From theoretical ecology to statistical physics and back: self-similar landscape metrics as a synthesis of ecological diversity and geometrical complexity

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Abstract

Biological diversity would apparently seem the most intuitive and easily studied of ecological concepts. The first and obvious way to study it simply consists in counting the number of species present at a given location. However, it has rapidly become clear that diversity measurements are a far more interesting and richer task than simple estimation of the number of species present. After the Second World War, several diversity indices have been proposed in order to quantify several aspects of biological diversity and their ecological implications. Since many theoretical foundations of biological diversity evolved at the cross-roads of theoretical ecology and statistical physics, in this paper I summarize the influences of statistical physics which mostly contributed to the understanding of biological diversity. Particularly, this review focuses on the observation that, despite the use of the same formalism, the ecological concept of diversity and the concept of geometrical complexity of strange attractors in statistical physics are based on very different theoretical assumptions. That is, ecologists do not simply rely on physical notation, but they generally re-interpret the theoretical foundation of statistical physics in an (ecological) meaningful way. © 2000 Elsevier Science B.V. All rights reserved.

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1. Rényi’s generalized entropy as a measure of biodiversity

Biological diversity or shorter (bio)diversity would apparently seem the most intuitive and easily studied of ecological concepts (Grassle et al., 1979). The first and obvious way to study it simply consists in counting the number of species present at a given location. However, since the concept of diversity can be related to numerous theories of community organization (Hill, 1973), it has rapidly become clear that diversity measurements are a far richer and more subtle task than simple estimation of the number of species present (Franc, 1998).

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After the Second World War, several quantitative diversity indices have been proposed (for a review see, e.g. Pielou, 1969; Margaruran, 1988; Rosenzweig, 1995). Imagine a community composed of \( N \) species where \( n_i \) is the number of individuals belonging to the \( i \)th species (\( i = 1, 2, \ldots, N \)), and let \( p_i \) denote the relative frequency of \( n_i \) (\( p_i = n_i / \sum_{j=1}^{N} n_j \)) such that \( 0 \leq p_i \leq 1 \), and \( \sum_{i=1}^{N} p_i = 1 \). The most widely used diversity indices in ecological literature, namely Shannon’s information theoretic entropy (Shannon, 1948) and Simpson’s index (Simpson, 1949), are both computed from the values of \( p_i \).

Ignoring the bias introduced by finite sample considerations, the information content or Shannon’s entropy is defined as:

\[
I = - \sum_{i=1}^{N} p_i \log p_i
\]

where \( p_i \log p_i = 0 \), for \( p_i = 0 \). For log base 2 the units of Shannon’s entropy are bits; for the natural log the units are nats, and for log base 10 the units are Hartleys (Finn, 1993).

The theoretical basis to interpret Shannon’s entropy as a measure of biodiversity relates to the connection between information theory and the entropy concept within classical statistical mechanics (Jaynes, 1957). Less technically, the information content (entropy) of a given community may be considered as a measure of uncertainty on prediction of relative abundance of species. It is trivial to show that the maximum value of Shannon’s entropy \( I_{\text{max}} = \log N \) is obtained in case of equiprobability, i.e. if \( p_i \) is the same for all \( i \)th species. In contrast, minimum entropy is obtained if there is a species having its probability equal to 1 (the probabilities of all the other species being null), which implies \( I_{\text{min}} = 0 \).

The first ecological application of Shannon’s entropy appeared in a paper of Mac Arthur (1955) to quantify trophic relationships among populations. Since then, it has rapidly become the most widely used measure of diversity and community structure in ecological literature (Margalef, 1958; Pielou, 1975).

While Shannon’s entropy has been widely used in ecological literature to characterize species diversity, it also provides the basis for entropy (diversity)-based landscape metrics (O’Neill et al., 1988; Riitters et al., 1995). Notice that, unlike the simple count of the number of species present, Shannon’s entropy is rather insensitive to the presence of rare species. For instance, if \( p_i > p_j, p_j \log p_j > p_i \log p_i \). This is a clarifying example on the conceptual disagreement among theoretical ecologists and field ecologists which considers rare species as a qualifying component of an ecosystem as far as biodiversity evaluation is concerned.

Conversely, the underlying (even though far from being obvious) assumption of Simpson’s work is that interactions between species are the primary source of biodiversity (see also Mac Arthur, 1955). In other words, the more interspecific interactions, the more diverse is the community (Franc, 1998).

Therefore, in ecological literature Simpson’s diversity index is generally defined as the complement to the total probability of interspecific interactions in the community:

\[
S = \sum_{i=1}^{N} p_i^2
\]

Notice that, not surprisingly, biodiversity as measured both by Shannon’s entropy or Simpson’s index is closely related to the variance of the distribution that statisticians mostly use to quantify disorder (e.g. Mukherjee and Ratnaparkhi, 1986; Franc, 1998), and, as a rule of the thumb, we might assume the more diverse is a given community, the greater is also its variance.

Following Rényi’s definition of a generalized entropy in statistical physics (1970), Hill (1973) proposed a unifying formulation for diversity measures which includes the three above mentioned indices, namely the total number of species, Shannon’s entropy, and Simpson’s index. For a distribution function characterized by its probabilities \( p_i = (p_1, p_2, \ldots, p_N) \), Rényi (1970) defined a generalized entropy of order \( \alpha \), such as:

\[
I_\alpha = \frac{1}{1-\alpha} \log \sum_{i=1}^{N} p_i^\alpha
\]

where \( \alpha \) is an arbitrary real number. Furthermore, Rényi proved that \( I_\alpha \) satisfies certain axioms which entitled it to be regarded as a measure of generalized entropy (Franc, 1998). Similarly,
Hill (1973) defined his generalized diversity index \( N_a \) as:

\[
N_a = \left( \sum_{i=1}^{N} p_i^a \right)^{1/a} \tag{4}
\]

Again, it is trivial to check that \( N_a = \exp I_a \). That is, \( N_0 = N \) (total number of species present), \( N_1 = \exp I \), and \( N_2 = 1/S \) (reciprocal of Simpson’s index). Therefore, according to Hill’s formulation, there is a continuum of possible diversity measures which differ only in their sensitivity to the presence of rare species. For instance, tuning the exponent \( a \) in Eq. (4) we can focus on different aspects of the partition of abundance among species (Hill, 1973; Franc, 1998).

From Eq. (4) it also follows that \( N \geq \exp I \geq 1/S \), where the equality holds for equiprobability (i.e. if \( p_i = p_j \) for all \( i \neq j \)). Shannon’s entropy represents therefore an intermediate way to consider the partition of abundance between species with respect both to the total number of species and to Simpson’s index.

2. Rényi’s generalized dimension as a measure of geometrical complexity

Mandelbrot (1982) developed fractal geometry as a tool to model much of the complexity apparent in natural objects and processes. Unlike more familiar Euclidean constructs, every attempt to split a fractal into smaller pieces results in the resolution of the same spatial pattern, no matter at which spatial scale the pattern is examined (Kenkel and Walker, 1996). This is because many natural objects are the result of iterative, diffusive processes which repeat themselves at different scales of observation (Johnson et al., 1995). Fractal objects and processes are therefore said to display scale-invariant or self-similar properties.

Scale-invariance manifests itself algebraically through power-law relationships. Imagine a set \( \Sigma \) consisting of a finite number of points \( n \) in a \( M \)-dimensional space. The set \( \Sigma \) is overlaid with a grid of \( M \)-dimensional square boxes of linear size \( \delta \). The number \( N \) of boxes of size \( \delta \) required to cover the set represents a \( \delta \)-cover of \( \Sigma \) (Hastings and Sugihara, 1993). After using different \( \delta \)-cov-
box-counting method. Notice that the box-counting method is based only on the metric properties of the attractor. Generally speaking, we may therefore think of the fractal dimension of an attractor as a measure of its geometrical complexity.

However, many natural fractals are generated by a large (or even infinite) number of processes operating at different scales. For such multifractal sets a single value of the fractal dimension is not enough to completely characterize their fractal properties (Stanley and Meakin, 1988). For instance, since the box-counting method has to do only with the geometrical structure of the attractor, regions of the attractor which contain many points contribute to the calculation of D with equal weights as regions which contain just few points (Scheuring and Riedi, 1994). We need therefore to extend the idea of fractal dimension (Hentschel and Procaccia, 1983; Halsey et al., 1986).

A first improvement of the box-counting method consists in transforming the number of points in each M-dimensional box to a probability method consists in transforming the number of points (Scheuring and Riedi, 1994). We need therefore to extend the idea of fractal dimension (Hentschel and Procaccia, 1983; Scheuring and Riedi, 1994). We need therefore to extend the idea of fractal dimension (Hentschel and Procaccia, 1983; Halsey et al., 1986).

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different dimensions (Kenkel and Walker, 1996). As shown in the previous paragraph, the equivalent in ecology is the allocation of individuals to species, where the equality $N = \exp I = 1/S$ holds in case of equiprobability. Similarly, from Eq. (7) it follows that the use of large positive values of $x$ accentuates the influence of the denser regions of the attractor (i.e. the influence of the boxes with the highest values of $p_i$) in the calculation of $D_x$. Conversely, for small values of $x$, the boxes with small values of $p_i$ will give the major contribution to $D_x$ (Scheuring and Riedi, 1994). The ecological equivalent to this property is the sensitivity of Hill’s generalized diversity index to the presence of rare species as a function of $x$.

As we can see, starting from Rényi’s formulation of a generalized entropy, similar indices have been independently developed both in ecological and physical literature in order to evaluate the biological diversity of a community and the strangeness of chaotic attractors, respectively. This analogy has been noted for the first time by Franc (1998). However, Franc did not mention a deep, even if subtle, conceptual difference between the ecological and the physical approach to Rényi’s generalized entropy. For instance, statistical physics assumes that fractal sets are composed by points of the same kind, while biotic communities generally contain many different kinds of points (Scheuring and Riedi, 1994). Therefore, despite the use of the same formalism, in statistical physics fractal sets are exclusively characterized on the basis of their metric/information theoretical properties.

3. The synthesis: self-similar landscape metrics

The term landscape ecology appeared for the first time at the end of the ‘30 (Forman, 1995a). However, most of its theoretical foundation was developed in the last twenty years, as the influence of global change on ecological research became more prominent.

Landscape ecology explicitly recognizes that the spatial arrangement of ecosystems, habitats, or communities has ecological implications and tries to understand the interactions between the structure of large spatially-heterogeneous areas and the ecological processes of landscape mosaics (for a review see, e.g. Forman and Godron, 1986; Forman, 1995b, and references therein). Since origin and ecological consequences of landscape patterns and processes are regulated by dynamics occurring simultaneously at several spatial (and temporal) scales, recognizing the spatial context of landscape ecology involves increasing attention to the scale of observation (Turner, 1990). For instance, due to the nested structure of terrestrial landscapes, patterns and processes important at one scale are generally less important and predictive at different scales. Therefore, before developing an ecological theory which explicitly takes into account the influence of landscape mosaics, improved analytical methods are needed to identify and quantify landscape mosaics capturing both the geometrical aspects and the ecological implications of spatially-heterogeneous landscapes (Turner, 1990; Milne, 1992). In this sense, since fractal and multifractal analysis explicitly relates the loss of information to changing scales of resolution, Rényi’s generalized dimension might be considered as the ideal tool to model much of the complexity apparent in landscape mosaics and to determine the appropriate self-similar range of scales of ecological process-pattern interactions.

Morse et al. (1985) emphasize that if animals perceive their (fractal) habitat in proportion to body length, there will be more apparent habitat space for smaller animals than for larger ones. Working with arthropods that live on plants, they found that predictions about the number of individuals based on body mass and metabolic rate consistently underestimated actual field values for the smaller species. Predictions were substantially improved when the fractal dimension of the habitat was taken into account. However, since in the field a three-dimensional cube-counting procedure for estimating the fractal dimension of plants (habitats) obviously cannot be considered, Morse et al. (1985) used photographs to determine the two-dimensional box dimension $(1 < D < 2)$ of plant outlines. Following Mandelbrot (1982), they estimated (rather broad) heuristic lower $(D + 1)$ and upper $(2D)$ limits of the habitat fractal dimension under the assumption that the photo-
A randomly-placed orthogonal plane. Despite the weak theoretical foundation of the proposed extrapolation procedure (see Kenkel and Walker (1996) and references therein), the empirical validity of this procedure has been successively confirmed by other researchers (Shorrocks et al., 1991; Gunnarsson, 1992; Jeffries, 1993).

Virkkala (1993) used a multiresolution analysis technique based on hierarchical grouping of adjacent 10 x 10 km2 to determine the box dimension of passerine bird distributions in Finland. Noting that the species ranges of short-distance migrants were associated with the largest box dimension values, He suggested that differences in the ranges of migratory groups reflect their ability to survive the severe climatic conditions of Finland. Successively, Gautestad and Mysterud (1994) proposed a correction to Virkkala’s approach. They also noted that the dilution effect induced by the coarse resolution of most species distribution maps can severely bias their fractal dimension estimates.

Loehle and Wein (1994) argue that since landscapes are not necessarily self-similar across many scales, scale-specific analyses are required to fully characterize multiresolution vegetation patterns. They estimated the information dimension of a landscape using an innovative transformation of raster data to probability space that incorporates a ‘degree of similarity’ between vegetation classes (Johnson et al., 1995). Starting with a raster vegetation map in a portion of the Hatchie River watershed in western Tennessee, the transformation is accomplished by obtaining principal component scores (based on vegetation composition) for each pixel. These component scores were then transformed to probability space (0 ≤ p ≤ 1 for i = 1,..., N (δ) pixels) such that for pixels with the mean ordination value p_i = 0, and all non-zero p_i values are a measure of the deviation from the mean. With nonvegetated areas assigned the mean ordination value of zero, the information dimension was then estimated between discrete measurement scales as:

\[ \sigma = \frac{\sum_{i=1}^{N(\delta)} p_i \log p_i - \sum_{i=1}^{N(\gamma)} p_i \log p_i}{\log(1/\delta) - \log(1/\gamma)} \]  

(8)

Where N(\delta) and N(\gamma) are the number of pixels at each measurement scale such that \( \delta < \gamma \).

Results show that at the finest scale of resolution the vegetation map exhibit high diversity (\( \sigma = 2.654 \)) while the larger measurement scales reveal lower diversity that corresponds to greater fragmentation (\( \sigma = 1.344 \)). For comparison, a binary map was created by assigning a value of 1 to vegetated pixels and 0 to nonvegetated pixels. The resulting information dimension values for the binary map fall just above 1.8 at all scales revealing statistical self-similarity over all measurement scales and indicating that vegetated vs. nonvegetated areas are fragmented in a similar way at all scales (Loehle and Wein, 1994).

In another application of Shannon’s entropy for assessing self-similar landscape properties, Costanza and Maxwell (1994) measured what they call spatial auto-predictability (\( P_a \)) and cross-predictability (\( P_c \)) of land use maps at different spatial resolutions. \( P_a \) is the ability to predict the state of a pixel in a scene given knowledge of the state of adjacent pixels in that scene, and is conceptually similar to a measure of contagion (O’Neill et al., 1988), while \( P_c \) is the ability to predict the state of a pixel in a scene given knowledge of the state of corresponding pixels in other scenes. Following Colwell (1974) and Turner et al. (1989), predictability is related to conditional uncertainty, which is in turn measured as entropy in the form of Eq. (1) (Costanza and Maxwell, 1994; Johnson, et al. 1995).

Both indices of spatial predictability were applied to digitized land use maps from the Kissimmee/Everglades Basin, Florida and the state of Maryland over a range of five different measurement scales. Decreasing the resolution of the land use maps was obtained by aggregating in each step a square of four pixels into a new coarser pixel and assigning the land use category of the original northwest pixel to the new aggregated pixel.

When the log of spatial predictability was plotted against the log of resolution (measured as the number of pixels per square kilometer) an increasing linear relation was observed for \( P_a \), while a decreasing linear relation was observed for \( P_c \). The authors argued that these linear relations
may justify the calculation of a fractal-like ‘predictability dimension’ \( D_p \) from the slope of the best-fitting line of the double-log plot. However, Johnson et al. (1995) noted that the theoretical foundation suggested by Costanza and Maxwell (1994) for extending the observed double-log linear scaling to a fractal dimension is incorrect in geometrical terms and offered a correction.

Pesin and Tempelman (1995) extended the use of informational characteristics in multiscale analysis to the study of the dimension of self-similar stochastic processes. They defined a ‘stochastic similarity dimension’ \( D = D_p + D_c \) where \( D_c \) is the component of deterministic origin and \( D_p \) is the component of stochastic origin due to the random nature of the analyzed spatial process. A detailed description of their model can be found in Johnson et al. (1995).

Milne (1992) introduced a method to estimate the co-occurrence of fractally distributed species and resources over the landscape. Imagine a square raster map composed of \( m \times m \) pixels representing the overlapping fractal distributions of \( S \) different states (species or resources) over the landscape. As usual, if the map is overlaid with a grid of square boxes of linear size \( \delta \), the number \( N \) of boxes of size \( \delta \) required to cover the \( i \)th of the \( S \) states scales as \( N(\delta) = k\delta^{-D_i} \) (see Eq. (5)) where \( k \) is a constant. Consequently, the proportion of total grid cells occupied by the \( i \)th state varies as:

\[
\Pi_i(\delta) = \frac{k_i\delta^{-D_i}}{m(\delta)^2}
\]  

(9)

where \( D_i \) is the box dimension of the \( i \)th state and \( (m/\delta)^2 \) is the number of cells of size \( \delta^2 \) over the entire raster map. It follows that, if all states are characterized by independent fractal distributions, the co-occurrence of \( S \) states over the landscape (i.e. the proportion of the landscape simultaneously occupied by \( S \) different states) can be derived from the following neutral model:

\[
\Pi_S(\delta) = \prod_{i=1}^{S} \frac{k_i\delta^{-D_i}}{(m/\delta)^2}
\]  

(10)

The neutral model of Eq. (10) can be further extended to the co-occurrence of fractally distributed states whose distributions are contingent on each other or on a limiting resource. Such a conditional neutral model is defined as (Milne 1992):

\[
\Pi_{Sj}(\delta) = \prod_{i=1}^{S} \frac{k_i\delta^{-D_i}}{(m/\delta)^2} \min(k_i\delta^{-D_i})
\]  

(11)

In Eq. (11) the proportion of grid cells occupied by the \( j \)th state is measured only in grid cells that are in turn occupied by the \( i \)th state whose coverage of the landscape at scale \( \delta \) is less than any other of the \( S \) states. The constrained distributions of the \( j \)th states are described by \( k_{ij}\delta^{-D_{ij}} \) where the constant \( k_j \) and the box dimension \( D_j \) are contingent on the underlying distribution \( \min(k_i\delta^{-D_i}) \).

As far as I know, Milne (1991) was also the first to propose a multifractal model to quantify the self-similar geometrical complexity of landscapes. Following Voss (1988), he introduced a probability–density function \( \Pi(n, \delta) \) which gives the probability of finding \( n \) pixels of a given land-cover class in a moving window of length \( \delta \). The multifractal spectrum \( D_n \) of the analyzed distribution can then be calculated from \( \Pi(n, \delta) \).

Milne (1991) estimated the probability density function \( \Pi(n, \delta) \) of a grassland from the Sevilleta National Wildlife Refuge, New Mexico, to quantify its self-similar spatial complexity. Successively, studying herbivore strategies as a function of landscape geometry and body size of herbivores, Milne et al. (1992) emphasized that the fractal moments of the probability-density distributions of simulated landscapes and foraging success are strongly correlated.

Solé et al. (1993) calculated the multifractal spectrum of gaps occurring on a rain forest and compared it with the spectrum of a simple artificial model describing the dynamics of gap formations. They concluded that, under certain conditions, the actual and the simulated multifractal spectra are in good agreement with each other.

More recently, Scheuring and Riedi (1994) further extended the application of multifractals for analyzing landscapes that consist of many different point sets, such as soil moisture, disturbances, vegetation cover, etc. Let us assume \( p_i \), \( l_i \), \( l_{i1}, \ldots, l_{im} \) is the proportion of type \( j \) points in the \( i \)th
cell, provided that at least one point from each of
the sets $l_1, \ldots, l_m$ also occurs in the same cell, Eq.
(7) can be expressed as:

$$D_a(l_j|l_1, \ldots, l_m) = \frac{1}{a - 1} \lim_{\delta \to 0} \frac{\log \sum_{i=1}^{N(\delta, l_1, \ldots, l_m)} (p_i(l_j|l_1, \ldots, l_m))^a}{\log \delta}$$

(12)

A computer-simulated example demonstrates
the use of statistical functions and illustrates its
applicability in vegetation science. The authors
used an artificial computer-generated pattern to
simulate two different spatial distributions of two
competing hypothetical species and computed
their multifractal moments. Their results show
that while the independent multifractal moments
based on Eq. (7) do not differ significantly within
each species, the conditional multifractal moments
based on Eq. (12) indicated much greater differ-
ences in their geometrical structure. This simple
example suggests that estimates of conditional
multifractal dimensions may provide a tool for
assessing the dependence of the pattern of one
species or resource on the patterns of other spe-
cies or resources.

However, despite the vast variety of fractal and
multifractal applications in landscape ecology,
most of these authors generally use the terms
‘complexity’ and ‘diversity’ as synonymous (e.g.
Loehle and Wein, 1994 p. 314, Scheuring and
Firstly because, unlike in physical applications of
multifractal analysis, terrestrial landscapes generally
include multiple land cover types, and, sec-
ondly because in ecological literature the concept
of diversity is deeply associated to Rényi’s work
(e.g. Hill, 1973). For these reasons, they don’t
explicitly realize that associating the concept of
diversity to Rényi’s generalized dimension is not
only an elegant answer to an emergent ecological
question, but also a major conceptual difference
with regard to statistical physics which roots his
theoretical foundation in Hill’s work.

As a conclusion, in the last thirty years most
conceptual developments regarding biological di-
versity evolved at the cross-roads of theoretical
ecology and statistical physics (Franc, 1998). On
this basis, I feel that further studies of multifractal
geometry might feed a deeper understanding of
new aspects of biological diversity and of its
spatial implications.

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