SVD entropy reveals the high complexity of ecological networks

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Tanya Strydom (1,2)
Timothée Poisot (1,2,*)

(1) Université de Montréal
(2) Québec Centre for Biodiversity Sciences
(*) `timothee.poisot@umontreal.ca`

Quantifying the complexity of ecological networks has remained elusive. Primarily, complexity has been defined on the basis of the structural (or behavioural) complexity of the system. These definitions ignore the notion of 'physical complexity', which can measure the amount of information contained in an ecological network, and how difficult it would be to compress. We present relative rank deficiency and SVD entropy as measures of 'external' and 'internal' complexity respectively. Using bipartite ecological networks, we find that they all show a very high, almost maximal, physical complexity. Pollination networks, in particular, are more complex when compared to other types of interactions. In addition, we find that SVD entropy relates to other structural measures of complexity (nestedness, connectance, and spectral radius), but does not inform about the resilience of a network when using simulated extinction cascades, which has previously been reported for structural measures of complexity. We argue that SVD entropy provides a fundamentally more 'correct' measure of network complexity and should be added to the toolkit of descriptors of ecological networks moving forward.

Introduction

Ecologists have turned to network theory because it offers a powerful mathematical formalism to embrace the complexity of ecological communities (Bascompte and Jordano 2007). Indeed, analysing ecological systems as networks highlighted how their structure ties into ecological properties and processes (Proulx, Promislow, and Phillips 2005; Poulin 2010), and there has been a subsequent explosion of measures that purport to capture elements of network structure, to be related to the ecology of the system they describe (Delmas et al. 2018). Since the early days of network ecology, ecological networks have been called "complex". This sustained interest for the notion of complexity stems, in part, from the strong ties it has to stability (Landi et al. 2018). As such, many authors have looked for clues, in the network structure, as to why the networks do not collapse (Borrelli 2015; Staniczenko, Kopp, and Allesina 2013; Gravel, Massol, and Leibold 2016; Brose, Williams, and Martinez 2006). Yet decades of theoretical refinements on the relationship between complexity and stability had a hard time when rigorously tested on empirical datasets (Jacquet et al. 2016); although ecological networks may be complex, our current measures of complexity do not translate into predictions about stability.

Surprisingly, *complexity* itself has proven an elusive concept to define in a rigorous way. It has over time been defined as connectance (Rozdilsky and Stone 2001), as measures of the diversity of species or their interactions (Landi et al. 2018), or as a combination of species richness and trophic diversity (Duffy et al. 2007). In short, network ecology as a field readily assumes that because we have more information about a system, or because this system has more components, or simply because this system can be expressed as a network, it follows that the system is complex. But such a diversity of definitions, for a concept that is so central to our quest to understand network stability, decreases the clarity of what complexity means, and what all of these alternative definitions do actually capture. This is a common thread in some measures of ecological network structure, as has been discussed at length for the various definitions of nestedness (Ulrich, Almeida-Neto, and Gotelli 2009).

None of the previous definitions of complexity are formally wrong, in that they do capture an aspect of complexity that ultimately ties to the behaviour of the system, *i.e.* its low predictability over time. Yet Adami (2002) provides a compelling argument for why the complexity of the behaviour does not necessarily reflects the complexity of the system; in fact, one would be very hard pressed to think of a more simple system than the logistic map used by May (1976) to illustrate how easily complexity of behaviour emerges. Rather than yielding to the easy assumption that a system will be complex because it has many parts, or because it exhibits a complex behaviour, Adami (2002) suggests that we focus on measuring "physical complexity", *i.e.* the amount of information required to encode the system, and how much signal this information contains. Complex systems, in this perspective, are those who cannot easily be compressed - and this is a notion we can explore for the structure of ecological networks.

Ecological networks are primarily represented by their adjacency matrices, *i.e.* a matrix in which every entry represents a pair of species, which can take a value of 1 when the two species interact, and a value of 0 when they do not. These matrices (as any matrices) can easily be factorised using Singular Value Decomposition (Forsythe and Moler 1967; Golub and Reinsch 1971), which offers two interesting candidate measures of complexity for ecological networks (both of which we describe at length in the methods). The first measure is the rank of the matrix, which works as an estimate of "external complexity", in that it describes the dimension of the vector space of this matrix, and therefore the number of linearly independent rows (or columns) of it. From an ecological standpoint, this quantifies the number of unique "strategies" represented in the network: a network with two modules that are distinct complete graphs has a rank of 2. The second measure is an application of the entropy measure of Shannon (1948) to the non-zero singular values of the matrix obtained through SVD. This so-called SVD entropy measures the extent to which each rank encodes an equal amount of information, as the singular values capture the importance of each rank to reconstruct the original matrix; this approach therefore serves as a measure of "internal complexity".

In this manuscript, we evaluate both the rank and the SVD entropy as measures of the complexity of ecological networks, by using a collection of 220 bipartite networks from various types of interaction, sizes, connectances, and environments. We show that while the rank of the adjacency matrix holds little information, SVD entropy functions as an appropriate quantification of the complexity of ecological systems. Notably, SVD entropy is an intuitive, robust, non-structural approach to defining the (surprisingly high) complexity of ecological networks, by relating them to their 'physical' as opposed to 'behavioural' complexity. In this process we showcase a breakdown in the assumption that all measures of complexity of networks are indicative of their robustness to extinctions. We propose that taking a physical approach to quantifying the complexity of ecological networks is a step in the right direction to unifying how we define complexity in the context of ecological networks, as it restores other measures (like connectance and nestedness) to their original role and signification.

Methods

We used all bipartite networks from the `web-of-life.es` database, taken from the `EcologicalNetworks.jl` package (Poisot et al. 2019) for the *Julia* (Bezanson et al. 2017) programming language. Using bipartite networks means that interacting species are split into two sets (or interacting groups) and along different dimensions in the interaction matrix. Thus, columns in the matrix represent one group (or type) of species and rows represent the other group of species involved in the interaction. Because SVD gives similar results on the matrix and its transpose, it captures the complexity of both sides of the system at once.

Estimating complexity with rank deficiency

The rank of $\mathbf{A}$ (noted as $r = \text{rk}(\mathbf{A})$) is the dimension of the vector space spanned by the matrix and corresponds to the number of linearly independent rows or columns; therefore, the maximum rank of a matrix ($M = \text{rk}_{max}(\mathbf{A})$) will always be equal to the length of the shortest dimension of $\mathbf{A}$, which ecologically speaking is the richness of the least species-rich compartment of the bipartite network (or the richness in the case of unipartite networks). A matrix is "full-ranked" when $r = M$, *i.e.* all of its rows/columns are unique. Matrices that are not full-ranked are called rank deficient, and we can measure rank deficiency using $d = M - r$. So as to control for the difference in species richness of the different networks, we report the relative rank deficiency, *i.e.* expressed as a ratio between rank deficiency and the maximal rank:

$$D = 1 - \frac{r}{M} \tag{1}$$

This measure returns values between 0 (the matrix is full ranked) and $1-M^{-1} \approx 1$ (the matrix has rank 1). This serves as a coarse estimate of complexity, as the more unique columns/rows are in the matrix, the larger this value will be. Yet it may also lack sensitivity, because it imposes a stringent test on uniqueness, which calls for more quantitative approaches to complexity.

Estimating complexity with SVD entropy

Singular Value Decomposition (SVD) is the factorisation of a matrix $\mathbf{A}$ (where $\mathbf{A}_{m,n} \in \mathbb{B}$ in our case, but SVD works for matrices of real numbers as well) into the form $\mathbf{U}\cdot\Sigma\cdot\mathbf{V}^T$. $\mathbf{U}$ is an $m\times m$ orthogonal matrix and $\mathbf{V}$ an $n\times n$ orthogonal matrix. The columns in these matrices are, respectively, the left- and right-singular vectors of $\mathbf{A}$. Σ is a diagonal matrix, where $\sigma_i = \Sigma ii$, which contains the singular values of $\mathbf{A}$. When the values of σ are arranged in descending order, the singular values are unique, though the singular vectors may not be.

After the Eckart-Young-Mirsky theorem (Eckart and Young 1936; Golub, Hoffman, and Stewart 1987), the number of non-zero entries (after rounding of small values if required due to numerical precision issues in computing the factorisation) in σ is the rank of matrix $\mathbf{A}$. For the sake of simplicity in notation, we will use $k = \text{rk}(\mathbf{A})$) for the rank of the matrix. Because only the first k elements of σ are non-zero, and that the result of the SVD is a simple matrix multiplication, one can define a truncated SVD containing only the first k singular values.

Intuitively, the singular value i (σ_i) measures how much of the dataset is (proportionally) explained by each vector - therefore, one can measure the entropy of σ following Shannon (1948). High values of SVD entropy reflects that all vectors are equally important, *i.e.* that the structure of the ecological network cannot efficiently be compressed, and therefore indicates high complexity (Gu and Shao 2016). Because networks have different dimensions, we use Pielou's evenness (Pielou 1975) to ensure that values are lower than unity, and quantify SVD entropy, using $s_i = \sigma_i/\text{sum}(\sigma)$ as:

$$J = -\frac{1}{\ln(k)}\sum_{i=1}^{k} s_i \cdot \ln(s_i) \tag{2}$$

Uncovering the extreme complexity values at a given connectance

We used simulated annealing (Kirkpatrick 1984) to generate networks with the highest, or lowest, possible SVD entropy values. From a set network size (30 species, 15 on each side) with a random number of interactions (spanning the entire range from minimally to maximally connected), we reorganised interactions until the SVD entropy was as close to 0 or 1 as possible. We repeated the process 25 times for every number of interactions. We also measured the relative rank deficiency of the generated networks. This allows identifying the boundaries of both measures of complexity.

SVD entropy compared to traditional measures of network complexity

We compared SVD entropy to some of the more common measures of complexity, namely nestedness (η, following Bastolla et al. (2009)), connectance (Co), and the spectral radius of the network (ρ, following Staniczenko, Kopp, and Allesina (2013)). All of these measures are positively correlated, especially over the range of connectances covered by empirical bipartite ecological networks.

The nestedness of a network is a measure of the degree of overlap between species links (or strategies), where larger assemblages are made up of a subset of smaller ones that share common interactions. Networks with a higher degree of nestedness could be considered simpler when compared to networks with a lower degree of nestedness. Connectance is the realised number of interactions (links) in an ecological network and is calculated as the fraction of the total number of realised interactions (or links) and the maximum number of possible interactions in a network (Martinez 1992). This has been shown to be a good estimate of a community's resilience to perturbation (Dunne, Williams, and Martinez 2002). The spectral radius of a matrix is the largest absolute value of its eigenvalues, which, in addition to being presented as a measure of network complexity has also been suggested as an indicator of the ability of a system to dampen disturbances (Phillips 2011).

Assessing robustness through targeted extinctions

One approach to calculating the overall structural robustness of an ecological network is by simulating extinction events through the sequential removal of species, which allows constructing an extinction curve that plots the relationship between species removed and cumulative secondary extinctions (Dunne, Williams, and Martinez 2002; Memmott, Waser, and Price 2004). Extinction events can be simulated in a manner of different ways, either by removing 1) a random individual, 2) systematically removing the most connected species (one with the highest number of interactions with other species) and 3) the least connected species (Dunne, Williams, and Martinez 2002). After each extinction event, we remove species from the network that no longer have any interacting partners, thereby simulating secondary extinctions. This is then repeated until there are no species remaining in the network. Furthermore, we can restrict extinction events to only one dimension of the interaction matrix, *i.e.* removing only top-level or bottom-level species, or alternatively removing a species from any dimension of the matrix. Extinction curves are then constructed by plotting the proportion of species remaining against those that have been removed; it stands to reason that a flatter curve 'maintains' its species pool for a longer number of cumulative extinctions, and could be seen as more resilient, when compared to a curve that has a much steeper decline. As per previous studies, we measure the robustness to extinction as the area under the extinction curve (AUC), calculated using the Trapezoidal rule. AUC values close to 0 means that a single extinction is enough to collapse the network almost entirely, and values close to 1 means that most species persist even when the number of extinctions is really high.

Results and discussion

Most ecological networks are close to full-rank

The majority (63% of our dataset) of bipartite ecological networks have a relative rank defficiency of 0 (fig. 1), which indicates that all species have different and unique interaction lists. Interestingly, the networks that had a comparatively larger relative rank deficiency tended to be smaller ones. Yet because most of the networks return the same value, matrix rank does not appear to be a useful or discriminant measure of network complexity. Another striking result (from fig. 1) is that the SVD entropy of ecological networks is really large – although the value can range from 0 to 1, all ecological networks had SVD entropy larger than 0.8, which is indicative of a strong complexity.

As expected following the observation that ecological networks are overwhelmingly full ranked, we do not see a relationship between SVD entropy and relative rank deficiency, neither do we observe differences between interaction types (fig. 2). Based on these results, we feel confident that SVD entropy provides a more informative measure of the complexity of ecological networks, and will use it moving forward.

Plant-pollinator networks are slightly more complex

Although we don't observe clear differences in the relationship between different interaction types when comparing amongst various measures of complexity, we do find that different types of interaction networks have differing SVD entropies. When comparing calculated SVD entropy between interaction types using an ANOVA (after excluding Plant-Ant and Plant-Herbivore interactions due to their small sample size in our dataset) we find a signifi-

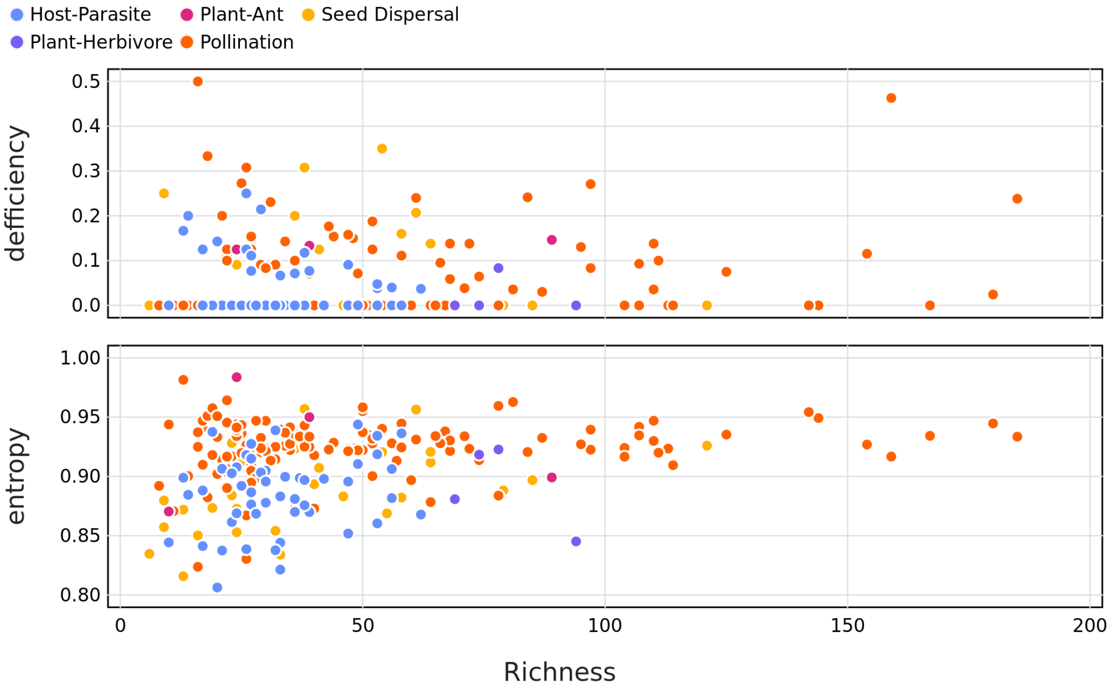

Figure 1: The relationship between network richness and relative rank deficiency, and SVD entropy. The different types of interactions are indicated by the colours.

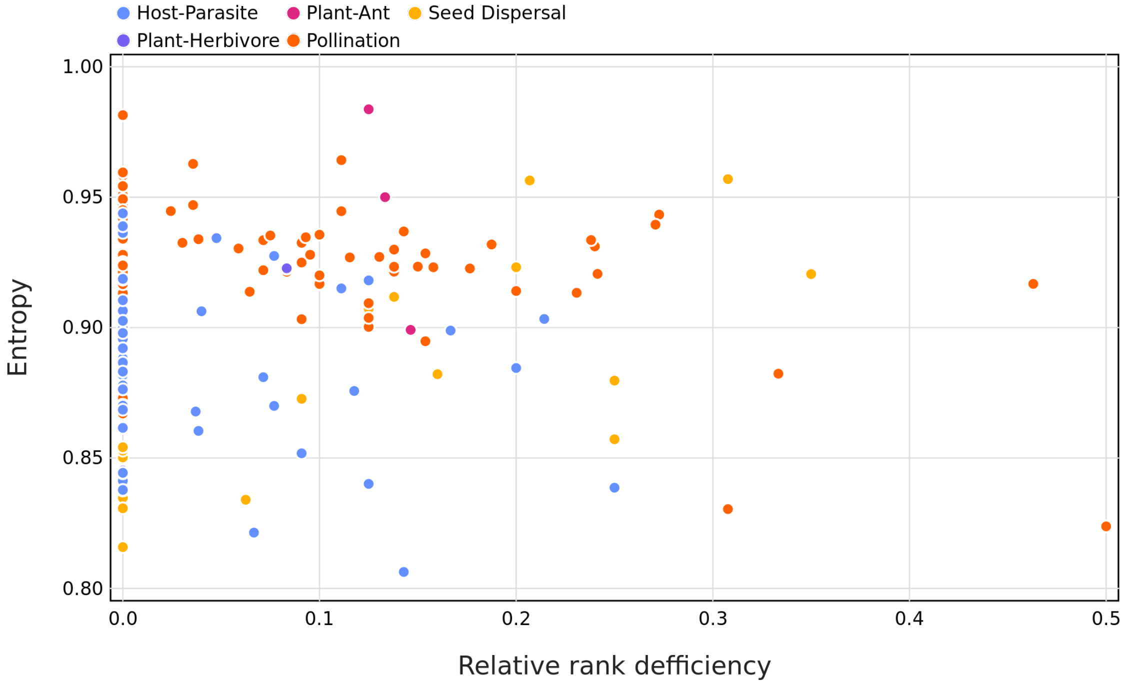

Figure 2: The relationship between SVD entropy and the relative rank deficiency of different species interaction networks Colours indicate the different interaction types of the networks.

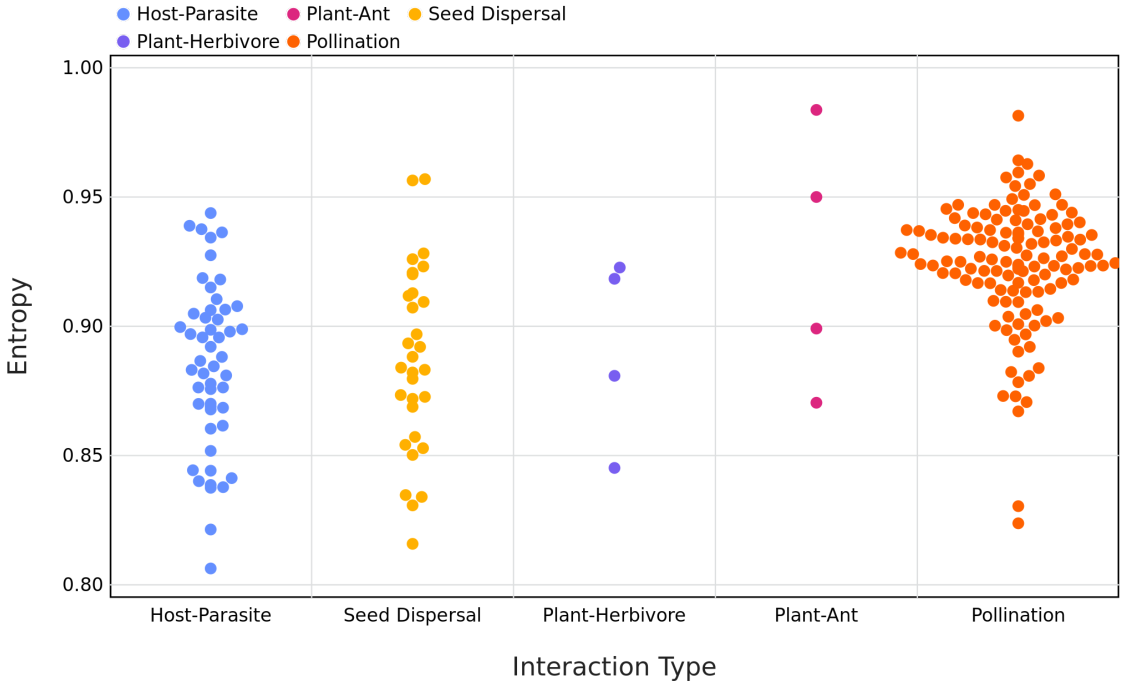

Figure 3: The calculated SVD entropy of different interaction networks of different interaction types

cant difference between group means ($F = 47.047, p < 10^{-3}$). A Tukey's HSD test reveals that plant-pollinator networks ($\mu = .924$) are more complex than both host- parasite networks ($\mu = .885, p < 10^{-3}$) and seed dispersal ($\mu = .888, p < 10^{-3}$). Host-parasite and seed dispersal networks had apparently no difference in average complexity ($p = .889$). These results suggest that mutualistic networks may be more complex, which matches with previous literature: these networks have been shown to minimise competition (Bastolla et al. 2009) and favour unique interactions, thereby increasing network complexity. This specific structure can appear as a side-process of either ecological (Maynard, Serván, and Allesina 2018) or evolutionary (Valverde et al. 2018) processes, but nevertheless leaves a profound imprint on the complexity of the networks.

Connectance constrains complexity (but also rank deficiency)

By exploring the minimal and maximal values of SVD entropy for networks of a given size, we can show that the range of complexity that a network can express varies as a function of connectance (fig. 4). As reported by Poisot and Gravel (2014), there is no variation when the networks are either minimally or maximally connected, but any connectance in between can give rise to networks of varying complexities. This being said – minimally connected networks always show the largest complexity, and an increase in connectance will always decrease complexity. Interestingly, this relationship is monotonous, and there is no peak of complexity where the maximal number of possible networks combination exists, *i.e.* around Co ≈ 0.5 (Poisot and Gravel 2014). This is an intriguing result – ecological networks are indeed extremely complex, but whereas ecologists have usually interpreted connectance as a measure of complexity, it is in fact sparse networks that are the complex ones, and connectance acts to decomplexify network structure.

The right panel of fig. 4 shows the average rank deficiency of networks for which SVD entropy was either maximised or minimised. Complex networks (meaning, maximally complex given their connectance) had a lower deficiency, indicating that except at extreme connectances, there are combinations of networks for which all species can interact in unique ways – this is a natural consequence of the results reported by Poisot and Gravel (2014), whereby the number of possible networks is only really constrained at the far ends of the connectance gradient. Minimally complex networks, on the other hand, saw their rank deficiency increase with connectance. This hints at the fact that the decrease in complexity with connectance may be primarily driven by the infeasibility of having enough species for them to all interact uniquely as connectance increases. Because non-unique interactions tend to result in competition (Bascompte and Jordano 2007), this can "push" networks towards the full-rank configuration (as suggested by the results in fig. 1), thereby maximising complexity regardless of connectance.

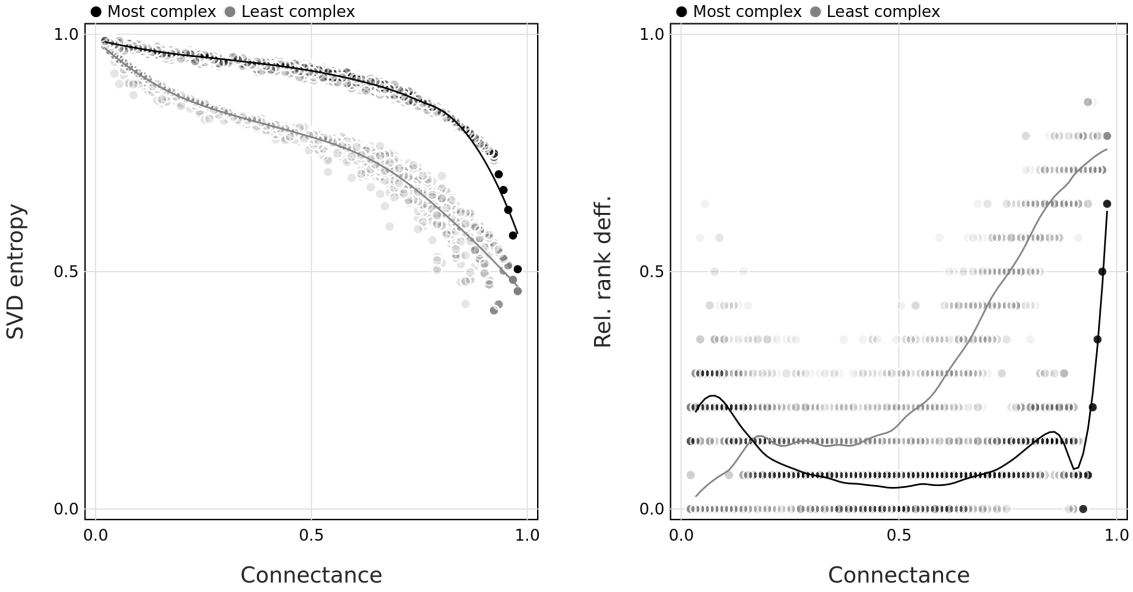

Figure 4: The relationship between the maximum and minimum value of SVD entropy of a collection of random interaction networks (using simulated annealing) for a given connectance spanning from 0 to 1 (left panel) and how this relates to the relative rank deficiency of networks (right panel)

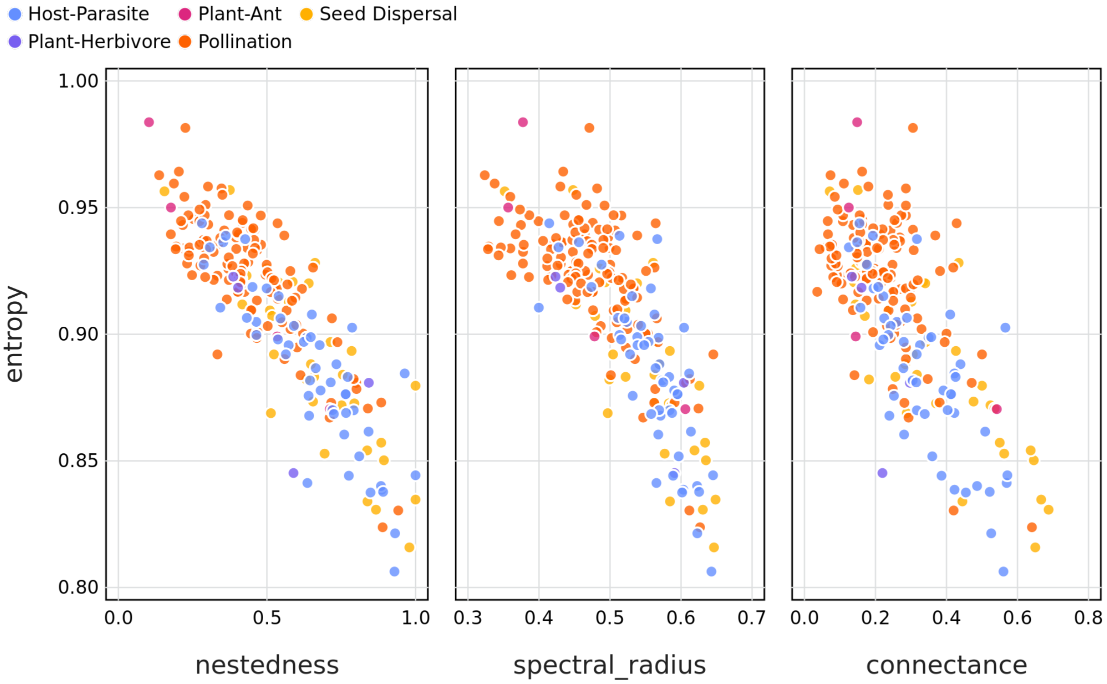

Figure 5: The relationship between SVD entropy and the nestedness (left panel), spectral radius (central panel) and connectance (right panel) of ecological networks. Colours indicate the different interaction types of the networks.

Most elements of network structure capture network complexity

We find that SVD entropy has a clear negative relationship with nestedness, spectral radius, and connectance (fig. 5). As in fig. 3, mutualistic networks tend to be more complex, and they also are both sparser and less nested than other types of networks. Bastolla et al. (2009) give a convincing demonstration that mutualistic networks are shaped to minimise competition – this can be done by avoiding to duplicate overlap in interactions, thereby resulting in a network that is close to full rank, and with high SVD entropy. Interestingly, fig. 5 suggests that both nestedness and connectance measure the *lack* of complexity in an ecological network, which contrasts to how they may commonly be viewed (Landi et al. 2018).

Complex networks are not more robust to extinction

When looking at the relationship between SVD entropy and the area under an extinction curve (as a proxy for resilience to extinction) we find differences depending on both the extinction mechanism as well as along which dimension the species removal occurred (fig. 6). As a whole we do not observe any obvious relationships between SVD entropy and resilience, nor for different interaction types. We do however see differences in the resilience of networks depending on how the extinctions were simulated. Generally we see a higher resilience in networks where species of only a specific group are removed or in networks where species were either randomly removed or based on an increasing number of interactions.

As highlighted in fig. 5 SVD entropy can be used as an additional measure of network complexity. However, as shown in fig. 6, the assumption that network complexity begets resilience to extinction begins to unravel when we use a measure of physical complexity. This is in contrast to previous studies that have shown how connectance plays a role in the resilience of networks to extinctions (Dunne, Williams, and Martinez 2002; Memmott, Waser, and Price 2004). This does not discount the role of using *structural* measures of network complexity (*e.g.* connectance, nestedness or spectreal radius) as indicators of their resilience (although possibly hinting as to why there is no strong emerging consensus as to how structural complexity relates to this), but rather points to an erroneous assumption as to what aspects of a network we have previously used to define its complexity.

Conclusion

We present SVD entropy as a starting point to unifying (and standardising) how we should approach defining the complexity of ecological networks. The use of a unified definition will allow us to revisit how complexity relates to the ecological properties of networks using a standardised method, or further exploring why, despite the strong relationship between the physical and behavioural complexity of networks, they seem to be underpinning different aspects of network properties. One important result from using SVD entropy is that the

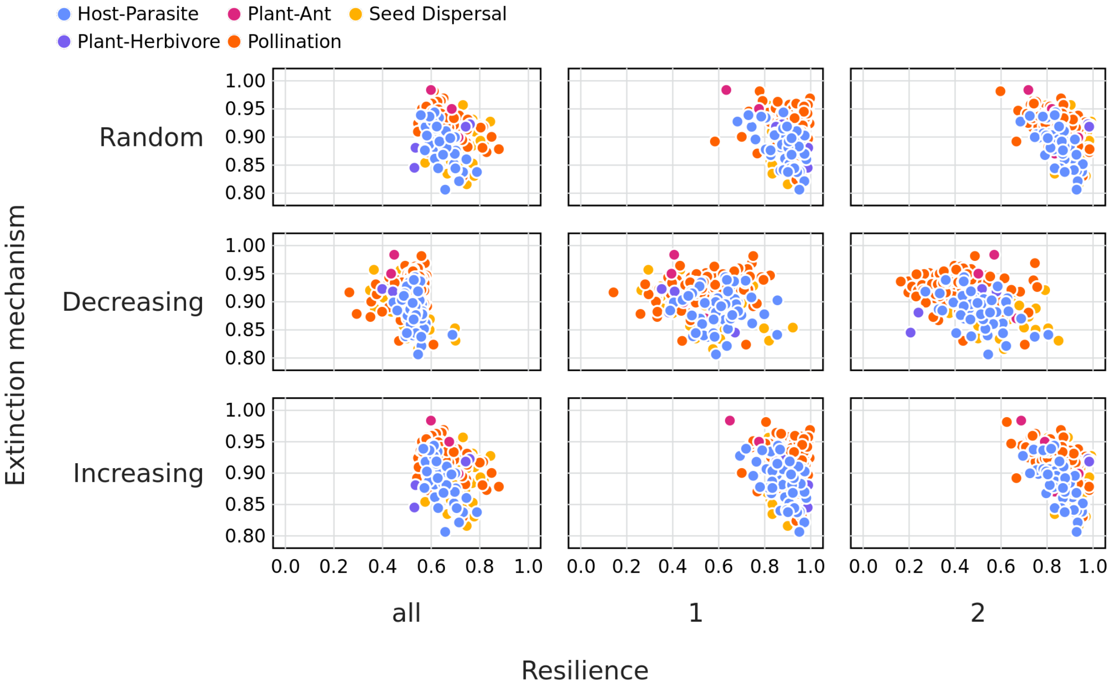

Figure 6: The relationship between SVD entropy and the area under an extinction curve (as a proxy for resilience to extinction) for both different extinction mechanisms (Random = the removal of a random species, Decreasing = the removal of species in order of decreasing number of interactions (i.e most to least number of interactions), Increasing = the removal of species in order of increasing number of interactions) as well as along different dimensions (species groups) of the network (all = any species, 1 = only top-level species, and 2 = only bottom- level species) Colours indicate the different interaction types of the networks.

complexity of ecological networks is indeed *immense*. This hints at the existence of mechanisms minimizing the overlap in interaction partners within networks, thereby increasing complementarity; for this reason, we are hopeful that the analysis of physical complexity will lead to emerging questions about what shapes ecological networks.

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