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Complexity of lakes in a latitudinal gradient

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ABSTRACT

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.

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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

species (Rohde, 1998). Furthermore, the study of gradients in ecology has just been related to diversity (Hawkins, 2001). Thus, little is known about latitudinal gradients of complexity.

Throughout this manuscript, it will be argued that lakes are significant examples of complex systems by having a rich variety of biological and environmental interactions. The spatio-temporal study of lakes considers different types of interactions between one or more subsystems, in one or more zones involving two or more variables. Additionally, ecological interactions that take place on different lakes, can be related to the patterns of persistence which corresponds to their latitudinal location. According to Amoros and Bornette (2002), complexity presented in lakes is a natural consequence produced by the integration of spatial scales on longitudinal, lateral and vertical dimensions of the landscape.

2.1. Simulations

Data were collected using *The Aquatic Ecosystem Simulator - "AES"* (Randerson and Bowker, 2008). This analysis was carried out using computer simulations based on numerical integration of 27 differential equations. The default timescale of this research was set to one year. However, outcomes produced by this simulation were analyzed in terms of days, weeks, months and in some cases season of the year.

Eq. (1), shows the general form of the equations applied and integrated by Euler's method. Units were $mg/m_3/day$.

$$\text{Rate of Change} = \text{Rate of Gain} - \text{Rate of Loss} \tag{1}$$

Some examples of specific components are give in Eqs. (2)–(4).

$$\frac{dPhy}{dt} = GPP - R - NM - SBZ - IZ - EO \tag{2}$$

where *dPhy* = Rate of Change of Phytoplankton; *GPP* = Gross Primary Production (Nutrient Uptake & Photosynthesis); *R* = Respiration; *NM* = Natural Mortality; *SBZ* = Sinking to Benthic Zone; *IZ* = Ingestion by Zooplankton, and *EO* = Efflux to Outflow.

$$\frac{dPN}{dt} = IFI + RBZ + RR\&EP - NUP\&M - EO \tag{3}$$

where *dPN* = Rate of Change of Planktonic Nutrients; *IFI* = Influx from Inflow; *RBZ* = Reflux from Benthic Zone via Mixing; *RR* & *E-P* = Recycling via Respiration & Excretion in Planktonic Zone; *NUP* & *M* = Nutrient Uptake by Periphyton & Macrophytes, and *EO* = Efflux to Outflow.

$$\frac{dPD}{dt} = NMPO + ITD - SB - IZ\&F - EO \tag{4}$$

where *dPD* = Rate of Change of Planktonic Detritus; *NMPO* = Natural Mortality of Planktonic Organism; *ITD* = Influx of Terrestrial Detritus; *SB* = Sinking to Benthic Zone; *IZ* & *F* = Ingestion by Zooplankton & Fish, and *EO* = Efflux to Outflow.

According to the equations previously stated, a set of simulations of physicochemical and trophic dynamics for four freshwater ecosystems were carried out. It is important to note that these four ecosystems contain functional groups (guilds) of organisms forming planktonic and benthic food webs.

Data were gathered from multiple sources: (i) The macrophyte zone, mainly composed of aquatic plants which are rooted or submerged. (ii) The planktonic zone, corresponding to open surface waters in which organisms drift passively (phyto and zooplankton). (iii) The benthic zone, or the lowest level of a body of water that is related to the substratum including the sediment and subsurface layers.

Within the zones explained earlier, it has been considered three subsystems: physicochemical, limiting nutrients and biomass. The physicochemical subsystem includes physical variables such as: light and temperature but also hydrological variables of inflow and outflow such as: retention time and zone mixing. It should be noted that chemical variables are also included: dissolved oxygen, conductivity and hydrogen potential *pH* (see Table 1). In the limiting nutrient subsystem case, this includes essential components for photosynthesis e.g., nitrates, phosphates and carbon dioxide. In general, this subsystem is associated with the biogeochemical cycles of nitrogen, phosphorus and carbon. It should be mentioned that silicates and detritus are also incorporated in this subsystem (see Table 2). Finally, The biomass subsystem is composed of photoautotrophic biomass (Diatoms, Cyanobacteria, Green Algae, Macrophytes) which is the basis for trophic web establishment but also consist of first and second-grade consumers: zooplankton and fish (see Table 3).

In order to avoid variations in our simulations it has been chosen a deterministic and closed model. In this regard, four different lakes corresponding to the following areas were taken into account: Arctic region (*Ar*), North Highland (*NH*), North Lowland (*NL*) and Tropical zone (*T*). The criteria for selecting these lakes were as follows: firstly, location of each one in a latitudinal gradient from the Polar to the Tropical zone *(Ar-T)*, and secondly, light and temperature conditions. A full description of the four lakes studied can be found in Appendix A.

To make possible the measuring of emergence, self-organization, complexity, homeostasis and autopoiesis, data from simulations was normalized to base 10 in order to obtain a finite alphabet

Table 1
Physicochemical variables.

Variable	Units	Acronym
Surface light	$MJ/m^2/day$	*SL*
Planktonic Light	$MJ/m^2/day$	*PL*
Benthic Light	$MJ/m^2/day$	*BL*
Surface Temperature	°C	*ST*
Planktonic Temperature	°C	*PT*
Benthic Temperature	°C	*BT*
Inflow and Outflow	m^3/s	*IO*
Retention Time	Days	*RT*
Evaporation	m^3/day	*Ev*
Zone Mixing	%/day	*ZM*
Inflow Conductivity	μS/cm	*ICd*
Planktonic Conductivity	μS/cm	*PCd*
Benthic Conductivity	μS/cm	*BCd*
Surface Oxygen	mg/litre	*SO*
Planktonic Oxygen	mg/litre	*PO*
Benthic Oxygen	mg/litre	*BO*
Sediment Oxygen	mg/litre	*SdO*
Inflow Ph	pH Units	*IpH*
Planktonic Ph	pH Units	*PpH*
Benthic Ph	pH Units	*BpH*

Table 2
Limiting nutrients variables.

Variable (all in mg/m^3)	Acronym
Inflow silicate	*IS*
Planktonic silicate	*PS*
Benthic silicate	*BS*
Inflow nitrate	*IN*
Planktonic nitrate	*PN*
Benthic nitrate	*BN*
Inflow phosphate	*IP*
Planktonic phosphate	*PP*
Benthic phosphate	*BP*
Inflow carbon dioxide	*ICD*
Planktonic carbon dioxide	*PCD*
Benthic carbon dioxide	*BCD*
Planktonic detritus	*PDe*
Benthic detritus	*BDe*

Table 3
Biomass variables.

Variable (all in mg/m^3)	Acronym
Inflow silicate	*IS*
Planktonic silicate	*PS*
Benthic silicate	*BS*
Inflow nitrate	*IN*
Planktonic nitrate	*PN*
Benthic nitrate	*BN*
Inflow phosphate	*IP*
Planktonic phosphate	*PP*
Benthic phosphate	*BP*
Inflow carbon dioxide	*ICD*
Planktonic carbon dioxide	*PCD*
Benthic carbon dioxide	*BCD*
Planktonic detritus	*PDe*
Benthic detritus	*BDe*

(values between 0 and 9). Thus, the following equation was applied to all points x of all variables X:

$$f(x) = \lfloor b \cdot \frac{x - \min X}{\max X - \min X} \rfloor, \tag{5}$$

where $\lfloor x \rfloor$ is the floor function of x and b is the base (10 in this case).

2.2. Measures

The proposed measures applied in this research have been recently developed and compared to other approaches e.g., Gershenson and Fernández (2012) and Fernández and Gershenson (2014). In the following lines our proposed set of measures: Emergence, Self-organization, Homeostasis and Autopoiesis will be defined. The term emergence (E) refers to a set of novel properties related to a specific phenomenon. In other words, it can be said that emergence occurs in an event when this phenomenon produces information. Therefore, it is possible to measure emergence in terms of Shannon's information I; $E = I$.

The term self-organization (S) has been used to refer situations in which there is an increase in order i.e., a reduction of entropy (Gershenson and Heylighen, 2003). Thus, it is possible to find the case where emergence implies an increase of information which is analogous to entropy and disorder: S should be anti-correlated with E ($S = 1 - I = 1 - E$).

Alternatively, according to Langton (1990), Kaufmann (1993), it has been argued that life and computation require a balance between change and regularity in order to achieve adaptation. This balance has been defined as complexity itself by following a study carried out by López-Ruiz et al. (1995), where change is described by emergence, whereas order and robustness are defined by self-organization (Fernández and Gershenson, 2014; Gershenson and Fernández, 2012). Hence, the present study proposes: $C = 4 \times E \times S$, where the constant 4 is added to normalize the measure to [0, 1].

This research considers to E, S, C as statistical measures, these measures are not able to distinguish a temporal order of values only their statistical distributions. However, they can be effective to distinguish between different dynamical regimes (ordered, complex and chaotic). In order to increase the reliability of these measures the range of measuring has been split into five categories as shown in Table 4. These categories are ordered by range, color and a word classification (adjectives). This classification was inspired by water pollution indexes that belongs to the Colombian classes (Fernández and Solano, 2003; Ramírez et al., 2003; Fernández et al., 2004).

Another important measure is homeostasis (H), which refers to a change in the system according to its own variables over time. In this context, this analysis was based on the conceptual framework proposed by the Hamming distance (Hamming, 1950); the Hamming distance d measures the percentage of different symbols in two strings X and X'. Then, $1 - d$ indicates how similar two strings are. Thus, homeostasis is finally found when there is a clear similarity between a pair of strings. In order to assess homeostasis it is necessary to compute the average of those similarities. It should be noted that H compares all variables of a system between two-time slices, while E, S, C consider the probability distributions of each variable i.e., they are orthogonal cases to H.

Finally, our last proposed measure is autopoiesis (A), in this study we have considered that an adaptive system requires a high level of C to be able to cope with changes in its environment (Langton, 1990; Kaufmann, 1993). Specifically, to compute A it is necessary to compare the trajectory of the variables of a system X against the trajectory of the variables in the system's environment Y. In this case, complexity of X (C_X) should be at least as higher as the complexity of Y (C_Y) due to this system requires the maintenance of its integrity depending on the dynamics of the environment. Consequently, $A = C_X/C_Y$. X and Y may differ depending on the scale at which the system is studied. For instances, at a lower scale, X can be a single variable and Y all other variables which are related to X, whereas at a higher scale X can be a system composed of a considerable amount of variables.

2.3. Measuring Tsallis information

Tsallis entropy (S_q) is considered as a generalized form of the standard Boltzmann–Gibbs entropy (see Eq. (6)). A major advantage of Tsallis entropy is that it can be used to determine whether there is a strong correlation between different micro-states in a system.

$$S_q = \frac{K}{q-1}\left(1 - \sum p_i^q\right) \tag{6}$$

In Eq. (6) p_i, is a discrete set of probabilities and q stands for a real number called entropic-index that measures how much correlated are the microstates. In this case, when q approaches to 1,

Table 4
Categories for classifying E, S, and C.

Category	1	2	3	4	5
Range	[0.8, 1]	[0.6, 0.8)	[0.4, 0.6)	[0.2, 0.4)	[0, 0.2)
Clasification	Very High	High	Fair	Low	Very Low
Color	Blue	Green	Yellow	Orange	Red

S_q is reduced to a Boltzmann–Gibbs entropy. In ecology, S_q is particularly useful to measure diversity. With regard to K, this variable refers to a positive constant that can be adapted for multiple scales of computation. Usually, the base is assumed to be binary meaning that $K = 1$. However, in this research we have set the base (b) to ten and K can be obtained using Eq. (7).

$$K = \frac{1}{Log_2(b)} \tag{7}$$

3. Results

Results are described in the following subsections. Firstly, details about physicochemical, limiting nutrients and biomass complexity are assessed and discussed. Graphical results for each variable belonging to a different subsystem and lake are summarised in Appendix B. The autopoiesis results of the phytoplanktonic subsystem are shown in the second subsection. A comparative analysis in terms of homeostasis is set out in the third part. Finally, the fourth part provides a set of similarities between our proposed complexity measure and Tsallis information.

3.1. Subsystem complexity of lakes

This section will examine complexity variations in three different subsystems corresponding to four lakes. Preliminary results of the physicochemical variables are shown in Appendix B.

In order to identify the characterization and variables of the lakes in terms of complexity, they were adapted to two multivariate techniques with an hybrid approach: principal component analysis (*PCA*) and hierarchical clustering (*HCPC*) (Le and Worch, 2015). *PCA* was used to examine the interrelations among *E*, *S*, and *C* of the four lakes to identify the underlying structure of these factors. *HCPC* was carried out on *PCA* for identifying groups of similar variables of each subsystem. The results obtained from the preliminary analysis of *PCA* were 12 combinations between the type of lakes (*Ar*, *NH*, *NL*, *T*) and these properties: *E*, *S*, *C*. These combinations are listed as follows: (1) emergence of lakes *ArE*, *NHE*, *NLE* and *TE*; (2) self-organization *ArS*, *NHS*, *NLS* and *TS* and finally, (3) complexity *ArC*, *NHC*, *NLC* and *TC*. Thus, these combinations were considered as factors in *PCA*.

Specifically, with the aim to establish a criterion in terms of a normal distribution, it was carried out a v-test on the variables and properties related to the lakes. Similarly, a p-value was computed to establish the significance of a given deviation among variables. Based on a v-test value, it was possible to test the following null hypothesis ($H0$): *the variables grouped in a particular cluster does not characterize a particular property in a lake*. In this case, the v-test was considered informative when the average of a property for a particular lake was equal to the general average. Thus, lakes were sorted in a descending order (p-values < 0.05) (Le and Worch, 2015).

3.1.1. Complexity in the physicochemical subsystem

The results obtained from the multivariate analysis are set out in Fig. 1. Additionally, a statistical analysis based on clusters was reported in Table 5.

To distinguish between these physicochemical variables it has been proposed five clusters (see Fig. 1a). Cluster one contains *SL*, *PL* and *BL*. this cluster describes the light measured on surface, planktonic and benthonic depths.

The most interesting aspect of this graph is that the light was the most emergent variable for *NH* and *Ar*. Similarly, in Fig. 1b, it can be seen that *NHE* and *ArE* are on the left side, close to the *X* axis. As previously stated, a closer inspection of the Table 5 shows that the characterization of light was the most emergent variable in the highest latitudes. From this data, it can be seen that the mean values related to *PL*, *SL* and *BL* in *NH* were 0.94, classified in category one. On the other hand, the overall average for the emergence of the same variables was 0.602, classified in class three.

Cluster two was effectively associated in all the layers of lakes to variables related to oxygen and temperature. These variables are as follows: *SO2*,*PO2*,*BO2*, *ST*, *PT* and *BT*. It is important to note that two more variables were added in this cluster; the first one was evaporation (*Ev*) and the second one was benthic *pH* (*BpH*).

With regard to cluster three, it is possible to find two additional forms of hydrogen potential: *pH* in inflow (*IpH*) and *pH* in planktonic zone (*PpH*). Interestingly, there were other different variables such as: time retention (*TR*), inflow and outflow (*IO*); and finally conductivity in the planktonic zone (*PCd*), it can be seen that *PCd* seems to be closed to other types of conductivity variables such as inflow (*ICd*) and benthic zone (*BCd*) which were arranged in cluster five.

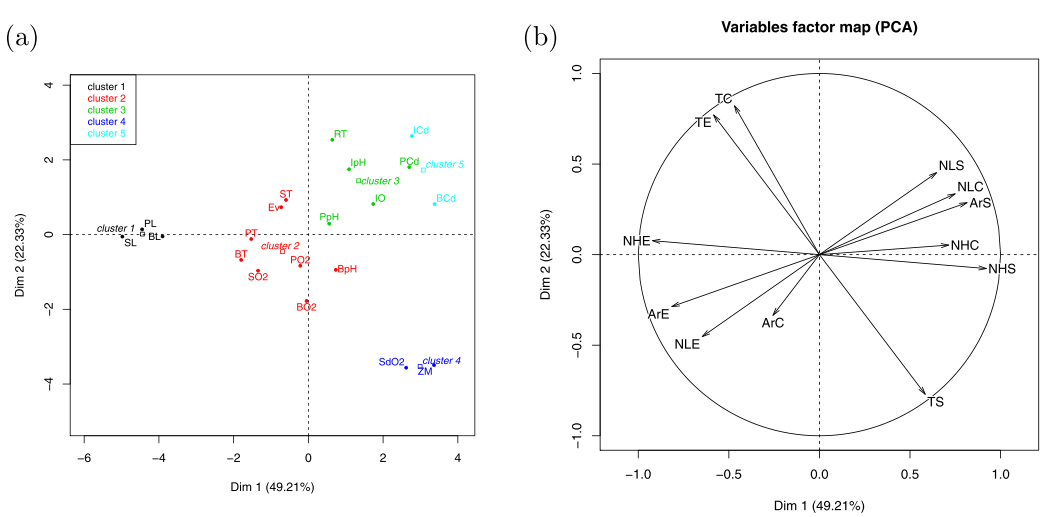

Fig. 1. Multivariate analysis of the physiocochemical subsystem. (a) Hierarchical classification analysis of physicochemical variables (clusters). (b) Principal component analysis ordination of the four lakes according to *E*,*S*,*C* properties.

Table 5
Statistical description of lakes and properties in the physicochemical subsystem. The sign in v-test corresponds to the direct or inverse relationship. Acronym NA: Non Applicable. NS: Non Significance. *: significance **: very high significance ***: extremely high significance.

Cluster	Variable Grouped	Lake	Property Associated	Property V.Test	Property μ in cluster	Property Overall μ	p-value
1	PL,SL,BL	NH	E	3.157	0.940	0.602	1.5964^{-03}***
		Ar	E	2.685	0.757	0.462	7.249^{-03}***
2	ST, PT, BT, Ev, SO2, PO2, BO2, BpH	NL	E	2.064	0.821	0.750	0.039*
3	IO,RT,ICd	NL	S	3.618	0.423	0.250	0.0003***
	IpH, BpH	NL	C	3.102	0.9678	0.691	0.002**
4	ZM,Sd02	T	S	3.262	1	0.632	1.105^{-03}***
5	ICd,BCd	Ar	S	3.341	1	0.538	8.353^{-03}***

In the case of cluster four, it was found oxygen in sediment (*SdO2*) and zone mixing (*ZM*). These two elements are the building blocks to determine self-organization in the Tropical zone. Further statistical tests revealed that their mean values were the highest in comparison with the overall mean (0.632). Finally, regarding cluster five, conductivity in inflow and benthos were the two variables observed. These variables were considered the most self-organized in the gradient due to their mean values 1 compared to the overall average of 0.538.

These results confirm the association between environmental conditions (light, temperature and oxygen) with emergence which in the latitudinal gradient *Ar-T* case shows a decreasing behavior. In addition, the current study found a type of regularity between *NL* and *T* but a lost of regularity on the conductivity (*Ar-NL*). What is interesting about the preliminary results is that the mix of water between lakes' layers and the oxygen in sediment permits to gain order in terms of the gradient. Finally, it can be seen that *pH* was the most complex variable in the middle of the latitudinal transect.

3.1.2. Complexity in the limiting nutrients subsystem

With respect to the limiting nutrients subsystem, the preliminary results were sorted into seven clusters (see Fig. 2b). These results further support the idea that there is significant level of disaggregation. This suggests a high dispersion of *E*, *S*, *C*. In this regard, cluster one showed a high density of phosphorous (*IP*) and nitrogen (*IN*) in inflow. On the other hand, cluster two revealed groups formed by nitrogen in planktonic (*PN*) and benthic layers (*BN*). Phosphorous and silicates: (*PP*, *BP*, *PS* and *BS*) were found in cluster three. In cluster four was observed the presence of carbon dioxide (*ICD*) and silicates in inflow (*IS*). Specifically, cluster five showed planktonic detritus (*Pde* and benthic detritus (*Bde*). Finally, a couple of variables related with carbon dioxide in planktonic and outflow sections of the lakes (*BCD* and *PCD*) were observed in cluster six and seven.

Further analysis showed that the planktonic and benthic dynamics were well defined for variables that revealed some level of self-organization such as: nitrogen, phosphorous and silicates. Fig. 2b provides an overview of how complexity in *Ar*, *NL* and *T* was related to a high level of emergence.

Table 6 presents a significant positive correlation between clusters, lakes and properties. Moreover, it should be noted that those clusters with a negative sign indicate that the correlation is inverse (clusters 1, 2 and 7). Similarly, a NULL value implies a no satisfactory variable for this case.

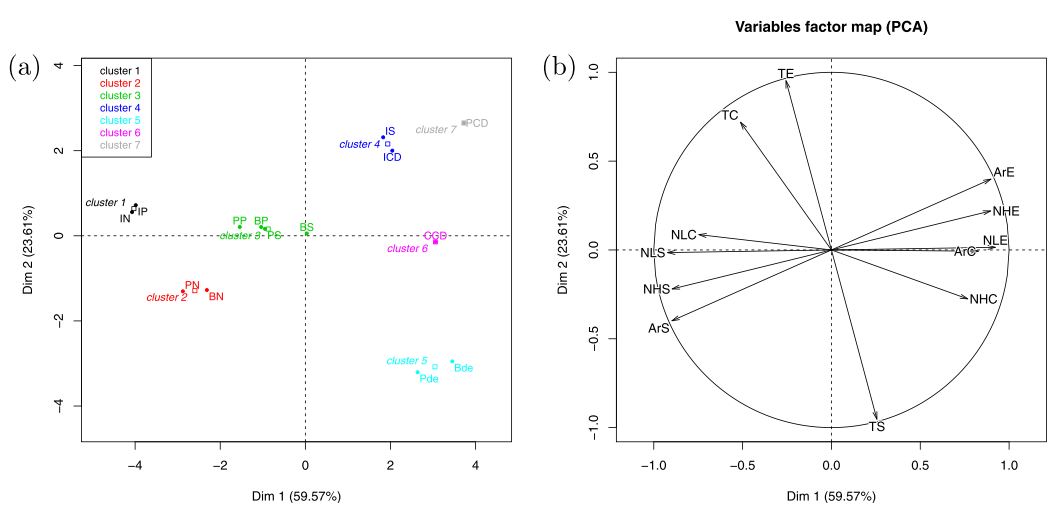

Fig. 2. Multivariate analysis of the limiting nutrients subsystem. (a) Hierarchical classification analysis of limiting nutrients variables (clusters). (b) Principal component analysis ordination of the four lakes according to *E*, *S*, *C*.

Table 6
Statistical description of lakes and properties in the limiting nutrient subsystem. The sign in v-test corresponding to the direct or inverse correlation. Acronym NA: Non Aplicable. NULL: Non variables or values associated. NS: Non Significance. *: significance **: very high significance ***: extremely high significance.

Cluster	Variable Grouped	Lake	Property Associated	Property V.Test	Property μ in cluster	Property Overall μ	p-value
1	IN,PN	Ar	C	-2.285	0	0.608	0.022 NS
		NH	C	-2.722	0	0.599	0.005*
2	PN,BN	Ar	C	-2.285	0	0.608	0.02 NS
3	PP,BP,PS,BS	NULL	NULL	NA	NA	NA	NA
4	IS, ICD	Ar	E	2.078	0.710	0.335	0.038*
5	Bde, Pde	T	S	2.801	1	0.578	0.005***
6	OCD	NULL	NULL	NA	NA	NA	NA
7	PDC	NL	C	-2.237	0.359	0.793	0.02 NS

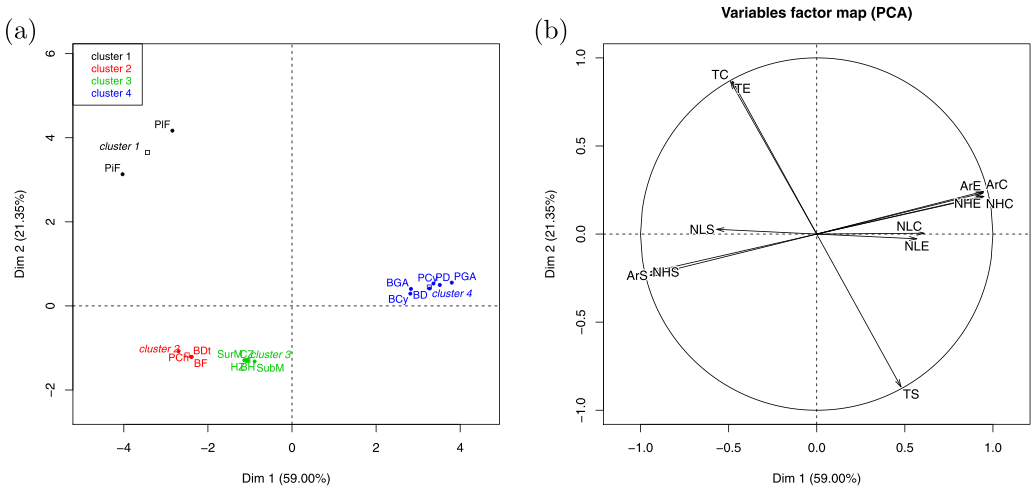

Fig. 3. Multivariate analysis of the limiting nutrients subsystem. (a) Hierarchical classification analysis of limiting nutrients variables (clusters). (b) Principal component analysis ordination of the four lakes according to the *E*, *S*, *C* properties.

3.1.3. Complexity in the biomass subsystem

Fig. 3 shows four clusters related to the biomass subsystem. In this particular case, planktonic (*PlF*) and piscivorous (*PiF*) fishes were found as the most complex species according to their proportion of emergence (see Table 7).

Further analysis showed that *NL* dynamics was significantly associated to the highest regularity (self-organization) of benthic detritivores (*BDt*), fish (*BF*) and planktonic chlorophyll (*PCh*). Variables such as: Benthic herbivorous (*BH*), planktonic zooplankton (*PZ*), herbivorous zooplankton (*HZ*), macrophytes in surface (*SurM*) and macrophytes submerged (*SubM*) were all well described by self-organization in cluster three. On the other hand, cluster four revealed the existence of benthic cyanobacteria, planktonic cyanobacteria, diatoms and benthic green algae.

The current study found that the influence of the seasonality and duration can lead to a change in the complexity of the photosynthetic taxa at the highest latitudes. These preliminary results suggest that the main factors that affect these dynamics are related to long periods of exposure to light and dark i.e., from summer to winter and vice-versa. Similarly, a regularity in detritivores located in middle latitudes with low altitude (*NH*) may be associated with seasonality.

3.1.4. Complexity in the latitudinal gradient from the arctic to the tropics (Ar-T)

Fig. 4 compares the summary statistics for the *C* averages of all variables in the *Ar-T* (annual cycle). These findings suggest that *NL* could be associated to a phase transition for *C* values. Turning now to the experimental evidence, the graph shows that there has been a marked drop in the physicochemical subsystem caused by the increasing level of $E = 0.75$. In this context, the graph reveals that the category of *C* gradually increase due to the rise of *S* (regularity in variables).

In terms of the limiting nutrients subsystem, complexity showed a gradual fall; then after it depicts an increase behavior heading to the high category in *NL* and *T*. It is important to note that a transition phase presented in *NL* is caused by *E* values (≈0.62 high category). With respect to biomass, a change in *NL* stems from *C* values that reach a higher category in the *Ar-T* transect (0.74). Turning now to *Ar* biomass and *NH* biomass, their *C* values were arranged in the low category.

3.2. Autopoiesis (A)

The term *A* from autopoiesis has come to be used to refer to the biological autonomy, which identifies living agents with a certain

Table 7
Statistical description of lakes and properties in the limiting nutrient subsystem. The sign in v-test corresponding to the direct or inverse correlation. Acronym NA: Non Applicable. NS: Non Significance. *: significance **: very high significance ***: extremely high significance.

Cluster	Variable Grouped	Lake	Property Associated	Property V.Test	Property μ in cluster	Property Overall μ	p-value
1	PlF, PiF	T	C	3.858	0.835	0.106	0.00011***
		T	E	3.834	0.301	0.038	0.00012***
2	BDt, BF, PCh	NL	S	2.992	0.967	0.580	0.00276**
3	BH, PZ, HZ	Ar	S	2.032	1	0.880	0.04209*
	SurM, SubM	NH	S	2.0212	1	0.860	0.04324*
4	PCy, BD, BCy	NH	C	3.8647	0.923	0.350	0.00011***
	BCy, PD	Ar	C	3.8634	0.860	0.326	0.00011***
	BGA	Ar	E	3.838	0.316	0.119	0.00012***
		NH	E	3.825	0.369	0.139	0.00013***

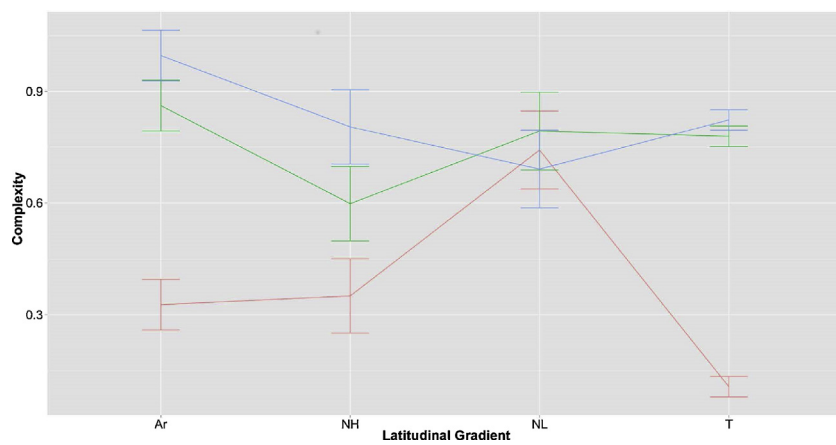

Fig. 4. Average complexity and its dispersion in the latitudinal gradient from the Arctic to the Tropic for: a biomass subsystem (red line), a limiting nutrients subsystem (green line) and a physicochemical subsystem (blue line).

way of organization (Maturana, 1980). However, in some contexts autopoiesis also reflects the autonomy of the system (Luisi, 2003; Froese et al., 2007). In this view, autopoiesisis is defined as the ratio of complexity of a system (C_X) and its environment (C_Y) i.e., $A = C_X/C_Y$. In this context, A can describe the independence relative of a particular element of the system.

The results of this study indicate that values related to A range as follows: $0 \leq A < \infty$. Thus, when a particular element presents a significant value of C, this can lead to present more autonomy $A > 1$. Otherwise, those elements with a lower value of C can result in less autonomy $0 \leq A < 1$. Additionally, there are different ways of assessing A. One of them is by estimating the A of each variable and the second one through the selection of some species. The next two sections describe results for both cases.

3.2.1. Autopoiesis (A) for variables

Appendix B compares the results obtained from the preliminary analysis of A. In summary, these results revealed that those variables arranged into categories one or two report a higher A. Therefore, autonomy may cause that variables with high or very high A show different states than others (variety). In this regard, these variables present a considerable amount of adaptability, and therefore, they are able to cope with environmental change (Gershenson, 2015).

3.2.2. Autopoiesis for biomass autonomy

Another way of estimating A in ecosystems is through the comparison of living agents against variables of different components (matter-energy flux). Specifically, the academic literature on photosynthetic organisms has revealed that these type of agents depend on solar radiation and nutrient availability. Hence, under these conditions it is possible to select variables that may affect organisms directly. Basically, this analysis is adopted to obtain further in-depth information on A, which can be interpreted as the autonomy of biomass in its physical and chemical environment. This method is particularly useful in studying how organisms respond to environmental changes. Table 8 provides those variables that were selected to be evaluated A.

It can be seen from the data in Table 9 that those cells colored in red correspond to the range $0 \leq A < 1$, these values confirm that complexity in the planktonic and benthic zones is higher in comparison to the phytoplanktonic biomass i.e., $A < 1$. It is apparent from this table that a lower environmental tolerance in T can result in a increasing radiation process, which generates more diversity in species. The rest of the values (Ar, NH and NL) suggest that the populations of photosynthetic biomass are able to balance environmental changes. Basically, the rest of the values may be less affected by physicochemical variations.

Table 8
Variables that were selected to be evaluated for autopoiesis of phytoplanktonic and phytobenthonic biomass.

Subsystem/Zone	Planktonic	Benthic
Physiochemical	Light, Temperature, Conductivity, Oxygen, pH	Light, Temperature, Conductivity, Oxygen, Sediment Oxygen, pH
Limiting Nutrients	Silicates, Nitrates, Phosphates, Carbon Dioxide	Silicates, Nitrates, Phosphates, Carbon Dioxide
Biomass	Diatoms, Cyanobacteria, Green Algae, Chlorophyta.	Diatoms, Cyanobacteria, Green Algae

Table 9
Lakes type A for phytoplanktonic and phytobenthic biomass: $A_{(B-Phy)}$ and $A_{(B-LN)}$. Values were computed for planktonic and benthic zones. Cells colored in blue $A > 1$ denote more autonomy of biomass and cells colored in red $0 < A < 1$ indicate that the environment controls dynamics of biomass.

	$A_{(B-Phy)}$		$A_{(B-LN)}$	
Location/Zone	Planktonic	Benthic	Planktonic	Benthic
Ar	0.7283	1.1527	1.1118	1.3157
NH	0.9740	1.1560	1.4105	1.4060
NL	1.0075	1.6360	0.89841	1.2440
T	0.0088	0.0000	0.0089	0.0000

Table 10
Homeostasis averages (H) for lakes.

Lake	Biomass $\pm\sigma$	Physicochemical $\pm\sigma$	Limiting Nutrients $\pm\sigma$
Ar	0.980 ± 0.044	0.959 ± 0.064	0.957 ± 0.065
NL	0.976 ± 0.0543	0.943 ± 0.092	0.915 ± 0.107
NH	0.917 ± 0.106	0.957 ± 0.075	0.945 ± 0.081
T	0.958 ± 0.115	0.965 ± 0.058	0.948 ± 0.073
Global	0.958 ± 0.036	0.956 ± 0.015	0.941 ± 0.018

According to Table 9 those cells colored in blue correspond to values where $A > 1$, revealing a high value of C in the phytoplanktonic biomass rather than in the environment. In addition, preliminary results show that photosynthetic organisms had more autonomy in benthic zones than in planktonic ones. In this context, a very high level on variety can lead to a very high level of complexity reflecting more independence and adaptability, which confers more autonomy of the taxa.

3.3. Homeostasis

In this section, it will be explained how homeostasis h between states is calculated by comparing daily values of all variables. In this regard, h can be defined as a temporal variation of states. This situation is more evident in the physicochemical subsystem of lakes where their responses are proportional to the seasonal changes (temperature and light). These results agree with recent studies indicating the importance of the temporal timescale i.e., h can vary considerably when states are compared every minute, daily or monthly (see Appendix B).

Table 10 compares the summary statistics for h. These results indicate that values of h were all sorted in the very high category owing to most of the lakes in consideration kept a quiet behavior for long periods of time. Moreover, It was observed that the biomass and physicochemical subsystems were slightly more stable in a year period than the limiting nutrients subsystem. In summary, Ar and T biomass were more regular than NH and NL.

3.4. Comparison of Tsallis information and C

Figs. 5 and 6 provide the results obtained from the preliminary analysis of self-organization patterns and emergence patterns. Contrary to expectations, this study did not find a significant correlation with C. however, a further analysis showed that when $q = 2$ correlations with C appears.

Previous studies observed that when C is compared to Fisher information, both measures are able to reach a maximal level between order and chaos in Boolean networks (Fernández et al., 2014). Additionally, C is expected to remain steady while Fisher information presents higher steepness. It should be noted that in order to compute C for any time step can result in a straightforward task whereas Fisher information requires a significant amount of time steps. With the aim to provide a proper assessment regarding C, it could be done via a continuous version of C recently developed by Santamara-Bonfil et al. (2016).

4. Discussion

4.1. Computational aspects of the ecological complexity

Recently, Biologists have shown an increased interest in S and E owing to these notions are very rooted to previous studies carried

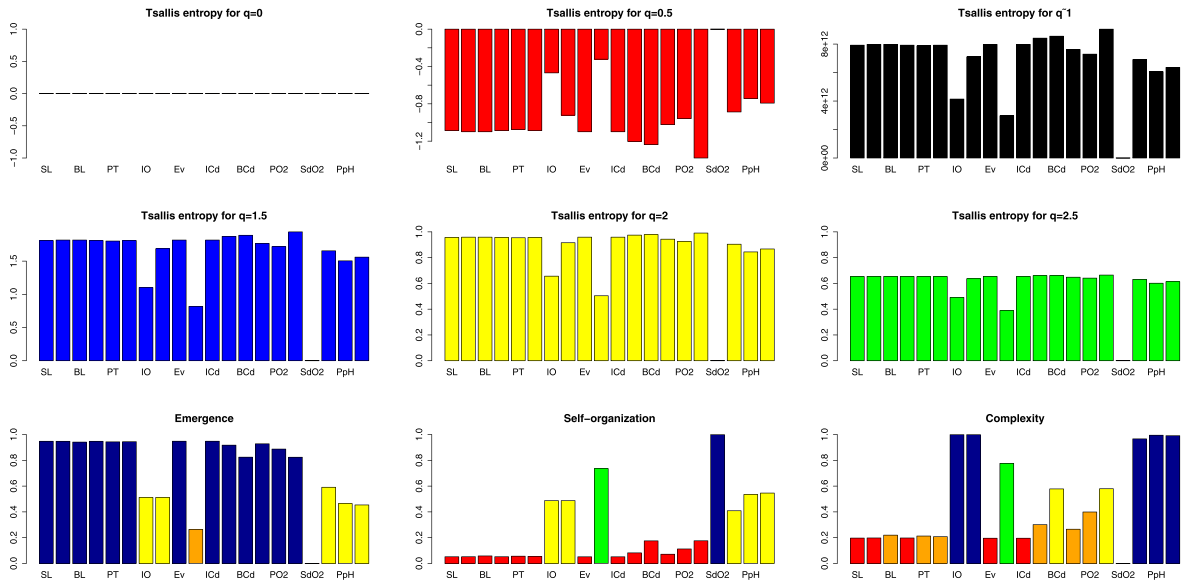

Fig. 5. *E*, *S*, *C* for the physicochemical subsystem (Tropical lake) are compared according to Tsallis information.

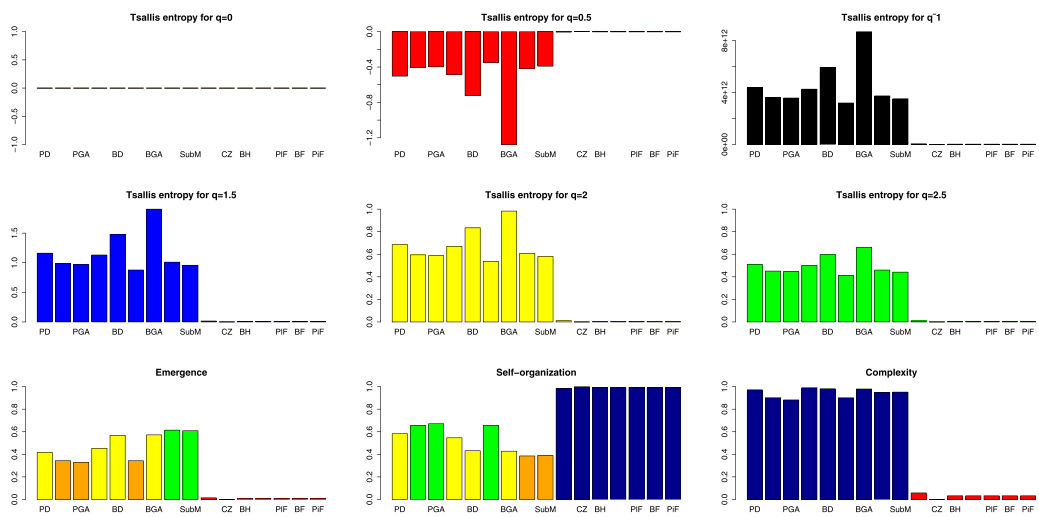

Fig. 6. *E*, *S*, *C* for the biomass subsystem (Artic lake) are compared according to Tsallis information.

out by Darwin and Mendel. In contrast, computer scientists describe complexity in terms of complex systems (the Kolmogorov–Chaitin Complexity), where complexity of an object is the length of the minimal Universal Turing Machine (UTM) program needed to reproduce it.

In general, this research analyses the impact of emergent patterns in terms of their behavior (order or chaos) (Gershenson and Fernández, 2012). Thus, it should be mentioned that chaotic patterns show a higher *E* than static patterns (ordered dynamics). In the case of ordered dynamics, they present the highest *S* which means the lowest entropy. Hence, living systems tend to reduce thermodynamic entropy to maintain themselves (Von Bertalanffy, 1968).

Integration of *S* and *E* into *C* is essential to reach a balance between regularity and variability, two necessary conditions to express adaptability. Thus, emergence is largest in chaotic systems ($E = 1, S = 0$), self-organization is largest in static (ordered) systems ($S = 1, E = 0$) and complexity is largest when *E* and *S* are in balance.

Further analysis showed that our complexity measure was able to cope with the complex dynamics of ecosystems. This resilience can be described in terms of the balance between regularity and variability of (micro)states. Consequently, *C* stands for the average dynamics and the different dynamic regimes that emerge from the interactions of the micro-states of the elements. It should be highlighted that our proposed measures may be useful to distinguish between random and non-random ecological processes. The former is related to a very high emergence (entropy) that involves many changes and patterns rupture. The second implies very high self-organization (very low entropy); it prevents complex patterns to emerge. For further details, this randomness can be examined in the probability distribution for any process or variable at different scales.

4.2. The ecological meaning and the proposed measures

The study used qualitative analysis in order to gain insights related to ecosystems at two scales: macroscopic and microscopic. With regard to microstates, it has been provided a degree of order or change to the ecosystems. Persistence of these microstates implies a higher regularity in the system (self-organization). Thus,

a microstates analysis confirms that in order to compute emergence it is necessary to obtain the probability values. Fig. 7 provides 365 values obtained for each variable of the physicochemical systems located in *Ar*. What is interesting about the figure is that those variables with an intermediate distributions, such as: *IO, RT, BO2, Sd02, IpH, PpH, BpH* reported a slight level of emergence and self-organization. On the other hand, variables with a higher heterogeneous distribution such as: *SL, PL, BL, ST, PT, BT, Ev, PCd, Bcd, SO2, PO2*, showed a significant level of emergence and a low level of self-organization. Finally, variables with a full heterogeneous distribution, such as: *ZM* and *ICd*, set out the highest level in emergence.

Interestingly, a higher self-organization of the tropical biomass was observed due to a low variation of microstates. However, it is possible to find a "steady state" of *T* when external perturbations are taken into consideration. It is important to note that in *Ar* and temperate lakes (*NH*, *NL*) seasonality may cause variations of biomass and physicochemical subsystems (irregular behavior). Therefore, there is a chance that during a year a single variable can provides more than one microstate.

A change of complexity has been positively correlated to the ecological process of succession. This process can lead to the replacement of species and permits the development of communities over time. In this regard, a high number of interspecific and intraspecific interactions is achieved generating more diversity. In this context, diversity in terms of species can be defined by the number of possible arrangements of *N* individuals distributed in certain *Sp* species. Hence, ecosystems with more species and similar densities among them (homogeneity) show more diversity; more variety of species the more information (more emergence).

The current study found that the Shannon–Wiener index (H') shows a positive correlation between *E* and diversity. Meanwhile a comparative analysis between H' vs. *C* showed a concave shaped curve, where *C* was set for 500 species due to the large proportion of absent species (see Fig. 8).

The findings mentioned earlier are consistent with data obtained in *Ar*, where there was a positive correlation between diversity and emergence (see Fig. 9). This emergence presents a linear trend (see Fig. 9a), meanwhile the correlation between complexity and diversity seems to be logarithmic (see Fig. 9b).

4.3. Spatial variation of complexity among lakes

Regarding the physicochemical results, it can be estimated $Ar \approx NH$; this situation can be related to the long periods of light and dark at highest latitudes. In contrast, physicochemical dynamics in an Arctic lake showed more regularity (self-organized) than in a North Lowland lake. Another important finding was that from the North Pole self-organization decreases whereas in the subtropical zone increases.

Preliminary results suggest that there is a differential trend of *C*. However, no significant global pattern was observed in *C*. In terms related to *NL*, it can be seen that seasonal scales have a significant effect on the complexity dynamics. In addition, *NL* showed the most emergent behavior in all components, which were computed monthly. Meanwhile, the scale of variations at *Ar* and *NH* were estimated daily and weekly. Similarly, at *T* the scale of change was computed monthly.

From these proposed measures, it can be seen that a very high *S* and a low *C* in *T* can lead to a low *A* in the biomass component.

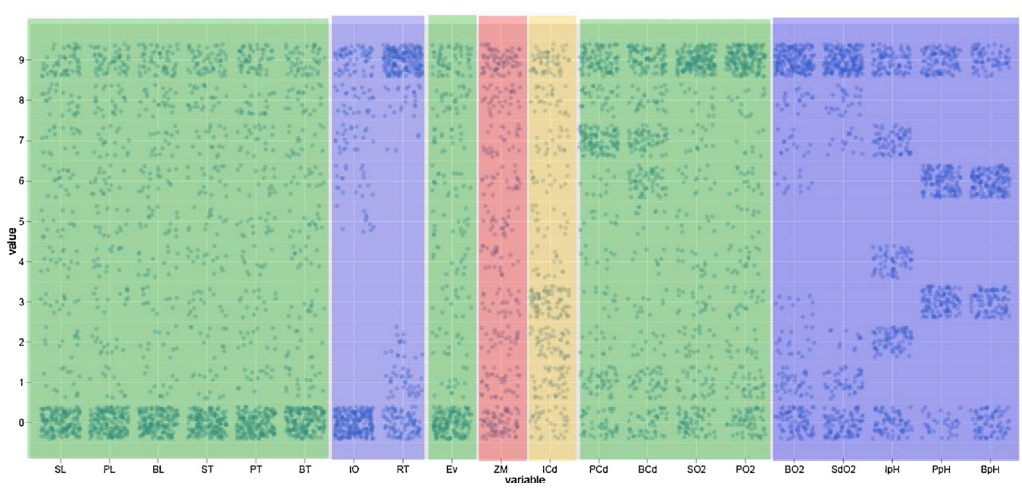

Fig. 7. Microstates for physicochemical variables distributed into ten categories.

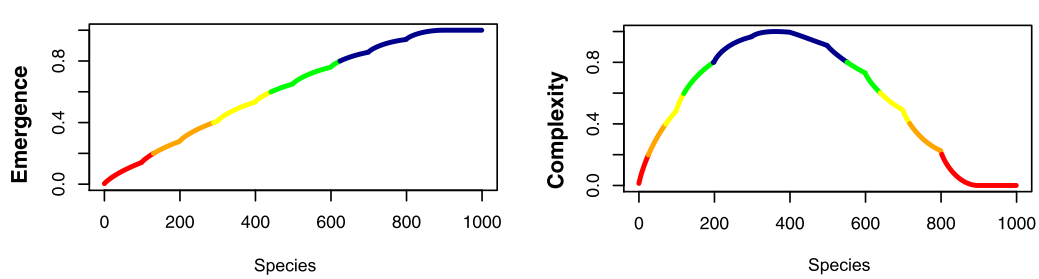

Fig. 8. Emergence and complexity vs. the incremental number of species from 1 to 1000. Lines correspond to the categories one to five for *E* and *C*.

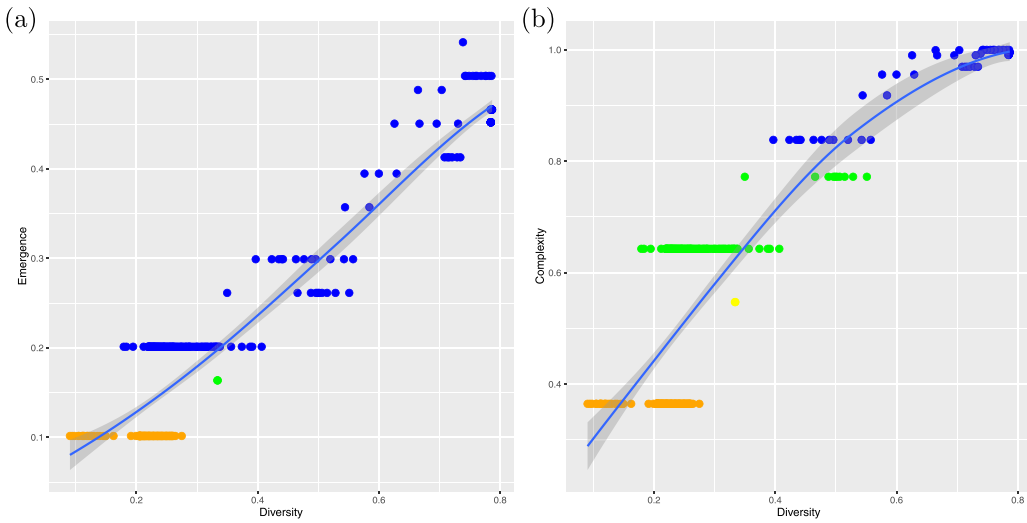

Fig. 9. Emergence and complexity computed with Shannon–Wiener index (H'). (a) E *vs.* H'. (b) C *vs.* H'. Points corresponding to categories one to five for E and C and coincides with the very low to very high qualifications.

Besides, a very high uniformity in T may cause a stable behavior at annual scales, it can be also suggested that tropical species are less resistant to environmental changes. In summary, these results show that our proposed measures contribute to the ecological interpretation of complexity through the characterization of different ecological configurations.

4.4. Complexity measures based on ecological complexity

Structural complexity can be described through a particular scale and interaction between elements. In this regard, an ecological structure can be determined in different scales such as: individuals (components) and population (system) (Clauset, 2014). In order to identify structural complexity, it is necessary on one hand, to provide a network approach where nodes are defined as species and links refer to a some sort of relationship (resource transference). On the other hand, structural complexity can be calculated through topological indicators e.g., node-degree distribution, clustering coefficient and average path length (Madrid et al., 2016).

In the case of dynamical complexity, it can be computed from the trajectories of the states. On the question of functional complexity, it can be analysed from the roles carried out by species. Thus, key ecological functions are as follows: primary consumer, secondary consumer, tertiary consumer, carrion feeder, cannibalistic, and coprophagous.

As mentioned earlier, our study defines complexity as a balance between self-organization (order) and emergence (chaos). Therefore, here it is necessary to characterize a structural, dynamical and functional complexity in ecosystems. These proposed measures were designed with the aim to evaluate and analyse dynamical complexity of lakes.

To develop a full picture of dynamical complexity in ecosystems, autopoiesis (A) was introduced, in order to analyse the adaptability of functional groups when facing changes in the environment. Finally, homeostasis (H) reports about the similarity of the states that involve a system during environmental changes.

5. Conclusions

This manuscript has argued that it is possible to describe ecological complexity in terms of information theory. Similarly, this study has shown that there is a reduced emergence and self-organization gain in the lakes located from the Arctic region to the Tropical zone. The previous results indicate that temporal variables such as: light, temperature and oxygen, present a significant influence on the limiting nutrients and biomass components. Thus, light and temperature may cause different ranges of seasonality in the gradient and may affect the availability of nutrients.

This research has identified variations in terms of daily and weekly scales for the response of the nutrients in the Arctic and temperate lakes, whereas in the tropical zone has identified that the scale of change can be measured monthly. Moreover, This study has found that generally the rhythms of biomass complexity caused by seasonality present variations related to the phytoplankton taxa and a regularity related to the macrophytes. The results of this study suggest that those variables with a homogeneous distribution of their states show higher values of self-organization, while variables with heterogeneous distribution show greater emergence.

E, S, C, H, A can be seen as ecological indicators at different scales due to they are able to provide a comparative analysis among ecosystems. In the case of C, it can contribute to the interpretation of a different sort of ecological complexity such as: structural, dynamical and functional.

Preliminary results presented in this manuscript are promising for the study of complexity of ecological systems. However, specific points should be explored e.g., (i) The relationship among the diversity of the species with its complexity in the different ecological succession states. (ii) Can these proposed measures be used to guide the self-organization of ecosystems? (iii) Can our proposed measures be used to promote complexity of ecological systems?. In addition, a further study could assess questions about the structural and dynamical complexity for instances: (iv) What does local-level structure look like? and (v) What does large-scale structure look like?.

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Appendix A. Case studied

Lakes are not uniformly distributed on Earth's surface. In consequence, their structure and function can vary at different latitudes. The latitudinal gradient from the Arctic to the Tropic of Cancer affects taxa composition and physicochemical dynamics in an annual cycle. The following description depicts the spatial and environmental factors of the four lakes considered for measuring complexity.

A.1. Arctic lake (Ar)

Arctic lakes are located close to the Arctic Polar Circle. Their mean surface temperature (*ST*) is around 3 °C. Their maximum is about 9 °C, and their minimum is 0 °C.

In general, Arctic ecosystems are sorted as oligotrophic due to their low primary production, represented in chlorophyll values of 0.8–2.1 mg/m^3. The lake's water column or limnetic zone is well-mixed; this means, there is no stratification (layers with different temperatures). During winter (October to March), the surface of the lake is covered by ice. During summer (April to September), ice melts and water flows and evaporation (*Ev*) increases. Consequently, the winter and summer in the Arctic region cause a typical hydrological behavior in the lakes. This hydrological behavior influences the physicochemical component of the lakes.

Limiting nutrients in the form of nitrates, silicates and carbon dioxide are between 90 and 100%. They are available for phytoplankton all year round. Phytoplankton and periphyton biomass are dominated by planktonic and periphytic diatoms (38.6% and 45% respectively). Zooplankton, 91.7% is dominated by herbivorous organisms. At the Benthic Zone, detritivores invertebrates dominates with a 86.8% of the total abundance. Benthic fish are dominated by piscivorous with 85.8%.

A.2. North Highland lake (NH)

NH corresponds to a mesotrophic ecosystem in a cool north-temperate climate (Mean = μ =5.3 °C). Levels of chlorophyll are between 2.2 and 6.2 mg/m^3. The surface is covered with ice in winter (end of November, December, January and early February). Ice covering forms a barrier to the wind which minimizes loss of water evaporation, while the bottom of the lake remains unfrozen. The water column is not thermo-stratified and is permanently well mixed with levels of 50% in summer and 90% in winter. The maximum flows are in spring and autumn (9.6 m^3/s) with minimum flow in summer (0.6 m^3/s). *Ev* is reduced because of cold water and low vapour–pressure gradients (μ = 9262 m^3/d). Retention Time (*RT*) is maximum in summer with 100 days. Oxygen concentration is up to 10 mg/lt on the surface, planktonic and benthic zones. *pH* mean values are around 7 to 7.3 units, but varies between 6.7 to 7.8 units from the surface to the bottom.

The association among variables is more seasonal in *NH* than in North Lowland lakes (*NL*). In *NH*, summer is related with high *RT* and with a higher *pH*. Winter is related with higher levels of oxygen in inflow and outflow. Moreover, there is a strong correlation of benthic and sediment oxygen (BO_2, SdO_2).

Limiting nutrients such as nitrates, silicates, and carbon dioxide are around 95% available for phytoplankton. Phosphates show less availability, around 80% all year. Biomass composition is dominated by planktonic (46.7%) and benthic (41%) diatoms (*PD,BD*). Zooplankton composition is almost entirely herbivorous zooplankton (*HZ* 91.4%). Carnivorous zooplankton (*CZ*) reaches a 8.6%. In the group of benthic invertebrates, detritivores dominates with 87.5%. The fish community is dominated again by benthic fish (*BF*), but in a higher proportion (88.9%).

A.3. North Lowland lake (NL)

NL is an eutrophic lake, located in a warm north-temperate climate (average of 14 °C). Primary production expressed in mg/m^3 of chlorophyll is around 6.3–19.2.

There are four seasons in a year: winter, spring, summer and autumn. In summer, the flow variations between inflow and outflow fall to 3.5 from 25.2 m^3/s. Retention time (*RT*) increases to 100 days. The lack of the wind and high temperatures (24 °C), causes a thermal stratification of the water column. Stratification is expressed in the formation of two layers with different density due to a temperature difference. At the border of these layers, temperature changes dramatically (24 °C in the surface, 20.6 °C in the planktonic layer, 17.3 °C in the benthic layer). Water above and below layers do not mix. The water is warmer near the surface while it is colder, and it has more density near the bottom.

In winter, there is no ice covering the surface. Otherwise, in summer (when the flow is minimum), in spring, and autumn, the water column overturns (*RT* of 14 days and Zone Mixing-*ZM* of 100%). This causes an increment in conductivity. In summer, depletions of oxygen at the three layers are more drastic than Arctic lakes (below 8.7 mg/lt). Oxygen is directly correlated with *ZM*, inflow, and outflow, and inversely associated with *pH* and *RT*.

All limiting nutrients are available for phytoplankton in all seasons (above 90%). The phytoplankton and periphyton biomass composition are dominated by planktonic (47%) and benthic (34.3%) diatoms. This way, 100% of zooplankton composition is herbivorous zooplankton. The fish community is dominated by benthic fish (67.6%).

A.4. Tropical lake (T)

T is a hypereutrophic ecosystem (Chlorophyll >19.2 mg/lt) located in a moist tropical climate, at the North of the Equator, near the Tropic of Cancer. Their mean temperature is 25 °C at the surface. Tropical lakes have a wet season and a dry season. A higher radiance of the sun rays leads to higher temperatures and smaller thermal differences between water layers. For that reason, the water column is permanently warm and stratified. Stratification is due to the heat exchange, but is less permanent than stratification in lakes at the higher latitudes, because the wind can have a substantial incidence in the mixing of the water column. Thus, intra-seasonal variations have a stronger effect on the thickness of the mixed layer than other morphometrically similar temperate lakes (Randerson and Bowker, 2008). The maximum flow of water is in the wet season, and the minimum flow is in the dry season. Episodes of heat and mixing affect the nutrient cycling and plankton dynamics. It is important to highlight that primary production in tropical lakes is about twice that of higher latitudes. Also, nitrogen is the most limiting nutrient.

Equitability among species inside phyto and periphyton communities is higher; around 33% for diatoms, green algae, and cyanobacteria. Zooplankton populations are dominated by herbivorous (90%). Benthos, by detritivores invertebrates (84.4%) and fish (87%).

Appendix B. Complexity for each component

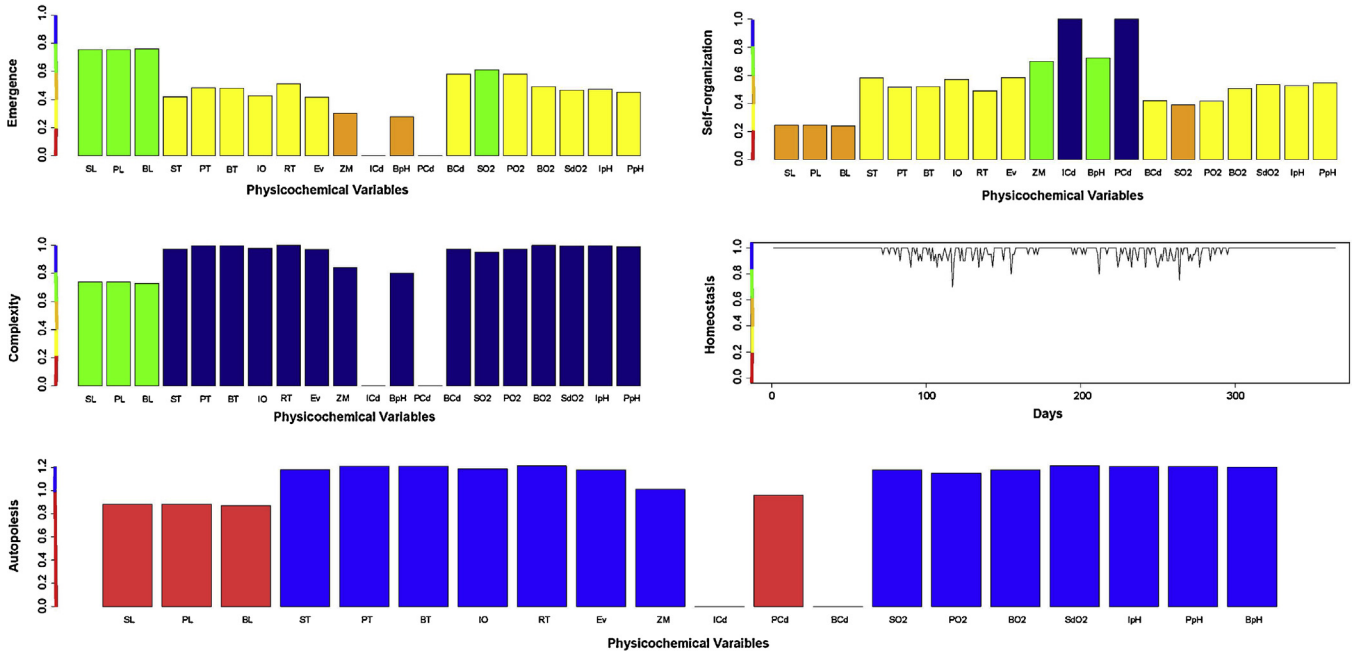

Fig. 10. Complexity in the physicochemical subsystem for an Arctic lake.

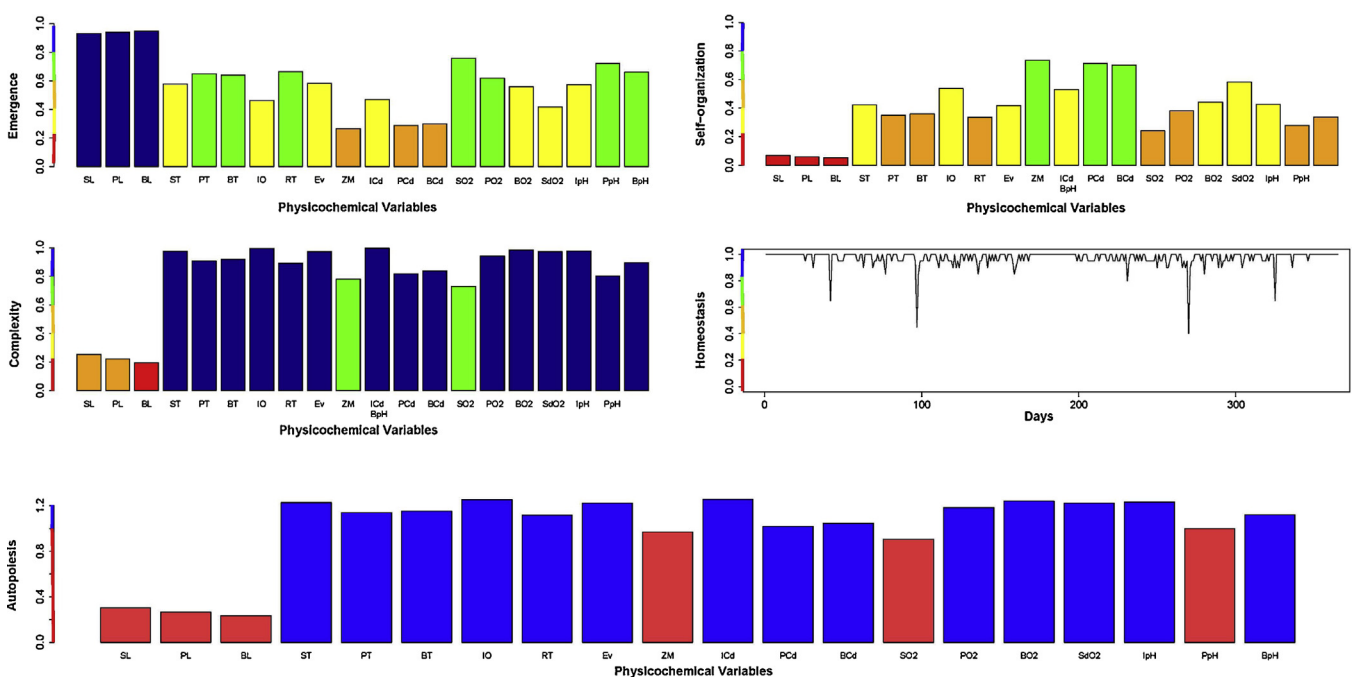

Fig. 11. Complexity in the physicochemical subsystem for a North Highland lake.

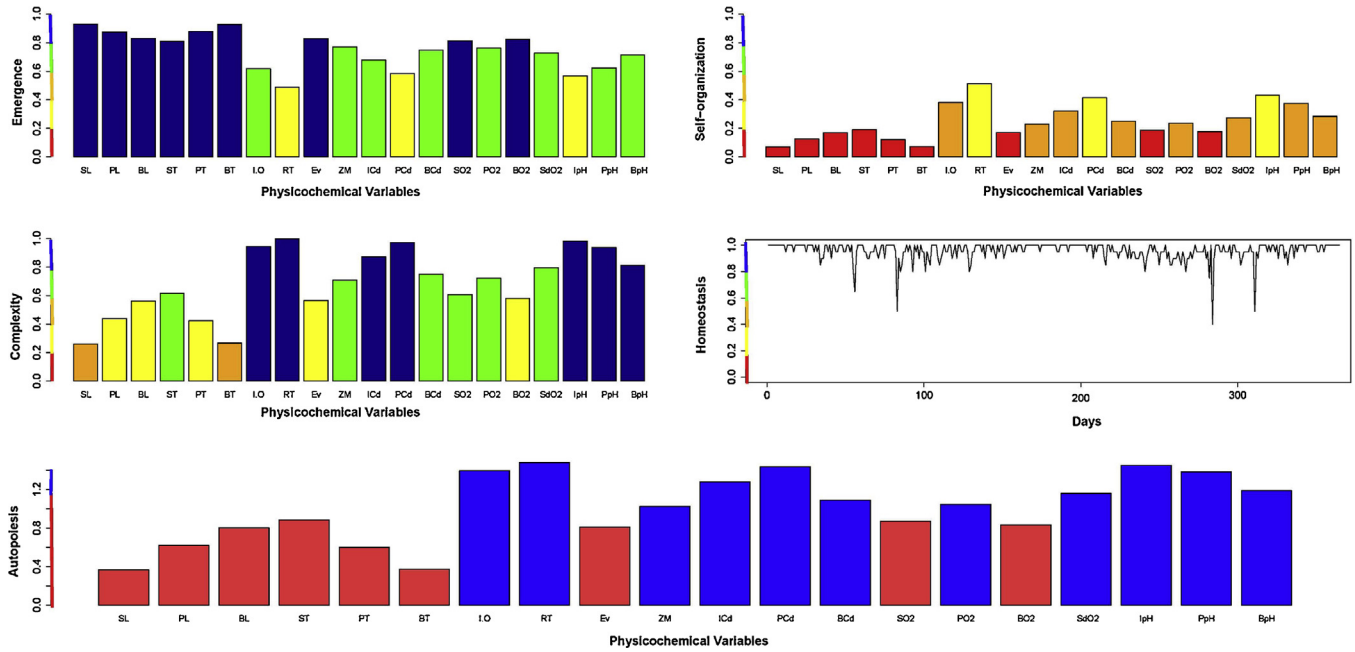

Fig. 12. Complexity in the physicochemical subsystem for a North Lowland lake.

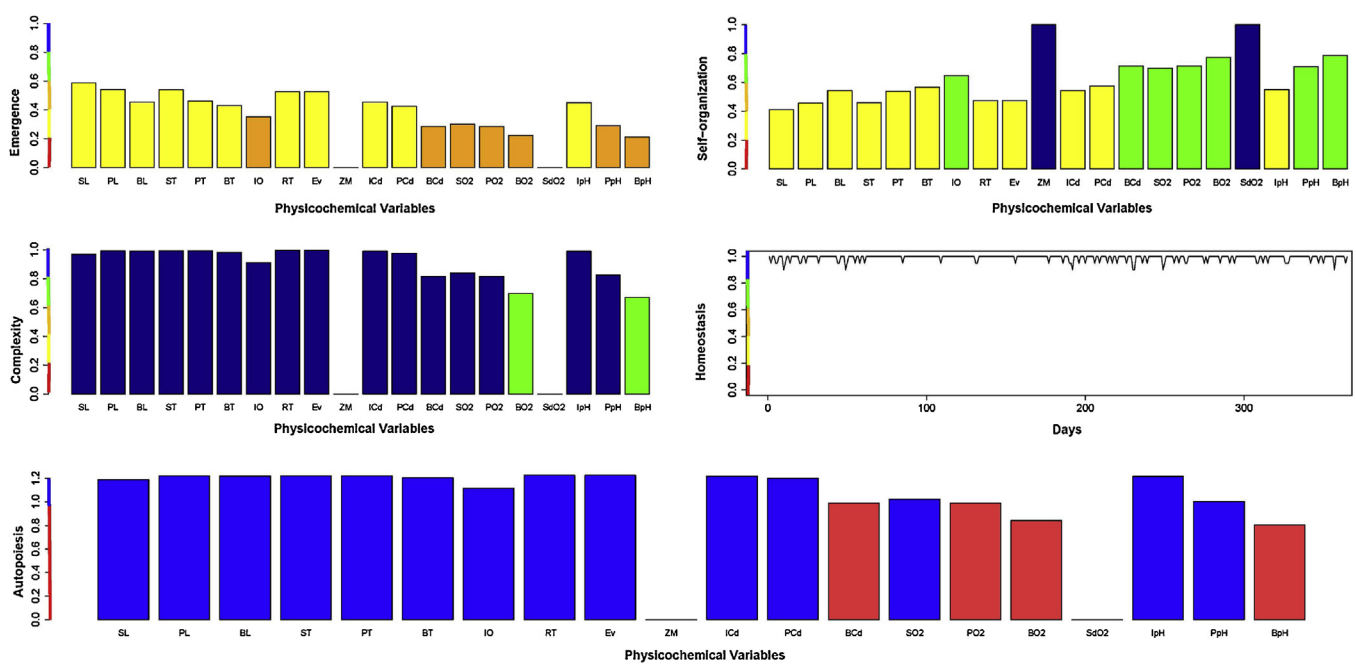

Fig. 13. Complexity in the physicochemical subsystem for a Tropical lake.

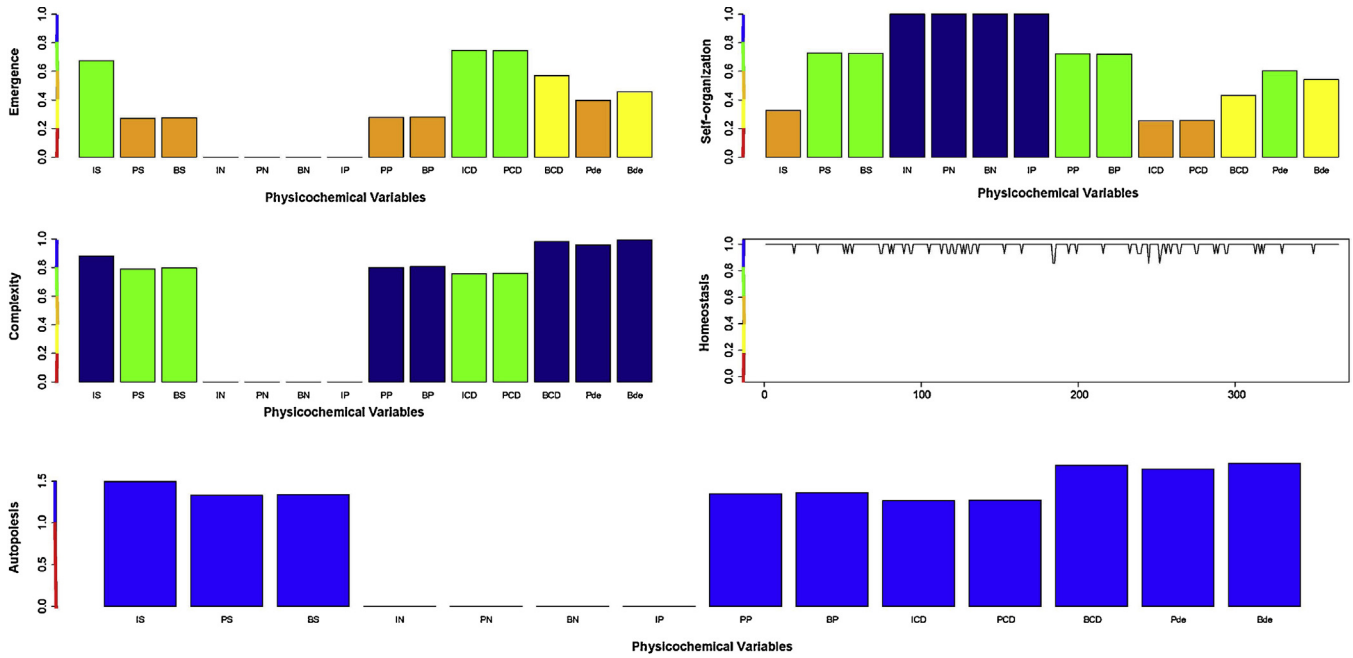

Fig. 14. Complexity in the limiting nutrients subsystem for an Arctic lake.

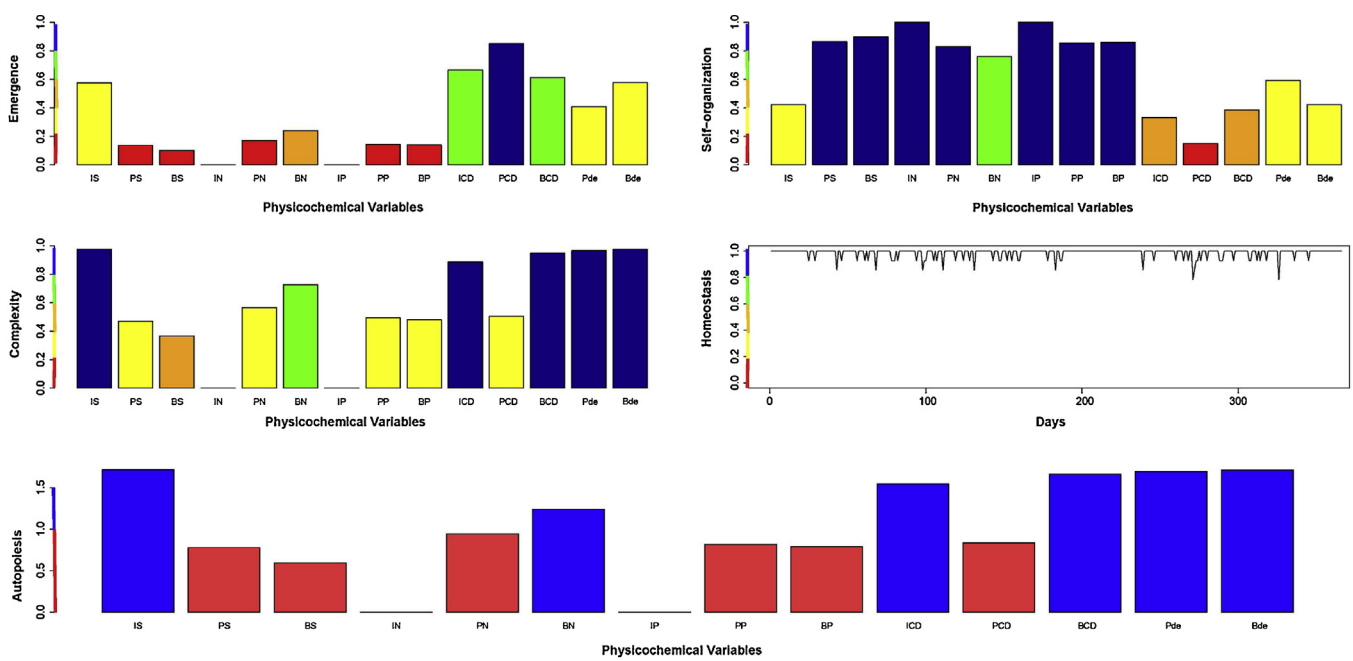

Fig. 15. Complexity in the limiting nutrients subsystem for a North Highland lake.

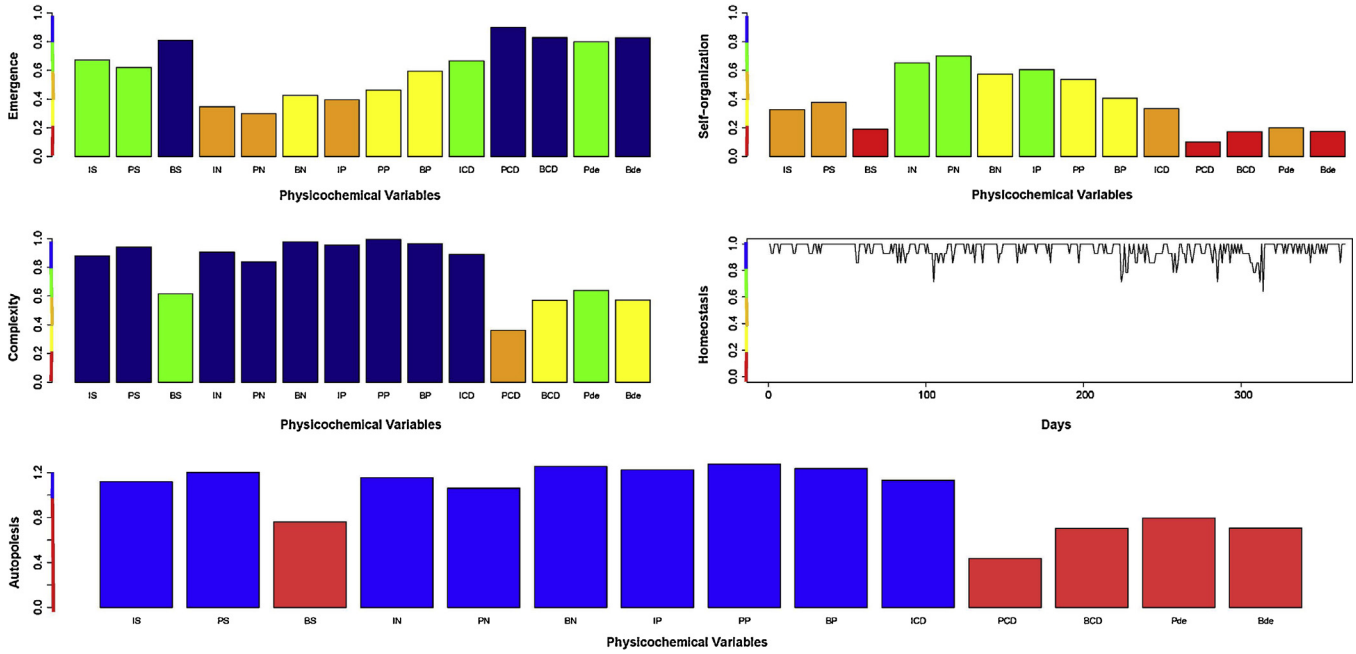

Fig. 16. Complexity in the limiting nutrients subsystem for a North Lowland lake.

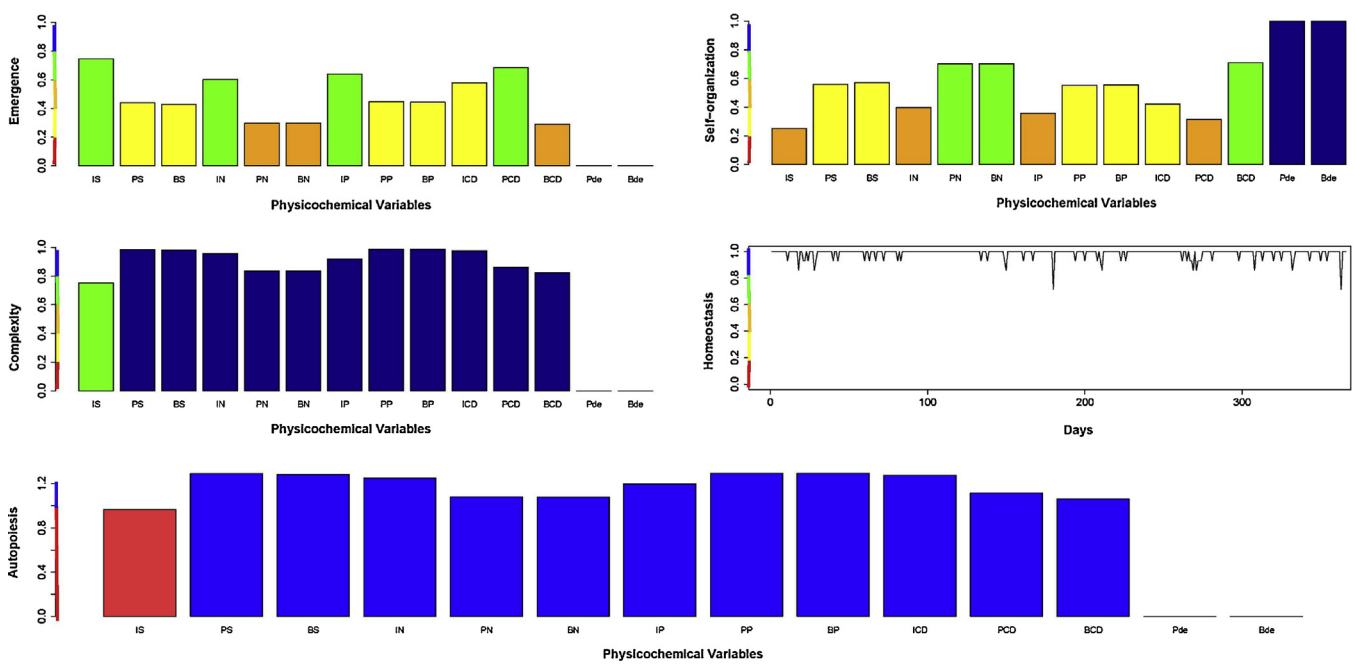

Fig. 17. Complexity in the limiting nutrients subsystem for a Tropical lake.

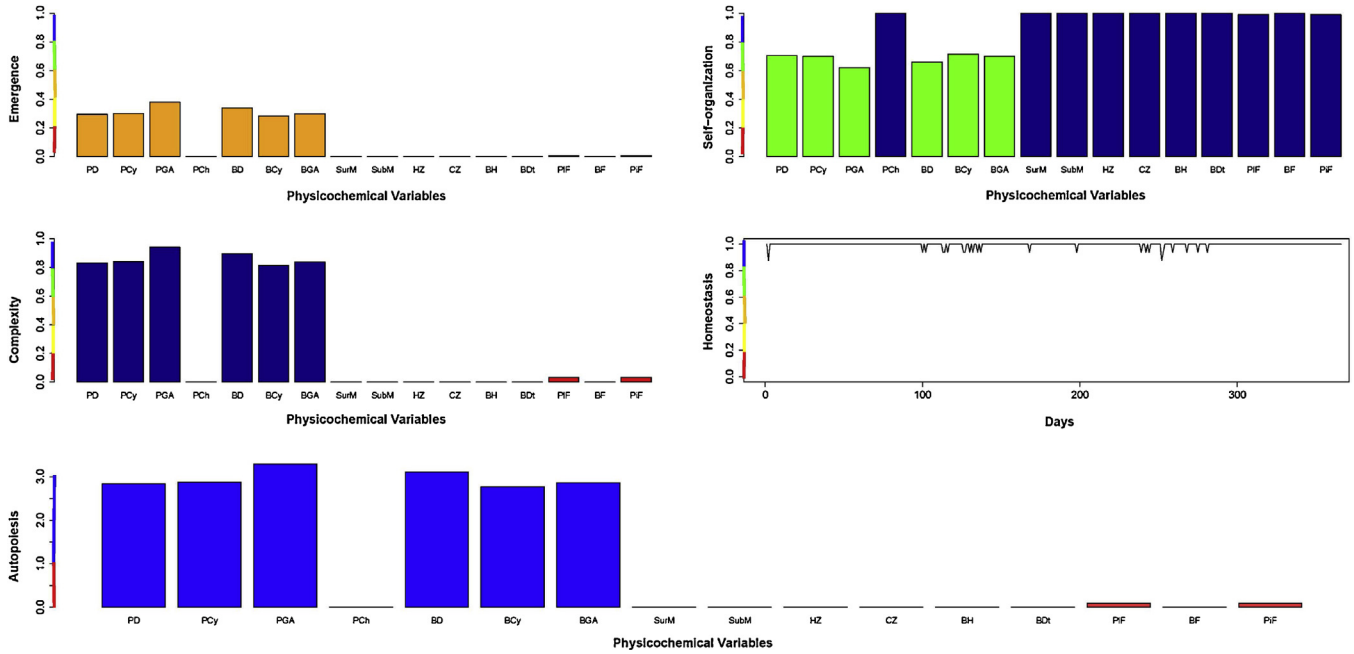

Fig. 18. Complexity in the biomass subsystem for an Arctic lake.

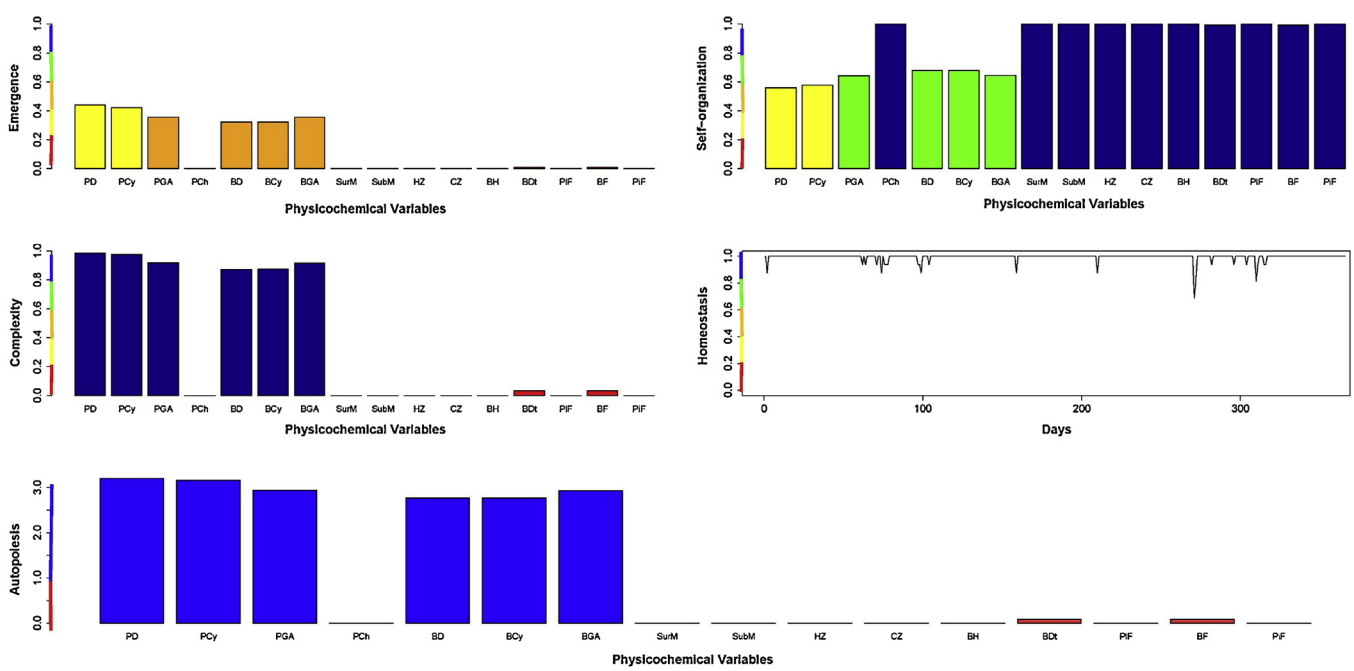

Fig. 19. Complexity in the biomass subsystem for a North Highland lake.

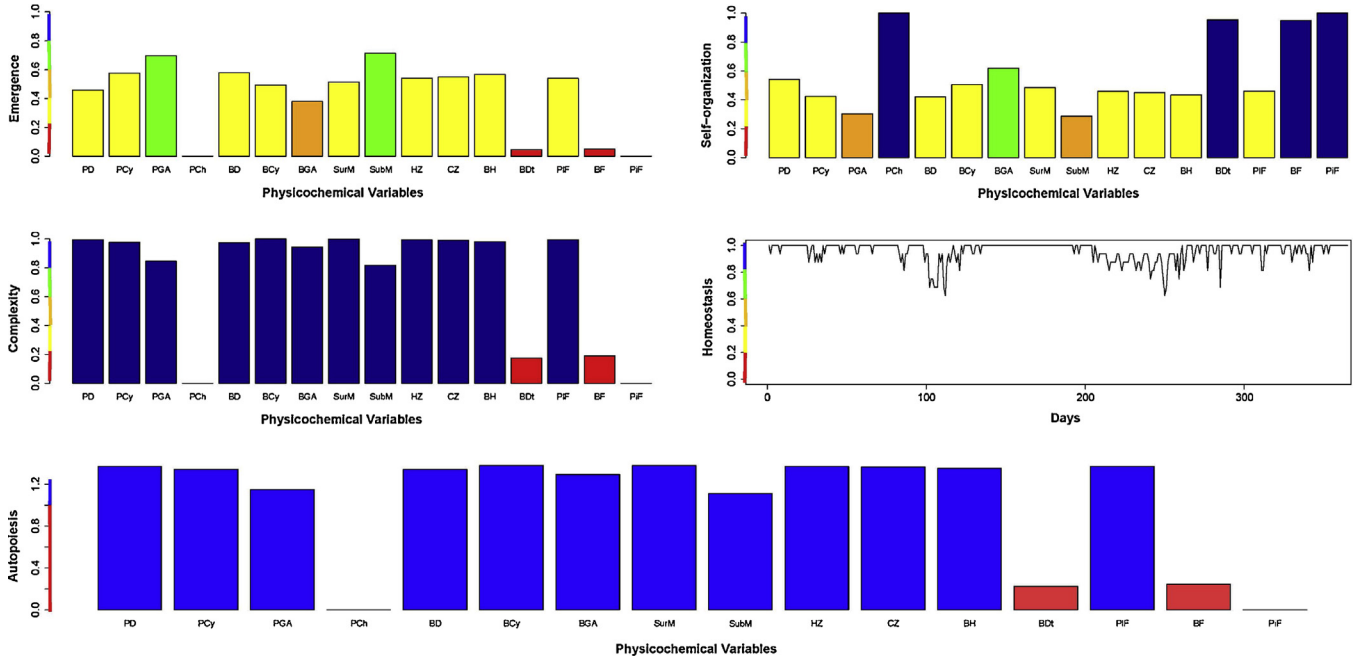

Fig. 20. Complexity in the biomass subsystem for a North Lowland lake.

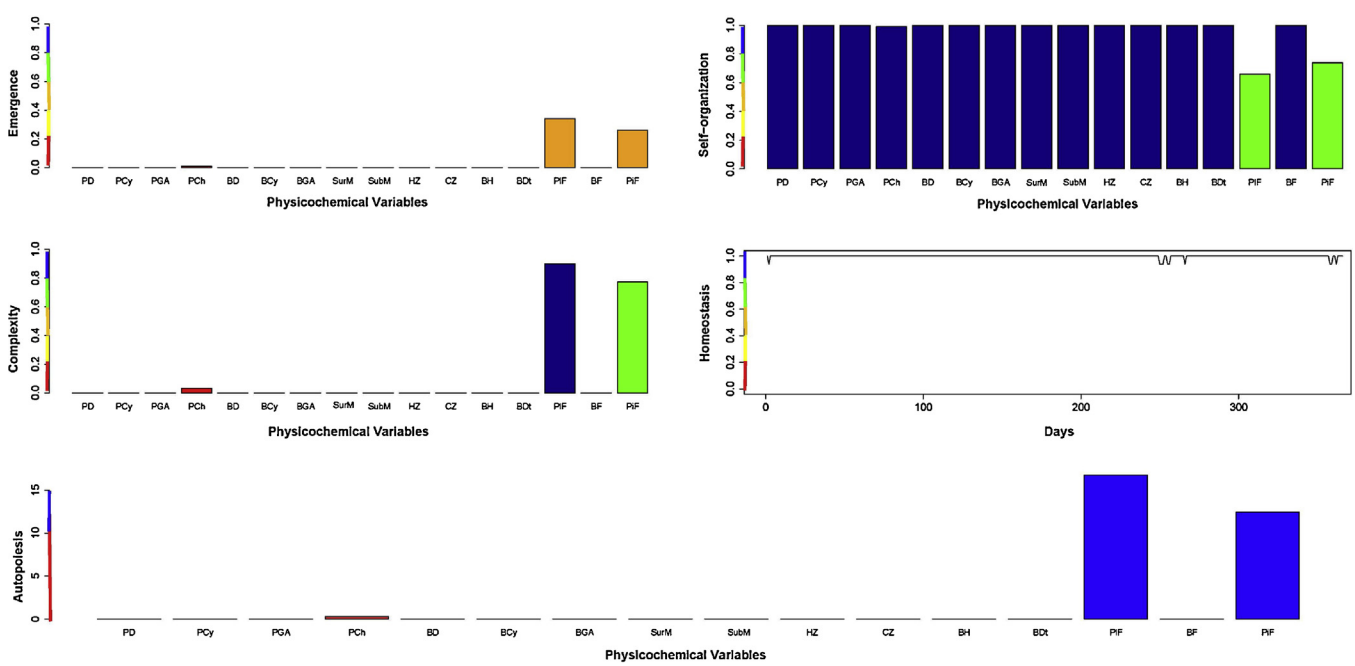

Fig. 21. Complexity in the biomass subsystem for a Tropical lake.

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