Multifractal diversity-area relationship at small scales in dune slack plant communities

Basil N. Yakimov, Beatris Bossuyt, Dmitry I. Iudin and David B. Gelashvily

B. N. Yakimov (damelfly@yandex.ru), D. I. Iudin and D. B. Gelashvily, Dept of Ecology, Faculty of Biology, Nizhni Novgorod State Univ., prosp. Gagarina 23, RU-603950 Nizhny Novgorod, Russia. – B. Bossuyt, Dept of Biology, Univ. of Ghent, Ledeganckstraat 35, BE-9000 Gent, Belgium.

The species-area relationship (SAR) is the core of spatial community ecology. This relationship has a distinguished reputation as one of the firmly established “laws” of community ecology (Rozenzweig 1995, Lawton 1999). The history of SAR investigation lasts for more than a century and is still going on. The most popular form of SAR, which was analytically derived by Arrhenius (1921, 1923) is the power-law:

\[ S = cA^z \]  

(1)

where \( S \) is species richness, \( A \) is area and \( c, z \) are constants.

Objects that can be described by a power law can often be considered as self-similar (Feder 1988, Schroeder 1991), and, in that case, the object itself is called fractal. A pattern is by definition self-similar if it does not vary with spatial scale (Hastings and Sugihara 1993). Harte et al. (1999) explicitly established this pattern for the SAR in ecological communities. Power-law SAR indicates a self-similar community spatial structure, allowing (1) treating the community itself as a fractal and (2) interpreting of the slope \( z \) as a fractal dimension. With spatial structure, we mean here the spatial pattern of characteristics of community composition or constitution, including species diversity. Such a “fractal” formulation of a classic power-law SAR appears as an evident consequence of the fractal paradigm in natural sciences that was formulated more than two decades ago (Mandelbrot 1982).

However, the SAR itself is a rather rough measure of community spatial structure, because it takes only the number of species occurring within a particular area, or the species richness, into account. This means that patterns of species abundance distribution, such as dominance or rarity, are completely ignored, although it is likely that this strongly affects community spatial structure. These patterns of species abundance distribution may be incorporated by the assessment of spatial distribution of species diversity, or, in other words, by transition from the analysis of SAR to the analysis of diversity-area relationship (DAR). An extension of SAR to DAR may have important applications, since a self-similar pattern of diversity implies that observed species abundance patterns can be extrapolated over different scale levels.

Fractal analysis of spatial distribution of separate species and their communities have come to ecology at the very end of the last century. Initially, the concept of fractals was applied to the description of animal home ranges (Loehle 1990, 1994, Gautestad and Mysterud 1994). Afterwards, fractal models were used for the study of plant distribution patterns in relation to area (Kunin 1998, Kunin et al. 2000, Witte and Torfs 2003, Halley et al. 2004), and finally for a fractal interpretation of SAR (Harte et al. 1999, 2001, Kinzig and Harte 2000, Lennon et al. 2002, Green et al. 2003, Sizling and Storch 2004). All steps of the application of fractal geometry in community ecology went along with considerable debate (He and Gaston 2000, Kunin et al. 2000, Maddux 2004, Ostling et al. 2003). The next logical step of the incorporation of fractal models into community ecology is an application of multifractal analysis to community spatial structure (Borda-de-Agua et al. 2002), which allows transition from conventional SAR to DAR.
DAR may be described by the generalization of a standard fractal analysis – multifractal analysis. The application of multifractal analysis to community characteristics was independently introduced by Borda-de-Agua et al. (2002) and Ludin and Gelashvily (2003). Multifractal analysis of community diversity is based on the investigation of scaling of species diversity components which are usually expressed as indices, among which the Shannon or the Simpson index. Species diversity measures are linked to each other via the Rényi’s generalized entropy function (Rényi 1970, Hill 1973). Previous works, dealing with multifractal analysis of community spatial structure, concentrated on obtaining the generalized Rényi dimensions’ spectrum (Borda-de-Agua et al. 2002, Zhang et al. 2006), but received spectra with obvious anomalies. Although theoretically, self-similar patterns of species diversity are assumed to be a general law (Borda-de-Agua et al. 2002), no study up to now has been able to provide clear evidence for this.

The use of Rényi dimensions’ spectrum has several limitations, among which the most prevalent is that it cannot be interpreted in operational terms but only describes the global behavior of a particular measure (Harte 2001). This substantially limits its utility for empirical studies. However, there exists an alternative for the Rényi spectrum to characterize a multifractal structure, known as the so-called multifractal spectrum or singularity spectrum (Falconer 1997). A multifractal spectrum allows an interpretation in terms of subsets of structures and their occupancies. In the context of the spatial structure of ecological communities, a multifractal spectrum can be interpreted in terms of subsets of species and their diversities.

In this study, we investigated the multifractal structure of dune slack plant communities within 14 nested plots situated at the Belgian and north French coast, at a scale level from several centimeters to meters. The existence of a power-law SAR for that scaling range was widely established (Arrhenius 1921, Green et al. 2003) and was indeed evidenced before for these particular plant communities (Bosuyt and Hermy 2004). We executed a complete multifractal analysis, using both Rényi spectrum and multifractal spectrum, and discussed the ecological implications of the results.

**Material and methods**

**Data collection**

Data were collected in four nature reserves situated in the dune landscape at the Belgian and north French coasts. In this landscape, dune slacks are formed by wind erosion. Once a dune slack has been formed, a primary succession process starts (Bossuyt et al. 2003). Fourteen dune slacks in the same successional stage were selected. When selecting the dune slack, we tried to keep community composition as similar as possible, and therefore, selection was based on the occurrence of some indicator species for a specific successional stage (e.g. Parnassia palustris, Epipactis palustris, Carex flacca, Euphrasia stricta, Prunella vulgaris) (Bossuyt et al. 2003). Within each of these slacks, a $2 \times 2$ m$^2$ nested plot was situated at random within a homogeneous vegetation in the centre of the slack (area $A_0 = 4$ m$^2$).

This nested plot was then subdivided into four plots of $1 \times 1$ m$^2$, (area $A_1 = 1$ m$^2$) which were each further divided into four plots of $50 \times 50$ cm$^2$ ($A_2 = 2500$ cm$^2$), and 16 plots of $25 \times 25$ cm$^2$ ($A_3 = 625$ cm$^2$). This resulted in a nested plot design with four levels, in which $A_i = A_{i-1}/4$ (Fig. 1). In each of the subplots, the percentage cover of all vascular plant species, including young plants and seedlings, was recorded.

**Brief overview of standard multifractal analysis**

Basic fractal analysis consists of calculation of a fractal dimension as a peculiar measure of a set density. The most popular algorithm for such calculation is box-counting. The set is covered by a grid of boxes of some size $\varepsilon$ and the number of occupied boxes $N(\varepsilon)$ is counted. Procedure is repeated for several values of box size $\varepsilon$ and fractal dimension is calculated as a slope of plot $\log(N)$ vs $\log(\varepsilon)$. Obviously, such a procedure cannot distinguish between homogenous and heterogeneous sets.

To study heterogeneous set new characteristics are introduced. For a given coverage of a set for all occupied boxes the number $n_i(\varepsilon)$ of points contained in the box are counted. These numbers are converted to relative abundances $p_i(\varepsilon)$ via division by the total number of points. On the basis of $[p_i]$ moments of distribution are defined as:

$$M_{q}(\varepsilon) = \sum_{i=1}^{N(\varepsilon)} p_i^q \propto \varepsilon^{d(q)}$$

where $q$ is called moment order. It varies from $-\infty$ to $\infty$ and defines the relative contribution to the sum of boxes with low (for negative $q$) or high (for positive $q$) abundances. The second proportionality in Eq. 2 determines scaling of moments.

![Fig. 1. Overview of the sampling design. For reasons of clarity, only one subdivision per plot was shown.](image-url)
Generalized Rényi dimensions are defined as follows (Hentschel and Procaccia 1983):

\[ D_q = \lim_{\varepsilon \to 0} \left( \frac{1}{q-1} \frac{\ln M_q}{\ln \varepsilon} \right) = \frac{\tau(q)}{q-1} \quad (3) \]

Rényi dimensions’ spectrum \( D_q \) is a non-increasing function of the moment order \( q \), which gives a full representation of multifractal object structure. Generalized dimensions, however, are not fractal dimension sensu stricto (Falconer 1997, Pesin 1997). That is why the multifractal spectrum function \( f(x) \) is used along with Rényi dimensions. Its derivation is achieved by a Legendre transformation of function \( \tau(q) \):

\[ \begin{align*}
\alpha(q) &= -\frac{d}{dq} \tau(q) \\
f(\alpha(q)) &= q\alpha(q) + \tau(q)
\end{align*} \quad (4) \]

Values of \( f(\alpha) \) are fractal dimensions of some homogenous fractal subsets of a multifractal.

**Application of multifractal analysis to community spatial structure**

The core of a multifractal analysis of a community spatial structure is a multiscale analysis of the distribution of a species abundance measure (Borda-de-Agua et al. 2002). We should register species abundances for all detected species abundance measure \( Borda-de-Agua et al. 2002 \). Structure is a multiscale analysis of the distribution of a community spatial structure.

Application of multifractal analysis to community spatial structure

The main condition to apply a multifractal analysis is a power-law scaling of moments (Eq. 6). Because power-law relations are easily convertible to linear relations via a logarithmic function, a verification of a power-law scaling can be reduced to a test of linearity. However, standard methods of regression analysis are not applicable in this case because regression significance testing implicitly assumes linearity. Moreover, there are no absolutely correct methods of statistical analysis on multiscale data (Borda-de-Agua et al. 2002, Halley et al. 2004), due to a lack of independence between different scales (large quadrates consist of small quadrates). Standard regression analysis may provide only a rough measure of the approximation quality by \( r^2 \). For these reasons, we applied the rather technical approach introduced by Berntson and Stall (1997). We fitted the relationship between \( \log(M_q) \) and \( \log(A) \) by a second-order polynomial and executed a test of significance for the quadratic term. Significance indicates substantial nonlinearity of the relationship, while the lack of significance means that there is no reason for rejecting the linear hypothesis which corresponds to power-law scaling.

Another issue is the estimation of variation in multifractal structure parameters, i.e. the construction of confidence intervals for spectra. We have 14 distinct independent plots. We estimated spectrum parameters \( (D_q, D, f(x)) \) for each of the plots separately and constructed a confidence interval via standard methods. Such a procedure implies that all plots belong to the same community.
Results

In the 14 nested plots, 77 species occurred. Species richness for the whole plot \( A_0 \) ranged between 15 and 30. The mean Jaccard similarity coefficient over the 14 nested plots was 0.38. When the similarity coefficient was calculated separately for each of the four nature reserves in the study area, we obtained values of 0.47 (two nested plots), 0.39 (average value over three nested plots), 0.40 (average value over six nested plots) and 0.38 (two nested plots). This indicates that the position of the plots had only a marginal impact on community composition.

Figure 2 shows the relationship between \( \log(M_q) \) and \( \log(A) \) for several values of order \( q \). We displayed one moment with negative order \( q \) \( (M_{-2}, \text{Fig. 2A}) \), one moment with positive order \( (M_2, \text{Fig. 2C}) \) and the zero-order moment \( (M_0, \text{Fig. 2B}) \). The zero-order moment is just the number of species, i.e. \( M_0 = S \), and the relation of \( M_0 \) with \( A \) corresponds hence with SAR. Similarly, \( M_2 \) represents the relation of the Simpson diversity index with area.

Moments with order \( q < 1 \) increased with area, while moments with order \( q > 1 \) decreased with area. The plots in Fig. 2 were satisfactorily approximated by linear function, which was indicated by the significance of the linear regression (in all cases \( p < 0.001 \)). Approximation quality (measured as \( r^2 \)) substantially decreased with \( q \). However, the linear fit could in all cases not be rejected, because of the lack of significance of quadratic term in the second-order polynomial fit (in all cases \( p^* > 0.05 \)).

The linear relationship between \( \log(M_q) \) and \( \log(A) \) reveals power-law scaling of moments. It indicates that our object (plant community diversity) had a multifractal structure in the considered range of scales from 25 cm to 2 m. We presented both forms of multifractal structure representation: Rényi generalized dimensions’ spectrum (Fig. 3) and multifractal spectrum function (Fig. 4). The solid line on these figures is the spectrum constructed for the whole community, analyzing all the plots together, and the confidence intervals indicate the variation of spectra derived from each of 14 \( 2 \times 2 \) m \( ^2 \) plots considered separately. As theoretically expected, the generalized Rényi dimensions’ spectrum was strictly decreasing. The multifractal spectrum function manifested however one anomaly: its right decreasing branch went to the negative quadrant. However, the abscissa axis is covered by the confidence interval for that branch so it is hard to judge on the importance of that anomaly.

Discussion

Multifractal analysis is a powerful tool for the description of complex objects (Falconer 1997, Harte 2001), developed in the field of statistical physics and applied nowadays in a wide range of sciences. In ecological research, the technique was used to characterize different environments (Kirkpatrick and Weishampel 2005, Montero 2005), to describe ecological time series such as dynamics of plankton biomass in the intertidal zone (Seuront et al. 1999, Seuront and Lagadeuc 2001) and to describe the spatial distribution of biomass and single species (Sole and Manrubia 1995, Appleby 1996, Seuront and Spilmont 2002). At the community level, multifractal analysis was proposed to characterize community structure in spatial (Borda-de-Agua et al. 2002) and nonspatial contexts (Iudin and Gelashvily 2003).
Up to now, we are aware of two studies on detailed multifractal analysis of community spatial structure. Borda-de-Agua et al. (2002) have performed a multifractal analysis of plots in the tropical rainforest tree layer in the range of scales from 0.04 to 50 ha. They derived generalized dimensions’ spectrum with obvious anomaly: values of $D_q$ began to increase in their spectrum for $q > 2$ whereas theory predicts the function $D_q(q)$ to be strictly non-increasing. Borda-de-Agua et al. (2002) were the pioneers to describe the methodology of multifractal analysis of community spatial structure, but they did not succeed entirely in an empirical verification of the introduced hypothesis. Zhang et al. (2006) applied the methodology proposed by Borda-de-Agua et al. (2002) to analyse the spatial structure of a mountain forest community with large spatial heterogeneity in abiotic conditions. They used a transect method with plots in the scale range from 10 m to 1 km. They obtained generalized Rényi dimensions’ spectra for three layers: trees, shrubs and herbs. However, these spectra contained a similar anomaly, as they were not strictly decreasing.

The previous studies dealt with DAR of forest communities and were executed in scale range from meters to hundreds of meters, while we investigated DAR of dune slack plant community, which only contains herbaceous species, in a much smaller scale range, from several centimeters to meters. We provided a quantitative application of multifractal analysis to that community. We found that power law could satisfactorily approximate the scaling of species distribution moments, so there are no reasons to reject the multifractal hypothesis. However, the values of the determination coefficients ($r^2$) of the relationship between $\log(M_q)$ and $\log(A)$ were very low, which may be attributed to the fact that we did not average species abundance values over all quadrates with the same area within one plot but used all possible points in our analysis. Although this resulted in a low approximation quality, it allowed for the first time deriving generalized Rényi dimensions’ spectrum without anomalies for diversity patterns in a plant community.

Our success in getting well-shaped spectra can be mainly attributed to two factors. First, we quantitatively (although not strictly statistically) tested the required assumption of power-law scaling of moments (using a curvilinearity test which was first introduced in the context of fractal analysis by Berntson and Stall (1997)). Previous studies used for this purpose only standard regression analysis which assumes a linear relationship. A significant linear regression does hence not indicate linearity of the relation. For example, Borda-de-Agua et al. (2002) found an approximately power-law scaling region (1–25 ha) of SAR at the Barro Colorado Island 50-ha plot on the basis of visual inspection of the derivative plot (their Fig. 2c). However, the lack of self-similarity in the whole range of scales within the 50-ha plot was shown for BCI and other tropical forest plots (Plotkin et al. 2000). It is likely that the anomaly of Borda-de-Agua’s spectrum is due to the application of multifractal analysis on a non-fractal object.

Secondly, we used no average values, neither for areas nor for plots, in the regression analysis, but incorporated all data points for all possible quadrats for slope estimation. Averaging resulted indeed with our data in general problems with spectra interpretation. The Rényi spectrum lost its nonincreasing property and the multifractal spectrum got characteristic ‘horns’ on its branches (plots not shown).

Generalized Rényi dimensions’ spectra have two major limitations: (1) generalized dimensions are not fractal dimensions sensu stricto (Harte 2001) and (2) the spectra can not be directly interpreted in ecological terms. As a solution, we propose making the next step in the application of multifractal analysis in community spatial structure and using a multifractal spectrum function (or simply multifractal spectrum), which is derived via a Legendre transformation (Eq. 3) of the function $\tau(q)$ and can be interpreted in ecological terms.

A multifractal object is a complex structured set, associated with a particular supporting measure. In the simplest geometrical case, the measure is a density of points. The set is heterogeneous, in the sense that at all scale levels it contains separate parts differing in values of the supporting measure. There are areas supporting large values of the measure and areas supporting small values. This heterogeneity is characterized by the so called Hölder exponent $\alpha$, or singularity index (Feder 1988): the higher
this index, the lower the supported measure. Multifractals can hence be considered as sets consisting of separate subsets with different Hölder exponents. These subsets are homogeneous and have fractal dimensions equal to \( f(\alpha) \). The fractal dimensions of the different subsets together represent the multifractal spectrum which provides hence a “portrait” of the multifractal object.

An ecological community can be considered as a heterogeneous object, at least in the sense of the spatial distribution of species abundances. It is possible to distinguish subsets of species with a similar relative abundance over all scale levels, such as subset of dominants, subdominants, rare species etc. Parameter \( \alpha \) characterizes the relative abundance of species in such subsets and constitutes the \( x \)-axis of the spectrum. The presence of points in the plot lying close to zero on the \( x \)-axis \( (\alpha) \) of the spectrum plot indicates the presence of strongly dominating species in the community (the lower the value of \( \alpha \), the stronger the dominance). The presence of points having a high value for \( \alpha \), in contrast, means that rare species occur in the community. The distance between the end-points of the spectrum can hence be interpreted as an inverse measure of evenness. The \( x \)-axis of the spectrum represents the fractal dimension of a subset, which can be interpreted as the amount of diversity in the corresponding subset of species. The height of the spectrum indicates hence the species diversity in the different subsets of species.

Concerning the observed spectrum for the analysed dune slack plant community (Fig. 4), we found a decreasing branch went into the negative area on the \( y \)-axis. Since the value of \( f \) is interpreted as the fractal dimension of species subset with a particular relative abundance negative values have no meaning. However, confidence intervals show that the accuracy of spectrum estimation in that area does not allow making unequivocal conclusions.

The obtained multifractal spectrum for small-scale spatial structure of the dune slack plant community (Fig. 4) has a left ascending branch laying close to the \( y \)-axis, i.e. the dominance in the community is rather high. That branch does not reach the \( x \)-axis, which means that the diversity in the subset of dominating species is not infinitesimal and there are several dominants. The right descending branch of the spectrum goes to the point \((1, 0)\). This means that there is a group of extremely rare species and that the species richness in that group is very small. The overall width of the spectrum is high indicating that evenness is very low. We also achieved an estimate of the variability of spectra parameters in the form of confidence intervals, providing opportunities for a strict quantitative comparison of spectra for different communities.

We believe that multifractal analysis is a powerful tool for community spatial structure analysis. Its utility was shown for forest communities at the scale range from meters to 1 km. In this study, we achieved a multifractal description of the small-scale spatial structure of a non-forest community. Future studies, empirically testing the patterns hypothesized by multifractal analysis in a wide range of organisms and scale levels are urgently needed to verify their generality for adequately describing the spatial structure of ecological communities.

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