**Oikos 121: 1810–1820, 2012**
doi: 10.1111/j.1600-0706.2011.20423.x

Subject Editor: Thorsten Wiegand. Accepted 25 November 2011

# Multifractal growth in periphyton communities

**Leonardo Ariel Saravia, Adonis Giorgi and Fernando Momo**

*L. A. Saravia (lsaravia@ungs.edu.ar) and F. Momo, Inst. de Ciencias, Univ. Nacional de General Sarmiento, J. M. Gutierrez 1159, (1613) Los Polvorines, Buenos Aires, Argentina. – A. Giorgi, CONICET, Depto de Ciencias Básicas, Univ. Nacional de Luján, C.C. 221, (6700) Luján, Argentina.*

Periphyton is an aquatic community composed by algae, bacteria, fungi, and other microorganisms that can develop a complex architecture comparable to tropical forests. We analyzed the spatial pattern of a periphyton community along a succession developed in experimental tanks. Our aim was to identify regularities that may help us to explain the patchiness of this community. Therefore, we estimated the spatial pattern of periphyton biomass using a non-destructive image analysis technique to obtain a temporal series of the spatial distribution. These were analyzed using multifractal techniques. Multifractals are analogous to fractals but they look at the geometry of quantities instead of the geometry of pattern. To use these techniques the object of study must show scale invariance and then can be characterized by a spectra of fractal dimensions. Self-organization describes the evolution of complex structures that emerge spontaneously driven internally by variations of the system itself. The spatial distribution of biomass showed scale invariance at all stages of succession and as the periphyton developed in a homogeneous landscape, in a demonstration of self-organized behavior. Self-organization to a critical state (SOC) is presented in the complex systems literature as a general explanation for scale invariance in nature. SOC requires a mechanism where the history of past events in a place influence the actual dynamics, this was termed ecological memory. The scale invariance was found from the very beginning of the succession thus self-organized criticality is a very improbable explanation for the pattern because there would be not enough time for the build-up of ecological memory. Positive interactions between algae and bacteria, and the existence of different spatial scales of colonization and growth are the likely causes of this pattern. Our work is a demonstration of how large scale patterns emerge from local biotic interactions.

Patchiness seems to be the rule in nature and can be observed at different organizational stages from cells to ecosystems (Holling 1992, Wiens 1999). Ecological studies and environmental monitoring programs should be designed and analyzed taking into account this fact (Wagner and Fortin 2005). Most ecological processes are inherently spatial as they operate between neighboring units (Levin 1992), this could be seen in competitive interactions (Stoll and Prati 2001), tree dispersal (Seidler and Plotkin 2006) and productivity (Pringle et al. 2010) to cite a few of them. Processes also interact with environmental conditions varying in space and time and with other processes, resulting in complex interwoven patterns at multiple spatial and temporal scales. Different theoretical and field studies have emphasized the importance of local biotic interactions in producing such complexities, like predator–prey (De Roos et al. 1998), competition between termite mounds (Pringle et al. 2010), facilitation between plants (Rietkerk et al. 2004) and others. The existence of these interactions can produce complex spatial patterns even in homogeneous environments (Rietkerk and van de Koppel 2008). In cases where these patterns are produced from fine-scale interactions owing to internal causes, they are called self organizing (Rohani et al. 1997).

Self-organization is defined as a set of dynamical mechanisms whereby structures appear at the global level of a system from interactions among their lower-level components. The interactions between the constituent units are determined by local information, without reference to the global pattern, which is an emergent property (Solé and Bascompte 2006).

The characteristics of a self-organizing process are: a) the creation of space-time structures from an homogeneous medium; b) the possible existence of multiple stable states, because the structures emerge through the amplification of random fluctuations; c) the existence of thresholds where a tiny change in a parameter can lead to a qualitative change in the behavior of the system, these are called bifurcations. In this context, the details of the particular biological interactions could be irrelevant for the dynamics of the system, thus a very simple model can describe it successfully (Solé and Goodwin 2000).

Some of these structures display scale invariance and therefore can be characterized by using fractal (power-law) spatial distributions, commonly associated with criticality (Solé et al. 1999). In its classical form criticality comprises an abrupt shift in state following only slight changes in an external parameter, and is related to threshold behavior in ecological systems (Scheffer and Carpenter 2003).

Spatial patterns which develop from local interactions following a power law show a complete lack of characteristic or dominant spatial scale. Ecological systems for which such behavior is suspected include the size distributions of gaps in tropical forests (Solé and Manrubia 1995), clusters in intertidal mussel beds (Guichard et al. 2003), wind disturbed (Kizaki and Katori 1999) and fire disturbed forests (Malamud et al. 1998), vegetation cover in the Kalahari (Scanlon et al. 2007) and biomass in intertidal microphytobenthos (Seuront and Spilmont 2002). However, the existence of this kind of power law spatial pattern is not enough to identify a critical behavior because the correspondence between patterns and underlying biological processes is not unique (Solow 2005).

There are three classes of critical behavior in the field of ecology which correspond to different kinds of driving mechanisms (reviewed by Pascual and Guichard 2005): 1) classical criticality: here we can observe that under the influence of a parameter external to the system (i.e. an environmental condition such as wind force) having a minimal change, the system undergoes a sudden shift called phase transition which happens at a critical point. Near this point power law patterns emerge (Scheffer 2009). It follows that criticality in this case implies a high sensitivity to environmental changes, as observed in predator–prey intertidal systems (Robles and Desharnais 2002). 2) Self organized criticality: in these cases there is no sudden shift associated with an external parameter and a critical point is not defined for them. The system takes itself to the critical state through its own dynamics and a slow external force (Rhodes et al. 1997). In these systems large and intermittent temporal fluctuations are produced due to its internal dynamics. 3) Robust criticality: here power law scalings occur in a broad region of parameter space, even though there exists a critical point where the connectedness of the patches changes dramatically. In addition, there are no drastic changes in the abundance of species neither from large temporal fluctuations (as in 2), nor from high sensitivity to an external parameter or environmental conditions (as in 1).

Thus scale invariance is one of the regularities that can help us to understand the nature of ecosystems (Pueyo et al. 2010), it is closely connected with criticality and therefore both these issues have relevance for ecological theory and its applications.

Scale invariance or fractal spatial distributions have been observed at different successional stages (Alados et al. 2003, 2004) and it is common to estimate one fractal dimension. However, it is likely that the spatial distributions present spatial correlations (Wagner and Fortin 2005) which were produced by several processes operating at different scales. In these cases a single fractal dimension is not enough to completely characterize their fractal properties (Stanley and Meakin 1988, Ricotta 2000), a set of fractal dimensions is required. This is called multifractal spectrum.

We hypothesize that the periphyton successional assembly is a spatial self-organized phenomenon where several processes are likely to operate at different spatial scales. Therefore we expect to find spatial correlations and we used multifractals to analyze the succession. Additionally, there are geometrical reasons (explained in methods) to use multifractal analysis.

We monitor the development of a periphyton community in the laboratory and estimate the spatial distribution of biomass over 11 weeks. We analyze it using multifractal methods to test for the presence of spatial self-organization. We discuss the processes that might cause it and the possible robust critical behavior. This opens the possibility to further study the behavior of an ecological system which seems to show robust criticality and spatial power-laws. The understanding of the mechanisms by which power laws arise from spatially organized ecosystems has potential applications for their management and conservation (Kéfi et al. 2011). These applications could be applied without regarding one particular ecological system while the condition of robust criticality is maintained.

## Methods

### Study system

We call periphyton a complex community composed of several organisms including algae, bacteria, fungi, animals, inorganic and organic detritus, which grows attached to submerged surfaces (Wetzel 1983). Periphyton can be responsible for most primary production in the shallow waters of streams, lakes, coastal waters and wetlands (Vadeboncoeur et al. 2001). It is also a chemical modulator in aquatic systems, transforming many inorganic chemicals into nutrients for its organic forms (Stevenson 1996), something that makes possible its use to purify polluted waters (Vymazal 1988). Furthermore, periphyton has been used as an indicator of water quality due to its property of integrating the effects of different effluents and its rapid response to environmental changes (Lowe 1996).

One of the descriptive characteristics of periphyton communities is biomass, defined as the amount of organic matter (or carbon) that has accrued from the production per surface unit. Biomass is a measure that integrates the interactions of individual characteristics of species, abiotic environmental controls and the effects of herbivory (Biggs et al. 1998).

In turn, the spatial distribution of biomass is the result of processes of colonization, growth, competition, and grazing, among others. Colonization occurs in random places that act as seeds for the development of biomass. As growth progresses, periphyton communities develop complex architectures similar to those of tropical forests, where competition for light and nutrients plays an important role (Lowe 1996).

We monitored the development of a periphyton community in the laboratory using ten 15 liters tanks, which were each illuminated by 10 fluorescent lamps with a photoperiod of 12/12 hours, and an average photon-flux density of 40 mmol $s^{-1}$ $m^2$. In each tank we placed 12 plates of high impact white polystyrene, 1 mm thick, with a size of $8 \times 8$ cm attached to ceramic tiles of the same size to keep them anchored to the bottom. Tanks were filled with 5 l of water from the Puelchense subaquifer. We used groundwater since the chemical characteristics of surface water are highly variable, and groundwater has proven to have more stable properties over time (Momo et al. 1999). Then we added 50 cm$^3$ of water with a high density of algae obtained by scraping from submersed macrophytes (*Egeria densa*), filtered with a mesh of 200 microns. Macrophytes were collected in the Las Flores stream, part of the Luján River basin (Feijoó et al. 1999).

To estimate the spatial distribution of biomass we used a nondestructive photographic method to obtain the development in time of the periphyton community (Saravia et al. 1999). The method uses digital photography to estimate biomass using a mathematical relationship previously calibrated with standard methods for chlorophyll *a* determination.

We identified one plate per tank for the photographic determination, on which measurements were made throughout the experiment. The frequency of sampling was weekly and lasted 11 weeks, from September to November 1999 (Fig. 1). On the same day that we made the photographic estimate another plate was selected at random and extracted from all the tanks. The plate was divided into three sections: one for chlorophyll *a* determination using the modified Lorenzen method (Aminot 1983) with methanol extraction, other to determine ash-free dry weight, and the third section was fixed to determine the taxonomic composition. We also measured physical characteristics such as water temperature (circa 22°C), the photon flux density (circa 40 mol quanta m$^{-2}$ s$^{-1}$), which did not vary significantly throughout the experiment.

Each week we added 50 cm$^3$ of concentrated algae to simulate the algae colonization that the community would receive in a natural environment. Groundwater was also added to compensate for evaporation when necessary.

## Multifractal analysis

Multifractals and fractals are techniques to characterize scaling behavior of a system, the difference is that fractals look at the geometry of presence/absence patterns, while multifractals look at the arrangement of quantities like population densities or biomass (Halley et al. 2004). An option to analyze this system would be to discretize it using a threshold and then calculate the fractal dimension for each slice. Some studies analyze a range of thresholds and obtain different values of the fractal dimension for each one (Seuront and Spilmont 2002, Kellner and Asner 2009). The natural choice is to use multifractal analysis and then there is no need to discretize the object at arbitrary thresholds.

Multifractals have been applied by other researchers for the characterization of bacterial biofilms (Hermanowicz et al. 1995) – which form an essential part of periphyton communities – and to characterize microphytobenthos communities (Seuront and Spilmont 2002). In ecology, multifractals have been used in the analysis of temporal variability in plankton biomass (Pascual et al. 1995) as a model of extinction and origin of species (Plotnick and Sepkoski Jr. 2001), and to analyze the spatial distribution of gaps caused by falling trees in the rainforest (Solé and Manrubia 1995). In the latter case the existence of multifractal distribution was taken as evidence that the forest could be in a critical state (Solé and Alonso 1998).

The fractal dimension *D* is usually used to characterize a fractal object, which measures the object's capacity to fill the space. Instead multifractal objects are characterized by a spectrum of fractal dimensions. We analyzed the images of

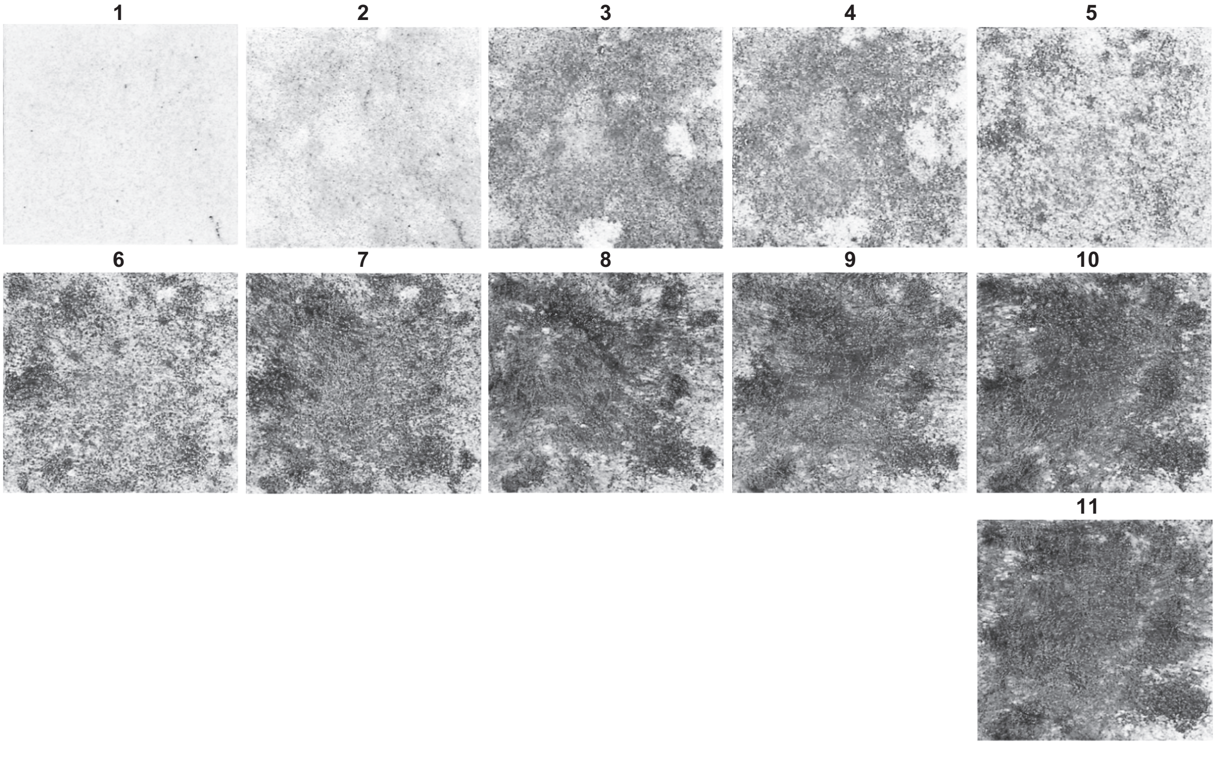

Figure 1. Time development of periphyton's spatial biomass distribution for one plate. The numbers on the top of each image correspond to weeks of development. Darker areas correspond to higher biomass, brighter areas to low biomass. The gray levels of the first week were modified to enhance the visualization of the pattern.

periphyton using the spectrum of generalized dimensions $D_q$ and the singularity spectrum $f(\alpha)$.

### Generalized dimensions spectrum

Generalized dimensions are exponents that establish the non-uniformity of a measure and were originally developed to characterize chaotic systems (Hentschel and Procaccia 1983). To estimate them we used the method of moments based on box-counting (Halsey et al. 1986). The image is covered with a grid, which divided it into $N(\varepsilon)$ squares of side $\varepsilon$, allowing to calculate the biomass $\mu_i(\varepsilon)$ in each of them. Then the so called partition function is computed as:

$$Z_q(\varepsilon) = \sum_i^{N(\varepsilon)} \left(\mu_i(\varepsilon)\right)^q \tag{1}$$

Where $q$ is called moment order. The operation is performed for different values of $\varepsilon$ and $q$, within a predetermined range. The generalized dimension is calculated as:

$$D_q = \frac{1}{q-1} \lim_{\varepsilon \to 0} \frac{\log\left(Z_q(\varepsilon)\right)}{\log \varepsilon} \tag{2}$$

though in fact the limit can not be assessed. Then the second term in $D_q$ is calculated as the slope of the $\log(Z_q)$ versus $\log(\varepsilon)$. This is done for different $q$, provided that it is a real number. Using a range of $q$ that includes negative and positive numbers yields a graph of $D_q$ in terms of $q$, called the spectrum of generalized dimensions. The parameter $q$ determines which squares have a greater contribution to the sum of Eq. 1 and therefore more influence on Eq. 2. When $q$ is a relatively large positive number, the main contribution comes from higher $\mu_i$. However, when $q$ is a negative number, large in absolute value, the highest contribution comes from smaller $\mu_i$. Thus an image with large peaks surrounded by a relatively uniform values of biomass will have higher $D_q$ for positive $q$ and an image with sharp holes of biomass will have higher $D_q$ for negative $q$. An image with both will have the biggest range of $D_q$.

The spectrum of generalized dimensions, $D_q$ takes the shape of a sigmoidal curve and it is a decreasing function of $q$ (Grassberger 1983).

When $q = 1$, the denominator of the first term in $D_q$ is undefined, so it must be replaced by the following expression:

$$D_q = \lim_{\varepsilon \to 0} \frac{\sum_i^{N(\varepsilon)} \mu_i(\varepsilon) \log\left(\mu_i(\varepsilon)\right)}{\log \varepsilon} \tag{3}$$

and we proceed to calculate the slope of the numerator in terms of $\log(\varepsilon)$.

The assumption that must be met in all cases is that the relationship $\log(Z_q)$ versus $\log(\varepsilon)$ should be linear. These linear relationships are estimated using the least squares method. Different $\varepsilon$ which are used to calculate the sums in Eq. 1 and 3 are determined so as to be equidistant points on the axis of the independent variable $\log(\varepsilon)$.

The generalized dimension is an exponent because it is derived from the definition 2, yielding:

$$\log(Z_q) \approx D_q(q-1)\log(\varepsilon) \tag{4}$$

The symbol $\approx$ is used here to mean that the term on the left approaches a constant times the term on the right at the limit of small $\varepsilon$. If we raise Eq. 4 to the power of 10 to remove the log:

$$Z_q \approx \varepsilon^{D_q(q-1)} \tag{5}$$

Expression 5 is called a power law, and determines how $Z_q$ varies with scale represented by $\varepsilon$. The relations of expression 5 are the signature of multifractal and fractal objects, in fact, when $q = 0$, (Eq. 5) becomes the standard fractal dimension. For a fractal object the calculation of $D_q$ in a range of $q$ can be performed but it would result in a constant value equal to $D_0$.

The exponential relationship (Eq. 5) only holds for all scales in theoretical multifractals. In nature though there are upper and lower limits for scales in which this relationship applies (Davis et al. 1994). The first limitation is imposed by the extent and resolution of the experimental method. In addition there are restrictions imposed by the method of estimation. At scales of less than 4 or 5 resolution elements (pixels), image structure is severely compromised (Chappell and Scalo 2001), this sets the lower limit. The upper limit of the scale used in the estimation should be significantly less than the size of the image otherwise edge effects distort the results (Chappell and Scalo 2001).

The second limitation is that natural processes have multifractal properties in a bounded range of scales due to their own dynamics. This is determined by observing the scales at which they maintain the linear relationship of $\log(Z_q)$ versus $\log(\varepsilon)$ (Pascual et al. 1995). This range of scales should be retained for all $q$ where $D_q$ is defined.

A caveat of generalized dimensions is that they do not have a clear interpretation in geometrical terms, except for three special cases: $D_0$ is the standard fractal dimension, $D_1$ is the information dimension that describes how the information content changes with scale, and is related to the Shannon index of diversity. Finally $D_2$ is the correlation dimension that measures how density accumulates as the area changes, $D_2$ is related to the Simpson diversity index. In fact $D_q$ might be considered as a measure of the the speed of increasing of Hill's generalized diversity index (Hill 1973) as the area changes (Ricotta 2000).

### Spectrum of singularities

This method can be used to overcome the problems of interpretation of generalized dimensions. A multifractal can be thought of as the sum of subsets with different fractal dimensions and this method characterize the different subsets and its associated fractal dimensions.

We start defining the coarse Hölder exponent: given a point $x$ on the plane where the object is defined, we place a square with side $\varepsilon$ centered on $x$ and calculate the value of the biomass contained therein $\mu(\varepsilon, x)$. Then for any point $x$, the exponent is defined as:

$$\alpha = \frac{\log\left(\mu(\varepsilon, x)\right)}{\log(\varepsilon)}$$

In the limit where the size of the square tends to zero, $\alpha$ measures how biomass integrated around a point $x$ varies with distance according to the relationship:

$$\mu(\varepsilon, x) \approx \varepsilon^{\alpha}$$

this means that increasing the scale in $\varepsilon$ the biomass increases or decreases according to $\alpha$. The smaller the value of $\alpha$ the faster this increase will be at the smallest scales of $\varepsilon$. Thus if the region around the point $x$ has a relatively uniform density, the value of $\alpha$ will be relatively high. If point $x$ have very high value with respect to the contiguous zone of the image, a singular value, the exponent $\alpha$ will be smaller (Pascual et al. 1995).

If we count the number of squares $N(\alpha)$ where the biomass $\mu(\varepsilon, x)$ has an exponent ranging between $\alpha$ and $\alpha + d\alpha$, with $d\alpha$ being a small value with respect to $\alpha$, then we define:

$$f_{\varepsilon}(\alpha) = -\frac{\log(N_{\varepsilon}(\alpha))}{\log(\varepsilon)}$$

When $\varepsilon$ tends to 0, $f_{\varepsilon}(\alpha)$ has a well-defined value $f(\alpha)$ that can be interpreted as the fractal dimension of the set of boxes with a singularity exponent $\alpha$:

$$N(\alpha) \approx \varepsilon^{-f(\alpha)}$$

In other words, within the biomass distribution there are overlapping sets each marked with a singularity exponent $\alpha$ and a fractal dimension $f(\alpha)$. The method of estimation is given in supplementary material (Supplementary material Appendix 2).

Both spectra are related and they provide the same information but from a different point of view. The singularity spectrum provides a naturally intuitive description of a multifractal object in terms of interwoven sets and the generalized dimensions correspond to the scaling exponents for the $q$th moments of the object (Chhabra and Jensen 1989).

### Estimation

Since the methods to estimate the two spectra use the same grids both were calculated at the same time. The images of biomass obtained from the succession of the periphyton community had a resolution of $470 \times 470$ elements or pixels, so we chose a grid size range of $\varepsilon$ in powers of two with a minimum of $2^2 = 4$ and maximum of $2^7 = 128$ pixels. Because different sizes of $\varepsilon$ do not divide the image exactly, the total area covered by the squares is not the same for each $\varepsilon$ – something which leads to deviations in the estimate. To avoid that we used a sliding window, taking a smaller portion of the image that it was exactly divisible by all values of $\varepsilon$, $2^8 = 256$ pixels. This window was located at the four corners of the image and the values of the spectra for each window were averaged. Using a $q$ range from $-24$ to 24, one plate was followed through time for each of the tanks and ten images were obtained, so we examined the development of 10 independent series of colonizations.

To test if the colonization patterns were different to a random one, we performed a randomization test. We use $D_1$ because this is theoretically the most informative dimension in the spectrum, and also is one of the least affected by sampling problems (Marshak et al. 1997). We shuffle the pixel position and recalculate the information dimension $D_1$ and obtained a confidence interval for a random pattern performing 1000 repetitions (Crowley 1992). If the actual values of $D_1$ falls outside the interval, then the spatial pattern is not random.

## Results

We observed that the linear relation necessary for the biomass distribution to be multifractal was achieved for all dates sampled and all $q$ used to determine the spectrum of generalized dimensions (Supplementary material Appendix 1 Fig. A1). We also noticed that the linear relation was maintained throughout the range of scales considered. The data used to determine $Z_q$ at each scale was not independent because the squares used for smaller $\varepsilon$ values are nested in the greater ones. This violates the assumptions implicit when performing statistical tests but does not invalidate the least square method to determine the best line through all points. We calculated the coefficient of determination $R^2$ as a descriptive measure of goodness of fit (Borda-de-Água et al. 2002). All $R^2$ were higher than 0.99 in all cases, indicating a very good fit.

There was a wide variation in the spectrum of generalized dimensions for different times of development of the periphyton community (Fig. 2). The theoretical prediction that $D_q$ should be a monotonically decreasing function of $q$ was maintained in all cases, that is, that for all $q_1 \geq q_2$ the generalized dimension must be $D_1 \leq D_2$ (Grassberger 1983).

In the case of a monofractal – when biomass exhibits a simple fractal structure – the spectrum of generalized dimensions should be a constant line, a pattern not observed in any case (Fig. 2).

A uniform spatial distribution of biomass, that is a constant value of biomass over all the plate would give a $D_q$ equal to two. Thus the more different the value is from two the more different from a uniform surface the colonized plate is.

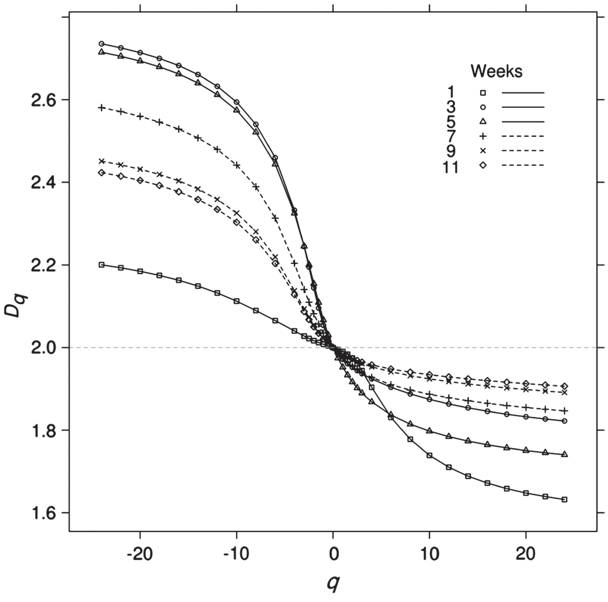

Figure 2. Spectrum of generalized dimensions $D_q$ versus $q$ for different times of development of the periphyton community. The values shown are the means for each colonization time.

In the first week of development $D_q$ showed the smallest distance from two for negative $q$ and the largest distance for $q$ positive, this means a uniform pattern of low biomass with some abrupt peaks of relatively high biomass (Fig. 2, 3). In the following weeks the regions of low biomass tend to grow but small regions of low biomass remain, creating holes. These singularities grow until the third week when the values of $D_q$ for $q$ negative show the maximal distance from two. Then the holes begin to fill, so $D_q$ values get closer to two.

For $q$ positive, the peaks of high biomass become less pronounced until the third week; then there is a secondary growth, new peaks of high biomass are formed, this might be caused by a replacement of species. The fifth week shows the maximal for these singularities. Then $D_q$ for $q$ positive tends to get closer to two and the biomass distribution as a whole tends to be more uniform.

The development of the periphyton biomass is what generates the multifractal pattern so the range of $D_q$ variation should increase or at least be modified with time. This is what has been observed experimentally with a maximum peak at fiveweeks of development, this is the point of greater heterogeneity of the biomass distribution from which the variation of $D_q$ decreases (Fig. 3).

All values of $D_q$ seems to stabilize in the last two weeks. From the point of view of spatial biomass distribution the succession appears to reach a steady state by the week ten, this can be seen in the last images of Fig. 1. That does not mean that the specific composition or other parameters of succession stabilize too, this could be the subject of future studies.

Another way to see the degree of heterogeneity of the spatial biomass distribution is to calculate the range of $D_q$ for a given value of $q$ ($\Delta D_q$). We can compare it with the information dimension $D_1$ and they roughly follow the same pattern: a peak of heterogeneity at five weeks and low heterogeneity at the beginning and at the end of succession (Table 1). The values of $\Delta D_{20}$ in Table 1 have roughly a coefficient of variation of 10% and the ones of $D_1$ are around 1%, this corresponds to the fact that $D_q$ for large $q$ (negative or positive) are determined by low or high intensity patterns that are relatively rare, so for statistical purposes it should be more convenient to use low values of $q$ (in the range of 5 to $-5$).

For all times in all plates the spatial distribution of biomass is not random, the region corresponding to a random spatial distribution is very narrow (Fig. 4), this means that $D_1$ is very sensitive index of spatial pattern. Besides initial colonization could be random the growth of periphyton quickly modifies the spatial pattern.

With regard to the spectrum of singularities, good fits were observed in the determination of $\alpha$ for all $q$ at all dates sampled (Supplementary material Appendix 1 Fig. A2). The $R^2$ value was higher than 0.99 in all cases.

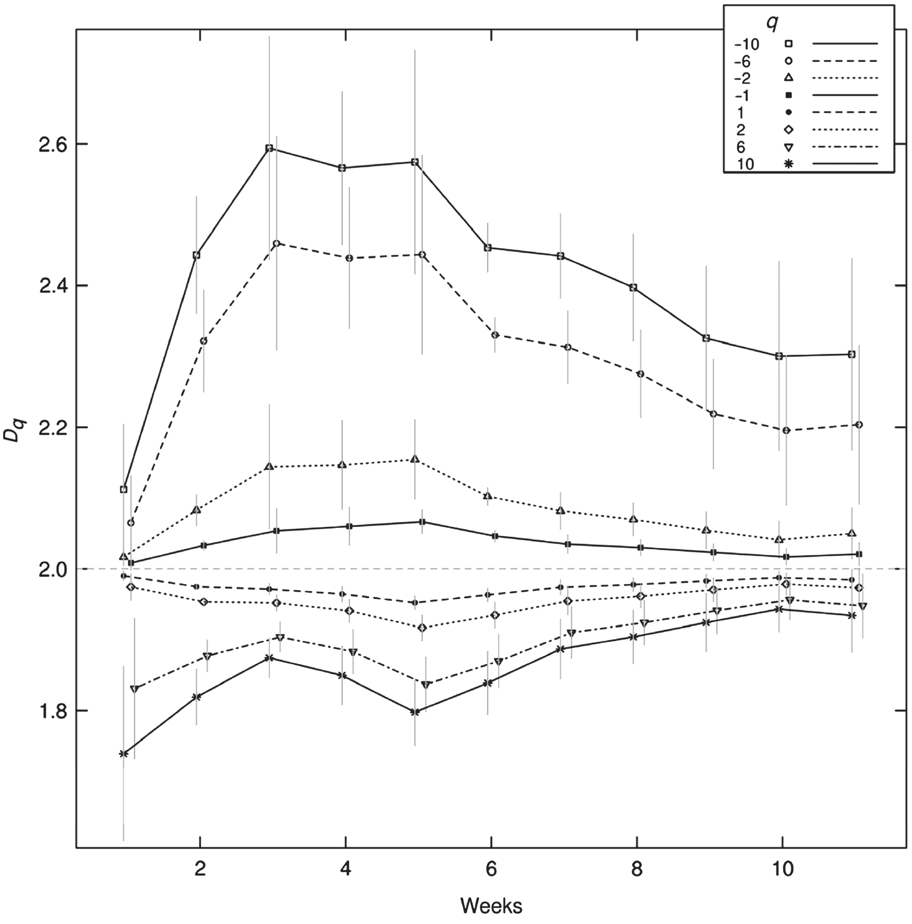

Figure 3. Plot of the generalized dimensions $D_q$ versus time for different values of $q$. The values of $D_q$ are averages of ten plates for each colonization time.

Table 1. Time evolution of variables extracted from the generalized dimension and singularities spectrum. $\Delta D_{20}$ is the range of generalized dimensions $D_q$ at $q = 20$ calculated as $D_{-20} - D_{20}$. $D_1$ is the information dimension. $\Delta\alpha_{20}$ is the range of the exponent of singularity calculated at $q = 20$ as $\alpha_{-20} - \alpha_{20}$. The variables are averages for the ten tanks and the numbers in parenthesis below each variable are standard deviations.

| | Weeks | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |
| $\Delta D_{20}$ | 0.5368 | 0.8054 | 0.8815 | 0.8776 | 0.9428 | 0.7681 | 0.7049 | 0.6375 | 0.5335 | 0.4844 | 0.4918 |
| | (0.1989) | (0.0886) | (0.1518) | (0.0953) | (0.1582) | (0.0603) | (0.0842) | (0.0925) | (0.1344) | (0.1608) | (0.1773) |
| $D_1$ | 1.9904 | 1.9750 | 1.9714 | 1.9645 | 1.9523 | 1.9633 | 1.9741 | 1.9778 | 1.9830 | 1.9878 | 1.9847 |
| | (0.0068) | (0.0031) | (0.0083) | (0.0107) | (0.0096) | (0.0095) | (0.0109) | (0.0094) | (0.0095) | (0.0091) | (0.0143) |
| $\Delta\alpha_{20}$ | 0.7278 | 1.0107 | 1.0770 | 1.0719 | 1.1371 | 0.9509 | 0.8856 | 0.8144 | 0.6990 | 0.6440 | 0.6495 |
| | (0.2082) | (0.0951) | (0.1542) | (0.1020) | (0.1680) | (0.0697) | (0.0885) | (0.1000) | (0.1487) | (0.1720) | (0.1898) |

For $f(\alpha)$ we observed the expected deviations from linear behavior for large $q$ in absolute value (Supplementary material Appendix 2), resulting from the arbitrary choice of $\varepsilon$ sizes. For $q$ in the range of $-4$ to $+6$, $R^2$ was always higher than 0.95. Outside this range, the poorer fits were observed, in the first week for positive $q$ and from the second week onwards for negative $q$ (Supplementary material Appendix 1 Fig. A3).

In a plate without algae or a plate with a uniform distribution of biomass the spectrum will collapse to a point where $\alpha = f(\alpha) = 2$. Theoretically, this value also corresponds to a completely random distribution of biomass. The difference is that in a empty plate $\alpha$ and $f(\alpha)$ would not have variations and on a plate with random biomass we would observe a narrow curve extending downwards (Chappell and Scalo 2001). We found instead, for all cases analyzed, singularity spectra with broad ranges of $\alpha$ and $f(\alpha)$ which demonstrate the multifractal nature of the distribution of periphyton biomass (Fig. 5).

Development stages of the community differ much more in the area of $\alpha > 2$, i.e. for $q$ negative. A greater range in the exponent of singularity $\alpha$ indicates a greater heterogeneity of the image, since there are homogeneous areas characterized by $\alpha > 2$ and areas with large fluctuations characterized by $\alpha < 2$. We can calculate the range of $\alpha$ for a given value of $q$ ($\Delta\alpha_q$). The wider range was observed at about five weeks of development (Table 1). As expected both methods show the same patterns, indicating a greater heterogeneity about five weeks and a clear difference for the first week with respect to the others.

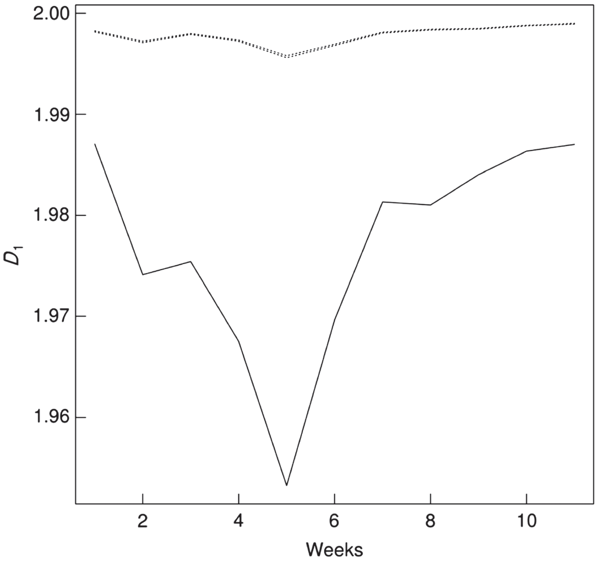

Figure 4. The information dimension $D_1$ as a function of time for one plate. The solid line represents $D_1$, dashed lines are 95% confidence intervals for testing against a random spatial distribution of periphytons' biomass. All other plates showed similar patterns.

As a dimension, $f(\alpha)$ does not accept negative values, but they tend to appear in certain stochastic multifractals describing very rare events. This means that as $\varepsilon$ tends to zero we find a decreasing amount of the corresponding $\alpha$ (Chhabra and Sreenivasan 1991). They can also be caused by the effect of the finite size of the sample and the estimation errors. In our case we observed the presence of negative values for $q$ where the fits are poorer. These were observed in the first week for the positive values of $q$, corresponding to the left of the curve, and on the following weeks for negative values of $q$, to the right of the curve. This suggests that the negative values of $f(\alpha)$ come from sampling errors and the effects of finite size of the sample rather than from very rare events.

## Discussion

We study the spatial distribution of periphyton's biomass and the results indicate that is multifractal, meaning that it could be seen as a composite of several fractal sets with various fractal dimensions. These different sets can be interpreted as different views about how the community is organized in space and the nature of the correlations between individuals (Solé and Bascompte 2006). This observation can be used when building a model to explain the mechanism of the community assembly to restrict the type of models that reproduce the field observations.

Moreover multifractality implies that the spatial distribution is self-similar with respect to the scale of observation. This means that if we look at the image with different lenses that can magnify or reduce the image, we would observe a similar distribution of biomass within a certain range. In the range used in this experiment from 0.7 to 22 mm there is no preferred scale, which does not imply that the distribution of biomass is homogeneous and constant, but that its irregularity or heterogeneity is invariant. The same set of processes should be acting over these scales generating this characteristic distribution.

The communities were developed in homogeneous environments, so in principle the spatial pattern has to be caused by biological processes generated by the community itself, that is the community shows self-organization.

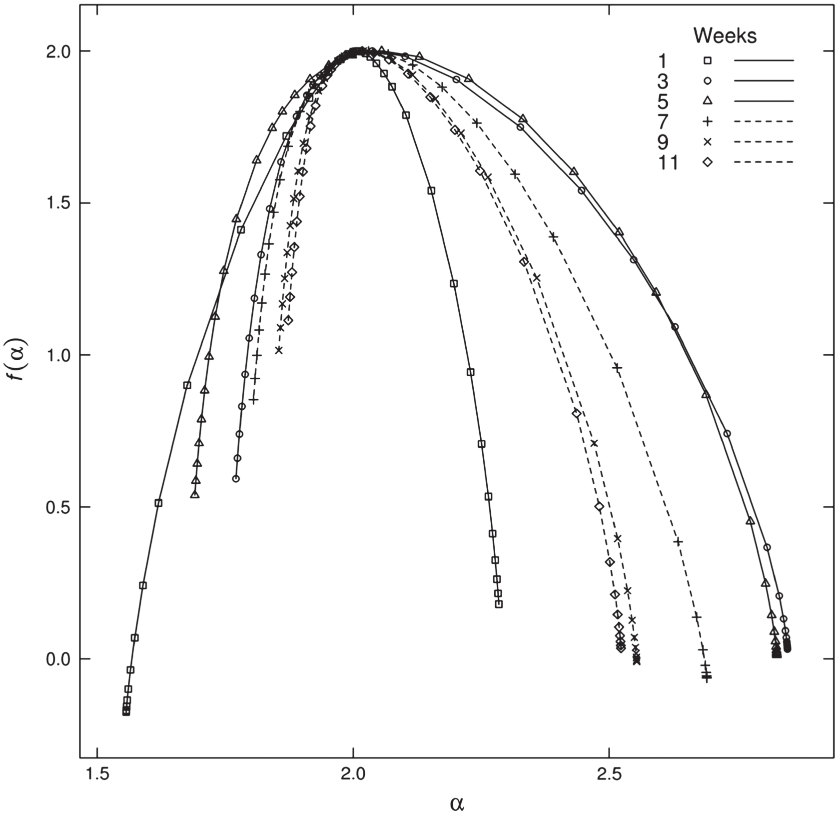

Figure 5. Spectrum of singularities α versus $f(\alpha)$ for different times of development of the periphyton community. The values shown are the means for each colonization time.

These two characteristics of the periphyton communities (self-similarity and self-organization) suggest that some kind of criticality may be operating.

Classical criticality requires the fine tuning of an external parameter such as temperature but in our study system all external parameters were kept constant, with the exception of nutrients. In any case, the community shows multifractality in all the analyzed periods (not only at a particular time), which would rule out the possibility of this type of criticality. Although there is a possibility that the environmental conditions in which we performed the study were exactly at the critical point. This could be excluded because we previously measured a similar periphyton's colonization under slightly different enviromental conditions with exactly the same results.

In systems that exhibit SOC there exists an external force that slowly drives the development of the system. In the case of ecological systems in general and periphyton in particular, this can be thought of as the immigration of new species (Solé et al. 2002). In our experimental system this is simulated by the added water with algae (see study system) that could potentially establish in the community. This pressure of individuals trying to colonize is called a force.

This force accumulates internally and was called ecological memory in the context of wildfire ecosystems (Zinck and Grimm 2009). The accumulation continues up to a certain point where there is a release or relaxation of the system that happens at a time scale much shorter than the accumulation, this phenomenon is known as a separation of temporal scales. In the case of ecological systems, the arrival of new species should reach a point where we would observe a cascade of local extinctions as a result of dynamic equilibrium.

Besides the observed self-similar spatial patterns, the temporal development of the system should exhibit fractal properties. If you observe the system long enough extinctions of all sizes would be detected (Solé and Goodwin 2000). Such temporal fluctuations are typical of SOC systems and are called 1/f noise. To determine whether the biomass behaves like 1/f noise requires a minimum of 50 points (Miramontes and Rohani 2002), making it impossible to apply this analysis for the biomass time series obtained in this experiment. In addition the species composition should be analyzed because extinctions might not cause biomass fluctuations. Further, it seems very unlikely that this mechanism is working because other similar experimental studies showed no trace of this kind of extinctions (Rodríguez 1992, 1994), at least for time scales of ecological interest.

Other mechanism that could produce SOC in the biomass' dynamics of the periphyton's succession is self-generated detachment: a sizeable and rather sudden loss of biomass. This perturbation, mainly caused by bacterial degradation of the periphyton mat (Bouletreau et al. 2006), does not seem to propagate fast enough to produce the separation of time scales required. Besides, it generally occurs in mature stages of the succession, thus we should not observe multifractal spatial distributions in the first weeks of the experiment. This leads us to disregard SOC as a possible mechanism.

The third type of criticality, robust criticality, is regarded as an explanation of the widespread observation of power-laws in ecological systems, and does not have the requirements of the previous two, does not need separation of scales nor fine tunning of external conditions. Thus is quite possible that our experimental communities show this kind of criticality, is hypothezised that systems that combine local stochastic birth and dead process will have this behavior (Kéfi et al. 2011), and periphyton communities belong to this class of systems. But the exact properties of robust critical systems are still poorly understood so this is an issue that will require further study.

Recent studies that combine field data with spatial models have demonstrated the importance of positive local interactions to generate self-organized and self-similar spatial patterns as those observed here (Kéfi et al. 2007, Scanlon et al. 2007). Within the periphyton community bacteria can produce facilitation in the colonization of new substrates by algae (Hodoki 2005), and there are interactions of mutual benefit between these communities with respect to recycling of nutrients (Scott et al. 2008). On the other hand, when the periphyton develops algal communities it may be limited primarily by attenuation of light (Asaeda and Duong 2001). These mechanisms acting locally could be respectively the activators and inhibitors required for the formation of spatial patterns (Rietkerk and van de Koppel 2008), and the establishment of a robust criticality regime. Self-similar spatial patterns are produced in this regime but it is not necessary to have large temporal fluctuations, drastic changes in the abundance of species or extreme sensitivity to environmental conditions, criticality here is related to the existence of a critical point where the connection between patches radically changes (Pascual and Guichard 2005). The positive interaction seems to be closely connected with the disturbance process involved in the development of bacteria, thus local recovery and disturbance rates should be comparable, a key assumption for the establishment of robust criticality.

Another mechanism is that colonization of the substrate occurs globally, that is periphyton might colonize any point of the plate with equal probability, though, growth is local. This combination of factors is similar to the invasion of an environment for a given species with events of long-distance dispersal (Kot et al. 1996). This type of invasion also produces self-similar spatial patterns and is regarded as a robust indication of self-organization (Marco et al. 2011). A similar mechanism of separation of spatial scales could be acting in the periphyton.

There is still another possibility: neutral clustering. This refers to the species aggregation produced in neutral spatial models, typically used to study species-area relationships (Rosindell and Cornell 2009). This aggregation is produced in stochastic birth–death models mainly by the effect of individual discreteness (Houchmandzadeh and Vallade 2003). It was demonstrated analytically that in three dimensions species aggregate in clusters with power-law distribution of sizes, in two dimensions clusters are formed but at equilibrium one species dominates and clustering vanish. We hypothesize that also the transient cluster distribution could be fractal.

Combining these with the dynamics of succession it is probable that in the first weeks the dominating mechanisms where related with stochastic colonization/growth and in the later stages of succession the mechanisms of positive interactions became more relevant. In contrast, neutral clustering could be acting along the entire succession. The next challenge is to find characteristics to differentiate which mechanism is acting or which ones are most important at different stages of succession.

This could be done using a mathematical models, but with a different approach to that used in most studies up to now. Usually the equilibrium state of the models is analyzed and the transient discarded, but in the case of the succession of periphyton the transient state is the important part to focus on. The succession of periphyton, and many natural systems, fail to reach an equilibrium state, and therefore we should study the transient dynamics from the perspective of self-organization and complex systems.

*Acknowledgements* – We thank the National University of Lujan for financial support. To Diana Marco and Graeme Ruxton and for kindly reading the manuscript and to Thorsten Wiegand for useful comments on an earlier version of the manuscript.

## References

Alados, C. L. et al. 2003. Quantitative characterization of the regressive ecological succession by fractal analysis of plant spatial patterns. – Ecol. Modell. 163: 1–17.

Alados, C. L. et al. 2004. Change in plant spatial patterns and diversity along the successional gradient of Mediterranean grazing ecosystems. – Ecol. Modell. 180: 523–535.

Aminot, A. 1983. Dosage de la chloropyhlle et des phéopigments par spectropfhotmétric. – In: Aminot, A. and Chausspied, M. (eds), Manuel des analyses chimiques. Centre National pour l'exploitation des Océans, Québec, pp. 177–189.

Asaeda, T. and Duong, H. S. 2001. A model of the development of a periphyton community: resource and flow dynamics. – Ecol. Modell. 137: 61–75.

Biggs, B. J. F. et al. 1998. A habitat matrix conceptual model for stream periphyton. – Arch. Hydrobiol. 143: 21–56.

Borda-de-Água, L. et al. 2002. Species–area curves, diversity indices, and species abundance distributions: a multifractal analysis. – Am. Nat. 159: 138–155.

Bouletreau, S. et al. 2006. Assessing the importance of a self-generated detachment process in river biofilm models. – Freshwater Biol. 51: 901–912.

Chappell, D. and Scalo, J. 2001. Multifractal scaling, geometrical diversity, and hierarchical structure in the cool interstellar medium. – Astrophys. J. 551: 712–729.

Chhabra, A. B. and Jensen, R. V. 1989. Direct determination of the f(alfa) singularity espectrum. – Phys. Rev. Lett. 62: 1327–1330.

Chhabra, A. B. and Sreenivasan, K. R. 1991. Negative dimensions: theory, computation and experiment. – Phys. Rev. A 43: 1114–1117.

Crowley, P. H. 1992. Resampling methods for computation-intensive data analysis in ecology and evolution. – Annu. Rev. Ecol. Syst. 23: 405–447.

Davis, A. et al. 1994. Multifractal characterization of nonstationarity and intermitency in geophysical fields: observed, retrieved or simulated. – J. Geophys. Res. 99: 8055–8072.

De Roos, A. M. et al. 1998. Pattern formation and the spatial scale of interaction between predators and their prey. – Theor. Popul. Biol. 53: 108–130.

Feijoó, C. S. et al. 1999. Temporal and spatial variability in streams of a pampean basin. – Hydrobiologia 394: 41–52.

Grassberger, P. 1983. Generalized dimensions of strange attractors. – Phys. Lett. A 97: 227–230.

Guichard, F. et al. 2003. Mussel disturbance dynamics: signatures of oceanographic forcing from local interactions. – Am. Nat. 161: 889–904.

Halley, J. M. et al. 2004. Uses and abuses of fractal methodology in ecology. – Ecol. Lett. 7: 254–271.

Halsey, T. C. et al. 1986. Fractal measures and their singularities: the characterization of strange sets. – Phys. Rev. A 33: 1141–1151.

Hentschel, H. G. E. and Procaccia, I. 1983. The infinite number of generalized dimensions of fractals and strange attractors. – Physica D 8: 435–444.

Hermanowicz, S. W. et al. 1995. Fractal structure of biofilms: new tools for investigation of morphology. – Water Sci. Technol. 32: 99–105.

Hill, M. O. 1973. Diversity and evenness: a unifying notation and its consequences. – Ecology 54: 427–432.

Hodoki, Y. 2005. Bacteria biofilm encourages algal immigration onto substrata in lotic systems. – Hydrobiologia 539: 27–34.

Holling, C. S. 1992. Cross-scale morphology, geometry and dynamics of ecosystems. – Ecol. Monogr. 62: 447–502.

Houchmandzadeh, B. and Vallade, M. 2003. Clustering in neutral ecology. – Phys. Rev. E 68: 061912.

Kellner, J. R. and Asner, G. P. 2009. Convergent structural responses of tropical forests to diverse disturbance regimes. – Ecol. Lett. 12: 887–897.

Kizaki, S. and Katori, M. 1999. Analysis of canopy-gap structures of forests by Ising Gibbs States – equilibrium and scaling property of real forests. – J. Phys. Soc. Jpn 68: 2553–2560.

Kot, M. et al. 1996. Dispersal data and the spread of invading organisms. – Ecology 77: 2027–2042.

Kéfi, S. et al. 2007. Spatial vegetation patterns and imminent desertification in Mediterranean arid ecosystems. – Nature 449: 213–217.

Kéfi, S. et al. 2011. Robust scaling in ecosystems and the meltdown of patch size distributions before extinction. – Ecol. Lett. 14: 29–35.

Levin, S. A. 1992. The problem of pattern and scale in ecology. – Ecology 73: 1943–1967.

Lowe, R. L. 1996. Periphyton patterns in lakes. – In: Stevenson, R. J. et al. (eds), Algal ecology: freshwater benthic ecosystems. Academic Press, pp. 341–373.

Malamud, B. D. et al. 1998. Forest fires: an example of self-organized critical behavior. – Science 281: 1840–1842.

Marco, D. E. et al. 2011. Comparing short and long-distance dispersal: modelling and field case studies. – Ecography 34: 671–682.

Marshak, A. et al. 1997. Scale invariance of liquid water distributions in marine stratocumulus. Part II: Multifractal properties and intermitence issues. – J. Atmospheric Sci. 54: 1423–1444.

Miramontes, O. and Rohani, P. 2002. Estimating 1/f scaling exponents from short time-series. – Physica D 166: 147–154.

Momo, F. R. et al. 1999. Mapping the water quality of the Puelchense subaquifer in Lujan (Argentina). – In: Brebbia, C. A. and Anagnostopoulod, P. (eds), Water pollution. V. Modelling, measuring and prediction. WIT Press, pp. 493–501.

Pascual, M. and Guichard, F. 2005. Criticality and disturbance in spatial ecological systems. – Trends Ecol. Evol. 20: 88–95.

Pascual, M. et al. 1995. Intermittency in the plankton: a multifractal analysis of zooplankton biomass variability. – J. Plankton Res. 17: 1209–1232.

Plotnick, R. E. and Sepkoski Jr., J. J. 2001. A multiplicative multifractal model for originations and extinctions. – Paleobiology 27: 126–139.

Pringle, R. M. et al. 2010. Spatial pattern enhances ecosystem functioning in an African savanna. – PLoS Biol 8: e1000377.

Pueyo, S. et al. 2010. Testing for criticality in ecosystem dynamics: the case of Amazonian rainforest and savanna fire. – Ecol. Lett. 13: 793–802.

Rhodes, C. J. et al. 1997. On the critical behaviour of simple epidemics. – Proc. R. Soc. B 264: 1639–1646.

Ricotta, C. 2000. From theoretical ecology to statistical physics and back: self-similar landscape metrics as a synthesis of ecological diversity and geometrical complexity. – Ecol. Modell. 125: 245–253.

Rietkerk, M. and van de Koppel, J. 2008. Regular pattern formation in real ecosystems. – Trends Ecol. Evol. 23: 169–175.

Rietkerk, M. et al. 2004. Self-organized patchiness and catastrophic shifts in ecosystems. – Science 305: 1926–1929.

Robles, C. and Desharnais, R. 2002. History and current development of a paradigm of predation in rocky intertidal communities. – Ecology 83: 1521–1536.

Rodríguez, M. A. 1992. An empirical analysis of community structure regulation in periphyton. – Oikos 65: 419–427.

Rodríguez, M. A. 1994. Succession, environmental fluctuations and stability in experimentally manipulated microalgal communities. – Oikos 70: 107–120.

Rohani, P. et al. 1997. Spatial self-organization in ecology pretty patterns or robust reality. – Trends Ecol. Evol. 12: 70–74.

Rosindell, J. and Cornell, S. J. 2009. Species-area curves, neutral models, and long-distance dispersal. – Ecology 90: 1743–1750.

Saravia, L. A. et al. 1999. A photographic method for estimating chlorophyll in periphyton on artificial substrata. – Aquat. Ecol. 33: 325–330.

Scanlon, T. M. et al. 2007. Positive feedbacks promote power-law clustering of Kalahari vegetation. – Nature 449: 209–212.

Scheffer, M. 2009. Critical transitions in nature and society. – Princeton Univ. Press.

Scheffer, M. and Carpenter, S. R. 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. – Trends Ecol. Evol. 18: 648–656.

Scott, T. J. et al. 2008. Does nutrient enrichment decouple algal–bacterial production in periphyton? – J. N. Am. Benthol. Soc. 27: 332–344.

Seidler, T. G. and Plotkin, J. B. 2006. Seed dispersal and spatial pattern in tropical trees. – PLoS Biol. 4: e344.

Seuront, L. and Spilmont, N. 2002. Self-organized criticality in intertidal microphytobenthos patch patterns. – Physica A 313: 513–539.

Solow, A. R. 2005. Power laws without complexity. – Ecol. Lett. 8: 361–363.

Solé, R. V. and Manrubia, S. C. 1995. Are rainforest self-organized in a critical state. – J. Theor. Biol. 173: 31–40.

Solé, R. V. and Alonso, D. 1998. Random walks, fractals and the origin of rainforest diversity. – J. Complex Systems 1: 1–22.

Solé, R. V. and Goodwin, B. 2000. Signs of life: how complexity pervades biology. – Basic Books.

Solé, R. V. and Bascompte, J. 2006. Self-organization in complex ecosystems. – Princeton Univ. Press.

Solé, R. V. et al. 1999. Criticality and scaling in evolutionary ecology. – Trends Ecol. Evol. 14: 156–160.

Solé, R. V. et al. 2002. Self-organized instability in complex ecosystems. – Phil. Trans. R. Soc. B 357: 667–681.

Stanley, H. E. and Meakin, P. 1988. Multifractal phenomena in physics and chemistry. – Nature 335: 405–409.

Stevenson, J. R. 1996. An introduction to algal ecology in freshwater benthic habitats. – In: Stevenson, R. J. et al. (eds), Algal ecology: freshwater benthic ecosystems. Academic Press, pp. 3–30.

Stoll, P. and Prati, D. 2001. Intraspecific aggregation alters competitive interactions in experimental plant communities. – Ecology 82: 319–327.

Vadeboncoeur, Y. et al. 2001. Whole-lake fertilization effects on distribution of primary production between benthic and pelagic habitats. – Ecology 82: 1065–1077.

Vymazal, J. 1988. The use of periphyton communities for nutrient removal from polluted streams. – Hydrobiologia 166: 225–237.

Wagner, H. H. and Fortin, M.-J. 2005. Spatial analysis of landscapes concepts and statistics. – Ecology 86: 1975–1987.

Wetzel, R. G. 1983. Limnology. – Saunders.

Wiens, J. A. 1999. Ecological heterogeneity: an ontongeny of concepts and approaches. – In: Hutching, M. J. et al. (eds), The ecological consequences of environmental heterogeneity. Cambridge Univ. Press, pp. 9–31.

Zinck, R. D. and Grimm, V. 2009. Unifying wildfire models from ecology and statistical physics. – Am. Nat 174: E170–185.

Supplementary material (available online as Appendix O20423 at <www.oikosoffice.lu.se/appendix>). Appendix 1–2.