p tends to yield networks with larger degrees on average, while a value of $p = 0$ corresponds to a disconnected network. Figure 3a illustrates what appears to be an independent behaviour of the calculated ratio with respect to the size of the network. Indeed, this observation aligns with our analytical result indicating that stable coexistence can occur for large networks whenever the maximum degree of the network is constrained. As illustrated in figure 3b, the tightness of the bound does depend on p and improves when p is smaller.

(b) Case 2: general competition

The result from the previous section can be expanded to a broader setting, where growth rates are represented by a positive vector $\mathbf{r} \in \mathbb{R}_{>0}$, and the interaction matrix is defined as $M = -T - D$. Here, T is a symmetric matrix with strictly non-negative entries, and D is a diagonal matrix with strictly positive entries. Let D_{\min} and D_{\max} represent the minimum and maximum elements of the diagonal of D , respectively, while r_{\min} and r_{\max} denote the minimum and maximum elements of the vector \mathbf{r} . Let

$$\Delta = \max_{i \in \{1, \dots, n\}} \sum_{j=1}^n T_{ij}$$

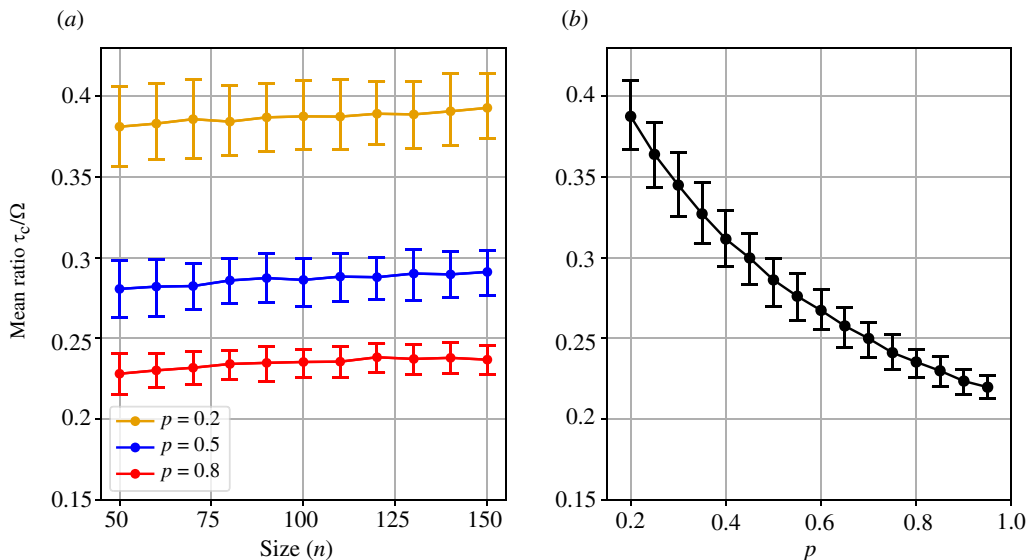


Figure 3. The ratio of the bifurcation value τ_c to our bound Ω as a function of the network size and connectivity. We generate networks of size 100 with binomially distributed degree sequences using the parameters $d_{\max} = 30$ and varying the connectivity parameter p . Note that the maximum degree of any constructed network cannot exceed 30. We verify whether the degree sequence is graphical, and if it is, we generate the network using the configuration model. We use exhaustive searching to ensure that the generated networks are connected. (a) The ratio of the bifurcation value τ_c to the conceived bound Ω , averaged over 500 runs. The error bars represent the 95% confidence intervals of the data. Note the apparent independence of the ratio on the network size while showing a strong dependency on the success probability p . (b) The ratio of the bifurcation value τ_c to the conceived bound Ω is determined for different connection probabilities p and averaged over 500 runs for each probability value. The error bars represent the 95% confidence intervals of the data.

denote the maximum outgoing edge weight, and let β represent the ratio between the minimum outgoing edge weight and Δ . Applying analogous steps as in Case 1, we derive an upper bound for Δ below which a transcritical bifurcation does not occur:

$$x_k^* := \left((T + D)^{-1} \mathbf{r} \right)_k \quad (2.9)$$

$$= \sum_{i=0}^{\infty} (-1)^i \left[(D^{-1}T)^i D^{-1} \mathbf{r} \right]_k \quad (2.10)$$

$$\geq \frac{D_{\max} D_{\min}^2 r_{\min} - D_{\max} r_{\min} \Delta^2 - D_{\max}^2 r_{\max} \Delta + r_{\max} \beta^2 \Delta^3}{(D_{\max}^2 - \beta^2 \Delta^2)(D_{\min}^2 - \Delta^2)}. \quad (2.11)$$

Setting the numerator of the last fraction to zero and solving for Δ , finding the smallest positive root Ω , we conclude that $x_k^* > 0$ for $\Delta < \Omega$, where:

$$\Omega := \frac{D_{\max}^2 - 2\sqrt{D_{\max}^4 + \frac{3\beta^2 D_{\max} r_{\min}}{r_{\max}}} \sin\left[\frac{1}{3} \arcsin(\theta)\right]}{3\beta^2},$$

$$\theta = \frac{\sqrt{\frac{r_{\max}}{D_{\max}} (2D_{\max}^5 r_{\max} + 9\beta^2 r_{\min} (D_{\max}^2 - 3\beta^2 D_{\min}^2))}}{2(D_{\max}^3 r_{\max} + 3\beta^2 r_{\min})^{3/2}}. \quad (2.12)$$

To show that a pitchfork bifurcation does also not occur for $\Delta < \Omega$, we constrain the eigenvalue spectrum by examining the disks in the complex plane centred around the points $-D_{ii}$, each with a radius $\sum_{j \neq i} T_{ij}$. All these disks are situated within the negative complex half-plane when

Table 1. Asymptotic regimes of Ω .

regime	parameters	θ	Ω
constant interaction	$\mathbf{r} = \mathbf{1}$, $T = \tau A$, $D = \mathbb{I}$	$\frac{2 + 9\alpha^2 - 27\alpha^4}{2(1 + 3\alpha^2)^{3/2}}$	$\frac{1 - 2\sqrt{1 + 3\alpha^2}}{3\alpha^2} \sin\left[\frac{1}{3}\arcsin(\theta)\right] \frac{1}{d_{\max}}$
large self-inhibition	$D_{\max} \rightarrow \infty$	1	0
large growth rate	$r_{\max} \rightarrow \infty$	1	0
small growth rate	$r_{\min} \rightarrow 0$	1	0

$\Delta := \max_{i \in [n]} \sum_{j \neq i} |T_{ij}| < D_{\min}$. This establishes a bound on the maximum outgoing edge weight, ensuring that for all values below this threshold, a pitchfork bifurcation does not occur. Note that the numerator from equation (2.11) evaluated at the point D_{\min} evaluates to $-D_{\max}^2 + \beta^2 D_{\min}^2$ which is always negative. The numerator of equation (2.11) at D_{\min} is $-D_{\max}^2 + \beta^2 D_{\min}^2$ which is always negative. Hence, the bound Ω is always smaller than the bound for a pitchfork bifurcation. Combining these observations, we establish an upper bound Ω on the maximum outgoing edge weight Δ thereby ensuring the absence of both transcritical and pitchfork bifurcations.

Similar to constant interaction systems, we observe the existence of a subset within the parameter space where stable coexistence is maintained. Note that the derived bound does not diminish when the network size increases indefinitely, given fixed values for D_{\max} and r_{\max} . Hence, even in the limit of large n , stable coexistence persists under these parameters.

One can use the parameter set $\mathbf{r} = \mathbf{1}$, $D = \mathbb{I}$ and $T = \tau A$ to get back the original bound for the constant interaction case (2.4). We examine different regimes of the parameter space, identified with ecologically meaningful cases, which are outlined in table 1. Large self-inhibition D_{\max} makes the system collapse, as the species die out too soon to have meaningful dynamics. Large maximum growth rate r_{\max} does not allow for coexistence, as the neighbours of v_i are heavily influenced by node v_i and therefore they cannot coexist. In the case of vanishing r_{\min} , we will also not obtain coexistence, as the corresponding species will not grow and therefore will die out in the long run.

Finally, the converse statement to our main result is also true; when the maximum degree k diverges with network size, at least one species will necessarily become extinct. To see why this is the case, consider the star graph S_k in which all but one node have degree 1, and one node has degree $k - 1$. Note that any graph G with adjacency matrix A and maximum degree k contains S_k as a subgraph. The minimum eigenvalue of S_k is $-(k - 1)^{1/2}$, and due to the eigenvalue interlacing theorem, we know that $\lambda_{\min}(A) \leq \lambda_{\min}(S_k)$. Consequently (at least) one pitchfork bifurcation must occur for $\tau > (k - 1)^{-1/2}$. Since k grows indefinitely, this value converges to zero, indicating that a pitchfork bifurcation must occur for networks with diverging degree. This proof easily generalizes to our general case of weighted graphs, as we can bound the minimum eigenvalue of the interaction matrix (due to negative definiteness) by the minimum eigenvalue of the binary adjacency matrix of the network scaled by the maximum element of T . Therefore, by the same reasoning, a pitchfork bifurcation must occur when k diverges.

3. Conclusions

This study examines coexistence in the Lotka–Volterra system with an undirected network of symmetric competitive interactions. We prove that when the degrees are bounded, regardless of system size, there is a globally stable coexistence state for a parameter set of non-zero measure. This observation resolves the diversity–stability paradox by demonstrating that stable species coexistence is possible even in large systems. When applied to weighted networks, we show that stable species coexistence can be maintained for an arbitrary large number of species when the sum of edge weights is bounded for each vertex. The converse statement is also shown to be true: if the largest degree diverges with system size, this necessarily leads to extinction of at least one species.

Additionally to resolving the paradox, an immediate implication of our results for the ecological modelling community is that a subtle choice between the network models that does or does not allow for limiting the maximum degree will have drastic implications on the dynamics of the interacting species. Rephrasing this in the language of statistical physics, choosing the interaction network from microcanonical or canonical ensembles might determine the fate of species coexistence in the Lotka–Volterra model.

It still remains an open question whether similar type of behaviour is also characteristic for directed networks and networks with mixed mutualistic–competitive interactions. While interactions of this type have been explored in Erdős–Rényi networks, their implications in bounded degree networks can lead to significantly different conclusions. Even though we show that the diversity–stability paradox does not exist *per se*, we note that our finding does not diminish the relevance of other possible explanations of diversity, for example, related to competition for time [24], space [25], higher order interactions [8,9] or cyclic food chains [26].

Finally, let us mention that this result is potentially relevant in ecology, since networks with sparse structures, and hence presumably bounded degrees, are common in ecology [15], for example in the context of tropical forests [17,18], where the underlying interaction network is possibly better represented as sparse rather than as an Erdős–Rényi graph. When there is a rationale to assume a bounded degree network, it is essential to acknowledge that the conclusions drawn for other network models may no longer be applicable.

Data accessibility. The data accompanying this paper can be found at [27]. The code accompanying this paper can be found at [28].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. M.N.M.: conceptualization, formal analysis, investigation, methodology, validation, visualization, writing—original draft; M.B.: conceptualization, funding acquisition, supervision, writing—review and editing; A.S.v.d.H.: conceptualization, funding acquisition, supervision, writing—review and editing; I.K.: conceptualization, funding acquisition, investigation, methodology, supervision, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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