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Original Research Article

Complexity of lakes in a latitudinal gradient

Nelson Fernández [a,b,c,d,*], José Aguilar [c], C.A. Piña-García [e], Carlos Gershenson [e,f,g,h,i,**]

[a] *Laboratorio de Hidroinformática, Universidad de Pamplona, 543050 Pamplona, Colombia*
[b] *Grupo de Investigación en Ecología y Biogeografía, Universidad de Pamplona, 543050 Pamplona, Colombia*
[c] *Centro de Micro-electrónica y Sistemas Distribuidos (CEMISID), Universidad de los Andes, 5101 Mérida, Venezuela*
[d] *Laboratorio Nacional de Ciencias de la Sostenibilidad, Instituto de Ecología, Universidad Nacional Autónoma de México 70275, 04510 Ciudad de México, Mexico*
[e] *Departamento de Ciencias de la Computación, Instituto de Investigaciones en Matemáticas Aplicadas y en Sistemas(IIMAS), Universidad Nacional Autónoma de México, 04510 Ciudad de México, Mexico*
[f] *Centro de Ciencias de la Complejidad (C3), Universidad Nacional Autónoma de México, 04510 Ciudad de México, Mexico*
[g] *SENSEable City Lab, Massachusetts Institute of Technology, Cambridge, MA 02139, USA*
[h] *MoBS Lab, Northeastern University, Boston, MA 02115, USA*
[i] *ITMO University, 199034 St. Petersburg, Russian Federation*

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A B S T R A C T

Measuring complexity is fast becoming a key instrument to compare different ecosystems at various scales in ecology. To date there has been little agreement on how to properly describe complexity in terms of ecology. In this regard, this manuscript assesses the significance of using a set of proposed measures based on information theory. These measures are as follows: emergence, self-organization, complexity, homeostasis and autopoiesis. A combination of quantitative and qualitative approaches was used in the data analysis with the aim to apply these proposed measures. This study systematically reviews the data previously collected and generated by a model carried out on four aquatic ecosystems located between the Arctic region and the tropical zone. Thus, this research discusses the case of exploring a high level of self-organization in terms of movement, distribution, and quality of water between the northern temperate zone and the tropics. Moreover, it was assessed the significance of the presence of a complex variable (*pH*) in the middle of the latitudinal transect. Similarly, this study explores the relationship between self-organization and limiting nutrients (nitrogen, phosphorus and silicates). Furthermore, the importance of how a biomass subsystem is affected by seasonal variations is highlighted in this manuscript. This case study seeks to examine the changing nature of how seasonality affects the complexity dynamics of photosynthetic taxa (lakes located in northern temperate zone) at high latitudes, and it also investigates how a high level of self-organization at the tropical zone can lead to increase the amount of planktonic and benthic fish which determines the dynamics of complexity. This research also compares the emerging role of how a biomass subsystem has a highest temporal dynamics compared to he limiting nutrients' subsystem. In the same way, the results associated to autopoiesis reflect a moderate degree of autonomy of photosynthetic biomass.

It is also discussed the case of how complexity values change in the middle of the latitudinal gradient for all components. Finally, a comparison with Tsallis information was carried out in order to determine that these proposed measures are more suitable due to they are independent of any other parameter. Thus, this approach considers some elements closely related to information theory which determine and better describe ecological dynamics.

* Principal corresponding author at: Laboratorio de Hidroinformática, Universidad de Pamplona, 543050 Pamplona, Colombia.
** Corresponding author at: Departamento de Ciencias de la Computación, Instituto de Investigaciones en Matemáticas Aplicadas y en Sistemas(IIMAS), Universidad Nacional Autónoma de México, 04510 Ciudad de México, Mexico.
E-mail addresses: nfernandez@unipamplona.edu.co (N. Fernández), cgg@unam.mx (C. Gershenson).

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1. Introduction

To date there has been little agreement on what complexity really is. In this sense, it can be said that complexity has a pervasive meaning i.e., it can be found in most disciplines and phenomena with different definitions. In this regard, a complex system is observed when its components are difficult to separate due to relevant interactions among their elements (Gershenson, 2013).

Complex systems are fundamental to study ecosystems due to they are highly interwoven units that may generate significant information as a result of relevant interactions. This information can be considered as emergent e.g., symbionts are not able to survive on their own, they depend directly on their relations with the environment. It is important to note that if interactions are neglected, it will not be possible to properly describe the most important features in ecology. Specifically, it can be said that some elements are continuously interacting to self-organize themselves in order to carry out a task i.e., these elements present a global pattern from local dynamics, as it can be found on fish schools where there is no central or external control, but interactions between fish lead to global regularities, so a high degree of organization is achieved (as opposed to random patterns). While emergence is related to generate information, self-organization is associated with order and regularity (Gershenson and Fernández, 2012; Fernández et al., 2014). Balance between change (chaos) and stability (order) has been proposed as a characteristic of complexity (Langton, 1990; Kaufmann, 1993). Thus, considering that chaotic systems generate enough information (emergence), complexity can be defined as the balance between emergence and self-organization (López-Ruiz et al., 1995; Fernández and Gershenson, 2014).

Interactions are present in the generation of two additional properties. Firstly, *homeostasis*: this term refers to a self-regulation property where ecosystem and their elements maintain steady states of operation during internal and external changes (Cannon, 1932). Interactions also enable feedback control loops, which help ecosystems to regulate themselves in their internal states and reach a dynamic equilibrium. Secondly, *autopoiesis*: it is a particular form of homeostasis and was originally understood as the self-production and regeneration of living systems. Thus, it can be said that an autopoietic ecosystem possess the potential to develop, preserve and produce organization (Varela et al., 1974). Similarly, autopoiesis has also been related to autonomy (Ruiz-Mirazo and Moreno, 2004), an essential aspect of living systems.

Recently, there has been renewed interest in complexity in terms of self-organization, emergence and criticality (Cadenasso et al., 2006; Boschetti, 2008, 2010). Previous research of complexity in ecology has been associated with aspects of richness, abundance and hierarchical structure (Azhar et al., 2013). As a result, different mathematical approximations for measuring ecological complexity have been explored (Parrott, 2005; Boschetti et al., 2008; Proulx and Parrott, 2008). Developing complexity measures plays a critical role in studying and comparing ecosystems. Thus, it should be noted that a sounded mathematical formalism is still an open task (Gershenson, 2008).

There is evidence that information theory is fundamental in developing measures of complexity (Prokopenko et al., 2009). It is only since the extensive research of MacArthur in MacArthur (1955) that the study of ecological communities and information theory has gained a renewed interest (Piqueira et al., 2009; Anand et al., 2010; Ulanowicz, 2004, 2011). On the other hand, it should be mentioned that entropy measures have also been used to describe the structural topology and dynamical change in time in ecosystems (Ricotta and Anand, 2006; Parrott, 2010).

A large and growing body of literature has investigated how complexity can be correlated to other types of information measures such as: Fisher information (Prokopenko et al., 2011) and Tsallis information (Tsallis, 2002). Early examples of Fisher information include a model to explore details of critical phenomena and order-disorder transitions. Fisher information has been carried out by (Karunanithi et al., 2008; Mayer et al., 2006) in aquatic and terrestrial ecology with the aim to detect transitions between multiple dynamic regimes. In the case of Tsallis information, it can be considered as a measure of uncertainty in the relative abundances of species and it describes species diversity in ecological communities (Zaccarelli et al., 2013).

Recent studies carried out by (Gershenson and Fernández, 2012) and (Fernández et al., 2014) involved a significant analysis and discussion on measures of emergence, self-organization, complexity, homeostasis and autopoiesis. However, much uncertainty still exists about the relationship between these type of measures with ecological systems. Similarly, in another qualitative study conducted by (Santamara-Bonfil et al., 2016) a set of different distributions were explored with the aim to study a wide range of dynamical systems. These criteria were applied to an aquatic ecosystem (Fernández and Gershenson, 2014) but also to determine the presence-absence of modelling data related to mammals (Fernández et al., 2013).

There are a number of large cross-sectional studies which describe ecological dynamics using Shannon information. However, from previous work some questions still remain unanswered e.g., How to use quantitative indicators of complexity to study the dynamical properties of ecosystems in different climatic conditions? How to compare the complexity of different ecosystems? How to explore complexity along a gradient considering various subsystems and variables? And Finally, What is the main effect in terms of latitude on the ecological complexity? All these questions will be attempted to address in the following sections.

This study set out to investigate the suitability of our proposed measures: complexity, self-organization, emergence, homeostasis and autopoiesis. These measures will be applied to examine and compare lakes dynamics in the latitudinal gradient (Arctic region and the Tropical zone). In this context, this research systematically reviews the variables related to the physiochemical, nutrient and biomass subsystems. It is important to note that experimental data was obtained from the modelling and simulation corresponding to an annual cycle. Moreover, a fair comparison with Tsallis information will be examined and discussed. Similarly, the suitability and benefits of measuring complexity in ecological systems will be assessed. This investigation will enhance our understanding of indicators considering different subsystems and variables.

This manuscript is organized as follows: Section 2 shows the methodology related to simulations and mathematical aspects of the measures applied. Section 3 describes the results obtained by measuring complexity. In this section we also analyze which variables characterize emergence, self-organization and complexity in lakes located in the latitudinal gradient using multivariate analysis. Section 4 discusses computational aspects, ecological interpretations of the proposed measures, spatial variation of complexity, dynamics and function. We conclude in Section 5. Additional results related to the ecological description of the lakes and complexity for each subsystem are presented in Appendices A and B.

2. Methodology

The aim of this research is to explore the relationship between our proposed measures and regional lakes. In this context, a major advantage of selecting lakes as a part of our tests, is that fresh waters have received lesser attention than terrestrial or marine ecosystems, even though they contain 20% of the Earth's vertebrate