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Title Towards a cohesive understanding of ecological complexity

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Abstract
Ecological systems are quintessentially complex systems. Understanding phenomena typical of complex systems is, therefore, critical to progress in ecology and conservation amidst escalating global environmental change. However, myriad definitions of complexity and excessive reliance on traditional scientific approaches hamper conceptual advances and synthesis. Ecological complexity may be better understood by following the solid theoretical basis of complex system science (CSS). We review features of ecological systems described within CSS and conduct bibliometric and text-mining analyses to characterize articles that refer to ecological complexity. Our analyses demonstrate that the study of

complexity in ecology is a global, increasingly common, but highly heterogeneous endeavor that is only weakly related to CSS. Current research trends are typically organized around basic theory, scaling, and macroecology. We leverage our review and the generalities identified in our analyses to suggest a more coherent and cohesive way forward in the study of complexity in ecology.

Teaser

Grounding the study of ecological complexity in complex system science is key for progress in ecology and conservation amidst escalating global environmental change.

INTRODUCTION

Understanding nature's complexity is at the core of science (*1–6*). In ecology and conservation, studying complexity has led to both the development of theories (*2*, *7–11*) and considerations in policies and plans for environmental management (*12–16*). Understanding complexity is also becoming increasingly important in the face of accelerating global environmental change, because ecological systems exposed to multiple stressors often display phenomena typical of complex systems (*14*, *15*, *17–19*). 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*" (*20*).

Complexity fulfills a central role in ecology and conservation because ecological systems are quintessentially complex systems (*3*, *18*, *21*). Understanding their complexity may, therefore, be key for resolving the major environmental crises currently faced by our societies (*19*, *22*, *23*). For instance, the risk that ongoing climate change will result in abrupt shifts to alternative states in the Earth's climates is considerable, and this awareness will be crucial to inform radical climate policy aimed at preventing catastrophic scenarios (*15*). Climate change, in turn, affects ecosystems and food webs that are already eroded from thousands of years of human activities worldwide (*24*, *25*). Recognition of the potential for a planetary systemic failure due to climate-biodiversity feedback is therefore soberingly increasing (*14*, *19*, *22*, *26*). Nevertheless, the goal of untangling these complex dynamics of ecological systems is hindered by the fact that such systems are rarely studied as complex systems *per se*. Most research in the environmental sciences continues to follow traditional reductionist approaches (*27*) instead of capitalizing on developments in complex system science.

Complex system science (CSS) emerged in the 20th century from a confluence of disciplines that independently attempted to bypass the limitation of traditional reductionist approaches in the study of complex systems (*6*, *28*, *29*). CSS is tied to more traditional studies on complexity, but it distinguishes itself as an independent, quantitative field that attempts to identify general laws across complex systems of different types, including biological, social, or technological alike. Despite the historical epistemological and ontological difficulties in defining complexity (*3*, *30–32*), researchers in CSS have reached a consensus on what characterizes complex systems (*4–6*, *18*, *21*, *33*, *34*) (Table 1). Grounding the study of ecological complexity in CSS has, therefore, the potential to facilitate coordination and advancements in ecology and the study of complexity. Here, we provide a synthesis to help tie the two fields together.

Coordination is needed because, as much as the study and invocation of ecological complexity continue to grow in the scientific literature, there is also persistent imprecision in how ecologists refer to "complexity" in their work. 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; Fig. 1a). The 71 reviews captured by this search discuss a broad range of topics, from the evolutionary novelty of venoms (*35*) to the biogeochemistry of marine polysaccharides (*36*), but none directly addresses what ecological complexity is or how it emerges (Table S1). Instead, complexity is often used in a colloquial sense, implying that a study focuses on a system that is difficult to comprehend, "complicated". Based on these 71 reviews, the study of ecological complexity appears highly disorganized, with few common threads across an extensive body of literature. This lack of clarity will likely confound the communication of ideas, foster unnecessary debates, limit research progress, and hinder the translation of findings into practice (*37*). Given the importance of understanding natural systems in the face of global change, seeking common ground in how we study and define complexity is not merely a semantic problem, but rather a pressing challenge of our times.

To this end, we use a 'research weaving' approach (*38*) combining the strengths of a critical review, text mining, and 'science of science' (*39*) analyses (Fig.1). We first assess how ecologists conceptualize complexity, and then suggest a more cohesive approach to the study of complex ecological systems centered around principles of CSS, following a three-pronged approach: (i) we review CSS literature to identify a list of features typically attributed to complex ecological systems (Fig. 1b; Table 1); (ii) we empirically assess the ecological literature to understand how these features relate to the study of 'ecological complexity' (Fig. 1c,d; results from the analyses illustrated in Figs. 2–5); and (iii) we leverage our critical review and 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 understanding complexity in a novel way: instead of defining the study of complexity from first principle reasoning, we quantitatively assess the literature to understand how ecologists have conceptualized complexity. Before addressing current practice in ecology and how to improve apparent confusion in the study of ecological complexity, we contextualize our work by providing a brief account of the history of CSS and by describing the philosophy underlying CSS within the broader study of complexity.

A BRIEF HISTORY OF COMPLEX SYSTEM SCIENCE

Understanding the history of CSS helps to appreciate why progress in the study of ecological complexity following this paradigm has high potential to advance in ecology and conservation. In brief, CSS aims to discover general rules across biological, technological, social, and other types of complex systems (*6*, *21*, *40*). This broad objective has made CSS historically fluid and ever-evolving, gradually encapsulating various ideas, methods, and traditions (*5*, *41*). While CSS has roots in ancient philosophy (e.g., Aristotle's emergence in the *Metaphysics*), formal research into complex systems began only towards the 19th century. The scientific revolution of the 16–17th centuries revealed fundamental laws of nature, but the principle that nature can be perfectly predicted following such laws soon began to falter, particularly in micro- and cosmo-physics. For instance, in 1871, James Clerk Maxwell began to explore the limitations of the second law of thermodynamics, and, in 1890, Henri Poincaré identified strong dependence on initial conditions when predicting the motion of celestial bodies using the laws of gravitation, tracing the way for chaos theory (*6*, *10*).

In the 20th century, it became increasingly clear that the global properties of complex systems can be difficult to predict based on fundamental laws of nature that rule the parts composing such systems – as the adage goes, "the whole can be greater than the sum of its parts". In turn, authors began to argue that natural laws do constrain, but do not determine, the global properties of complex systems, where interactions among units can determine phenomena that emerge across hierarchical levels of complex systems (*4*, *5*, *29*, *42*, *43*). CSS embraced this need to consider interactions, providing a new paradigm for understanding reality beyond traditional scientific views. The birth of CSS was inspired by developments including the conceptualization of system theory, spearheaded in the 1930s by Ludwig von Bertalanffy, by mathematical work, e.g., on self-organization and dissipative systems by Ilya Prigogine or on chaos by Edward Lorenz in the 1960s, and finally by increasing reliance on computer simulations after World War II (*44*, *58*).

Following these early developments, the study of complex systems became an explicit research focus from the 1970's onward (*45*), especially with the establishment of the Santa Fe Institute (https://www.santafe.edu/) (*32*). Founded in 1984 by eight physicists, including Nobel Prize winner Murray Gell-Mann, the Santa Fe Institute was the first institution fully dedicated to research of complex systems. Since then, many centers for the study of complexity have opened across the planet. Today, the Santa Fe Institute connects a global network of scientists that are seeking a better understanding of complex systems and plays a key role in popularizing CCS outside academia (see, e.g., the Complexity podcast – https://complexity.simplecast.com/). Principles from CSS have been instrumental in meta-science (*39*), mathematics (*46*), physics (*28*), medicine (*47*), sociology (*48*), archeology (*49*), economy (*50*), social management (*51*), and computer science (*52*) among many other disciplines. Ecology is one of those disciplines, and it has been argued that CSS can provide important answers to many current crises faced by humanity (*21–23*).

In 1989, Heinz Pagels suggested that "*the nations and people who master the new sciences of complexity will become the economic, cultural, and political superpowers of the next century*" (*53*). Despite skepticism that has persisted around CSS since its inception (*52*), the diffusion of this paradigm in the last three decades, together with important developments documented across many fields of knowledge (*5*, *54*), is a testament to the vision of the pioneers in this field.

THE PHILOSOPHY OF COMPLEX SYSTEM SCIENCE

The study of complexity is a broad endeavor that includes both philosophical considerations on the epistemology and ontology of complexity (*6*, *30*), as well as assessments of complex systems following a CSS paradigm (*18*, *21*). It is an effort that spans from comparative religion, philosophy, and ethics to mathematics and physics. Because of these different viewpoints, defining "complexity" has been a long-standing challenge. For instance, some authors categorize their object of study as either complex or not, while others conceptualize complexity along a continuum (*30*). Complexity can also be defined differently across scientific domains, e.g., computer scientists may refer to the time and computational memory required to solve a problem (*56*, *57*), whereas mathematicians may refer to chaotic and nonlinear dynamics (*58*). It has been even suggested that complexity is "*a placeholder for the unknown*", a "*nomadic term that links disparate discourses*", and therefore a strict definition would only be an unwarranted constraint (*31*). This flexibility might underlie how some fields that leverage explicit metrics of complexity, like computer science, have advanced faster than others in their quest to understand complexity. Meanwhile, immoderate freedom also seemed to have hindered coordination and synthesis.

CSS bypasses most of these philosophical aspects and is thus more operational. Specifically, CSS is the quantitative field that seeks to discover laws that describe phenomena in complex systems. Decades of research in CSS, therefore, provide a robust and pragmatic framework to classify phenomena also in complex ecological systems. Ecologists turning to CSS, however, must be aware that this field demands a shift from the traditional scientific paradigm (*3*, *6*, *44*, *59*). Scientists have engaged complexity following three historically successful approaches: (i) determinism, i.e., systems can be explained by adequate mathematical models; (ii) reductionism, i.e., any system composed by many entities can be understood by studying such entities individually; and (iii) disjunction, i.e., the way to resolve cognitive problems is isolating them within specialized disciplines. These principles can fail, as (i) some systems cannot be easily predicted, even when they follow deterministic laws (*4*, *18*, *32*, *60*); (ii) organization of units in a system can determine the emergence of some properties and the inhibition of others, hindering efforts to predict systems by studying solely their parts (*6*, *27*, *30*, *59*); and (iii) capitalizing on approaches across disciplines has greatly increased our understanding of complex systems (*3*, *6*, *46*).

Due to these inconsistencies, the traditional scientific model has often failed ecologists interested in understanding complex systems (*27*). Conversely, CSS embraces these aspects and provides alternative insights – it explicitly recognizes the importance of emergence, and it is, by nature, integrative across disciplines. Transcending reductionism is a major divide in the study of complexity between two philosophical views – restricted complexity, of which CSS is an expression, and generalized complexity [see (*6*, *44*) for more comprehensive accounts on restricted and generalized complexity].

Restricted complexity is interested in the dynamics of complex systems composed of a large *number* of interacting parts (i.e., the more parts and interactions, the greater the complexity). Restricted complexity postulates that certain phenomena make systems more difficult than others to understand and predict, bypassing epistemological and ontological considerations on complexity, and aims at understanding laws determining those phenomena. Drawing inspiration from mathematics and physics, restricted complexity emerged to address the gap left from scientific discoveries that demonstrate how the traditional scientific paradigm is inadequate to predict phenomena typical of some systems (e.g., chaos, nonlinearities, tipping points). It is a search for the "laws of complexity", and therefore it follows a reductionist model (*32*). Our manuscript stems from views consistent with restricted complexity, a perspective that we consider appropriate given the strong quantitative focus of modern ecology.

Generalized complexity suggests complexity not only concerns all scientific disciplines, but also more broadly human systems of knowledge. Traditional scientific views are completely replaced, and reductionism is substituted by the seeking of a dynamic understanding of the relation between a whole and its parts, as well as their mutual implications. Rather than the number of parts interacting in a system, generalized complexity focuses on the *nature* of the interactions among the parts (i.e., more complex interactions lead to more complex systems). Generalized complexity sustains that our inference on complex systems can never be perfect because studying a system requires creating boundaries, an arbitrary process that excludes certain aspects of the system itself and of the environment hosting that system. Generalized complexity originated from the integration of post-structural philosophy with biology, and allows us to better identify the limits of our knowledge systems.

A balance between restricted and generalized complexity is needed to facilitate scientific progress. Restricted complexity emerged to aid in cases where traditional scientific methods failed, and generalized complexity emerged to counterbalance inflated claims that restricted complexity was seen to hold (*6*). However, we note that generalized complexity does not argue against reductionism – instead it recognizes some of its limitations. Understanding the world necessarily requires reduction, and a balance between conceptual advances and urgent action will be necessary to face the global environmental crisis (*61*, *62*).

UNTANGLING THE FABRIC OF ECOLOGICAL COMPLEXITY

To understand how ecologists conceptualize complexity, we proposed a research weaving exercise designed to identify general patterns in how authors conceptualize complexity in ecology (Fig. 1b-e; see Materials and Methods). Briefly, we first 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. Last, we use this dataset to describe spatiotemporal trends in the study of ecological complexity (Fig. 2), to analyze thematic diversity (Fig. 3), and to identify patterns in connections between feature usage (Fig. 4) and co-citation of the references cited in articles that explicitly refer to ecological complexity (Fig. 5).

Because the concept of complexity should recall similar ideas for different scientists, articles that explicitly refer to ecological complexity should more frequently mention features typical of complex systems than the *control* group articles (or "*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 biogeographical 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 the well-established principles we identified in reviewing relevant literature in CSS (Table 1).

Features of complex ecological systems identified from complex system science

We found that scientists in CSS identified a core set of concepts that characterize complex systems. Common narratives include the idea that complexity is typical of systems composed of multiple, diverse parts and structured across different organizational levels (*3–5*, *18*, *21*, *32*), a vision that puts networks (*52*, *63*) and hierarchies (*9*, *64*, *65*) at the core of ecological complexity. Other concepts include spatiotemporal scale dependencies (*27*, *66–68*), self-organization of the parts that compose a system in increasingly sophisticated modules (*9*, *21*, *32*, *69*, *70*), and feedbacks occurring both within and between each level of the system, which stabilize and constrain both the whole system and its parts (*6*, *18*, *30*, *66*, *68*). Chaotic dynamics 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*, *18*, *71*, *72*). We chose 23 representative features to synthesize more specific aspects that emerged consistently from this broad range of concepts (Table 1).

Spatiotemporal patterns in the study of ecological complexity

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. 2a), 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. 2b; see also Fig. S1).

The diversity of complexity articles

We ran a topic modelling analysis using the Latent Dirichlet Allocation (LDA) to verify whether the 23 features we selected through our critical review (Table 1) are relevant to characterize *complexity* articles, and to what extent these contribute more to *complexity* than *control* articles. All features except 'aggregation' appeared more often in the top 0.5% important features in topics from the *complexity* group compared to the *control*, and the average probability of a feature to characterize a document was higher for the *complexity* group (Fig. S2).

Having assessed the reliability of the 23 features we identified in our critical review, we compared *complexity* and *control* articles with respect to their reference to these features. *Complexity* articles included a significantly (α = 0.05) higher number of features than expected from a random sample of *control* articles from the ecological literature (Fig. 3a-b) and were more similar to each other than expected by chance alone (Fig. 3c-d). Specifically, *complexity* articles mentioned on average 9 out of 23 features, against the 6 observed in *control* articles ($F_{1,344}$ = 86.6, p < 0.0001; Fig. 3a). This result was consistent when accounting for features' relative abundances ($F_{1,344}$ = 68.53, p < 0.0001; Fig. 3b). 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 0.54 ± 0.10 ($F_{1,344}$ = 10.92, p = 0.001; Fig. 3c). 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 less commonly mentioned in other articles from our sample (Fig. 3d).

A network of complexity features

The features identified in our critical review formed a highly connected network (Relative Connectance = 0.988; Fig. 4). Most of the features co-occurred at least once, although the features "scaling", "interaction" and "dynamicity" contributed disproportionately more in terms of connection strength and node weight (Fig. 4, S3). By modeling the network using an Exponential Random Graph Model (ERGM), we found that *complexity* articles are more likely to form connections in the network (edges) than *control* articles (estimate ± SE: 0.47 ± 0.02, *z-value*: 27.67, p < 0.0001). Conversely, network homophily (i.e., similar nodes are more likely to connect than dissimilar ones) was not significant (estimate ± SE: –0.04 ± 0.02, z-value: –1.91, p = 0.06), indicating overall that *control* and *complexity* articles tend to be interconnected with each other. Some of the most important features for the extracted network (e.g., the terms "network" and "diversity") were not typically common to the *complexity* articles (Fig. 4, in gray).

Co-citation network for the ecological complexity literature

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. 5). Two clusters included 10 or fewer references and reflected the production of two research groups (Fig. 5; in gray). Conversely, three clusters included at least 19 references and involved several research groups. The first cluster includes, among others, the seminal work of Kuhn (*73*), Levins & Lewontin (*74*), and May (*2*), representing a tradition of basic theory, mathematics, and philosophy applied in the study of complexity (Fig. 5; in pink). The second cluster includes the work of Levin (*18*), Brown (*75*), Maurer (*76*) and Hubbell (*77*), and represents a tradition of macroecological approaches and large-scale system science (Fig. 5; in blue). The third cluster includes the work of Allen & Starr (*9*), Levin (*68*), and Petrovskii (*78*), representing a tradition of scaling approaches and application of hierarchy theory in the study of complex ecological systems (Fig. 5; in gold). Although these 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 seminal 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. The adjacency matrix showing the pairwise co-occurrence of all 100 articles can be found in the supplementary information (Fig. S4).

THEMES IN ECOLOGICAL COMPLEXITY

The concept of complexity has been historically intertwined with our understanding of nature (*3*, *31*, *32*, *80*), with many environmental challenges currently faced by humanity being "complex systems problems" (*13*, *14*, *16*, *19*, *21*, *22*). Solutions to these challenges might appear straightforward (e.g., reducing emissions of greenhouse gasses, halting habitat degradation), but because we lack unified theories, methods, and ultimately a comprehensive understanding of complex ecological systems, we can hardly predict whether ecosystem collapses are a legitimate threat given current or forecasted environmental conditions (*19*, *22*). Some phenomena might even be impossible to predict, a crucial aspect that scientists often fail to communicate effectively with the public (*61*). The study of ecological complexity will be central in clarifying these aspects in the coming century (*14*, *28*).

Nevertheless, our analysis suggests that the field of ecological complexity is disorganized, hampering a coordinated and optimized progress. The reviews that we assessed based on our preliminary literature survey (Fig. 1a, Table S1) focus on a broad spectrum of unrelated themes, and we could not assess *complexity* articles concerning CSS independently, because we only found 24 such articles. Furthermore, ecology and conservation are lagging behind recent developments in complexity science (*22*, *58*, *69*). For instance, a recent analysis suggests that deterministic chaos is not uncommon in nature (*81*), but attempts to reveal its influence on natural systems remain comparatively rare. Similarly, the potential for catastrophic scenarios is largely understudied (*19*), meanwhile recent evidence suggests that global warming is likely to trigger at least some climatic tipping points (*15*). These are dynamics that must be understood urgently, a goal which could be directly pursued following principles from CSS. In the following sections, we discuss how we could best achieve this objective.

What makes a system complex?

From the premise that complexity can be studied as an attribute of ecological systems (*40*, *72*, *82*, *83*) stems the idea that some ecological systems must be characterized by properties that make them more complex than others. Based on this principle, we conducted a critical review to identify features typical of complex systems as described in the CSS literature. Through this exercise we reduced very broad, interconnected aspects of complexity into a more tractable set of features typical of complex systems (Table 1). Our synthesis goes beyond applications within specific subfields and encompasses a broad range of perspectives, following both seminal references (*3–6*, *18*, *21*, *32*, *43*, *84–88*), and more recent work that focuses on application of the CSS paradigm in ecology and conservation (*10*, *11*, *30*, *37*, *54*, *58*, *66*, *69*, *72*, *82*, *89–91*). Therefore, we suggest that the list provided in Table 1 can be used as a template to organize the study of complex ecological systems around well-established themes in CSS.

We recognize elements of subjectivity in our work. For instance, we chose to omit some concepts developed in CSS from our list of features, including panarchy (*92*), heterarchy (*91*), brittleness (*93*), and criticality (*11*, *88*). These are important conceptual aspects of CSS but are less general than the features we selected, e.g., they rarely occur in the *complexity* papers we retrieved (Fig. 1c,d). Nevertheless, perhaps over-simplistically, the concepts embodied by these terms can be represented by combining different features proposed in our work. For instance, panarchy relates to stability and dynamicity, heterarchy to networks and hierarchies, brittleness to resilience and modularity, and criticality to dynamicity, fractality, scaling, and attractors (Table 1). We also purposely chose to represent some of our features using very general terms – for example the feature "diversity", with the term "biodiversity" alone being the object of volumes of discussion. Another relevant example is scaling, which has been used loosely to describe the property of some ecological phenomena to change across spatial scales, and more formally in the context of scale-invariant laws discovered in ecology (*11*) (see "efficient theories" below). Keeping these limitations in mind, we believe that the flexibility coming with the broad terms we chose will accommodate the many different phenomena that have been described in complex ecological systems under a broad, but organized, conceptual framework.

Because of these limitations, our review should be seen as the beginning of a general effort to explore CSS for ecologists interested in complexity, not as a definitive guide to the vast field of ecological complexity. Importantly, while some of our choices are arbitrary, we do not see a single objective way to replicate our studies while removing personal evaluations. Relying solely on bibliometric tools to identify alternative features to those we propose would have substantial limitations (*94*). For instance, different terminologies can be used by different authors to express the same concept [see, e.g., "complex adaptive systems" *sensu* (*3*) vs. (*4*)], and while the human mind can recognize these patterns, algorithms would likely fail to do so. Furthermore, text analysis would skew our assessments towards concepts in papers, neglecting books and letters that we have read and used to inform our assessment (*55*). For this reason, we preferred a critical review to a topic modeling approach for identifying the features synthesized in Table 1, which might be more broadly applied in the study of complexity in ecological systems. Acknowledged these aspects of our work, we next discuss how we used the template of 23 features to assess how ecological complexity has been conceptualized in the peer-reviewed literature.

How do authors conceptualize ecological complexity?

Our analyses found that the number of articles referring to 'ecological complexity' has increased exponentially in the last fifty years (Figs. 2, S1), 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. In parallel to reviewing CSS in relation to ecological systems (Fig. 1b,d), a second contribution of this manuscript is to provide a quantitative assessment of how authors have conceptualized ecological complexity in relation to the features identified in our critical review (Fig. 1c-e; Table 1).

Overall, we found limited 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. 3). The term complexity seems therefore to have been often used loosely, confirming the perspective that the word "complexity" is often used as a "*placeholder for the unknown*" (*31*). More specifically, it 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 different aspects 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. 4), and only about a third of the *complexity* articles contributing to the 100 most co-cited references (Fig 5). Together, these parallel lines of evidence suggest that the study of ecological complexity has lacked 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 might agree that more complex systems are complex owing to the interplay of a larger set of features. Furthermore, ~ 60% of the features identified in our review were significantly more likely to be related to *complexity* articles (14 out of 23 features; Fig. 4), with this number increasing to ~ 80% of the features (19 out of 23 features) when assessing occurrence of features rather than frequency of use. A caveat to these results is that not all analyses engaging with complexity require consideration of many features, e.g., macroecological models, and unnecessarily complicated models are indeed inconsistent with principles from CSS. Last, our analysis identified relationships expected based on current ecological theory, such as those between scales and hierarchies (*65*), and networks and interactions (*63*).

Most notably, the results of co-citation network analysis are consistent with three prominent philosophies in ecology (Fig. 5). The first co-citation cluster emerged from authors that refer to complexity in relation to a long tradition of basic theory and mathematics (*1*, *2*, *30*, *73*). The second co-citation cluster emerged from authors that refer to complexity in relation to the concepts of scales and hierarchies (*9*, *37*, *65*, *68*, *95*). The third co-citation cluster emerged from authors that refer to complexity in relation to macroecological theory and the study of large-scale systems (*76*, *77*, *96*–*98*). These schools of thought have been prominent in ecology for decades, and will likely continue to be so. Indeed, recent developments suggest that the role of theory in ecology will be crucial in the era of big data (*99*), that scales can be a mediator of seemingly irreconcilable ecological patterns (*100*), and that a macroecological approach might be our only way to escape local contingencies in the pursuit of generality (*27*).

Ultimately, despite confusion in the literature on ecological complexity and some limitations of text mining approaches, we found promising trends for coordination of research efforts.

TOWARDS A COHESIVE UNDERSTANDING OF ECOLOGICAL COMPLEXITY

We interpret the results of our research weaving exercise as evidence that studies targeting complexity in ecology should more frequently follow principles from CSS. This will be key because such studies have the potential not only to reveal how ecological systems are responding to global change, but also to advance theory in both disciplines. On the one hand, developments in CSS can provide ecology with new theories and tools. For instance, studies on the mathematics of fractals and of self-similarity permeate many fundamental theories in ecology (*101*, *102*); mechanistic simulations such as cellular automata and agent-based models, developed by computer scientists in the 1950s, are increasingly used to explore emergent biological phenomena (*88*, *103*, *104*); and genetic algorithms (*84*) are now used in several ecological applications (*105*). On the other hand, ecology has held a special place in the development of theory for CSS. Ecological research on populations and ecosystems has provided many insights, e.g., on non-linear dynamics (*106*, *107*), chaos (*60*, *71*, *81*), tipping points (*12*, *15*, *108*), scaling (*11*, *68*, *109*), resilience (*110*, *111*), and natural computation (*58*). Better integration of principles from CSS in ecology will reinforce this virtuous cycle.

An example of successful integration between CSS and ecology comes from the application of principles from the three clusters outlined by our analysis – theory, scaling, and macroecology (Fig. 5) – in searching for efficient theories [*sensu* (*99*)]. These are typically "theories of averages" that identify regularities appearing in ecological systems at certain levels of organization (*11*, *21*). Efficient theories generate first principle predictions across scales of ecological organization, usually based on mathematical models, and ecologists have successfully dealt with the complexity of ecological systems by developing a number of these theories. Ecological theories developed in the last decades allow testing explicit predictions on a variety of phenomena including biodiversity (*101*, *112*, *113*), abundances and spatial distributions of species (*113*), distribution networks in animals and plants (*102*), or responses to temperature across levels of biological organization (*114*). The principles on which these theories are based include information theory (*115*, *116*), optimization of energy dissipation (*102*), metabolic rates (*117*), or chemical laws (*114*). While it has been argued that identifying such efficient theories should be the primary goal of ecologists (*61*), progress is slow because of the urgency to solve pressing environmental issues with other tools currently at hand (*62*).

This tension between a search for general, theoretical advancements, and resolving more specific case studies, is useful to advancing ecology, and there is no doubt that traditional scientific views will continue to provide important insights on ecological systems. Yet, approaches from CSS have already yielded fresh perspectives on historical dilemmas that could not be solved with traditional approaches. These include insights on the stability-diversity relationship [e.g., negative feedbacks in species interactions can promote stability in dynamic systems (*118*)], on critical thresholds in habitat loss and fragmentation [e.g., realized connectivity effects on genetic drift depend on thresholds of habitat area left in a landscape (*119*)], on the evolution of maladaptive characters [e.g, when considering spatial dynamics, maladaptive traits can be retained in a population despite their disadvantages (*120*)], on the regulation of emergent behaviors [e.g., simple rules can explain how fireflies coordinate their light pulses (*121*)], among many more topics (*58*, *69*).

This non-exhaustive list of contributions highlights how approaches from CSS, although often lacking common methodologies, are characterized by shared conceptual underpinnings that separate CSS from traditional scientific views. For instance, a key conceptual advancement owed to CSS is the awareness that very simple rules can produce a wide variety of patterns, with complexity stemming from simplicity (*6*, *23*, *60*, *85*, *122*, *123*). This powerful idea remains largely unexplored in ecology, but is central to approaches typical of CSS such as A-life, cellular automata, multi-agent models, and genetic programming that are based on the idea of interpreting natural processes as computation (*58*, *123*). More broadly, CSS is interdisciplinary by nature and scientists have been exceptionally creative in developing approaches to cope with the challenges typical of different features highlighted in our Table 1. We therefore suggest that ecologists and conservation biologists interested in these features of complex ecological systems will benefit from exploring how they have been addressed across other scientific disciplines.

Ultimately, a central message of our work is that developments in CSS will lead to developments in ecology and conservation (and *vice versa*) only if ecologists will conceptualize and use the word 'complexity' with more clarity and depth. We propose two simple principles that will help to this end. First, it is always desirable to specify what exactly one means when referring to complexity. While working on our critical review, we noticed that definitions of ecological complexity are extremely rare in the literature, with "complexity" being sometimes used as a buzzword (*124*). We therefore propose that the term complexity in ecology should be used carefully by studies that are not assessing ecological systems through the lenses of CSS. Second, attempts to measure the complexity of natural systems are very common (e.g., *40*, *82*, *83*, *125*), and we believe that these efforts could often be sharpened. When measuring properties of systems and referring to those as metrics of complexity, authors could first refer explicitly to the phenomenon that a metric represents, and then discuss their results in relation to ecological complexity, rather than conflating the two aspects. We provide a non-exhaustive list of metrics used to measure complexity as an example (Table 2), specifying the relations among these metrics and the features identified by our review. Importantly, many questions in ecology can be answered without appealing to concepts and approaches from CSS. For those studies, we suggest that referring to complexity only increases confusion in an already difficult field.

CONCLUDING REMARKS: UNDERSTANDING ECOLOGICAL COMPLEXITY IS CRITICAL IN AN AGE OF ENVIRONMENTAL AND SOCIAL URGENCY

The study of complex systems requires accepting the coexistence of concepts that have been historically considered antithetical in the sciences (*30*, *32*, *126*). When studying ecological complexity, one must embrace that the parts can constrain the whole and that the whole can constrain the parts, that both chaos and the laws of nature can co-determine phenomena across these systems, that simplicity can beget complexity, and that systems are ultimately both unity and diversity, cause and effect, life and death. Facing global change, we must embrace that we still need reductionism, but also that we need different views on ecological systems. Understanding the myriad of complex systems that we experience, including the Earth itself, will not be easy, and discovering new laws of nature alone might be insufficient to predict the directions and dynamics of those systems. However, one of the most important lessons learned from the development of CSS is that, with a proper focus, we can estimate and even predict how global environmental change will affect many types of complex systems (*20*).

Embracing ideas and approaches from the CSS perspective is therefore more urgent than ever. As we write, the Earth has experienced another season of records in climatic anomalies. The summer of 2022 was the hottest recorded in the history of Europe, as much as China has experienced the longest heatwave ever recorded. Severe drought affected several water bodies worldwide, including the Po, Rhine, and Loire rivers in Europe, the Colorado river in North America, and China's largest freshwater body, Poyang Lake. Africa was cursed by the worst drought in 70 years, while wildfires recently raged uncontrolled in large portions of Australia and Canada. These phenomena are impacting not only biodiversity and ecosystem functions, but also the supply of energy and primary services (e.g., water) to millions of people (*23*). CSS provides a relevant conceptual framework to assess ongoing environmental crises not only because of the conceptual advancements outlined in this review (*21*), but also because it recognizes the tight links connecting ecosystems and human societies into socio-political-ecological entities (*98*), embracing the important roles of sustainability, governance, politics, and ethics for applied biodiversity conservation in the face of global environmental change (*23*, *26*). This holistic understanding of environmental and social issues will be necessary as we embark in a critical transition to more sustainable and ethical societies, in an attempt to mitigate the effects of human activities on the Earth (*23*–*25*).

Ultimately, while we primarily provide guidelines to integrate CSS, ecology, and conservation, our hope is that this work will also promote the pursuit of consilience and integration with social aspects of the modern environmental sciences. We also hope that, by sharing the importance of reflecting on how we study and refer to ecological complexity, we will stimulate the sharing of new ideas from areas that likely have already participated in CSS, but whose contributions remain poorly known to the Western science. As history taught us (*3*, *6*), efforts will benefit from inclusion of perspectives from underrepresented regions, such as the Global South, which our analysis suggests remain marginalized in the study of ecological complexity (Fig. 2a). Likewise, 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 into CSS (*127*). Openness to new, transdisciplinary ideas has been a mantra of the study of complexity, and in an age of globalization and potentially catastrophic environmental changes, embracing the principles of CSS has never been more timely.

MATERIALS AND METHODS

Overview

Our manuscript is based on the premise that complexity is an attribute of ecological systems, and thus that we can identify properties of systems that are typically associated with the idea of complexity (*82*). This perspective relates to the paradigm of restricted complexity, and allows us to quantitatively assess the ecological literature. 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 (Fig. 1b-e). 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 (iv) identifying influential references in ecological complexity literature. We ran all analyses in R v.4.1.2 (*128*), using the 'tidyverse' suite v.1.3.1 (*129*) 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 began 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 (*66*, *69*)]. 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 (*130*), 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.

We refer to several documents for discussion of the features identified in our review (Table 1). These include books and book chapters (*3*, *5*, *6*, *21*, *43*, *58*, *84*–*86*), and various types of peer-reviewed scientific articles (hereafter, "articles"), particularly reviews (*4*, *10*, *11*, *18*, *30*, *32*, *37*, *54*, *66*, *69*, *72*, *82*, *87*–*91*). While other relevant perspectives certainly exist in the literature, we contend that this body of literature captured what characterizes complex systems reasonably well because we targeted the perspective of several independent groups of authors interested in CSS, often recognized as leaders in the study of complexity, and because we included recent reviews, thereby capturing ideas at the forefront of the study of ecological complexity.

Our critical review identified 23 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, and 'heterogeneity', e.g., in landscape ecology. 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 September 23rd, 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 the Web of Science categories. In all analyses, we looked at differences between *complexity* and *control* articles to understand if *complexity* articles were more consistent with CSS literature.

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 (*131*). 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 (*132*) and 'stringr' v.1.4.0 (*133*). 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 (*134*).

Topic modelling

We ran a topic modelling analysis using the LDA method (*135*) to verify whether the 23 features we selected through the critical review (Table 1) are meaningful to describe ecological complexity. LDA assumes that text documents are a mixture of topics, and topics are composed of a mixture of words (with individual words having differential probabilities of associating to a given topic). LDA is a mathematical method for finding the mixture of words that is associated with each topic, while also determining the mixture of topics that describes each document. First, we extracted the full-text of all articles in the *complexity* and *control* groups and preprocessed the text (e.g., removed stop words and punctuation, combined hyphenated words, and singularized all words). Next, we ran a LDA on the pre-processed text of all articles with the function LDA in the R package 'topicmodels' v. 0.2.12 (*136*), setting the number of topics to 100 and using the variational expectation-maximization algorithm. We then extracted the per-topic-per-word probability for each word (beta parameter; Fig. S2). Because LDA provides near-zero probability for most of the words in topics, we selected only the 0.5% highest probabilities of our data in each topic by taking only the values above the upper limit of the 0.99 Highest Density Interval (HDI) of our posterior distribution. Afterward, we ranked the beta values of each word within each topic and grouped them based on whether they ranked at the lowest (Q1) or the highest quantile (Q4). If the probability and the frequency of a feature was higher in the *complexity* group, we assumed it to be more important in characterizing this group.

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; *137*)], 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 (but see "*How do authors conceptualize ecological complexity?*" for discussion of caveats).

Additionally, we assessed the uniqueness of the features in each *complexity* and *control* article by analyzing the multivariate homogeneity of group dispersion (PERMDISP), as calculated using the package 'vegan' v.2.5.7 (*138*). 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 each 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 (*139*).

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 Model (ERGM; *140*). 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:

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

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 (*141–143*), 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 (*144*, *145*). We identify these clusters in an unsupervised way using a Louvain clustering optimization, a greedy optimization algorithm often used in network analyses due to its fast computation time and performance (*146*). This way, we let clusters emerge without imposing a fixed number of clusters *a priori*.

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Figures and Tables

Fig. 1. Analytical roadmap. Summary illustrating the different sections that compose our synthesis on ecological complexity.

Fig. 2. 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 articles mentioning "complexity" in their titles and abstract considering all the scientific fields (gray line) and separately for the ecology and environmental sciences, as approximated by the search term "ecological complexity" (red line).

Fig. 3. Comparison between *control* and *complexity* articles. Comparison between *control* (gray) 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 4. 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 5. 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 (*18* – in blue); scaling, hierarchies, and cross-scale dynamics (*68* – in gold); and macroecological theory and large-scale systems (*2* – in pink). Two additional clusters (*43*, *79* – in gray) 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 ecological systems. Features identified as typical of complex ecological systems through a critical review of the literature in complexity science. 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	Related concepts
Adaptation	The parts and/or a system change in response to pressures	adapt	Evolution, Niche, Plasticity, Phenological shifts
Aggregation	The parts that compose a system tend to organize into groups	aggregat	Consortia, Superstructures
Attractor	One of many states toward which a system tends to evolve	attractor	Criticality, Hysteresis, Tipping points, Stable-states
Chaos	Small differences in the initial conditions of a system results in great, deterministic differences among the potential states of that system	chaos + chaotic	Sensitivity, Phase space divergence
Diversity	The parts that compose a system are not equal	diversit	Entropy, Heterogeneity, Information, Variation
Dynamicity	The property of systems and parts change with time	dynamic	Evolution, Stasis, Transformation,
Emergence	The property of system characteristics that are not predictable based on the characteristics of their parts	emergen	Collective intelligence, Gestalt principles
Feedback	Processes in the system that increase or reduce the likelihood of the same process happening again	feedback	Reinforcement, Top-down causation
Flow	Exchange of material or information across the system	flow	Information, Linkages

Fractality	Self-similar regularities that repeat across scales	fractal	Regularity, Scale-invariance
Hierarchy	The system exhibits properties at multiple organizational levels	hierarch	Levels, Nestedness, Scales
Homeostasis	Self-regulating mechanisms that tend to maintain optimal conditions	homeosta	Control, Robustness
Interaction	The parts that compose a system affect each other	interact	Competition, Dependence, Parasitism, Mutualism, Synergy
Memory	Previous states of the system influence present and future states	memory + memories	Lagged responses, Markov processes
Modularity	The property of parts and systems of being composed by distinct units	modul	Cluster, Connectivity, Stability
Network	A representation of relationships (links) occurring between parts (nodes) in a system	network	Food webs, Feedbacks, Nodes
Non-equilibrium	The state of a system that has not reach a steady state	non-equilib + non equilib + nonequilib	Balance, Disturbance, Multiple stable states, Instability
Non-linearity	Local rules of interaction change as the system evolves	non-linear + non linear + nonlinear	Higher-order effects
Resilience	The capacity of a system to resist and recover from disturbance	resilien	Brittleness, Robustness, Stability
Scaling	The property of system patterns to change with scale (e.g., spatial, temporal, or taxonomic)	scal + scale-depend + scale depend	Discrete hierarchy, Grain, Levels
Self-organization	The tendency of a system to develop complex patterns from simpler states	self-orga + self orga + selforga	Evolution, Emergence, Multicellularity, Pattern formation
Stability	The tendency of a system to return to its equilibrium state	stabilit	Invasibility, Persistence, Resistance, Robustness
Threshold	The context in which a small change in the conditions of a system results in large change in the system itself	thresho	Criticality, Tipping point

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 the references (*63, 72, 82, 125*) for comprehensive reviews of metrics designed to measure complexity.

Feature	**Metric**	**Reference**
Chaos	Lyapunov exponent. It represents the rate of separation of infinitesimally close trajectories, measuring how a dynamic system is sensitive to initial conditions.	(*147*)
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.	(*72*)
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.	*(82)*
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.	(*82*)
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.	(*148*)
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.	(*82*)
Fractality	Power law: $P(x) = cx^{-\gamma}$. Measures the degree of pattern consistency across scales.	(*149*)
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).	(*63*)
Network	Connectance: the proportion of realized ecological interactions (m) among the potential ones (L), or L/m. Potential links are most often calculated as the squared species richness. Measures the fraction of all possible links that are realized in a network.	(*63*)
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.	(*63*)
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	(*150*)

	efficiently compressed.	
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.	(*125*)
Stability	Coefficient of variation: CV = σ/μ, 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.	(*151*)
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.	(*125*)

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Supplementary Materials for

Towards a cohesive understanding of ecological complexity

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This PDF file includes:

Table S1
Figures S1 – S4

Table S1.

List of review studies retrieved by the search on the Web of Science using the word "Complexity" in the "Ecology" and "Environmental Sciences" categories. The original search retrieved 23,703 manuscripts published between 2000 and 2021 (search conducted on July 14th, 2021), from which 71 were review studies.

Authors	Article Title	Source Title	Publication Year	DOI
Kappeler, PM	A framework for studying social complexity	BEHAVIORAL ECOLOGY AND SOCIOBIOLOGY	2019	10.1007/s00265-018-2601-8
Merow, C; Smith, MJ; Edwards, TC; Guisan, A; McMahon, SM; Normand, S; Thuiller, W; Wuest, RO; Zimmermann, NE; Elith, J	What do we gain from simplicity versus complexity in species distribution models?	ECOGRAPHY	2014	10.1111/ecog.00845
Chaplin-Kramer, R; O'Rourke, ME; Blitzer, EJ; Kremen, C	A meta-analysis of crop pest and natural enemy response to landscape complexity	ECOLOGY LETTERS	2011	10.1111/j.1461-0248.2011.01642.x
Donohue, I; Hillebrand, H; Montoya, JM; Petchey, OL; Pimm, SL; Fowler, MS; Healy, K; Jackson, AL; Lurgi, M; McClean, D; O'Connor, NE; O'Gorman, EJ; Yang, Q	Navigating the complexity of ecological stability	ECOLOGY LETTERS	2016	10.1111/ele.12648
He, P; Maldonado-Chaparro, AA; Farine, DR	The role of habitat configuration in shaping social structure: a gap in studies of animal social complexity	BEHAVIORAL ECOLOGY AND SOCIOBIOLOGY	2019	10.1007/s00265-018-2602-7

Tuck, SL; Winqvist, C; Mota, F; Ahnstrom, J; Turnbull, LA; Bengtsson, J	Land-use intensity and the effects of organic farming on biodiversity: a hierarchical meta-analysis	JOURNAL OF APPLIED ECOLOGY	2014	10.1111/1365-2664.12219
Arnosti, C; Wietz, M; Brinkhoff, T; Hehemann, JH; Probandt, D; Zeugner, L; Amann, R	The Biogeochemistry of Marine Polysaccharides: Sources, Inventories, and Bacterial Drivers of the Carbohydrate Cycle	ANNUAL REVIEW OF MARINE SCIENCE, VOL 13, 2021	2021	10.1146/annurev-marine-032020-012810
Parrish, B; Heptonstall, P; Gross, R; Sovacool, BK	A systematic review of motivations, enablers and barriers for consumer engagement with residential demand response	ENERGY POLICY	2020	10.1016/j.enpol.2019.111221
Vila, M; Espinar, JL; Hejda, M; Hulme, PE; Jarosik, V; Maron, JL; Pergl, J; Schaffner, U; Sun, Y; Pysek, P	Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems	ECOLOGY LETTERS	2011	10.1111/j.1461-0248.2011.01628.x
Sheriff, MJ; Peacor, SD; Hawlena, D; Thaker, M	Non-consumptive predator effects on prey population size: A dearth of evidence	JOURNAL OF ANIMAL ECOLOGY	2020	10.1111/1365-2656.13213
Casewell, NR; Wuster, W; Vonk, FJ; Harrison, RA; Fry, BG	Complex cocktails: the evolutionary novelty of venoms	TRENDS IN ECOLOGY & EVOLUTION	2013	10.1016/j.tree.2012.10.020
Brack, W; Ait-Aissa, S; Burgess, RM; Busch, W; Creusot, N; Di	Effect-directed analysis supporting monitoring of aquatic	SCIENCE OF THE TOTAL ENVIRONMENT	2016	10.1016/j.scitotenv.2015.11.102

Paolo, C; Escher, BI; Hewitt, LM; Hilscherova, K; Hollender, J; Hollert, H; Jonker, W; Kool, J; Lamoree, M; Muschket, M; Neumann, S; Rostkowski, P; Ruttkies, C; Schollee, J; Schymanski, EL; Schulze, T; Seiler, TB; Tindall, AJ; Umbuzeiro, GD; Vrana, B; Krauss, M	environments - An in-depth overview			
Sterner, T; Barbier, EB; Bateman, I; van den Bijgaart, I; Crepin, AS; Edenhofer, O; Fischer, C; Habla, W; Hassler, J; Johansson-Stenman, O; Lange, A; Polasky, S; Rockstrom, J; Smith, HG; Steffen, W; Wagner, G; Wilen, JE; Alpiza, F; Azar, C; Carless, D; Chavez, C; Corial, J; Engstrom, G; Jagers, SC; Kohlin, G; Lofgren, A; Pleijel, H; Robinson, A	Policy design for the Anthropocene	NATURE SUSTAINABILITY	2019	10.1038/s41893-018-0194-x
Carmona, CP; de Bello, F; Mason, NWH; Leps, J	Traits Without Borders: Integrating Functional Diversity Across Scales	TRENDS IN ECOLOGY & EVOLUTION	2016	10.1016/j.tree.2016.02.003

Sundqvist, MK; Sanders, NJ; Wardle, DA	Community and Ecosystem Responses to Elevational Gradients: Processes, Mechanisms, and Insights for Global Change	ANNUAL REVIEW OF ECOLOGY, EVOLUTION, AND SYSTEMATICS, VOL 44	2013	10.1146/annurev-ecolsys-110512-135750
Symonds, MRE; Moussalli, A	A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion	BEHAVIORAL ECOLOGY AND SOCIOBIOLOG Y	2011	10.1007/s00265-010-1037-6
Fino, D; Bensaid, S; Piumetti, M; Russo, N	A review on the catalytic combustion of soot in Diesel particulate filters for automotive applications: From powder catalysts to structured reactors	APPLIED CATALYSIS A-GENERAL	2016	10.1016/j.apcata.2015.10.016
Kim, KH; Kabir, E; Jahan, SA	Airborne bioaerosols and their impact on human health	JOURNAL OF ENVIRONMENT AL SCIENCES	2018	10.1016/j.jes.2017.08.027
Qiu, RJ; Lin, M; Qin, BJ; Xu, ZM; Ruan, JJ	Environmental-friendly recovery of non-metallic resources from waste printed circuit boards: A review	JOURNAL OF CLEANER PRODUCTION	2021	10.1016/j.jclepro.2020.123738
Swanson, ME; Franklin, JF; Beschta, RL; Crisafulli, CM; DellaSala, DA; Hutto, RL; Lindenmayer,	The forgotten stage of forest succession: early-successional ecosystems on forest sites	FRONTIERS IN ECOLOGY AND THE ENVIRONMENT	2011	10.1890/090157

DB; Swanson, FJ				
Orr, JA; Vinebrooke, RD; Jackson, MC; Kroeker, KJ; Kordas, RL; Mantyka-Pringle, C; Van den Brink, PJ; De Laender, F; Stoks, R; Holmstrup, M; Matthaei, CD; Monk, WA; Penk, MR; Leuzinger, S; Schafer, RB; Piggott, JJ	Towards a unified study of multiple stressors: divisions and common goals across research disciplines	PROCEEDINGS OF THE ROYAL SOCIETY B-BIOLOGICAL SCIENCES	2020	10.1098/rspb.2020.0421
Fisher, RA; Koven, CD; Anderegg, WRL; Christoffersen, BO; Dietze, MC; Farrior, CE; Holm, JA; Hurtt, GC; Knox, RG; Lawrence, PJ; Lichstein, JW; Longo, M; Matheny, AM; Medvigy, D; Muller-Landau, HC; Powell, TL; Serbin, SP; Sato, H; Shuman, JK; Smith, B; Trugman, AT; Viskari, T; Verbeeck, H; Weng, ES; Xu, CG; Xu, XT; Zhang, T; Moorcroft, PR	Vegetation demographics in Earth System Models: A review of progress and priorities	GLOBAL CHANGE BIOLOGY	2018	10.1111/gcb.13910
Belzer, C; de Vos, WM	Microbes inside-from diversity to function: the case of Akkermansia	ISME JOURNAL	2012	10.1038/ismej.2012.6
Bandeira, M; Giovanela, M; Roesch-Ely, M;	Green synthesis of zinc oxide	SUSTAINABLE CHEMISTRY	2020	10.1016/j.scp.2020.100223

Devine, DM; Crespo, JD	nanoparticles: A review of the synthesis methodology and mechanism of formation	AND PHARMACY		
Mesoudi, A; Thornton, A	What is cumulative cultural evolution?	PROCEEDINGS OF THE ROYAL SOCIETY B-BIOLOGICAL SCIENCES	2018	10.1098/rspb.2018.0712
Hardesty, BD; Harari, J; Isobe, A; Lebreton, L; Maximenko, N; Potemra, J; van Sebille, E; Vethaak, AD; Wilcox, C	Using Numerical Model Simulations to Improve the Understanding of Micro-plastic Distribution and Pathways in the Marine Environment	FRONTIERS IN MARINE SCIENCE	2017	10.3389/fmars.2017.00030
Wohl, E; Lane, SN; Wilcox, AC	The science and practice of river restoration	WATER RESOURCES RESEARCH	2015	10.1002/2014WR016874
Ahmad, M; Rajapaksha, AU; Lim, JE; Zhang, M; Bolan, N; Mohan, D; Vithanage, M; Lee, SS; Ok, YS	Biochar as a sorbent for contaminant management in soil and water: A review	CHEMOSPHERE	2014	10.1016/j.chemosphere.2013.10.071
Engler, RE	The Complex Interaction between Marine Debris and Toxic Chemicals in the Ocean	ENVIRONMENTAL SCIENCE & TECHNOLOGY	2012	10.1021/es3027105
Kim, KH; Kabir, E; Jahan, SA	Exposure to pesticides and the associated human health effects	SCIENCE OF THE TOTAL ENVIRONMENT	2017	10.1016/j.scitotenv.2016.09.009
Prakash, V; Singh, VP; Tripathi, DK; Sharma, S; Corpas, FJ	Crosstalk between nitric oxide (NO) and abscisic acid (ABA) signalling	ENVIRONMENTAL AND EXPERIMENTAL BOTANY	2019	10.1016/j.envexpbot.2018.10.033

	molecules in higher plants			
Baleta, J; Mikulcic, H; Klemes, JJ; Urbaniec, K; Duic, N	Integration of energy, water and environmental systems for a sustainable development	JOURNAL OF CLEANER PRODUCTION	2019	10.1016/j.jclepro.2019.01.035
Yu, XW; Manthiram, A	Electrode-electrolyte interfaces in lithium-based batteries	ENERGY & ENVIRONMENTAL SCIENCE	2018	10.1039/c7ee02555f
Giovannoni, SJ; Thrash, JC; Temperton, B	Implications of streamlining theory for microbial ecology	ISME JOURNAL	2014	10.1038/ismej.2014.60
Nayak, A; Bhushan, B	An overview of the recent trends on the waste valorization techniques for food wastes	JOURNAL OF ENVIRONMENTAL MANAGEMENT	2019	10.1016/j.jenvman.2018.12.041
Notarnicola, B; Sala, S; Anton, A; McLaren, SJ; Saouter, E; Sonesson, U	The role of life cycle assessment in supporting sustainable agri-food systems: A review of the challenges	JOURNAL OF CLEANER PRODUCTION	2017	10.1016/j.jclepro.2016.06.071
Siddique, MNI; Ab Wahid, Z	Achievements and perspectives of anaerobic co-digestion: A review	JOURNAL OF CLEANER PRODUCTION	2018	10.1016/j.jclepro.2018.05.155
Kelly, JR; Scheibling, RE	Fatty acids as dietary tracers in benthic food webs	MARINE ECOLOGY PROGRESS SERIES	2012	10.3354/meps09559
Mahmood, A; Wang, JL	Machine learning for high performance organic solar cells: current scenario and future prospects	ENERGY & ENVIRONMENTAL SCIENCE	2021	10.1039/d0ee02838j

Asbjornsen, H; Goldsmith, GR; Alvarado-Barrientos, MS; Rebel, K; Van Osch, FP; Rietkerk, M; Chen, JQ; Gotsch, S; Tobon, C; Geissert, DR; Gomez-Tagle, A; Vache, K; Dawson, TE	Ecohydrological advances and applications in plant-water relations research: a review	JOURNAL OF PLANT ECOLOGY	2011	10.1093/jpe/rtr005
Campanale, C; Massarelli, C; Savino, I; Locaputo, V; Uricchio, VF	A Detailed Review Study on Potential Effects of Microplastics and Additives of Concern on Human Health	INTERNATIONAL JOURNAL OF ENVIRONMENTAL RESEARCH AND PUBLIC HEALTH	2020	10.3390/ijerph17041212
Lai, CS; Locatelli, G; Pimm, A; Wu, XM; Lai, LL	A review on long-term electrical power system modeling with energy storage	JOURNAL OF CLEANER PRODUCTION	2021	10.1016/j.jclepro.2020.124298
Jiang, Y; Zevenbergen, C; Ma, YC	Urban pluvial flooding and stormwater management: A contemporary review of China's challenges and sponge cities strategy	ENVIRONMENTAL SCIENCE & POLICY	2018	10.1016/j.envsci.2017.11.016
Lead, JR; Batley, GE; Alvarez, PJJ; Croteau, MN; Handy, RD; McLaughlin, MJ; Judy, JD; Schirmer, K	Nanomaterials in the environment: Behavior, fate, bioavailability, and effectsAn updated review	ENVIRONMENTAL TOXICOLOGY AND CHEMISTRY	2018	10.1002/etc.4147
Martin, TG; Burgman, MA; Fidler, F; Kuhnert, PM; Low-Choy, S; Mcbride, M; Mengersen, K	Eliciting Expert Knowledge in Conservation Science	CONSERVATION BIOLOGY	2012	10.1111/j.1523-1739.2011.01806.x

Torralba, M; Fagerholm, N; Burgess, PJ; Moreno, G; Plieninger, T	Do European agroforestry systems enhance biodiversity and ecosystem services? A meta-analysis	AGRICULTURE ECOSYSTEMS & ENVIRONMENT	2016	10.1016/j.agee.2016.06.002
Samways, MJ; Barton, PS; Birkhofer, K; Chichorro, F; Deacon, C; Fartmann, T; Fukushima, CS; Gaigher, R; Habel, JC; Hallmann, CA; Hill, MJ; Hochkirch, A; Kaila, L; Kwak, ML; Maes, D; Mammola, S; Noriega, JA; Orfinger, AB; Pedraza, F; Pryke, JS; Roque, FO; Settele, J; Simaika, JP; Stork, NE; Suhling, F; Vorster, C; Cardoso, P	Solutions for humanity on how to conserve insects	BIOLOGICAL CONSERVATIO N	2020	10.1016/j.biocon.2020.108427
Filbee-Dexter, K; Scheibling, RE	Sea urchin barrens as alternative stable states of collapsed kelp ecosystems	MARINE ECOLOGY PROGRESS SERIES	2014	10.3354/meps10573
Sifakis, S; Androutsopoul os, VP; Tsatsakis, AM; Spandidos, DA	Human exposure to endocrine disrupting chemicals: effects on the male and female reproductive systems	ENVIRONMENT AL TOXICOLOGY AND PHARMACOLO GY	2017	10.1016/j.etap.2017.02.024
Dong, LJ; Tong, XJ; Li, XB; Zhou, J;	Some developments and new insights of	JOURNAL OF CLEANER PRODUCTION	2019	10.1016/j.jclepro.2018.10.291

Wang, SF; Liu, B	environmental problems and deep mining strategy for cleaner production in mines			
Ramanujam, J; Singh, UP	Copper indium gallium selenide based solar cells - a review	ENERGY & ENVIRONMENTAL SCIENCE	2017	10.1039/c7ee00826k
Manaia, CM; Rocha, J; Scaccia, N; Marano, R; Radu, E; Biancullo, F; Cerqueira, F; Fortunato, G; Iakovides, IC; Zammit, I; Kampouris, I; Vaz-Moreira, I; Nunes, OC	Antibiotic resistance in wastewater treatment plants: Tackling the black box	ENVIRONMENT INTERNATIONAL	2018	10.1016/j.envint.2018.03.044
Kumar, SG; Rao, KSRK	Physics and chemistry of CdTe/CdS thin film heterojunction photovoltaic devices: fundamental and critical aspects	ENERGY & ENVIRONMENTAL SCIENCE	2014	10.1039/c3ee41981a
Paul-Pont, I; Tallec, K; Gonzalez-Fernandez, C; Lambert, C; Vincent, D; Mazurais, D; Zambonino-Infante, JL; Brotons, G; Lagarde, F; Fabioux, C; Soudant, P; Huvet, A	Constraints and Priorities for Conducting Experimental Exposures of Marine Organisms to Microplastics	FRONTIERS IN MARINE SCIENCE	2018	10.3389/fmars.2018.00252
Thomas, N; Dionysiou, DD; Pillai, SC	Heterogeneous Fenton catalysts: A review of recent advances	JOURNAL OF HAZARDOUS MATERIALS	2021	10.1016/j.jhazmat.2020.124082

Conti, C; Guarino, M; Bacenetti, J	Measurements techniques and models to assess odor annoyance: A review	ENVIRONMENT INTERNATIONAL	2020	10.1016/j.envint.2019.105261
Qin, YX; Li, GY; Gao, YP; Zhang, LZ; Ok, YS; An, TC	Persistent free radicals in carbon-based materials on transformation of refractory organic contaminants (ROCs) in water: A critical review	WATER RESEARCH	2018	10.1016/j.watres.2018.03.012
Wang, HX; Guerrero, A; Bou, A; Al-Mayouf, AM; Bisquert, J	Kinetic and material properties of interfaces governing slow response and long timescale phenomena in perovskite solar cells	ENERGY & ENVIRONMENTAL SCIENCE	2019	10.1039/c9ee00802k
Bucci, K; Tulio, M; Rochman, CM	What is known and unknown about the effects of plastic pollution: A meta-analysis and systematic review	ECOLOGICAL APPLICATIONS	2020	10.1002/eap.2044
Agrawal, AA	Current trends in the evolutionary ecology of plant defence	FUNCTIONAL ECOLOGY	2011	10.1111/j.1365-2435.2010.01796.x
Krzeminski, P; Tomei, MC; Karaolia, P; Langenhoff, A; Almeida, CMR; Felis, E; Gritten, F; Andersen, HR; Fernandes, T; Manaia, CM; Rizzo, L; Fatta-Kassinos, D	Performance of secondary wastewater treatment methods for the removal of contaminants of emerging concern implicated in crop uptake and antibiotic resistance	SCIENCE OF THE TOTAL ENVIRONMENT	2019	10.1016/j.scitotenv.2018.08.130

	spread: A review			
Pearlman, J; Bushnell, M; Coppola, L; Karstensen, J; Buttigieg, PL; Pearlman, F; Simpsons, P; Barbier, M; Muller-Karger, FE; Munoz-Mas, C; Pissierssens, P; Chandler, C; Hermes, J; Heslop, E; Jenkyns, R; Achterberg, EP; Bensi, M; Bittig, HC; Blandin, J; Bosch, J; Bourles, B; Bozzano, R; Buck, JJH; Burger, EF; Cano, D; Cardin, V; Llorens, MC; Cianca, A; Chen, H; Cusack, C; Delory, E; Garello, R; Giovanetti, G; Harscoat, V; Hartman, S; Heitsenrether, R; Jirka, S; Lara-Lopez, A; Lanteri, N; Leadbetter, A; Manzella, G; Maso, J; McCurdy, A; Moussat, E; Ntoumas, M; Pensieri, S; Petihakis, G; Pinardi, N; Pouliquen, S; Przeslawski, R; Roden, NP; Silke, J; Tamburri, MN;	Evolving and Sustaining Ocean Best Practices and Standards for the Next Decade	FRONTIERS IN MARINE SCIENCE	2019	10.3389/fmars.2019.00277

Tang, HR; Tanhua, T; Telszewski, M; Testor, P; Thomas, J; Waldmann, C; Whoriskey, F				
Vereecken, H; Schnepf, A; Hopmans, JW; Javaux, M; Or, D; Roose, DOT; Vanderborght, J; Young, MH; Amelung, W; Aitkenhead, M; Allison, SD; Assouline, S; Baveye, P; Berli, M; Bruggemann, N; Finke, P; Flury, M; Gaiser, T; Govers, G; Ghezzehei, T; Hallett, P; Franssen, HJH; Heppell, J; Horn, R; Huisman, JA; Jacques, D; Jonard, F; Kollet, S; Lafolie, F; Lamorski, K; Leitner, D; McBratney, A; Minasny, B; Montzka, C; Nowak, W; Pachepsky, Y; Padarian, J; Romano, N; Roth, K; Rothfuss, Y; Rowe, EC; Schwen, A; Simunek, J; Tiktak, A; Van Dam, J; van der Zee, SEATM; Vogel, HJ; Vrugt, JA;	Modeling Soil Processes: Review, Key Challenges, and New Perspectives	VADOSE ZONE JOURNAL	2016	10.2136/vzj2015.09.0131

Wohling, T; Young, IM				
Bellwood, DR; Streit, RP; Brandl, SJ; Tebbett, SB	The meaning of the term 'function' in ecology: A coral reef perspective	FUNCTIONAL ECOLOGY	2019	10.1111/1365-2435.13265
Adao, T; Hruska, J; Padua, L; Bessa, J; Peres, E; Morais, R; Sousa, JJ	Hyperspectral Imaging: A Review on UAV-Based Sensors, Data Processing and Applications for Agriculture and Forestry	REMOTE SENSING	2017	10.3390/rs9111110
Keesstra, S; Nunes, JP; Saco, P; Parsons, T; Poeppl, R; Masselink, R; Cerda, A	The way forward: Can connectivity be useful to design better measuring and modelling schemes for water and sediment dynamics?	SCIENCE OF THE TOTAL ENVIRONMENT	2018	10.1016/j.scitotenv.2018.06.342
Heino, J	A macroecological perspective of diversity patterns in the freshwater realm	FRESHWATER BIOLOGY	2011	10.1111/j.1365-2427.2011.02610.x
Lenoir, J; Svenning, JC	Climate-related range shifts - a global multidimensional synthesis and new research directions	ECOGRAPHY	2015	10.1111/ecog.00967
Groeneveld, J; Muller, B; Buchmann, CM; Dressler, G; Guo, C; Hase, N; Hoffmann, F; John, F; Klassert, C; Lauf, T; Liebelt, V;	Theoretical foundations of human decision-making in agent-based land use models - A review	ENVIRONMENTAL MODELLING & SOFTWARE	2017	10.1016/j.envsoft.2016.10.008

Nolzen, H; Pannicke, N; Schulze, J; Weise, H; Schwarz, N				
Guimaraes, N; Padua, L; Marques, P; Silva, N; Peres, E; Sousa, JJ	Forestry Remote Sensing from Unmanned Aerial Vehicles: A Review Focusing on the Data, Processing and Potentialities	REMOTE SENSING	2020	10.3390/rs12061046
Andersen, AN	Responses of ant communities to disturbance: Five principles for understanding the disturbance dynamics of a globally dominant faunal group	JOURNAL OF ANIMAL ECOLOGY	2019	10.1111/1365-2656.12907

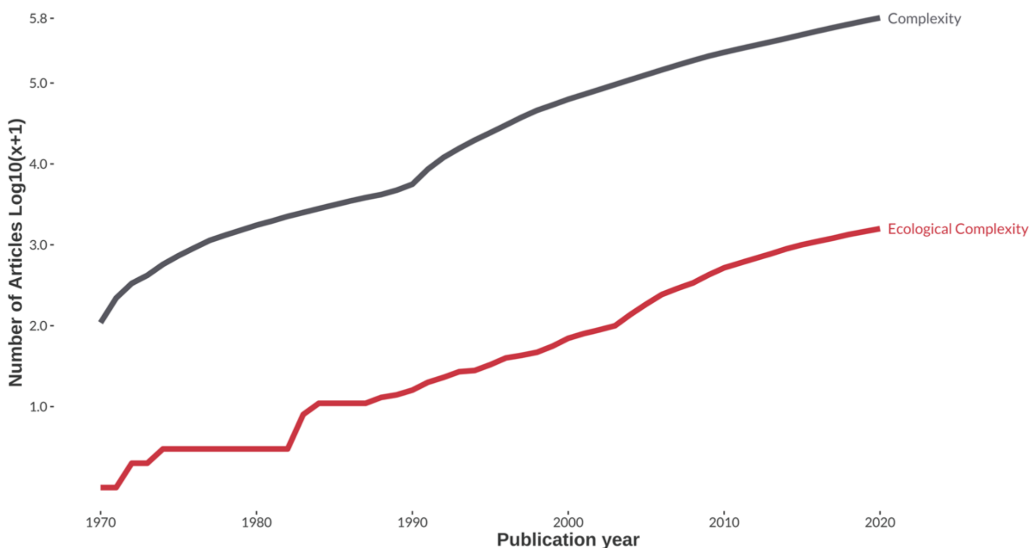

Fig. S1. Cumulative production of articles over time. Cumulative production (from 1970 to 2021) between articles mentioning "complexity" in their titles and abstract considering all the scientific fields (gray line) and separately for the ecology and environmental sciences, as approximated by the search term "ecological complexity" (red line). The number of articles were log-transformed [Log10(x+1)] to ease the comparison between groups.

	Control					Ecological complexity				
	Q1	Q2	Q3	Q4	Total	Q1	Q2	Q3	Q4	Total
Adaptation	8	8	13	12	41	7	16	8	32	**63**
Aggregation	1	6	8	3	**18**	6	3	3	5	17
Attractor	0	0	0	0	0	0	2	1	5	**8**
Chaos	1	0	0	1	2	1	3	3	9	**16**
Dinamicity	12	10	15	22	59	6	11	15	53	**85**
Diversity	6	12	6	29	53	11	10	13	31	**65**
Emergence	4	7	7	7	25	8	10	18	24	**60**
Feedback	0	1	3	2	6	3	8	9	6	**26**
Flow	7	6	10	14	37	8	10	8	15	**41**
Fractality	0	0	0	0	0	0	3	2	4	**9**
Hierarchy	0	3	5	2	10	6	9	2	12	**29**
Homeostasis	0	0	0	0	0	0	2	0	0	**2**
Interaction	5	11	17	41	74	4	9	22	50	**85**
Memory	0	1	0	0	1	4	3	1	1	**9**
Modularity	0	2	3	1	6	4	2	6	0	**12**
Network	1	2	2	5	10	4	8	13	27	**52**
Non−equilibrium	0	0	0	0	0	2	3	1	0	**6**
Non−linearity	1	2	0	2	5	5	6	11	7	**29**
Resilience	0	1	1	1	3	5	6	8	6	**25**
Scaling	11	10	18	25	64	2	8	18	48	**76**
Self−organization	4	3	2	1	10	7	9	12	27	**55**
Stability	0	4	2	2	8	3	4	9	10	**26**
Threshold	1	5	5	3	14	4	5	5	5	**19**

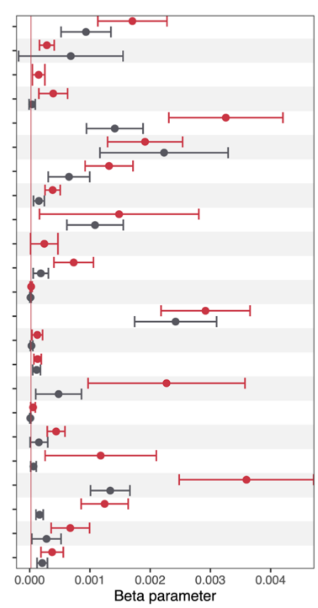

Fig. S2. Importance of features to characterize *control* group and *complexity* articles. The table reports the number of times each feature appears in each quantile (Q1–4) considering only the 1% most important terms in each article. The higher total value between groups is highlighted in bold (note that only the feature "Aggregation" appears more in the control group and some features do not appear at all in the *control* group). Graph on the right show the distribution of beta parameters for each feature without subselecting the 1% most important terms. Vertical line represents the average probability across all words.

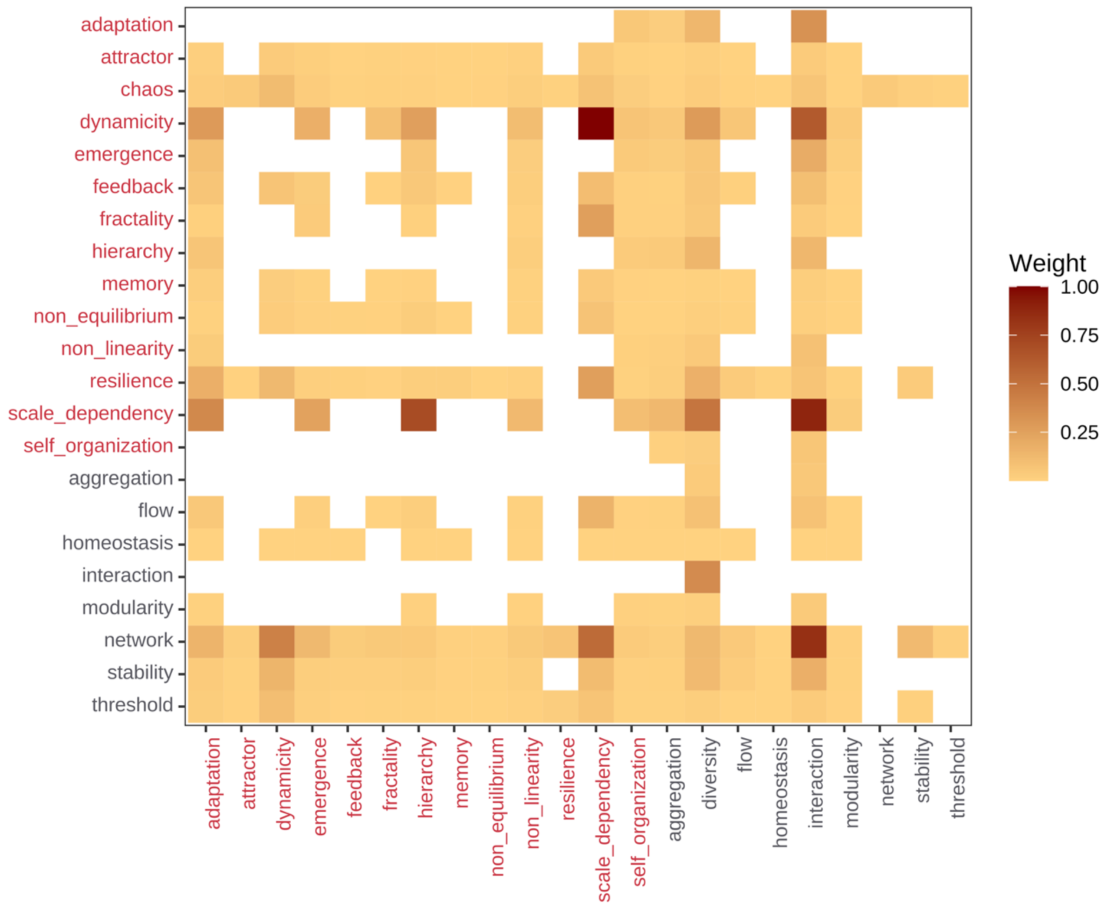

Fig. S3. Adjacency matrix for the co-occurrence of features. The colors in the name of the features indicate whether these are significantly related to *complexity* than the *control* articles based on Indicator Species Analysis. The filling gradient in the matrix represents the weight of the connection estimated as the sum of the edge weights of the adjacent edges of the node.

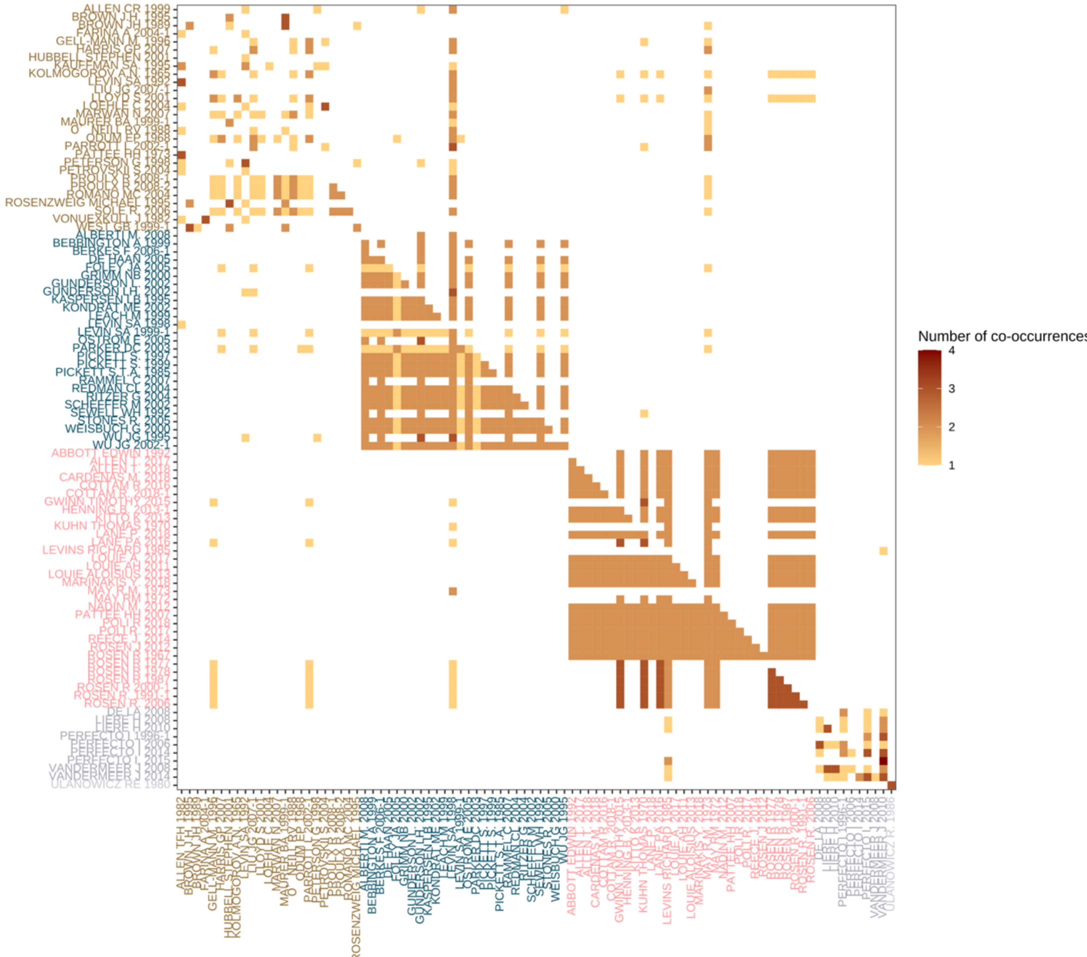

Fig. S4. Adjacency matrix for the co-citation of references. The colors in the name of the reference indicate the five clusters extracted using the Louvaine algorithm. The filling gradient in the matrix represents the number of articles citing the pair of references simultaneously.