

Review

Measuring ecological complexity

Lael Parrott*

Complex Systems Laboratory, Département de géographie, Université de Montréal, C.P. 6128 succursale "centre-ville", Montréal, Québec, Canada H3C 3J7

ARTICLE INFO

Article history:

Received 8 October 2009
 Received in revised form 3 February 2010
 Accepted 26 March 2010

Keywords:

Ecological complexity
 Complex systems
 Ecological orientors
 Entropy

ABSTRACT

Complexity is an elusive term in ecology that is often used in different ways to describe the state of an ecosystem. Ecological complexity has been linked to concepts such as ecological integrity, diversity and resilience and has been put forth as a candidate ecological orientor. In this article, the concept of complexity as a system attribute is presented and candidate measures of ecological complexity are reviewed. The measures are distinguished by their ability to characterize the spatial, temporal, structural or spatiotemporal signatures of an ecosystem. Many of these measures have been adapted from disciplines such as physics and information theory that have a long history of quantifying complexity, however more work needs to be done to develop techniques adapted to ecological data. It is argued that if appropriate measures are developed and validated for ecosystems, ecological complexity could become a key ecological indicator.

© 2010 Elsevier Ltd. All rights reserved.

Contents

| | |
|---|------|
| 1. Introduction..... | 1069 |
| 2. Measuring complexity..... | 1070 |
| 3. Example measures of ecological complexity..... | 1070 |
| 3.1. Temporal measures..... | 1070 |
| 3.2. Spatial measures..... | 1071 |
| 3.3. Spatiotemporal measures..... | 1072 |
| 3.4. Structural measures..... | 1072 |
| 4. Discussion: ecological complexity as an ecological orientor..... | 1074 |
| 5. Conclusion..... | 1075 |
| Acknowledgements..... | 1075 |
| References..... | 1075 |

1. Introduction

Many authors have claimed that an ecosystem is a prototypical complex system (Levin, 1998). Ecological theory has a long history of describing ecosystems in terms of material and energetic flows between multiple components in interaction (Odum, 1968; Jørgensen and Müller, 2000), providing a conceptual model which is very compatible with current conceptual models of complex systems. More recently, ecologists and others have proposed the idea that the structure and functioning of ecosystems may be understood according to theories of emergence, self-organization, network theory and non-linear dynamics, borrowed from the physical sciences (Levin, 1999; Solé and Bascompte, 2006). Modern

views in ecology present ecosystems as adaptive, dynamic networks of interacting components that should be studied in a context of non-equilibrium dynamics leading to innovation and surprise as a result of feedbacks and cross-scale interactions (Harris, 2007; Liu et al., 2007).

It seems natural to assume that if an ecosystem is a complex system, then any changes in its state will be reflected in established measures of the complexity of the system (Parrott, 2005). How to measure the complexity of a system, however, is an ongoing subject of debate and remains one of the key challenges in complex systems research. Ask yourself which ecosystem is more complex: A healthy, diverse coral reef or a degraded reef dominated by algae? A second growth temperate coastal forest that was subjected to clear cut harvesting 80 years ago, or an adjacent old growth stand that has not been disturbed for more than 800 years? Most readers will have an intuitive answer to this question, classifying different ecosystems as being more or less complex than others. Yet, how do

* Tel.: +1 514 343 8032; fax: +1 514 343 8008.
 E-mail address: lael.parrott@umontreal.ca.

we measure the complexity of an ecosystem? Can we quantify this seemingly system-level attribute? And if we could, would it serve as a useful ecological indicator, informing us about the state of the system?

Here, I argue that while complexity is, in many ways, related to other holistic measures of an ecosystems structure and functioning, it can be seen as a distinct attribute of a system. As such, it should be possible to measure and quantify this attribute, classifying some ecosystems as more or less complex. This paper describes a number of recent techniques that have been developed in fields such as physics and information theory and which are now being used to characterize the complexity of ecosystems. If successful, such measures of complexity may serve as aggregate indicators of ecosystem structure and dynamics.

2. Measuring complexity

Ecosystems, like all complex systems, typically display a non-linear dynamics in space and time that is extremely difficult to characterize using standard quantitative methods. The dynamics of a complex system has been said to lie “at the edge of chaos” (Langton, 1992) between the two extremes of order (equivalent to a uniform spatial pattern or temporal equilibrium) and disorder (equivalent to a random spatial distribution or white noise), exhibiting a balance between underlying regularity and complete unpredictability (chaos). Studies in graph theory show that the organizational structure, or interaction network, of the components making up a complex system also has a characteristic structure that is neither random nor completely ordered (Barabasi, 2009). Recent research has thus focused on developing methods to characterize the temporal, spatial or structural signatures of complex systems, classifying the system along a gradient of order to disorder. Measures of complexity tend to be of two types (Atmanspacher, 2007): Type 1 measures increase linearly with increasing disorder in the system, and Type 2 measures are a convex function, attributing their highest values to systems of intermediate regularity (Fig. 1).

Whichever type of measure is used, the objective is to differentiate between so-called simple systems versus those that are complex (Grassberger, 1988). Simple ordered systems, for example, may have patterns such as periodic cycles that repeat themselves predictably in time or in space and they may have a highly organized structure, in which each node in the system has the same number of connections, for example. Disordered systems have random spatial structure, display random dynamics and have a random organization of components. Such systems are simple in the sense that they can be easily described by a probability distribution function that can reproduce the main characteristics of the system. While early attempts to quantify ecological complexity proposed measures such as the number of significant axes in a principal components analysis of a data set (Meyer, 1988), the field has advanced to a search for more sensitive measures that may serve as ecological indicators. In the following section, measures of complexity that have, for the most part, been developed in fields such as information theory and physics are presented and their applicability to quantifying ecological complexity is discussed.

3. Example measures of ecological complexity

3.1. Temporal measures

Temporal measures of complexity can be used to characterize time series of different variables describing the dynamics of a system. Since a time series can be viewed as a symbol sequence, it is a natural candidate for the application of information-based

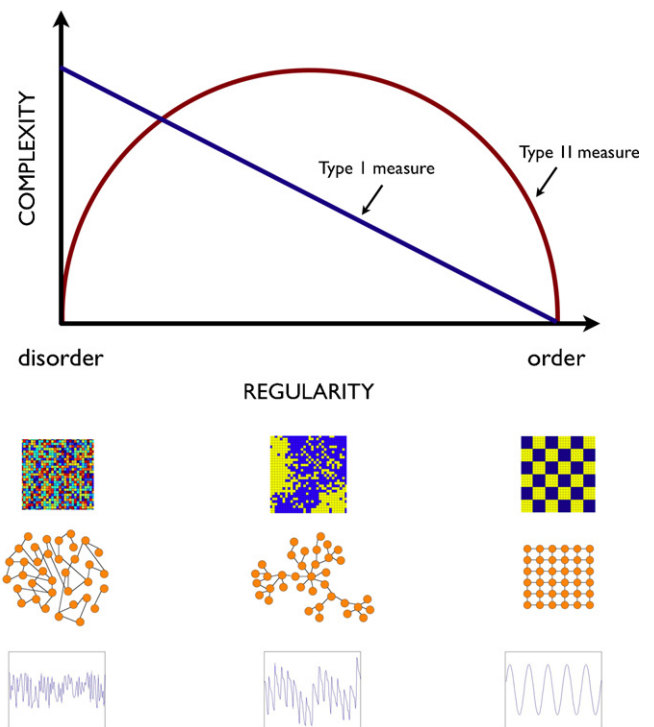


Fig. 1. Complexity versus regularity. Measures of complexity distinguish classes of structures or dynamics along a gradient of order to disorder. Type 1 measures assign the highest value to disordered systems, whereas Type 2 measures are convex functions that assign the highest value to systems falling between the two extremes of order and disorder. Examples of spatial, structural and temporal signatures corresponding to each class of system are also shown. Here, we argue that both highly ordered and highly disordered (random) systems are simple systems and that the most complex systems are situated in the intermediate zone of regularity.

measures of complexity, most of which have Shannon entropy or derivatives of Shannon entropy at their root (Kolmogorov, 1965; Chaitin, 1977; Gell-Mann and Lloyd, 1996; Lloyd, 2001). Such measures require that the data be categorized into binary or another fixed number of bins (“symbols”), entailing a loss of information for continuous valued data. Complexity measures then are based on the probability (p_i) of observing symbol i in the data, as well as on second order probabilities such as the frequency of observing symbol i next to symbol j or of observing particular sequences of symbols of length L in the series (known as L -words). For a binary symbol string, the number of possible words of length L that can be made is 2^L . The relative frequency of occurrence of each L -word in the symbol string is designated as ($p_{L,i}$) (for a random sequence, all words are equally probable). Both Type 1 and Type 2 complexity measures exist for symbol sequences. These can be used to classify and compare time series from different systems along an axis of order to disorder and have been widely applied to describe symbol sequences in the information sciences.

Two information-theoretic measures of complexity that have been applied to ecological time series are the mean information gain (MIG) (Wackerbauer et al., 1994) and fluctuation complexity (Bates and Shepard, 1993). MIG measures the amount of new information gained by reading an additional symbol in a time series and is maximal for a random series. MIG is thus a Type 1 measure of complexity. Fluctuation complexity is a measure that relates to the degree of structure in the time series and meets the criteria for Type 2 measures.

The mean information gain (H_G) is computed as follows:

$$H_G(L) = H_S(L + 1) - H_S(L) \quad (1)$$

where H_s is the Shannon entropy of the sequence:

$$H_s(L) = -\sum_{i=1}^n p_{L,i} \log_2 p_{L,i} \quad (2)$$

The fluctuation complexity (C_F) is equal to:

$$C_F = \sum_{i,j=1}^n p_{L,ij} \left(\log_2 \frac{p_{L,i}}{p_{L,j}} \right)^2 \quad (3)$$

where $p_{L,ij}$ is the probability of observing word j immediately following the word i . The fluctuation complexity thus takes into consideration, to some extent, the ordering of, and relationship between, words in a sequence.

MIG and C_F have been successfully applied to characterize different types of ecological time series. [Hauhs and Lange \(2008\)](#) showed that these measures can successfully discriminate between the complexity of runoff (discharge time series) from predominantly urban versus forested watersheds and between river systems from different parts of the globe. [Pachepsky et al. \(2006\)](#) used the same methods to characterize water flux time series through different soil profiles. [Meloche \(2005\)](#) applied these measures to flux tower data from the boreal forest and showed their ability to differentiate between forest stands in different states of development. While MIG and fluctuation complexity have the advantage of being founded in a clear tradition of information-based measures for describing complexity, the drawback of this approach is the loss of information that occurs in pre-treatment of the series, as well as the necessity of having fairly long (>1000 measurements) series in order to make meaningful conclusions. Future work should involve the development of new information-based measures adapted to shorter time series and more value classes (as opposed to binary classifications).

In addition to the various information-theoretic measures of complexity, methods of non-linear time series analysis may be used to characterize underlying structure in a data set and can give some insight into the nature of the systems temporal dynamics. Ecological data sets, however, have proven to be exceptionally difficult to analyze, due in part to the problem of distinguishing between noise and non-noise, as well as to the short length of most available time series. Efforts to detect chaos in ecological data sets by estimating Lyapunov exponents or reconstructing the underlying attractor, for example, have not met with incredible success ([Hastings et al., 1993](#)) although there are some recent, more promising examples with longer time series ([Benincà et al., 2008](#)). Less conventional methods, however, such as recurrence quantification analysis (RQA) may show structure in data that passed all other tests for randomness and are applicable to shorter time series ([Marwan et al., 2007](#)).

The RQA method is based on the recurrence plot (RP) of a time series, $\mathbf{B}_i(t)$, with $t = 1 \dots n$. The first step is to reconstruct the attractor in state space via Taken's theorem, in which a point v_j in the attractor Φ is defined as:

$$v_j = \langle \mathbf{B}_i(j), \mathbf{B}_i(j + \tau), \mathbf{B}_i(j + 2\tau), \dots, \mathbf{B}_i(j + (\omega - 1)\tau) \rangle$$

$$j = 1 \dots n - (\omega - 1)\tau \quad (4)$$

where ω is the embedding dimension and τ is the delay. The RP is created by filling the binary recurrence matrix \mathbf{R}_i according to the following rule:

$$\mathbf{R}_i(x, y) = \begin{cases} 1 & \text{if } d(v_x, v_y) < \delta, \\ 0 & \text{elsewhere.} \end{cases} \quad x, y \in \Phi, \quad (5)$$

where $d(v_x, v_y)$ is the Euclidean distance between two points on the attractor in the embedded state space. The threshold value given by δ represents the threshold distance for which two states are

considered to be on neighboring trajectories (recurrent) in state space. A multivariate RP can also be calculated, via the dot product of the RPs for different time series. This allows the identification of points in state space where the entire system state (as described by multiple dynamic variables) recurs ([Romano et al., 2004](#)).

RQA techniques are based on analysis of patterns in the recurrence plots, and can quantify the degree of randomness or determinism in the system dynamics. Measures of determinism in RQA may perhaps be linked to the complexity of a time series, serving as Type 1 measures of complexity. RQA has been successfully applied to characterize time series from many social and biological systems and recent work ([Proulx et al., 2008](#); [Proulx and Parrott, 2009](#)) has demonstrated the potential of RQA to characterize the dynamics of real and simulated ecological systems.

3.2. Spatial measures

Spatial measures of complexity must be able to characterize ordered, random and complex two-dimensional patterns. Spatial measures do not describe the dynamics or function of a system but rather describe its configuration in space at a particular moment in time. A few candidate information-based measures have been proposed and tested on spatial ecological data, including the Shannon entropy and mean information gain. In these cases, the measures are applied to raster-based data (such as photographs, satellite imagery or output from spatially explicit models). As for time series, these measures require preprocessing of the data into a reduced number of classes and are based on the probabilities (p_i) of observing certain pixel values in the raster. Second order probabilities such as the frequency that symbol j is in the neighborhood of i (p_{ij}) are also used, as are the probabilities of finding particular spatial configurations of values (e.g., in a 1×3 , 1×2 or 2×2 rectangle). [Proulx and Parrott \(2008\)](#) presented mean information gain (MIG) as being a candidate measure of spatial complexity for ecosystems. They showed that the MIG of photographs taken in the forest understory was positively correlated with plant species diversity and was able to differentiate between different habitat types ([Fig. 2](#)).

The fractal dimension is very commonly proposed as a measure of the spatial complexity of patterns. This measure is applicable to patterns that are self-similar over at least a certain range of spatial scales, which is often the case for physical landscape forms such as mountain ranges, coastlines and river networks ([Mandelbrot, 1983](#); [Barnsley, 1993](#)). It has been extensively used at the landscape scale to describe patterns of land use such as forest fragmentation as detected via aerial imagery or satellites ([Krummel et al., 1987](#); [Wiens and Milne, 1989](#)). It has also been used to describe the silhouettes of skylines in photographs of different categories of landscapes (e.g., urban versus forested) ([Hagerhall et al., 2004](#)). Increasing fractal dimension was shown to be positively correlated with scene "naturalness" and with human preferences for different landscape scenes. However, when a spatial pattern is not obviously self-similar, the application and calculation of the fractal dimension is problematic. In addition, some authors argue that complex systems are not necessarily self-similar across scales ([Wolpert and Macready, 2007](#)) and in ecology, the idea that ecosystems may have several characteristic spatial scales at which different structures and processes are present is becoming increasingly accepted. For this reason, the fractal dimension may have limited application as a measure of spatial complexity in ecology.

Landscape ecologists have devised a suite of metrics intended to describe patterns present on a landscape mosaic ([O'Neill et al., 1988](#)). Entropy and contagion (dispersion) metrics are good surrogates for Type 1 complexity measures, since they categorize the uniformity versus randomness of landscape patterns. Many other metrics are object-based; describing the shapes of identifiable patches in a spatial matrix. Methods of characterizing the

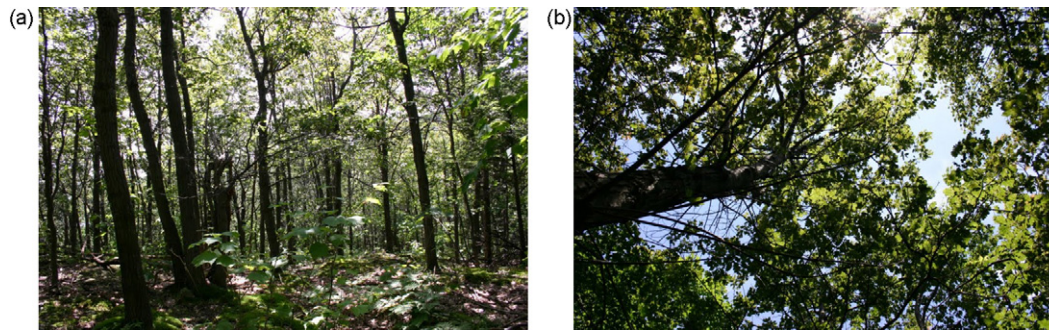


Fig. 2. Image analysis is an increasingly popular method for describing the spatial complexity of ecosystems and landscapes. In a study carried out by Proulx and Parrott (2008), the mean information gain was calculated for the pixel values of images of the forest understory (a) and canopy (b) in a mature mixed beech and maple forest. Results show a clear temporal signature of complexity over the growing season and the method is able to differentiate between different habitat types and between low and high diversity sites (photos taken by Joy Ding, Site B44, Gault Nature Reserve, Mont Saint Hilaire).

complexity of shapes include such simple measures as perimeter-area ratios and the ratio of patch area to the area of its bounding box. Moser et al. (2002) proposed a measure that describes landscape spatial complexity by the number of unique points required to trace boundaries between patches. They applied the measure to land cover data for agricultural landscapes and found a positive correlation with plant species richness. These types of shape-complexity metrics are analogous to Type 2 measures of complexity. These and similar metrics applied at the landscape scale, combined with site-specific indicators, could lead to insight into how habitat complexity and biodiversity are linked across spatial scales.

3.3. Spatiotemporal measures

Ultimately, the dynamics of ecosystems unfolds in space and time; however, methods of characterizing the complexity of such spatiotemporal dynamics are very limited. Kaspar and Schuster (1987) first demonstrated the use of the spatial autocorrelation function for detecting complex space-time patterns in two-dimensional data (one temporal and one spatial dimension). Other authors have done similar analyses on ecological point data measurements, but typically with the objective of detecting population synchrony across space (Bjørnstad et al., 1999). Parrott et al. (Parrott, 2005; Parrott et al., 2008) have proposed an information-based measure of spatiotemporal complexity that is applicable to three-dimensional raster data, such as space-time mosaics of land use or other variables. STC characterizes the complexity of three-dimensional structures (“blobs”) in space-time. STC gives a zero value to completely uniform space-time matrices, an intermediate value to random matrices and a value of one to matrices that have a power law distribution of blob volumes (e.g., a matrix occupied by mostly small, single-celled blobs, one or two large blobs with complex shapes and then many blobs of in-between shapes and sizes). STC has been successfully applied to the characterization of data from ecological models (Fig. 3), series of repeat photographs taken in a forest ecosystem (Parrott et al., 2008) and to remote sensing images of sea surface temperatures (Bottin, 2009).

3.4. Structural measures

Structural complexity measures describe the organization and relationships between components of a system. The natural application of these methods is in the analysis of networks, in which components are represented by nodes and relationships are represented by edges connecting 2 nodes together. Recent research in complex systems has shown that a wide variety of different systems

all share a similar, non-random structure characterized by short diameters (i.e., the shortest path required to traverse the network is much smaller than for a random network) and long-tailed degree distributions in which most nodes have 1 or 2 connections and a few “hubs” have many connections (Watts and Strogatz, 1998; Barabasi and Albert, 1999; Barabasi, 2009). This non-random yet irregular structure is thus a signature of a complex system and should be present in ecosystems as well.

Ecology has a long history of describing ecosystems as networks, starting with early conceptual models of ecosystems describing the flows of matter and energy through the systems major reservoirs (Odum, 1968). The food web concept, in which nodes represent species or functional groups and feeding relationships are represented by edges is another well-known network studied in ecology.

Recent work in food web analysis has shown that the structure of natural food webs is indeed irregular and non-random and, depending on the resolution of the studied food web, may be characterized as being complex using measures from graph theory (Bascompte, 2009; Ings et al., 2009, Fig. 4). Analysis of empirical data describing food webs from aquatic and terrestrial ecosystems has shown ecosystems to be “small-world” networks, characterized by path lengths between two randomly chosen species that are considerably shorter than would be expected for a random or regularly structured network (Montoya and Solé, 2002; Williams et al., 2002).

The implications of a non-random structure are important, since scale-free systems in particular are robust to the random loss of nodes (a node selected at random is unlikely to be highly connected) but highly vulnerable to the loss of hubs (Albert et al., 2000). If ecosystems are indeed structured like other complex systems, this type of analysis could help conservation managers identify highly connected “hub” species that should be the focus of conservation efforts. It is also possible that ecosystem “hubs” are keystone species. Analysis of the robustness of empirical food webs to the loss of species has shown them to respond similarly to other complex systems (Dunne et al., 2002), with a threshold point after which the network is too fragmented to be functional. Interpretation and analysis of ecosystems from a network perspective may thus provide useful information to managers on the potential effects (via links in the network) of interventions. Current research is going beyond the food web concept to study more general ecological interaction webs, in which all types of ecological interactions (exploitation, mutualism, facilitation, neutralism, etc.) are included (Ings et al., 2009). These studies may contribute additional insight into the long-standing diversity-stability debate, started by May with early multi-species models (May, 1973) and may help identify the role of weak or positive interactions in community structure (McCann,

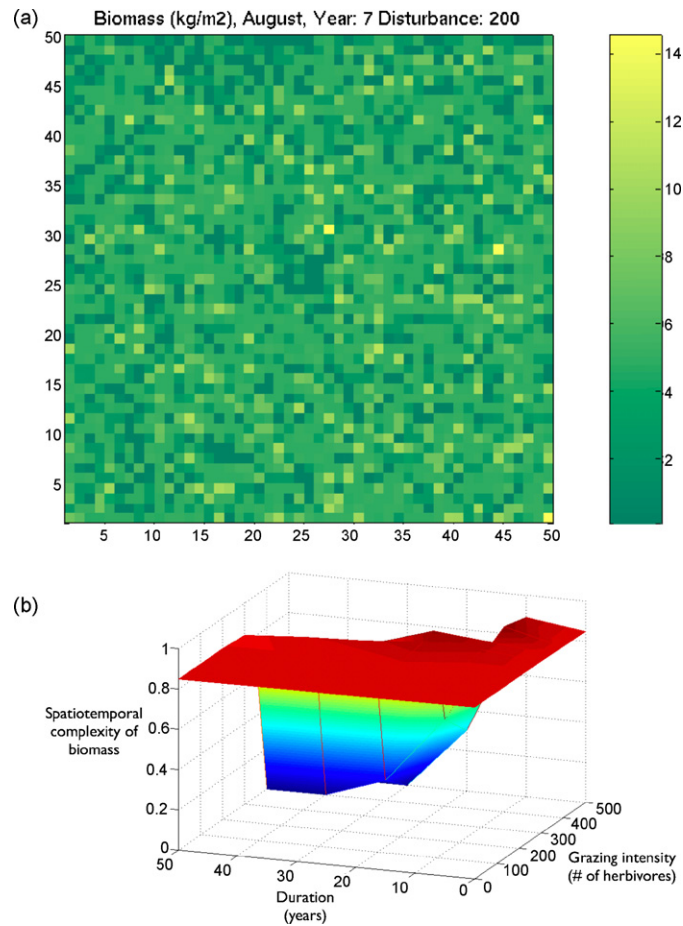


Fig. 3. Relationship between grazing intensity and spatiotemporal complexity in a model ecosystem. In this study, increasing numbers of herbivores were added to a grassland ecosystem for different lengths of time to explore the effects of grazing intensity and duration on the vegetative community. Simulations were carried out with the spatially explicit, individual-based model, WIST (Parrott and Kok, 2006). Simulations were run for a period of 50 years and the biomass of standing vegetation was recorded for 10 m × 10 m grid cells on a monthly basis (see (a) for an example). The spatiotemporal complexity of the biomass series was computed for each combination of grazing intensity and duration ((b), see text for details about the method). Results show that the spatiotemporal complexity remains high for low levels of grazing intensity or for any level of grazing intensity so long as the duration is sufficiently short to allow the system to recover. A threshold effect occurs after which the spatiotemporal complexity of the system decreases rapidly, followed by a corresponding decrease in species diversity (not shown).

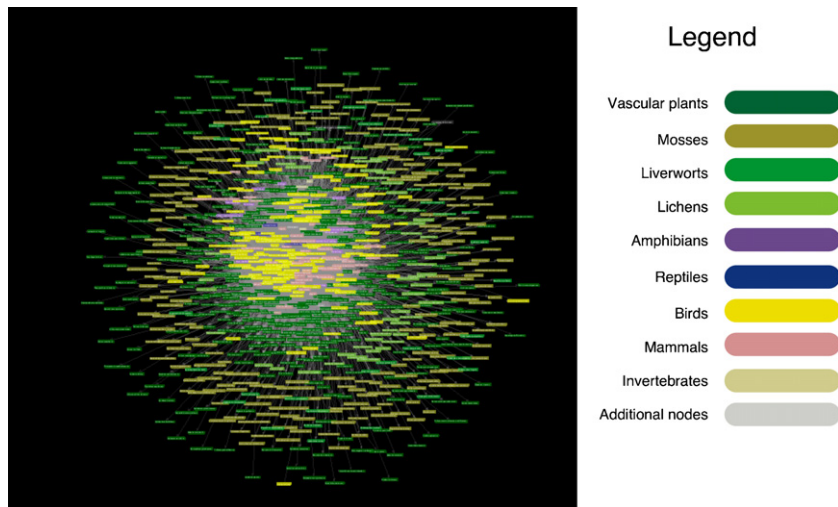


Fig. 4. Network analysis can be used to describe the structural complexity of an ecosystem. This figure shows the food web for 913 species inhabiting Mont Saint Hilaire in Québec, Canada. Nodes (colored rectangles) represent species and links represent predator–prey relationships between species. Analysis of the degree distribution (distribution of the number of links per node) of this food web shows a non-random structure that is typical of many types of complex networks (Arii et al., 2007). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

2000). Lastly, the study of such interaction webs should provide more accurate characterizations of the complex structural signature of ecosystems.

4. Discussion: ecological complexity as an ecological orientor

Recent research continues to confirm the presence of temporal, spatial, spatiotemporal and structural signatures that share common characteristic patterns across all types of complex systems. Measures of complexity are designed to quantify these patterns. Despite the growing acceptance of ecological complexity as an important system attribute, there are very few examples of studies applying complexity measures to analyze ecological data. In this review, I have summarized the key approaches that have been taken and identified where more research is needed.

Clearly, the concept of ecological complexity is important for ecology and there is a need to better define it. Ecological complexity is often linked to concepts such as ecological resilience and ecological integrity (Levin, 1999; Harris, 2007). Indeed, most ecologists would probably posit a positive correlation between the degree of complexity of an ecosystem and its “health” or “integrity”, both of which very likely increase a system’s resilience and robustness (Loreau et al., 2001; Hooper et al., 2005). Certainly the heterogeneity of components in a system, providing functional and structural redundancy, increases system complexity (in space, time and structure) and provides increased robustness and tolerance to disturbance (Carlson and Doyle, 2002). An appropriate measure of complexity should, therefore, also serve as a surrogate measure of robustness. Additionally, a positive correlation between habitat complexity and specific diversity is a long-standing hypothesis in ecology that has been confirmed by numerous field studies for both terrestrial and marine systems (MacArthur and MacArthur, 1961; Roth, 1976; Heck and Wetstone, 1977; August, 1983). Further work should be done to quantify habitat complexity using spatial and temporal complexity measures applied to currently available remote sensing and flux tower data. If a quantitative relationship were found between habitat complexity and biodiversity, such analyses could serve to identify priority areas for conservation. Complexity may, therefore, be a useful indicator of the state and health of an ecosystem.

Complexity may also serve as an indicator of the degree of maturity or organization of an ecosystem and is, in this sense, complementary to measures of self-organization. Müller (2005) postulated that the complexity of a natural ecosystem increases with its maturity and that via a process of “undisturbed complexifying development” certain features of an ecosystem tend towards an attractor state which is a function of site conditions and “prevailing ecological functions”. Indeed, many authors have argued that it is the processes of self-organization and adaptation that serve to maintain a complex system in a state of maximal complexity, in the intermediate zone between order and disorder (Nicolis and Prigogine, 1977; Kay, 1991; Fath et al., 2004; Müller, 2005). Fig. 5 presents a synthesis of the hypothetical relationship between this state of maximal complexity and the degree of organization of a system. In this figure, it is hypothesized that, for a given set of environmental conditions, the process of self-organization will draw an undisturbed system towards a local optimum, that can be measured as the state of maximal complexity. In this context, Type 2 measures of complexity (as opposed to Type 1) are perhaps more meaningful as indicators of ecosystem state. Working from a similar hypothesis, Kutsch et al. (2001) used a collection of indicators, including information-based complexity measures, as a means of quantifying the degree of self-organization of different ecosystems, linking self-organization, complexity, and ecosystem

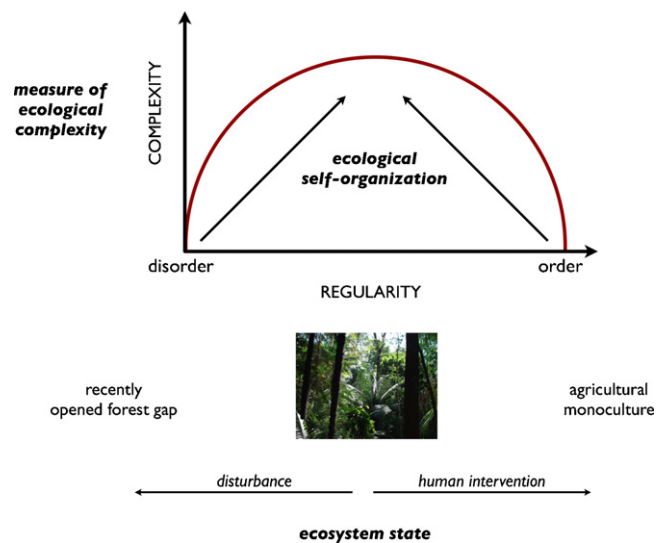


Fig. 5. Ecological complexity as an ecological indicator. An ecosystem tends towards greater complexity via the process of self-organization, which draws the system away from the two extremes of order and disorder to a state of maximal complexity. This state of maximal complexity is a site-specific attractor which is constrained by prevailing physical and environmental conditions. Natural disturbance events may cause an ecosystem state to tend towards greater disorder, whereas human intervention in the form of energy input can move the system state towards greater order than might be attainable naturally. Here, an agricultural monoculture, such as a cornfield planted in rows, serves as an analogy for an ordered ecosystem, whereas a recently opened gap in a forest, in which seeds have randomly fallen and just begun to germinate, may be an example of a disordered ecosystem. An undisturbed, ancient tropical rainforest (central image) is probably the best example of one of the Earth’s most complex ecosystems.

state. They concluded that a mature beech forest was more complex and more self-organized than an agricultural field located nearby and that this difference could be detected using appropriate indicators. Future work should focus on detecting more subtle differences between similar ecosystems in different stages of development.

Ecosystems are open-systems that, through the process of self-organization, optimize their internal structures and processes so as to achieve maximum complexity, in part through the development of dissipative structures (Nicolis and Prigogine, 1977; Kay, 1991). I hypothesize that an ecosystem naturally tends towards this state, maintaining maximal complexity over time even as internal components are adapted and replaced. Human interventions or natural disturbances can draw a system away from this state of maximal complexity. Conversely, restoration efforts may help the system to self-organize towards a state of higher complexity (Parrott, 2002). If the system has been totally degraded to a point that makes this natural attractor unattainable, e.g., in the case of extreme soil degradation or pollution, or the prevailing environmental conditions have changed, the ecosystem may find an alternative stable state which is a local maximum for complexity. Such a change is equivalent to a catastrophic shift (Scheffer et al., 2001; Scheffer and Carpenter, 2003).

Proulx and Parrott (2008) proposed complexity as an ecological orientor (*sensu* (Müller and Leupelt, 1998; Müller et al., 2000)): a property of a system that is optimized as an ecosystem develops via the process of self-organization. Such ecological orientors are global level state variables that Müller et al. (2000) argue may serve as “aggregated indicators for ecological integrity”. Complexity, as an indicator, has an operational advantage over ecological integrity, in that it is a well-defined concept that can be measured relative to a known baseline of total randomness or total order. In this sense, it can be more easily implemented as a holistic indicator in an ecological monitoring program, as opposed to ecological integrity, which defines the state of an ecosystem relative to a sup-

posed “natural” or reference state. More research needs to be done to validate hypotheses linking complexity with other measurable indicators of the physical and biological environment. If complexity can be adequately quantified, then optimization of complexity should be added to the list of eight ecological orientors, related to material and energetic flow, biomass production and heterogeneity, originally proposed by Müller et al. (2000).

5. Conclusion

The search for an appropriate measure of ecological complexity is similar to the search for any holistic indicator of ecosystem state: managers and policy makers need a limited number of indicators upon which they can base environmental assessments and policy statements. Appropriate ecological indicators may provide leverage for conservation, preservation and also rehabilitation projects. Given the high dimensionality of natural ecosystems, there is probably no one particular measure or approach that will suffice to give a complete picture of the system state. The holistic nature of complexity, however, makes it an appealing candidate amongst ecological indicators. Certainly, the studies cited here do conclude that measures of complexity capture at least some system-level aspects of ecosystem state. Many of these measures are data demanding, and clearly ecological indication should not be based on sparse or incomplete data. The recent increase of automated monitoring systems being installed in research sites, as well as the availability of high-resolution satellite based remotely sensed data, should greatly contribute to the development and application of new and existing measures of complexity over the next decade, rapidly improving our understanding of the complex structures and dynamics of ecosystems.

Acknowledgements

I would like to thank Friedrich Recknagel who strongly encouraged me to publish these ideas and gave me the final impetus that I needed to write this manuscript. The network visualization in Fig. 4 was done by Rodolphe Gonzales. I would also like to acknowledge Holger Lange, Raphaël Proulx and Bai-Lin (Larry) Li with whom I have had stimulating discussions about the problem of measuring ecological complexity. The Natural Sciences and Engineering Research Council of Canada (NSERC) provided funding for this research.

References

- Albert, R., Hawoong, J., Barabasi, A., 2000. Error and attack tolerance of complex networks. *Nature* 406.
- Arii, K., Derome, R., Parrott, L., 2007. Examining the potential effects of species aggregation on the network structure of food webs. *Bulletin of Mathematical Biology* 69, 119–133.
- Atmanspacher, H., 2007. A semiotic approach to complex systems. In: Mehler, A., Köhler, R. (Eds.), *Aspects of Automatic Text Analysis*. Springer, Berlin, pp. 79–91.
- August, P., 1983. The role of habitat complexity and heterogeneity in structuring tropical mammal communities. *Ecology*, 1495–1507.
- Barabasi, A., 2009. Scale-free networks: a decade and beyond. *Science* 325, 412–413.
- Barabasi, A., Albert, R., 1999. Emergence of scaling in random networks. *Science* 286, 509–512.
- Barnsley, M., 1993. *Fractals Everywhere*. Academic Press, London.
- Bascompte, J., 2009. Disentangling the web of life. *Science* 325, 416–419.
- Bates, J.E., Shepard, H.K., 1993. Measuring complexity using information fluctuation. *Physics Letters A* 172, 416–425.
- Benincà, E., Huisman, J., Heerkloss, R., Jöhnk, K., Branco, P., Van Nes, E., Scheffer, M., Ellner, S., 2008. Chaos in a long-term experiment with a plankton community. *Nature* 451, 822–825.
- Bjørnstad, O., Ims, R., Lambin, X., 1999. Spatial population dynamics: analyzing patterns and processes of population synchrony. *Trends in Ecology & Evolution* 14, 427–432.
- Bottin, Z., 2009. Spatio-Temporal Complexity of the Sea Surface Temperatures of the Philippines. The University of the Philippines, Diliman, Quezon City.
- Carlson, J.M., Doyle, J., 2002. Complexity and robustness. In: *Proceedings of the National Academy of Science*, 99, pp. 2538–2545.
- Chaitin, G., 1977. Algorithmic information theory. *IBM Journal of Research and Development* 21, 350–359.
- Dunne, J.A., Williams, R.J., Martinez, N., 2002. Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecology Letters* 5, 558–567.
- Fath, B., Jørgensen, S., Patten, B., Straskraba, M., 2004. Ecosystem growth and development. *BioSystems* 77, 213–228.
- Gell-Mann, M., Lloyd, S., 1996. Information measures, effective complexity and total information. *Complexity* 2, 44–52.
- Grassberger, P., 1988. Complexity and forecasting in dynamical systems. In: Peliti, L., Vulpiani, A. (Eds.), *Measures of Complexity*. Springer-Verlag, Berlin, pp. 1–22.
- Hagerhall, C.M., Purcell, T., Taylor, R., 2004. Fractal dimension of landscape silhouette outlines as a predictor of landscape preference. *Journal of Environmental Psychology* 24, 247–255.
- Harris, G., 2007. *Seeking Sustainability in an Age of Complexity*. Cambridge University Press.
- Hastings, A., Hom, C., Ellner, S., Turchin, P., Godfray, H.C.J., 1993. Chaos in ecology: is mother nature a strange attractor? *Annual Review of Ecological Systems* 24, 1–33.
- Hauhs, M., Lange, H., 2008. Classification of runoff in headwater catchments: a physical problem? *Geography Compass* 2, 235–254.
- Heck Jr., K., Weststone, G., 1977. Habitat complexity and invertebrate species richness and abundance in tropical seagrass meadows. *Journal of Biogeography* 4, 135–142.
- Hooper, D., Chapin III, F., Ewel, J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J., Lodge, D., Loreau, M., Naeem, S., 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* 75, 3–35.
- Ings, T., Montoya, J., Bascompte, J., Blüthgen, N., Brown, L., Dormann, C., Edwards, F., Figueroa, D., Jacob, U., Jones, J.I., Lauridsen, R., Ledger, M., Lewis, H., Olesen, J., Veen, F.J.F.v., Warren, P., Woodward, G., 2009. Ecological networks – beyond food webs. *Journal of Animal Ecology* 78, 253–269.
- Jørgensen, S., Müller, F. (Eds.), 2000. *Handbook of Ecosystem Theories and Management*. Lewis Publishers, Washington, DC, p. 584.
- Kaspar, F., Schuster, H.G., 1987. Easily calculable measure for the complexity of spatiotemporal patterns. *Physical Review A* 36, 842–848.
- Kay, J., 1991. A non-equilibrium thermodynamic framework for discussing ecosystem integrity. *Environmental Management* 15, 483–495.
- Kolmogorov, A., 1965. Three approaches for defining the concept of information quantity. *Problems of Information Transmission* 1, 3–8.
- Krummel, J., Gardner, R., Sugihara, G., O'Neill, R., Coleman, P., 1987. Landscape patterns in a disturbed environment. *Oikos*, 321–324.
- Kutsch, W., Steinborn, W., Herbst, M., Baumann, R., Barkmann, J., Kappen, L., 2001. Environmental Indication: a field test of an ecosystem approach to quantify biological self-organization. *Ecosystems* 4, 49–66.
- Langton, C., 1992. Life at the edge of chaos. *Artificial Life II* 10, 41–91.
- Levin, S., 1998. Ecosystems and the biosphere as complex adaptive systems. *Ecosystems* 1, 431–436.
- Levin, S., 1999. *Fragile Dominion*. Perseus Publishing, Cambridge, p. 250.
- Liu, J., Dietz, T., Carpenter, S.R., Alberti, M., Folke, C., Moran, E., Pell, A.N., Deadman, P., Kratz, T., Lubchenco, J., et al., 2007. Complexity of coupled human and natural systems. *Science* 317, 1513.
- Lloyd, S., 2001. Measures of complexity: a non-exhaustive list. *IEEE Control Systems* 21, 7–8.
- Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J., Hector, A., Hooper, D., Huston, M., Raffaelli, D., Schmid, B., 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* 294, 804.
- MacArthur, R.H., MacArthur, J.W., 1961. On bird species diversity. *Ecology* 42, 594–598.
- Mandelbrot, B.B., 1983. *The Fractal Geometry of Nature*. W.H. Freeman and Company, New York.
- Marwan, N., Carmen Romano, M., Thiel, M., Kurths, J., 2007. Recurrence plots for the analysis of complex systems. *Physics Reports* 438, 237–329.
- May, R., 1973. *Stability and Complexity in Model Ecosystems*. Princeton University Press, New York.
- McCann, K., 2000. The diversity-stability debate. *Nature* 405, 228–233.
- Meloche, F., 2005. Caractérisation de l'auto-organisation et de la complexité des écosystèmes. Université de Montréal, Montréal.
- Meyer, J.-A., 1988. Complexity in ecological systems. In: Peliti, L., Vulpiani, A. (Eds.), *Measures of Complexity*. Springer-Verlag, Berlin, pp. 139–145.
- Montoya, J., Solé, R., 2002. Small world patterns in food webs. *Journal of Theoretical Biology* 214, 405–412.
- Moser, D., Zechmeister, H.G., Plutzer, C., Sauberer, N., Wrabka, T., Grabherr, G., 2002. Landscape patch shape complexity as an effective measure for plant species richness in rural landscapes. *Landscape Ecology* 17, 657–669.
- Müller, F., 2005. Indicating ecosystem and landscape organisation. *Ecological Indicators* 5, 280–294.
- Müller, F., Leupelt, M. (Eds.), 1998. *Eco Targets, Goal Functions and Orientors*. Springer, Berlin.
- Müller, F., Hoffmann-Kroll, R., Wiggering, H., 2000. Indicating ecosystem integrity – theoretical concepts and environmental requirements. *Ecological Modelling* 130, 13–23.
- Nicolis, G., Prigogine, I., 1977. *Self-Organization in Nonequilibrium Systems: From Dissipative Structures to Order Through Fluctuations*. Wiley, New York.
- O'Neill, R.V., Krummel, J.R., Gardner, R., Sugihara, G., Jackson, B., DeAngelis, D.L., Milne, B.T., Turner, M., Zygmunt, B., Christensen, S.W., Dale, V.H., Graham, R.L., 1988. Indices of landscape pattern. *Landscape Ecology* 1, 153–162.

- Odum, E., 1968. Energy flow in ecosystems: a historical review. *Integrative and Comparative Biology* 8, 11.
- Pachepsky, Y., Guber, A., Jacques, D., Jiri Simunek b, Genuchten, M.T.V., Nicholson, T., Cady, R., 2006. Information content and complexity of simulated soil water fluxes. *Geoderma* 134, 253–266.
- Parrott, L., 2002. Complexity and the limits of ecological engineering. *Transactions of the ASAE* 45, 1697–1702.
- Parrott, L., 2005. Quantifying the complexity of simulated spatiotemporal population dynamics. *Ecological Complexity* 2, 175–184.
- Parrott, L., Kok, R., 2006. Use of an object-based model to represent complex features of ecosystems. In: Minai, A., Bar-Yam, Y. (Eds.), *Unifying Themes in Complex Systems*. Springer, Berlin, pp. 169–179.
- Parrott, L., Proulx, R., Thibert-Plante, X., 2008. Three-dimensional metrics for the analysis of spatiotemporal data in ecology. *Ecological Informatics* 3, 343–353.
- Proulx, R., Parrott, L., 2008. Measures of structural complexity in digital images for monitoring the ecological signature of an old-growth forest ecosystem. *Ecological Indicators* 8, 270–284.
- Proulx, R., Parrott, L., 2009. Structural complexity in digital images as an ecological indicator for monitoring forest dynamics across scale, space and time. *Ecological Indicators* 9, 1248–1256.
- Proulx, R., Cote, P., Parrott, L., 2008. Use of recurrence analysis to measure the dynamical stability of a multi-species community model. *The European Physical Journal-Special Topics* 164, 117–126.
- Romano, M., Thiel, M., Kurths, J., von Bloh, W., 2004. Multivariate recurrence plots. *Physics Letters A* 330, 214–223.
- Roth, R.R., 1976. Spatial heterogeneity and bird species diversity. *Ecology* 57, 773–782.
- Scheffer, M., Carpenter, S.R., 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends in Ecology & Evolution* 18, 648–656.
- Scheffer, M., Carpenter, S., Foley, J., Folkes, C., Walker, B., 2001. Catastrophic shifts in ecosystems. *Nature* 413, 591–596.
- Solé, R.V., Bascompte, J., 2006. *Self-Organization in Complex Ecosystems*. Princeton University Press, Princeton, NJ.
- Wackerbauer, R., Witt, A., Atmanspacher, H., Kurths, J., Scheingraber, H., 1994. A comparative classification of complexity measures. *Chaos, Solitons & Fractals* 4, 133–173.
- Watts, D., Strogatz, S., 1998. Collective dynamics of 'small-world' networks. *Nature*, 393.
- Wiens, J., Milne, B., 1989. Scaling of 'landscapes' in landscape ecology, or, landscape ecology from a beetle's perspective. *Landscape Ecology* 3, 87–96.
- Williams, R.J., Berlow, E., Dunne, J.A., Barabasi, A., Martinez, N., 2002. Two degrees of separation in complex food webs. *PNAS* 99, 12913–12916.
- Wolpert, D.H., Macready, W., 2007. Using self-dissimilarity to quantify complexity. *Complexity* 12, 77–85.