Towards a cohesive understanding of ecological complexity

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Abstract

Understanding phenomena typical of complex systems is key for progress in ecology and conservation amidst escalating global environmental change. However, myriad definitions of complexity hamper conceptual advancements and synthesis. Ecological complexity may be better understood by following the strong theoretical basis of complexity science. We conduct bibliometric and text-mining analyses to characterize articles that refer to ecological complexity in the literature, in relation to features of complex systems described within complexity science. Our analyses demonstrate that the study of ecological complexity is a global, increasingly common, but highly heterogeneous endeavor that is only weakly related to complexity science. Current research trends are typically organized around basic theory, scaling, and macroecology. To increase clarity, we propose streamlining the study of ecological complexity around specific features of complex systems in lieu of the vague term "complexity", embracing complexity science, appreciating different philosophies, and integrating ideas from researchers beyond the "Global North".

Teaser

Combining a review and quantitative analyses, this study provides a unique perspective on the study of complexity in ecology.

MAIN TEXT

Introduction

Understanding nature's complexity is traditionally at the core of scientific endeavors (*1*, *2*). In ecology and conservation, studying complex systems has led to both the development of theories (*2*–*5*), and consideration in policies and plans for environmental management (*6*–*9*). Understanding complexity is becoming increasingly important in the face of accelerating global environmental change, because natural systems exposed to multiple stressors often display phenomena typical of complex systems (*10*–*13*). Advancements in the study of complexity are therefore crucial, to the point that the 2021 Nobel prize in Physics was awarded to Parisi, Manabe and Hasselmann for their "*groundbreaking contributions to our understanding of complex systems*" (*14*). Despite these important aspects, defining what exactly ecological complexity is – and thus the properties of complex natural systems – has been historically difficult (*15*–*17*).

Complexity remains challenging to define due to its multifaceted nature, which transcends observational scales, emerges in different forms, and contains variables that through feedbacks, enter models as causative factors and consequences of phenomena. Complexity is therefore typically conceptualized differently by authors based on the particular aspects being studied (*15*, *17*, *18*). For instance, some authors categorize their object of study and epistemological approach as either complex or not, while others conceptualize complex systems along a continuum, from less to more complex (*15*). Some propose quantifying the complexity of different systems through use of specific metrics (e.g., *19*, *20*), in contrast to approaches that rely on qualitative definitions (*21*, *22*). Furthermore, complexity can be defined differently across scientific domains, e.g., computer scientists may refer to the time and computational memory required to solve a problem (*23*, *24*), whereas mathematicians may refer to chaotic and nonlinear dynamics (*21*). It has been even suggested that complexity is "*a placeholder for the unknown*", a metaphor that facilitates us in understanding reality by behaving like a "*nomadic term that links disparate discourses*", and therefore a strict definition would only be an unwarranted constrain (*16*).

While we lack consensus for a single, comprehensive definition of complexity, the study and invocation of ecological complexity continues to grow in the scientific literature. A search on the Web of Science for the word "Complexity" in the "Ecology" and "Environmental Sciences" categories matched 23,703 manuscripts published between 2000 and 2021 (search conducted on July 14th, 2021). The 71 reviews captured by this search discuss a broad range of topics, from the evolutionary novelty of venoms (*25*) to the biogeochemistry of marine polysaccharides (*26*), but none addresses directly what ecological complexity is (Table S1). Rather, complexity is often only used in a colloquial sense, implying that a study focuses on a system difficult to comprehend, rather than referring to a clear heuristic (*16*). Since a lack of clarity in science confounds the communication of ideas, fosters unnecessary debates, limits research progress, and hinders the translation of findings into practice (*18*, *27*, *28*), seeking common ground in how we define and study complexity is not merely a semantic problem, but rather a pressing challenge of our times.

Notably, confusion in the study of ecological complexity is not due to a lack of theoretical background. Attempts to define complex natural systems and their properties abound (*17*), typically in relation to 'complexity science' (or 'complex system science'). Complexity science arose to more formally seek generalities in our understanding of complex systems (*29*, *30*), but ecology and conservation have lagged behind recent developments in this field (*9*, *22*). Furthermore, even within complexity science, different definitions of complexity exist due to subjective preferences, philosophical views, and peculiarities of different subfields (*15*, *17*, *18*). Ultimately, there seems to be confusion in ecology, expressing itself as how and when authors choose to refer to 'complexity' in their work.

Here, our goal is synthesizing how ecologists conceptualize and study complexity to propose a more cohesive approach to the study of complex natural systems. We follow a three-pronged approach: (i) we review the complexity science literature to identify a list of features typically attributed to complex systems; (ii) we empirically assess the ecological literature to understand how these features relate to the study of 'ecological complexity'; and (iii) we leverage generalities identified in our analysis to suggest a cohesive way forward in the study of complexity in ecology. This empirical approach allows us to face the historical challenge of defining and understanding complexity in a novel way: instead of defining complexity by first principle reasoning, we investigate the literature to understand how complexity has been conceptualized by the ecological community.

We quantitatively assess the literature on ecological complexity following a 'research weaving' approach, combining the strengths of a critical review, text mining, and scientometrics analyses (*31*). Specifically, we first review complexity science literature to identify a set of features typical of complex systems in ecology and the environmental sciences (Table 1). We then quantify how often these features have been used in all the articles that are explicitly related to ecological complexity in the Web of Science database and compare those to control articles randomly selected from ecological studies that do not refer to ecological complexity. We used this dataset to describe spatiotemporal trends in the study of ecological complexity (Fig. 1), to analyze thematic diversity (Fig. 2), and to identify patterns in connections between feature usage (Fig. 3) and co-citation of the references cited in articles that explicitly refer to ecological complexity (Fig. 4).

Because the concept of complexity should recall similar ideas for different scientists, we predict that articles that explicitly refer to ecological complexity should mention more frequently features typical of the study of complexity than control articles. We also predict that articles that explicitly refer to ecological complexity should be more similar amongst themselves than control articles, because ecology is a vast field with studies ranging from behavioral responses to macroecological patterns. For the same reason, we predict that patterns in how ecological complexity is conceptualized should differ across subfields, e.g., with certain features being more likely to be discussed together, and/or with some subfields citing different subsets of the literature. Support for these predictions would suggest that some of the authors who refer to ecological complexity do so while relating to a set of shared ideas, and therefore that – at least in principle – there is potential to organize the study of ecological complexity around well-established principles in complexity science. Given that progress in the study of complexity will be crucial moving forward, we conclude by proposing five prescriptive actions that can be taken to minimize confusion around complexity in ecology.

Materials and Methods

Overview

Our manuscript is based on the premise that complexity is an attribute of natural systems, and thus that we can identify properties of systems that are typically associated with the idea of complexity (*19*). This is a perspective that allows us to quantitatively assess the ecological literature. However, we note that it relates marginally to other more abstract perspectives on complexity (e.g., *15*, *16*). We also avoid exploring the ontology of complexity, which is a difficult philosophical matter (*15*) — but stress the importance of this discourse to understand the roots of complexity. More pragmatically, we propose that the widespread use of the word 'complexity' justifies an attempt to formally organize its use and study in ecology and undertake this task.

We prepared and analyzed a dataset to assess how often the features typical of complex systems are used in the literature referring to complexity in ecology. This required identifying features typical of ecological complexity, extracting those features from *control* and *complexity* articles, and quantifying their use in *control* and *complexity* articles. The analysis followed four steps: (i) describing general patterns in *complexity* articles, (ii) comparing the diversity of features in *complexity* vs. *control* articles, (iii) exploring the relationships among complexity features within *complexity* articles, and (4) identifying influential references in ecological complexity literature. We ran all analyses in R v.4.1.2 (*32*), using the 'tidyverse' suite v.1.3.1 (*33*) for data wrangling and visualizations. We refer readers to the Data Availability Statement for information on scripts and data used in this study.

Data preparation

Identifying features typical of ecological complexity

We begin by compiling a list of features that are typically associated with the study of complexity in the scientific literature. An initial screening showed that different articles that mention and define complexity highlight different features (Table S1). For instance, we tried searching for reviews summarizing ideas from complexity science in ecology with little success (but see *9*, *34*). We concluded that identifying the features typical of complex systems in ecology as described in complexity science was not possible based on an automatic procedure. This is because different authors use complexity to describe very different ideas and processes or use different words to refer to the same concept, which makes the design of a systematic review prohibitive. We, therefore, chose an unstructured, critical review approach (*35*), based on a mixture of article retrieval with fixed search strings (e.g., 'complexity' AND 'ecology' AND 'review') and scouting of the references cited in seminal articles that we deemed relevant for our exercise.

Among several ($n > 100$) articles evaluated during this exercise, we refer to 16 documents for discussion of the features identified in our review (Table 1). These include books (*21*, *30*, *36*), and various types of peer-reviewed scientific articles (hereafter, "articles"), particularly reviews (*9*, *12*, *15*, *17–19*, *29*, *34*, *37–41*). While other relevant perspectives certainly exist in the literature, we contend that this body of literature captured what makes natural systems 'complex' reasonably well because (i) we targeted the perspective of several independent groups of authors, often recognized as leaders in the study of complexity (e.g., on average, well above 100 citations per document, which is typically a sign of high impact (*42*)); (ii) we focused on concepts from complexity science, the field that emerged as a formal attempt to synthesize generalities across a variety of fields that study complex systems; and (iii) we typically selected recent reviews (all the reviews listed above are < 15 years old, and half are < 5 years old), thereby capturing ideas at the forefront of the study of ecological complexity.

Our critical review identified 22 major features typical of ecological complexity (Table 1). We note that some features initially under consideration, including the terms 'hysteresis', 'panarchy', and 'heterarchy', were removed because they appeared in less than 10% of the articles assessed in our analysis. We used single words to represent each of the selected features, aiming to ensure comparability on the frequency of use of different features across studies (Table 1). These words were carefully chosen to be as broadly representative of the features as possible. For example, a common feature emerging in the literature is the idea that complex systems are composed of units that differ among themselves; this is typically discussed as 'diversity', but can be also associated with 'entropy', e.g., in biodiversity science (*43*), and 'heterogeneity', e.g., in landscape ecology (*44*). We selected a single word to represent each of the compiled features to ensure comparability in features' counts among articles and acknowledge that our results might be sensitive to the word selected. Additionally, any two articles might share similar features, but address them with different approaches. These nuances are challenging to capture when conducting broad-scale bibliometric analyses, and our results should be evaluated keeping this in mind.

Systematic mapping of the literature

Next, we retrieved articles representing research on ecological complexity to compare them with more general articles in the field of ecology. This was carried out through literature searches on the Web of Science Core Collection database over all the citation indices, all document types, and all years (exploratory queries between May and July 2021; final query on 23rd September 2021). In an exploratory scoping phase, we trialed different search terms by running searches and considering the relevance of the first references. We found that using overly broad terms (e.g., <ALL = "ecology" AND "complexity">) yielded a large number of articles (n >14,000). On the opposite end, incorporating specific terms typically associated with ecological complexity either matched a limited number of articles (e.g., 'homeostasis') or captured several articles not relevant to the question posed (e.g., the term 'network' generated articles on industrial ecology and energy infrastructure). We found a balance between specificity and quantity by searching for general terms but restricting the search to the title (TI) and keywords (AK). The final query was <_TI = "ecolog* complex*" OR AK = "ecolog* complex*"_>, which returned 188 results (henceforward '_complexity'_ articles). We assumed these articles to be a random sample of literature that generally refer to complexity in ecology and the environmental sciences, i.e., that the study of 'ecological complexity' is not an independent avenue of research from the broader study of complexity in ecology. As a control (henceforward '_control'_ articles), we randomly selected 188 articles from the ecological literature, using the query <_WC = "Ecology" NOT (TI = "ecolog* complex*" OR AK = "ecolog* complex*"_>, where WC is used for searching through Web of Science categories.

Text mining

The last step of our dataset preparation was to quantify how often each of the features listed in Table 1 occurred in each article. We did this by performing text mining analyses on the full-text file of each of the articles returned by our searches. We first downloaded all full-text files as .pdf files and extracted their text using the package 'pdftools' v.3.1.0 (*45*). Because we could not retrieve 24 files (16 *complexity* and 8 *control* articles), the final sample size for the text mining analysis was 172 *complexity* articles and 180 *control* articles. Once we extracted the text from the articles, we screened them to obtain all the n-grams (strings of one or more adjacent words, henceforth 'words') within each article using the package 'tidytext' v.0.3.2 (*46*) and 'stringr' v.1.4.0 (*47*). Some of the features could be found either as single or composite words (Table 1), thus we extracted both unigrams and bigrams from articles using strings compatible with both British and American spellings. For single words (e.g., 'scale'), we cross-referenced the string with the unigrams extracted from the text (i.e., every single word in the article). For two-part words (e.g., 'self-organization'), we cross-referenced the search string with all bigrams extracted from the text (i.e., every combination of two consecutive words). For the features that could be found either as single, hyphenated, or two-part words (e.g., 'nonlinear' vs. 'non-linear' vs 'non linear') we cross-referenced the strings separately using both approaches. Lastly, we summed the results from the cross-reference to determine the total number of times each feature appeared in each article and to calculate the relative frequency of each feature as the ratio between the number of uses of a given feature and the total number of words in that article. We note that four *control* and two one-page-long *complexity* articles did not include any features from Table 1.

Analysis

Spatiotemporal patterns in the study of complexity

The first set of analyses was aimed at describing general patterns in *complexity* articles. We assessed the number of *complexity* articles published each year up to 2020 to determine whether research effort increased over time. We also extracted the affiliation of all authors from each article to investigate whether the collaborations were carried out nationally or internationally, and how these were globally distributed. We automatically retrieved the geographic coordinates for each affiliation using the package 'ggmap' v.3.0.0 (*48*).

The diversity of complexity articles

To compare *complexity* and *control* articles, we ran a series of analyses inspired by classical community-level biodiversity analyses. In these analyses, we treated each complexity feature as a 'species', and each article as a 'site'. We calculated feature richness (i.e., number of features discussed in each article) and the effective number of features of first order (i.e., exponential of the Shannon entropy calculated using the relative frequency of features used in each paper; *43*), to evaluate whether *complexity* articles tend to encompass more of the features typical of ecological complexity compared to *control* articles. Given how we delimited the terms associated with complexity, we assumed that articles referring to more features should generally capture the idea of complexity better.

Additionally, we assessed the uniqueness of the features in each *complexity* and *control* article by analyzing the multivariate homogeneity of group dispersion (PERMDISP), using the package 'vegan' v.2.5.7 (*49*). A common measure of multivariate dispersion (i.e., variance) for a group of samples (i.e., articles) is to calculate the average distance of group members (i.e., *control* vs. *complexity* articles) to their spatial median, and test if the dispersions are different with analysis of variance. PERMDISP requires a symmetrical matrix of dissimilarities between pairs of articles, which we calculated using the Bray-Curtis dissimilarity metric applied to feature relative frequency. Lastly, we tested what features were typical of *complexity* or *control* articles using an indicator species analysis with 'indicspecies' v.1.7.9 (*50*).

Network of complexity features

We explored relationships among the complexity features using a network approach. Specifically, we constructed a bipartite (i.e., containing two node types) directed network to link *complexity* articles with the features retrieved from our review (Table 1). In this network, the first node type represents individual articles, and the second node type represents the features. We weighted edges connecting the two node types in the bipartite network by the relative usage of each feature within each article. Once we constructed the bi-partite network, we projected it as a single mode or 'unipartite' network for ease of visualization and analysis. In the unipartite network, all nodes are treated as the same type and directionality is lost. We calculated the importance of each node in the network as the sum of the edge weights of the adjacent edges of the node (henceforth 'strength'). We also estimated realized connectance (RC), namely the proportion of possible links between nodes that are realized as

$$RC = L\left[\frac{2}{S(S-1)}\right],$$

where S represents the number of nodes and L is the actual number of edges realized among all the nodes in the network. To estimate the degree of discrepancy between article types, we tested the probability of connection between *complexity* and *control* articles within the network by using exponential random graph models (ERGM; *51*). In ERGMs, Y_{ij} designates the probability of forming an edge between articles *i* and *j* with $Y_{ij} = 1$ if there is a network edge, and $Y_{ij} = 0$ otherwise. Each value y_{ij} specifies the observed value Y_{ij} in a system governed by a matrix of predictor variables **Y** and edges **y**—i.e., the network. The general form of ERGM can be derived as follows:

$$\Pr(\mathbf{Y} = \mathrm{y}) = \frac{exp(\theta\prime g(y))}{k(\theta)},$$

ERGM's assume that the structure of a graph can be explained by a vector of network statistics $g(y)$ relating to network configuration, and to model parameters θ associated with $g(y)$. The normalization term $k(\theta)$ ensures that probabilities sum to 1. Note that $g(y)$ can be interpreted as covariates in a model that predicts edge occurrence, and that here, it represents network homophily, i.e., the degree to which nodes are connected based on similarity of their attributes. For the analysis, we constructed a bipartite incidence network, starting from an incidence matrix that included both *complexity* and *control* articles. We projected the network to visualize the connections among articles through the features used. The projected network was introduced as a response variable in an ERGM fitted using the package 'ergm' v.4.1.2 (*52–54*), with the formula (in *R* notation):

Network ~ edge + nodeMatch("Group") + nodeFactor("Group"),

where "Group" is a categorical variable discriminating *complexity* and *control* articles, *nodeMatch* tests network homophily in terms of article type and *nodeFactor* tests the overall probability of nodes forming an edge based on their article type.

Network of co-citations

We extracted the reference list from all *complexity* articles and used it to build a co-citation network, seeking to identify broad trends within this research avenue. Co-citation networks describe the number of times a reference was cited alongside others, and how often these were co-occurring in the reference lists. Analysis of co-citation networks has been proposed as a tool to enhance transdisciplinary research because it allows identifying key articles that act as bridges between (sub)disciplines, as well as groups of authors focusing on similar research topics (*55*, *56*). To identify these groups, we used a Louvain clustering optimization, a greedy optimization algorithm often used in network analyses due to its fast computation time and performance (*57*).

Results

Bibliometric analysis and spatiotemporal patterns

We retrieved 172 articles that mention “ecological complexity” in their title or keywords. Institutions from all continents except Antarctica contributed to this pool of manuscripts (Fig. 1a), with North American (n = 266) and European (n = 185) institutions contributing disproportionately more. Considering the articles mentioning “ecological complexity” in all fields (i.e., title, keywords and abstract), we found a steady increase in research effort starting from the late 1990s, exceeding 2000 articles as of the end of 2021 (Fig. 1b).

The diversity of complexity articles

Based on the features typical of complex systems retrieved from our critical review (Table 1), *complexity* articles included a significantly ($\alpha = 0.05$) higher number of features than expected from a random sample of *control* articles from the ecological literature (Fig. 2a–b) and were more similar to each other than expected by chance alone (Fig. 2c–d). Specifically, *complexity* articles mentioned on average 9 out of 22 features, against the 6 observed in *control* articles ($F_{1,344} = 83.13$, $p < 0.001$; Fig. 2a). This result was consistent when accounting for features’ relative abundances ($F_{1,344} = 67.03$, $p < 0.001$; Fig. 2b). Regarding uniqueness, PERMDISP showed that *complexity* articles were, on average, 6% more similar to each other than *control* articles. The average distance to the median of *complexity* articles was 0.51 ± 0.09 while *control* articles showed an average distance to the median of 0.55 ± 0.10 ($F_{1,344} = 12.47$, $p < 0.001$; Fig. 2c). For both *complexity* and *control* articles, those mentioning less than five features were typically more distant from their respective group median than the other articles, which suggests that the features mentioned in those articles were rarely mentioned in other articles from our sample (Fig. 2d).

Network of complexity features

The features identified in our critical review formed a highly connected network (RC = 0.987; Fig. 3). Most of the features co-occurred at least once, although the features “scale dependency”, “interaction” and “dynamicity” contributed disproportionately more in terms of connection strength and node weight (Fig. 3). According to the ERGMs analysis, *complexity* articles were more likely to form edges than *control* articles (estimate ± SE: 0.47 ± 0.02, *z-value*: 27.67, $p < 0.0001$) whereas network homophily was not significant (estimate ± SE: –0.04 ± 0.02, z-value: –1.91, $p = 0.06$), indicating that *control* and *complexity* articles are interconnected with each other. Still, some of the most important features for the network (e.g., network and diversity) were not typically common to the *complexity* articles (Fig. 3, in gray).

Network of co-citations

When assessing the reference lists of all *complexity* articles, the Louvain clustering algorithm identified five clusters of co-citation among the top 100 most co-cited references (Fig. 4). Two clusters included 10 or fewer references and reflected the production of two research groups (Fig. 4; in grey). Conversely, three clusters included at least 19 references and involved several research groups. The first cluster includes among the others the seminal work of Kuhn (1969), Levins & Lewontin (1985), and May (1973), representing a tradition of basic theory, mathematics, and philosophy applied in the study of complexity (Fig. 4; in blue). The second cluster includes the work of Brown (1995), Maurer (1999) and Hubbell (2001), and represents a tradition of macroecological approaches and large-scales system science (Fig. 4; in pink). The third and last cluster includes the work of Allen & Starr (1982), Levin (1992), and Petrovskii (2004), representing a tradition of scaling approaches and application of hierarchy theory in the study of complex natural systems (Fig. 4; in red). Although clusters were found when considering the 100 most cited articles, such structure remained resistant to deviations in the number of nodes in the network, except for the cluster including two references by Ulanowicz. Overall, 68 *complexity* articles cited the references that determined patterns in the clusters, from which 58 cited only references from the three most important clusters.

Discussion

The concept of complexity has been historically intertwined with the study of natural systems (*16*). Indeed, many environmental challenges currently faced by humanity are ‘complex systems problems’ (*8*, *22*, *65*). Solutions to these challenges might appear straightforward (e.g., reducing CO_2 emissions, halting habitat degradation). However, because we lack unified theories, methods, and ultimately a cohesive understanding of complex systems, we can hardly predict whether ecosystemic collapses are a legitimate threat given forecasted – or even current – environmental conditions (*22*, *65*). The study of ecological complexity, therefore, will be central in the 21st century.

To progress in the study of complexity in natural systems, efforts should be coordinated and optimized. Yet, our preliminary literature surveys suggested that the field is disorganized (e.g., Table S1). Furthermore, ecology and conservation are lagging behind recent developments in complexity science, despite the fact that integration of ideas from this field has clear potential for advancements in our understanding of natural systems (*9*, *22*). Therefore, our goal here was to understand how complexity has been conceptualized in ecology and conservation in relation to widespread principles in complexity science and use this information to suggest ways to improve organization in the study of ecological complexity.

What is a complex system, and what is ecological complexity?

From the premise that complexity is an attribute of natural systems (*19*), stems the idea that some natural systems must be characterized by properties that make them more complex than others. Based on these definitions, the first contribution of our synthesis is identifying features typical of complex systems as described in the complexity science literature (Table 1). Unsurprisingly, we found no unequivocal agreement on what exactly constitutes a complex system (*16*, *17*), although many authors converged to a core set of concepts.

Common narratives include the idea that complexity is typical of systems composed of multiple parts and structured across different organizational levels, a vision that puts networks (*66*, *67*) and hierarchies (*5*, *68*, *69*) at the core of complexity. Other concepts include spatiotemporal scale dependencies (*34*, *63*, *70*–*72*), self-organization of the parts that compose a system in increasingly sophisticated modules (*5*, *9*, *73*), and feedback occurring both within and between each level of the system, which constrains both the whole system and its parts (*12*, *15*, *34*, *63*). Stochastic or chaotic phenomena and the potential for alternative states, which are often contingent on the initial conditions of a system and may operate at any organizational level, complete the typical recipe of a complex system (*2*, *12*, *17*, *74*, *75*). Note we did not include 'chaos' in our list of features (*2*, *74*) or 'stochasticity' (*75*, *76*). While these phenomena contribute to our perception of a given system as complex, we believe that they deserve separate discussions because they are difficult to conceptualize and not universally accepted as properties of systems (*74*, *75*).

With our critical review we reduced very broad, interconnected aspects of complexity into a more tractable set of features typical of complex systems (Table 1). This synthesis goes beyond applications within specific subfields and encompass a broad range of perspectives, following both seminal references in the study of complexity (*2*, *5*, *12*, *30*, *71*), and more recent work that also synthesized developments in complexity science, but within subfields in ecology (e.g., *9*, *17*, *29*, *34*). We suggest therefore that the features listed in Table 1 can be used as a template to study more broadly complexity in natural systems. We use this template to assess how ecological complexity has been conceptualized in the peer-reviewed literature.

How do authors conceptualize ecological complexity?

The number of articles referring to 'ecological complexity' has increased exponentially in the last fifty years (Fig. 1), mirroring the trend observed for articles that refer more broadly to 'complexity', and involving all continents except for Antarctica. Despite this growth, what authors conceptualize when referring to ecological complexity has remained to date largely unknown. Therefore, the second contribution of this study is a quantitative assessment of how authors have conceptualized ecological complexity in relation to the template of features identified in our critical review (Table 1).

Overall, we found surprisingly few differences between *complexity* and *control* articles. For instance, approximately a quarter of the *complexity* articles mentioned fewer features than the average *control* article, and *complexity* articles were only 6% more similar to each other than *control* articles (Fig. 2). The term complexity seems therefore to have been often used loosely, confirming the intuition of Proctor and Larson (2005) that it is often "*a placeholder for the unknown*". More specifically, it also suggests that many articles refer to ecological complexity inconsistently with pivotal concepts in complexity science—or that these articles focus on a few of the features typical of complex systems, rather than covering the multifaceted nature of complexity that emerged from our review. Similarly, assessing the co-occurrence of features revealed a highly connected network, with little structure and 98% of all possible connections fulfilled (Fig. 3), and only about a third of the *complexity* articles contributing to the 100 most co-cited references (Fig 4). Together, these parallel lines of evidence suggest that the study of ecological complexity still lacks coordination and structure.

One could argue that we failed to capture the true essence of ecological complexity with our features (Table 1). However, we identified meaningful patterns that suggest the contrary. For instance, a significantly higher number of features in *complexity* articles indicates that authors that appealed to ecological complexity agree, perhaps unconsciously, with the idea that complex systems are characterized by a set of different features. Furthermore, ~ 60% of the features identified in our review were significantly more likely to be related to *complexity* articles (13 out of 22 features; Fig. 3), with this number increasing to ~ 80% of the features (18 out of 22 features) when assessing occurrence of features rather than frequency of use. Even the fact that *complexity* articles were significantly more likely to form network edges is consistent with the idea that authors interested in understanding complexity recognize that this concept is multifaceted and results from the co-occurrence of multiple phenomena (here features). Our analysis also identified relationships expected based on current ecological theory, such as those between scales and hierarchies (*69*, *77*), and networks and interactions (*66*, *67*).

Most notably, the analysis of co-citation networks in our data is remarkably consistent with three prominent philosophies in ecology (Fig. 4). The first co-citation cluster emerged from authors that refer to complexity in relation to a long tradition of basic theory (*1*, *2*, *15*, *58*). The second co-citation cluster emerged from authors that refer to complexity in relation to the concepts of scales and hierarchies (*5*, *18*, *63*, *69*, *78*). The third co-citation cluster emerged from authors that refer to complexity in relation to macroecological theory and the study of large-scale systems (*61*, *62*, *79–81*). These schools of thought have been prominent in ecology for decades (*2*, *71*, *82*), and will continue to be so. Recent developments suggest that the role of theory in ecology will be crucial in the era of big data (*83*), that scales can be a mediator of seemingly irreconcilable ecological patterns (*84*), and that a macroecological approach might be our only way to escape local contingencies in the pursuit of generality (*70*).

Ultimately, despite confusion in the literature on ecological complexity, we found clear trends in how authors conceptualize complexity. We believe that these trends provide fertile ground for better coordination of research efforts.

Towards a cohesive understanding of ecological complexity

Integrating ideas from complexity science in ecology and conservation will be necessary to understand how natural systems will respond to unprecedented, potentially disastrous environmental conditions (*10*, *22*, *65*). Based on the general patterns found in our analysis, this has also the potential to aid in organizing the study of complexity in natural systems. Therefore, here we suggest using 22 features typical of complex systems (Table 1) as a template for organizing and clarifying the study of complexity in ecology and conservation. Practically, this means that authors referring to ecological complexity should do so consciously, and preferably in line with current theory developed in complexity science. To facilitate this transition towards a cohesive study of ecological complexity, we propose the following five prescriptive principles:

1) Prioritize clarity

It is always desirable to specify exactly what one means when referring to complexity, because of the different interpretations of this concept. Yet, we noticed that definitions of ecological complexity are extremely rare in the literature. Complexity seems to be used often as a buzzword, which makes it more challenging to find truly relevant literature, thus slowing progress (*85*, *86*). We suggest that the term complexity should be reserved to studies where many of the features listed in Table 1 are expected to determine the properties of a system. In cases where authors attempt to isolate one or a few of such features, authors should simply state the focus of their study because referring to complexity would only add an additional layer of confusion.

2) Integrate complexity science

Complexity science is an emerging field of research, and therefore, ecological complexity has not been well-understood in this context. For instance, our study could not assess *complexity* articles concerning 'complexity science' and 'complex system science' because the number of articles mentioning these terms was too limited ($n = 24$). Yet, integrating ideas from complex system science in ecology will not only provide an established theoretical framework, but also release important methodological advances. Approaches typical of complex system science such as Alife, cellular automata, multi-agent models, and genetic programming, based on the idea of interpreting natural processes as computation, remain underrepresented in ecology (*21*). These approaches have already provided fresh perspectives on traditional dilemmas including the stability-diversity relationship, critical thresholds in habitat loss and fragmentation, the evolution of maladaptive characters, and more (*9*, *21*, *87*).

3) *Understand metrics of complexity*

Attempting to measure the features identified in our review is already common practice in the study of ecological complexity (*19*). Therefore, the philosophy that we propose here – that complexity can be conceptualized, and thus measured, according to a set of well-established features – will not be novel to many readers. However, these efforts must be sharpened. When measuring properties of systems and referring to those as metrics of complexity, authors should first refer explicitly to the feature that a metric represents, and then discuss results in relation to ecological complexity. Mentioning complexity will not always be relevant (e.g., when focusing on just one of the features presented in Table 1). Similarly, conflating any metric with complexity itself only risks increasing confusion in an already difficult field. As an example, to facilitate this transition we provide a non-exhaustive list of metrics used to measure complexity (Table 2), specifying the relations among these metrics and the features identified by our review.

4) *Appreciate different philosophies*

Our analysis suggests that basic theory, scaling, and macroecology are three important heuristics to which ecologists appeal when studying complex systems (Fig. 4). While these approaches will remain important for the study of complexity in ecology, there are emergent perspectives that will complement and expand these traditional views. For instance, analysis of networks (*66*, *67*) and artificial intelligence (*87*) have been used increasingly often to accommodate the complexity of ecological systems — at times combining the strengths of more than one of these approaches. Notably, studies of complexity are often developed following a reductionist framework, but progressing in our understanding of complexity will require embracing also novel perspectives developed in complexity science (*21*, *88*). One key advance from the natural computation approaches described above is the awareness that very simple rules can produce a wide variety of patterns (*30*, *89*). This powerful idea remains largely unexplored in the study of ecological complexity.

5) *Maximize diversity of perspectives*

Similarly to many other subfields (*90*), we found strong geographical biases in the production of *complexity* articles and a striking lack of representation from the Global South (Figure 1a). While our results confirm that the study of complexity is of global importance and of growing interest in the environmental sciences, they also highlight that we are missing important perspectives from underrepresented regions. Maximizing collaborations beyond the limited scope of one's own research group and promoting international collaborations across country borders will be a key step to bring new ideas and hypotheses in the study of complex systems problems (*91*).

Conclusions

Our hope is that this manuscript will provide guidelines to integrating complexity science, ecology, and conservation, in pursuit of consilience. In our view, developments in complexity science will lead to developments in ecology and conservation – and vice versa – only if ecologists will conceptualize and use the word 'complexity' with more depth. As Richard Feynman (*92*) eloquently proposed, the difficult words we use to refer to natural phenomena rarely inform us about nature itself. Our article will be successful if authors that consider using complexity as a key concept in their work will do so after critically evaluating whether their study actually focuses on complex systems, and, if that is the case, which of the features identified in our critical review are important in that context. Many questions in ecology can be answered without appealing to concepts and approaches from complex system science, and for those studies we suggest that referring to complexity only increases confusion in an already difficult field. Moving forward, it will be important to carve a specific niche within ecology and conservation for studies of complexity, so that we can develop a strong theoretical and methodological background to improve our capacity to forecast how ecosystems will change in response to global change.

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Figures and Tables

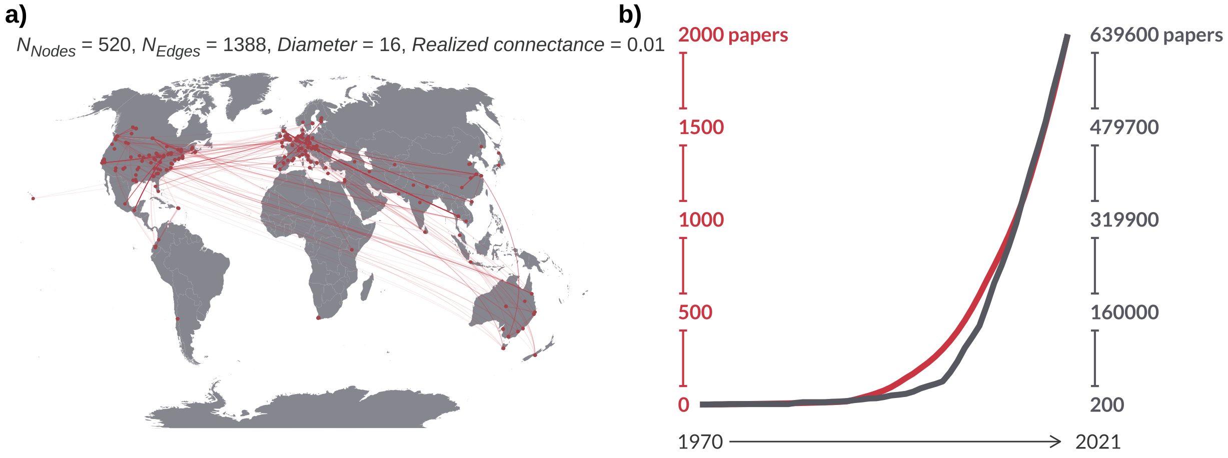

Fig. 1. The study of ecological complexity in space and time. a) Global network of collaborations considering all the authors from the articles that referred to "ecological complexity" in their title or keywords (*n* = 188). Points represent researchers' affiliation addresses, whereas lines indicate collaboration between authors. b) Cumulative production (from 1970 to 2021) between of articles mentioning "complexity" in their titles and abstract considering all the scientific fields (grey line) and separately for the ecology and environmental sciences, as approximated by the search term "ecological complexity" (red line).

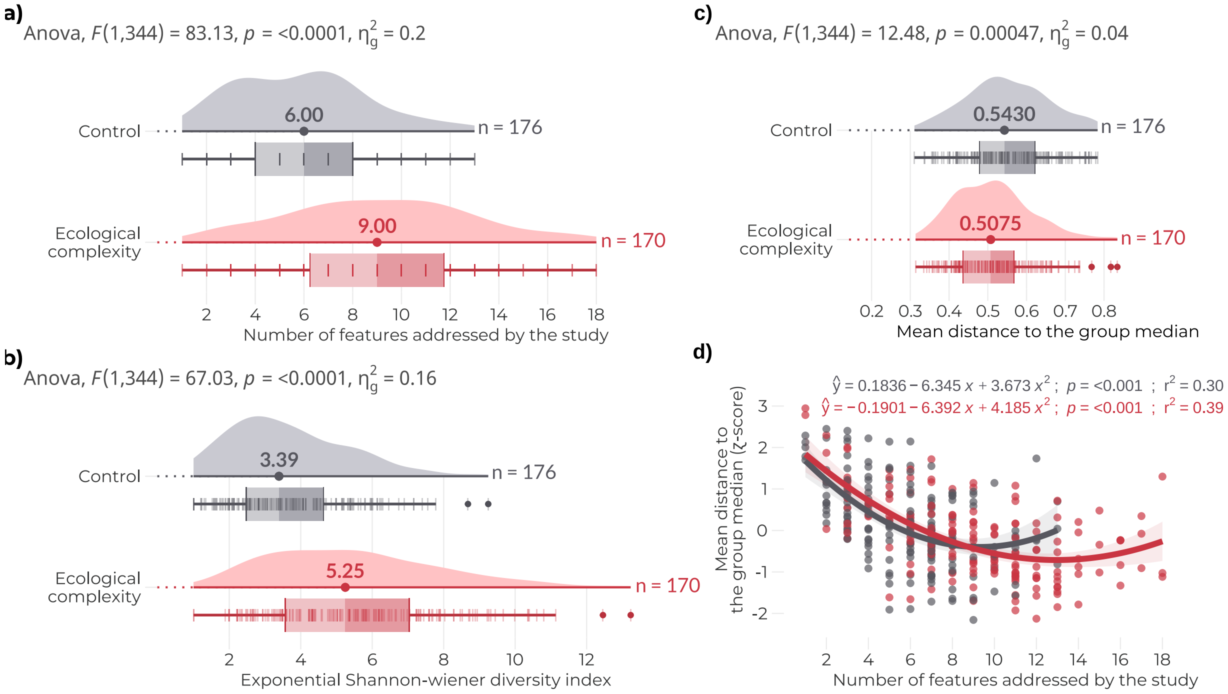

Fig. 2. Comparison between *control* and *complexity* articles. Comparison between *control* (grey) and *complexity* (red) articles considering the features retrieved by the systematic mapping (listed in Table 1). The *control* group (*n* = 176) includes articles randomly selected from the ecological literature and the *complexity* group (*n* = 170) includes articles explicitly referring to 'ecological complexity' in their

title or keywords. (a) The richness of features of each article and (b) the exponential of the Shannon entropy calculated on relative frequency of feature usage were significantly higher in the *complexity* articles. (c) Study uniqueness (i.e., the distance from each article to its group median) was smaller in *complexity* articles, indicating that these were typically more similar among themselves. (d) The relationship between study uniqueness and feature richness shows that articles mentioning fewer features were on average more distant from their group mean, suggesting that these features were rarely mentioned by other articles.

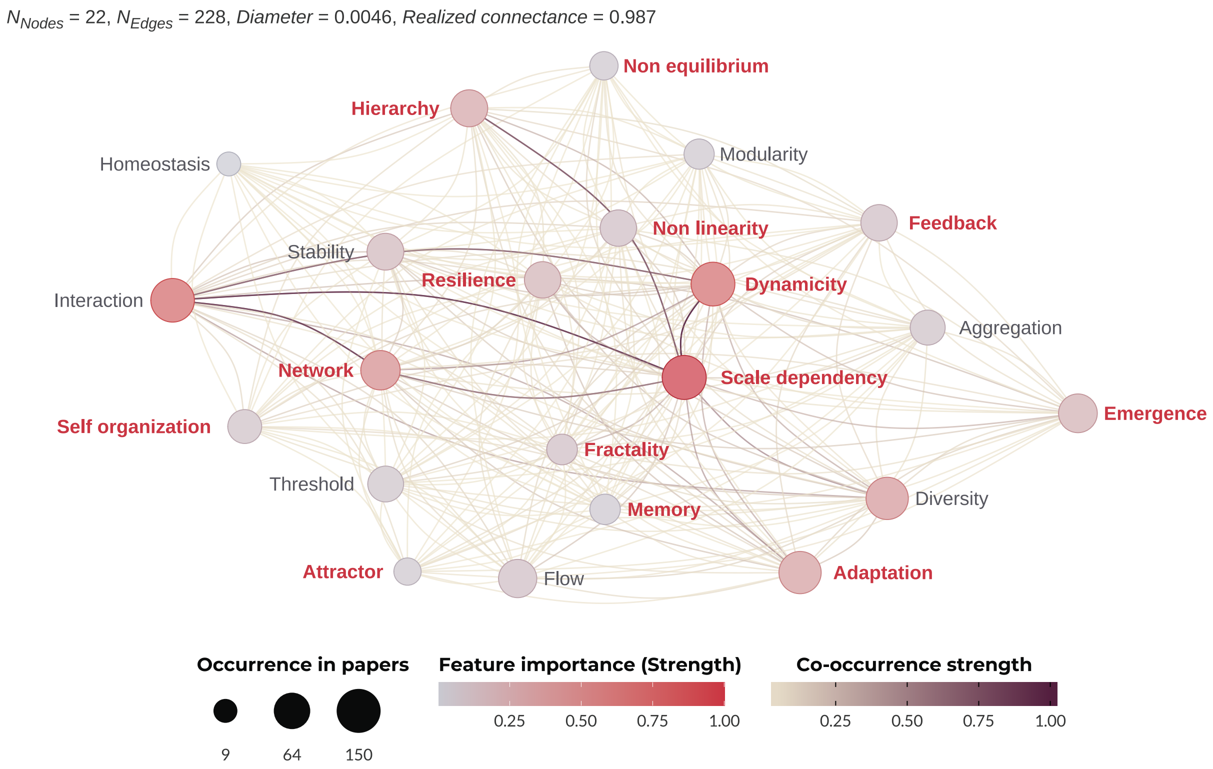

Fig 3. Connections among complexity articles in ecology based on its features. This unipartite network shows the projection of a bipartite network linking complexity articles through their usage of complexity features (Table 1). Features (Nodes of the network) are shown with more red color indicating that features are more significantly associated with complexity articles based on Indicator Species Analysis. Co-occurrence strength (edges) are represented by the sum of the edge weights of the adjacent edges of the node.

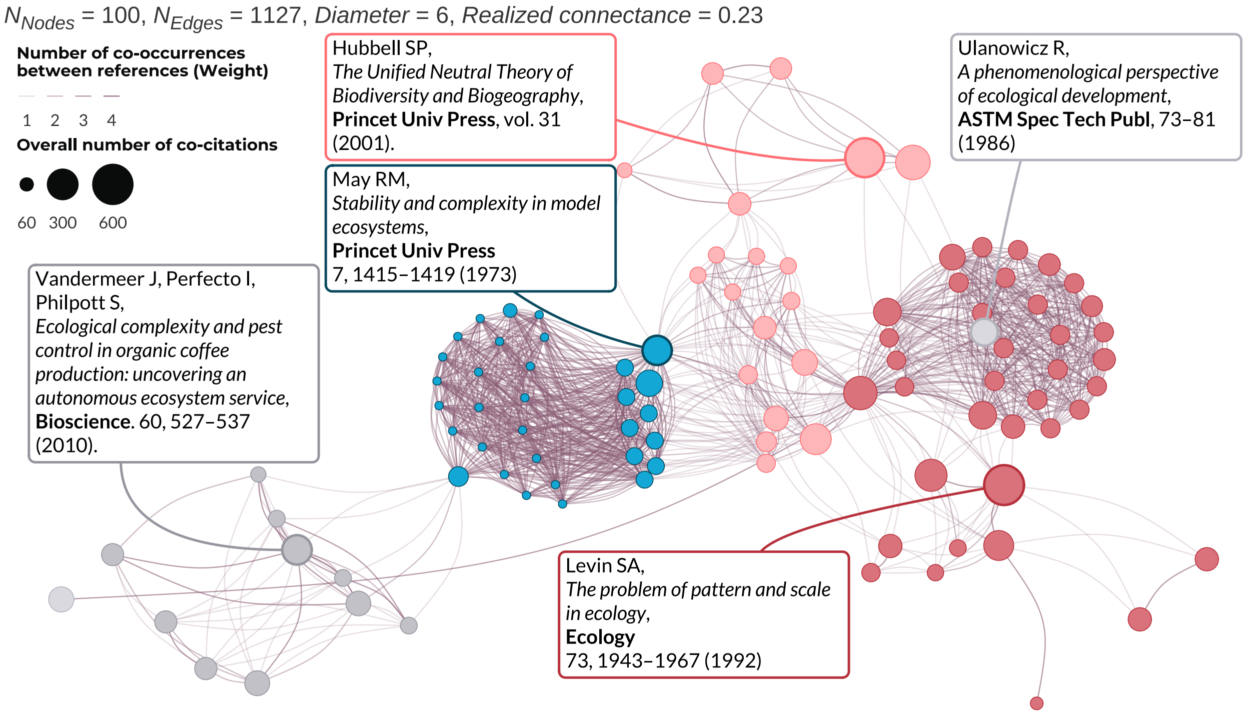

Fig 4. Seminal literature in ecological complexity. Weighted co-citation network for the top 100 co-cited articles in the *complexity* articles. The colors reflect co-citation clusters: foundational complexity theory (in blue); scaling, hierarchies, and cross-scale dynamics (in red); and macroecological theory and large-scale systems (in pink). Two additional clusters (in grey) count 10 or less articles and emerged from the use of "ecological complexity" in a more specific context (e.g., one research group).

Table 1. Features typical of complex natural systems. Features identified through a critical literature review of the literature in complexity science as typical of complex natural systems. Note that search strings are presented as word stem (e.g., 'self-orga') to capture plurals and alternative forms and spellings (e.g., self-organization, self-organisation, self-organising, etc.).

Feature	Definition	Search string
Adaptation	The parts and/or a system change in response to pressures	adapt
Aggregation	The parts that compose a system tend to organize into groups	aggregat
Attractor	One of many states toward which a system tends to evolve	attractor
Diversity	The parts that compose a system are not equal	diversit
Dynamicity	The property of systems and parts change with time	dynamic

Emergence	The property of system characteristics that are not predictable based on the characteristics of their parts	emergen
Feedback	Processes in the system that increase or reduce the likelihood of the same process happening again	feedback
Flow	Exchange of material or information across the system	flow
Fractality	Self-similar regularities that repeat across scales	fractal
Hierarchy	The system exhibits properties at multiple organizational levels	hierarch
Homeostasis	Self-regulating mechanisms that tend to maintain optimal conditions	homeosta
Interaction	The parts that compose a system affect each other	interact
Memory	Previous states of the system influence present and future states	memory + memories
Modularity	The property of parts and systems of being composed by distinct units	modul
Network	A representation of relationships (links) occurring between parts (nodes) in a system	network
Non-equilibrium	The state of a system that did not reach a steady state	non-equilib + non equilib + nonequilib
Non-linearity	Local rules of interaction change as the system evolves	non-linear + non linear + nonlinear
Resilience	The capacity of a system to resist and recover from disturbance	resilien
Scale-dependence	The property of system patterns to change with scale (e.g., spatial, temporal, or taxonomic)	scal + scale-depend + scale depend
Self-organization	The tendency of a system to develop complex patterns from simpler states	self-orga + self orga + selforga

Stability	The tendency of a system to return to its equilibrium state	stabilit
Threshold	The context in which a small change in the conditions of a system results in large change in the system itself	thresho

Table 2. A non-exhaustive list of metrics used in the ecological literature when assessing ecological complexity, and their relationship with the features identified in our article. We refer particularly to Parrot (2010), Ladyman et al. (2013), Delmas et al. (2018), and Wiesner and Ladyman (2019) for comprehensive reviews of metrics designed to measure complexity.

Feature	**Metric**	**Reference**
Diversity	Shannon entropy: $-\sum_i P\,(x_i) log P(x_i)$, where P is the probability of an event i. Measures the amount of information in an event drawn from that distribution.	(*17*)
Diversity	Mean information gain: $H_s(L+1) - H_s(L)$, where H_s is the Shannon entropy of the sequence of length L. Measures the amount of new information gained by knowing an additional step in time or space.	(*19*)
Diversity	Fluctuation complexity: $\sum_{i,j} P_{L,ij} log\left(\frac{P_{L,i}}{P_{L,j}}\right)^2$, where $P_{L,ij}$ is the probability of observing j immediately following i. Measures the degree of structure in a time series.	(*19*)
Dynamicity	Information theoretic measure of correlation between the two halves of a stochastic process $\lim_{t\to\infty} I(X_{-t}X_{-t+1}\ldots X_{-1}; X_0X_1\ldots X_t)$. Also known as effective measure complexity, predictive information, and excess entropy.	(*93*)
Fractality	Fractal dimension: $\log(N) / \log(r)$, where N is the number of self-similar pieces, r is a magnification factor. Measures the degree of self-similarity.	(*19*)
Fractality	Power law: $P(x) = cx^{-\gamma}$. Measures the degree of pattern consistency across scales.	(*94*)
Network	Modularity: $Q = \sum_i \left(e_{ij} - \left(\sum_j e_{ij}\right)^2\right)$, where e_{ij} are the fraction of edges that link nodes in cluster i to nodes in cluster j. Measures the strength of division of a network into groups (modules).	(*66*)
Network	Connectance: the proportion of realized ecological interactions (m) among the potential ones (L), or L/m.	(*66*)

	Potential links are most often calculated as the squared species richness. Measures the fraction of all possible links that are realized in a network.	
Network	Degree distribution: the distribution (P_k) of the number of links (interactions) per species; if $N(k)$ is the number of nodes with k interactions, and S is the total number of species in the network, then $P(k) = N(k)/S$. Measures the heterogeneity of a system: if all the nodes have the same degree k, the network is completely homogeneous.	(*66*)
Network	Singular Value Decomposition (SVD) Entropy: within a matrix i, the nonzero singular values (σ_i) and the number of nonzero entries (k) are extracted. SVD entropy is then calculated as: $$J = \frac{-1}{ln(k)}\sum_{i=1}^{k} s_i \times ln(s_i)$$ where $s_i=\sigma_i/sum(\sigma)$. Measures the number of vectors needed for an adequate explanation of the data set, where higher values indicate that the dataset cannot be efficiently compressed.	(*95*)
Stability	Eigenvalues of the Jacobian matrix: $[J_{ij}] = [\partial f_i/\partial x_j]$, where x is a state and $f_i = dx_i/dt$ at a fixed point. If all real parts of the eigenvalues are negative, this fixed point is a stable attractor, and the system returns to the steady state after perturbation.	(*20*)
Stability	Coefficient of variation: $CV = \sigma/\mu$, where σ is the standard deviation and μ the average of a time series. Measures the level of dispersion around the mean of a series.	(*96*)
Self-organization	Mutual information: measures the difference in uncertainty between the sum of the individual random variable (ex. X and Y) distributions and the joint distribution: $I(X;Y) = H(X) + H(Y) - H(X,Y)$, where H represents Shannon entropy. When two variables are completely independent from one another, $H(X) + H(Y) = H(X,Y)$ and the mutual information is zero. Any covariance between X and Y (i.e. self-organization or order) will result in an uncertainty in the joint distribution that is lower than the sum of their individual distributions.	(*20*)