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# Estimating Biodiversity and the Fractal Nature of Ecosystems

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**Abstract:** The problem of biodiversity impairment not only poses a global threat to the planet's biosphere and causes global health issues, it is also a cumbersome pièce de résistance for mathematical modeling. Already the definition of biodiversity requires knowledge of the hierarchical structure of an ecological environment and taxonomic complexity of life forms in all of their manifestations. Not only the enumeration of easily recognized, large vertebrate species, but an estimation of all living species present in a given area, forms the ultimate challenge for biodiversity estimation. This is an important goal for enabling a scientifically sound approximation of biodiversity impairment. In this paper, the analogy of the fractal geometry of nature and the fractal appearance of ecosystems is followed, in order to define a constitutive approach for estimating the local and global biodiversity of an ecosystem. Moreover, following the rationale of percolation theory and Mandelbrot's (1983) definition of the bounds of a critical fractal dimension in a hierarchically stratified system, the notions of critical biodiversity and biodiversity resilience strength (BRS) are proposed. It is concluded that in order to understand the dynamics of biodiversity change in a stressed, stratified environment such as the global biosphere, not only the stratification into trophic levels, but also short and long distance migration effects have to be considered.

**Keywords:** Biodiversity, Biodiversity Resilience Strength, Fractal Dimension, Similarity and Mass Dimension, Uniformity Index, Percolation Probability

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## 1. Introduction

The global decline of biodiversity has been assigned by the UN as one of the major challenges for human well-being in the new millennium [1, 2]. Estimating the biodiversity at a local scale, however, not only has been shown to be tedious because of the variety of assessment methods for animal abundance [3], or because of differences in nomenclature and determination of life forms, or in unacquainted backyards of living organization [4], but also because of the inherent complexity of population dynamics in ecosystems with multiple trophic levels and species [5].

In this paper, we start with a review of current biodiversity definitions (2. Theoretical Background). The dynamics of biodiversity change, in theory, can be derived from a matrix representation of local species abundances (following Fisher's formula) [6]. In order to incorporate dynamic, multiple species interactions into a so-called Biodiversity Tensor Equation (BTE), however, knowledge of the time-derivatives of biodiversity (change), both locally and globally, is lacking.

Moreover, the applicability of the dynamic equations is hampered by the problem of perturbations that aren't strictly local, because also long distance interactions following migration of species may occur.

Instead of a mean field approach, therefore, an approach is presented for incorporating the fractal, spatial structure of ecosystems, in analogy with the structural and scaling analysis of multifractal systems [7] (3. Modeling the Fractal Nature of Ecosystems). An important concept derived from percolation theory, the critical (percolation) probability is also used to characterize the critical dimensionality of a hierarchical cluster [8], which to our opinion characterizes the hierarchical nature of ecosystems with multiple trophic levels. This percolation notion, moreover, may become helpful to understand the notion of biodiversity resilience strength (4. Estimating the Biodiversity Dynamics in an Ecological Framework). In addition to the fractal approach, in analogy with Turing's use of Fibonacci series for describing plant phyllotaxis [9], a timeless, stepping stone approach for predicting biodiversity changes is also discussed.

## 2. Theoretical Background: Definitions of Biodiversity

### 2.1. Relative (Mean) Species Abundance

The earliest notions of a quantitative estimate of biodiversity resulted from statistical considerations on the abundance of species in a biological environment. In the *geometric series model* of Motomura [10, 11], the (relative) species level of abundance is a sequential, constant proportion of the total number of individuals in the community. This is in fact a simplification of Fisher's [6] *Log series* model, represented by the formula:

$$S = \alpha \ln\left(1 + \frac{N}{\alpha}\right)$$

with  $S$  = the number of species in the sampled community,  $N$  = number of individuals sampled and  $\alpha$  = a constant derived from the sample data set.

From this the number of species at a certain abundance is derived:

$$S_n = \frac{\alpha \cdot x^n}{n}$$

with  $S_n$  = the number of species with abundance  $n$  and  $x$  = positive constant ( $0 < x < 1$ ) derived from data set and generally approaching value:= 1. The parameter  $\alpha$  is called Fisher's dimensionless  $\alpha$  and is used as a measure of biodiversity (see below).

Alternatively, Preston [12] postulated that species abundances – when binned logarithmically in a so-called Preston plot – follow a Normal (Gaussian) distribution, partly as a result of the *Central Limit Theorem*. This resulted in a *Log normal distribution* meaning that the abundance distribution is lognormal, or  $n = n_0 e^{-(aR)^2}$  and, hence  $N = \frac{n_0 \sqrt{\pi}}{a}$

In this formula  $N$  represents the estimate of the total number of species (derived from the area under curve);  $n_0$  is the number of species in the modal bin (peak value), and  $n$  = the number of species in  $R$  bins distant from the modal bin,  $a$  = constant derived from the data set.

### 2.2. Biodiversity of Communities as Function of Biomass

In a more dynamical approach, Vandermeer and Lin [13] proposed to estimate biodiversity as function of prey biomass and functional response of predators, with biomass for  $i$ -th competitor resp. prey

$$\dot{X}_i = r_i X_i \left(1 - X_i - \sum_{j \neq i} \alpha X_j\right) - X_i \sum_j a_j P_j \Theta_j$$

where  $r_i$  is the intrinsic increase rate for species  $i$ ,  $a_j$  is the predation rate of species  $j$  on  $i$ , etc. The predator biomass of

species  $k$  is given by the formula:  $\dot{P}_k = a_k P_k X_i \Theta_i - m_k P_k$  with  $m_k$  the mortality rate of predator  $k$ , and  $\Theta_i = \frac{1}{(1 + b_i X_i)}$  the functional response of the  $i$ -th predator on  $X_i$ .

However, an important caveat has to be made, since interactions considered between competitors and predators occur at one or two trophic levels, at most!

### 2.3. Biodiversity Representation as Matrix of (Local) Abundances

When abundance data of (all) known species are available, they can be represented in a  $n \times n$  symmetric matrix, (1) provided  $n$  = the (maximum) abundance, and (2) that abundances can be measured accurately. Based on Fisher's formula (see 2.1) for  $S_n(i, j)$ , the  $i$ -th entry of the  $i$ -th row can be defined as  $\alpha \cdot x^i / i$

This may seem an interesting result from the viewpoint of matrix calculus, namely that when  $A$  represents the Biodiversity matrix with only positive, non-zero values on the diagonal, then:

$$\det A = \prod_i \frac{\alpha \cdot x^i}{i} \neq 0$$

represents a measure of Local Biodiversity.

However, it is an almost impossible task to estimate all species abundances in an ecosystem without causing interference, especially when also observations at different trophic levels have to be made so that visualization with remote sensing is not applicable.

Further applications of matrix calculations devoted to the biodiversity problem may be found in analogy with similar fields of research [14]. An intuitive notion of the “(affine) matrix subspace intersecting the cone of positive definite matrices” [15]<sup>1</sup> may be found in analogy with “finding the loci of the points in  $\mathfrak{R}^3$  satisfying the ‘general second-degree equation’ (for which no simple method exists for simplifying equations of degree greater than two)”. Solutions of these cone intersections may be represented by convolution surfaces of paraboloids, hyperboloids, ellipsoids. An important question is what can we might learn from a geometric representation of the biodiversity paradigm?

In the next section we will explore the potential benefits of a fractal approach of the physical phenomena in our planet. In the following section (in 4), we will investigate how biodiversity changes may fit into that fractal approach.

(1) For instance Parrilo and Jadbabaic [15] suggested that: “the problem of checking if a polynomial can be decomposed as a sum of squares is equivalent to verifying whether a certain affine matrix subspace intersects the cone of positive definite matrices, and hence an SDP feasibility problem.”

(Parrilo and Jadbabaic, p. 291). (\*SDP= semidefinite programming). Definition: A matrix  $A$  in  $\mathfrak{R}_{\text{sym}}^{n \times n}$  is positive definite if (I)  $A$  is symmetric and (II)  $X^* A X > 0$  for every non-zero  $X$  in  $\mathfrak{R}_n$  (note that  $X^* A X$  is a real number – a one-by-one matrix; alternatively, it is the value of a quadratic form at the point  $X^* = (x_1, x_2, \dots, x_n)$ ; so (II) makes sense. Hence, a matrix  $A$  is positive definite if (and only if) all of its eigenvalues are positive real numbers [16].

### 3. Modeling the Fractal Nature of Ecosystems

#### 3.1. Topological and Fractal Dimensions of Nature (theory)

The concept and methods of modeling the fractal geometry of nature date back to the foundational work of Benoit Mandelbrot [8]. As exemplified in Figures 1 and 2, the fractal nature of many biological (Figure 2) and geological objects can be described using the so-called Mandelbrot set (Figure 1).

Mandelbrot embarks on his journey into the fractal geometry of nature with three so-called classical fractals, e.g. with the question of the length of the Coast of Britain<sup>2</sup>. It appears that the observed total length depends on the scale of some prescribed length  $\varepsilon$  (called the yardstick length by Mandelbrot). Namely, with  $\varepsilon$  becoming increasingly smaller, the total length  $L(\varepsilon)$  tends to increase without limit. Mandelbrot acknowledges for the formula (following below) to the posthumously discovered work of the British mathematician Lewis Fry Richardson (1881-1953). Richardson empirically found a relation between the logarithm of the length of the side of equal-sided polygons (e.g. squares) and the logarithm of the total length of some coast lines and frontiers between different countries<sup>3</sup>.

For  $F$  the number of fragments of chosen length  $\varepsilon$ , the total length adds up to the length

$$L(\varepsilon) \approx F \varepsilon^{1-D} \quad [8]$$

with  $D$  ‘some’ exponent, which according to Richardson, had “no particular significance”, but appears to be the *fractal dimension*<sup>4</sup>. Mandelbrot compares Richardson’s formula with the following empirical formula for the triadic Koch curve [20] - intuitively it is obtained by progressively breaking up line segments and inserting a triangle at the breaking points -, where  $D$  appears to satisfy the equation<sup>5</sup>:

$$3^{D-1} = 4/3 \quad \text{which is the case when } D = \log 4 / \log 3 \quad [8]$$

For fractal objects, it is more convenient to speak about the *similarity dimension*<sup>7</sup>, where the similarity of each part to the

whole is deduced by the ratios:

$$r(N) = 1/b = 1/N \quad (\text{for a line divided in } N=b \text{ parts})$$

$$r(N) = 1/b = 1/N^2 \quad (\text{for a plane divided in rectangles})$$

$$r(N) = 1/b = 1/N^{1/D} \quad (\text{in general}), \text{ which can also be}$$

formulated as

$$\log r(N) = \log 1/N^{1/D} = -(\log N)/D \quad [8].$$

An alternative expression for this *similarity dimension* follows:

$$Nr^D = 1 \quad \text{which is equivalent to } D = \log N / \log 1/r^8$$

However, when self-similarity is not absolute, i.e. where unequal parts of  $r_i$  are allowed (ordered with increasing length  $r_m$ ), then the following important extrapolation results:

$$\sum_m r_m^D = 1 \quad [8]^9.$$

To explain the formula for  $D$  above, consider the *topological dimension* ( $d$ ) ( $D_T$  in the notation of Mandelbrot) of for instance a smooth curve of length  $l$ . It can be approximated by a polygonal of  $N(l)$  line segments ( $N$  representing the number of segments of length  $l$ ) which in the limit approaching zero, is given by the formula:

$$d = -\lim_{l \rightarrow 0} \frac{\ln N(l)}{\ln l} = 1 \quad [21].$$

Consider that in the above equation  $\ln N(l) / \ln l$  the zero-approaching limit for  $l$  tends to the indefinite ratio  $(\infty / -\infty)$ , which, using the method of G. de l’Hôpital (1661-1704), equals unity. In analogy, the *fractal dimension* of a set can be defined, using the box counting method, or packing or Tricot dimension [22]:

$$N(l) \approx l^{-\Delta(E)} \quad \text{with } \Delta(E) = -\lim_{l \rightarrow 0} \frac{\ln N(l)}{\ln l} \quad [21]$$

which coincides with the *topological dimension*, whenever the set  $E$  is regular. Moreover, if there exist a real  $D$  and a finite positive measure  $\mu$  (like the mass density), such that for all  $x \in E$ , with  $B_r(x)$  being the ball of radius  $r$  centered at  $x$ , the following theorem is used:

$$\frac{\log \mu[B_r(x)]}{\log r} \rightarrow D \quad \text{then } D = \dim E,$$

where  $D$  is called the *mass dimension*. If the convergence is uniform on  $E$ , then  $D = \dim E = \Delta(E)$  [21]. According to Marcelli [21], p. 11, “Mandelbrot has popularized the Hausdorff-Besicovitch dimension or mass dimension, since the measure (by which physical objects are measured) is very often a mass,  $\dim E$ , which turns out to be one of the most understandable dimensions for the majority of physics

(2) BB Mandelbrot [17] (*vide* Mandelbrot, 1983).

(3) BB Mandelbrot (1983), p. 33.

(4) In the work of Mandelbrot (1983) a formal distinction is introduced between the *topological dimension*  $D_T$  of a set, which is always an integer, and the *fractal dimension*  $D$ , which in fact is the dimension as formulated by Hausdorff [18] and put in final form by Besicovitch [19] (*vide* Mandelbrot 1983, p. 15). In case of the well-known Euclidean spaces, which are called dimensionally concordant sets, it appears that  $D_T = D$ . Then, according to Mandelbrot, “a fractal is by definition a set for which the Hausdorff Besicovitch dimension strictly exceeds the topological dimension.” (Mandelbrot, [8], p. 15).

(5) BB Mandelbrot (1983), p. 36.

(6) When inserting  $D = \log 4 / \log 3$  into Richardson’s formula (called the ‘coastline measure’ by Mandelbrot, p. 44), we obtain:

$$3^{(\log 4 / \log 3)^{-1}} = 3^{(\log 4 - \log 3) / \log 3} = 3^{\log 4 / \log 3} = 3^{\log_3 4} = 4 / 3$$

(7) For Mandelbrot (*ibidem*, p. 37) in most cases - and according to many mathematicians - this similarity dimension equals the Hausdorff dimension (see footnote <sup>3</sup> and also Marcelli, 2019), and, ‘in their context’ there is ‘no harm in thinking of the fractal dimension as being synonymous with similarity dimension’.

(8) BB Mandelbrot (*ibidem*), p. 37.

(9) BB Mandelbrot (*ibidem*), p. 57.

problems.”

Another important result of a fractal geometry of natural objects results from the notion of defining the critical percolation threshold of a network. According to Mandelbrot [8] the ‘percolation’ notion goes back to the work of Daniel Bernoulli (1700-1782), as for instance introduced by Shante and Kirkpatrick [23]. In the example of a Bernoulli lattice, e.g. made of sticks consisting of insulating vinyl or of conducting copper, it is easily imagined that a sufficient connectivity of conducting copper sticks in the lattice results in electric conductance throughout the entire network, called percolation of the network<sup>10</sup>. The ecological analogue of this percolation threshold, also called critical (percolation) probability ( $p_{crit}$ ) in terms of the biodiversity is discussed below (see 3.2 and 4.4). Earlier, the importance of the percolation notion was also recognized in immune networks [24, 25]<sup>11</sup> and, in ecology, in the role of habitat fragmentation [26].

### 3.2. Applying the Fractal Dimension to Ecosystems

We may wonder how the multiple interactions between species, and within species too, of an ecosystem could be described using abstract, mathematical tools such as fractals. However, according to Mandelbrot [8], fractals not only are useful to describe geometrical patterns in the geology and morphology of our planet, or the branching patterns of trees and river beds, or the anatomical folding of our brains and the ramifications of the lung bronchioles and even smaller structures, but also the spread of galaxies and galactic lacunae<sup>12</sup>. Intuitively, the distribution of niches occupied by biological species in an ecosystem, shows similarities with the abstract notion of Cantor ‘dust’, used by Mandelbrot [8] to describe any physical system revealing burst and gaps, also known as noise<sup>13</sup>. According to Mandelbrot, from a topological viewpoint all Cantor sets can be defined as sets of dimension  $D_T = 0$ , because “any point in the set is by definition cut from the other points, without anything having to be removed to cut it”<sup>14</sup>. Alternatively, the use of Peano curves [27]<sup>15</sup> – i.e. a variant of the Koch curves where points of self-contact are allowed – results in plane-filling curves, for which  $D$  approaches  $D_T = 2$ <sup>16</sup>. For the fractal dimension, one may either adhere to the notion of similarity dimension or to the notion of mass dimension (see 3.1).

(10) BB Mandelbrot (*ibidem*), p. 126, 216 ff.

(11) W Allaerts [25], p. 168.

(12) See modeling of galaxies and galactic lacunarity in Mandelbrot (*ibidem*), pp. 288-318.

(13) See BB Mandelbrot (*ibidem*), p. 74-82: Mandelbrot cautions for a lot of reserve among physicists (and others) against making reference to the ‘monstrous’, i.e. mathematically uncanny objects described by Cantor (but also to the Koch and Peano curves), even so that he had to “erase every mention of Cantor” in his work on Cantor dusts (p. 79). Historically, it was noted that Georg F.L.P. Cantor 1845-1918) not only was an outstanding mathematician, creator of Set theory and many others, but also that he met with harsh criticism and opposition, during his life and long after his death.

(14) BB Mandelbrot (*ibidem*), p. 78.

(15) G Peano (1890).

(16) BB Mandelbrot (*ibidem*), p. 58-73.

As to the notion of percolation of a fractal cluster, the critical threshold for percolation defines whether a network of clusters is coherent or whether it falls apart in non-connected clusters<sup>(10)</sup>. An ecological application of percolation theory was found in the effect of habitat fragmentation (in a neotropical rain forest) on the persistence of a population of army ants (*Eciton burchelli*) [26]. Using random-walk modeling, these authors found that a critical value of 0.4072 (or 40,72% of the patches being removed), resulted in extinction of the ant populations. So, even in huge reserves, habitat fragmentation may result in extinction of certain keystone species.

In order to call a structure a fractal, it is mandatory that some rule of self-similarity should apply. Analogous to Marcelli’s definition of mass dimension, we may define the fractal uniformity of an ecosystem in terms of the distance  $l_{IN}$  between neighbors (or couples) of the same species and the distance  $l_{NIN}$  to the nearest non-identical neighbor (predator or competing species):

$$U \propto \frac{\ln l_{NIN}}{\ln l_{IN}}$$

Biodiversity, however, is inversely related to this uniformity index  $U$ . From wildlife observation it follows that high biodiversity indices or so-called biodiversity hot spots<sup>17</sup> are often found in remote areas, at geological ridges (like mountain ranges) or in ecosystems with a maximum number of ecological ‘niches’ within short range, characterized by various physical parameters (like temperature, humidity, altitude above sea level, tree size and altitude above the ground, soil composition, presence of caves, etcetera, e.g. in tropical rain forests). The impact of these cumulative effects results in an ecological phase space, identifiable with a set of dimensions with fractal nature.

Consider the ecological niche of a species, basically, the niche habitat - being the physical space in which a species may live and find shelter for reproduction (i.e. in contrast with the behavioral niche) - could be de-composed in a number of foraging-sheltering dipoles  $fs_{i \rightarrow I}$  (Figure 3), where  $i$  is an index (positive integer number) reflecting the trophic level of the species. The distances  $\hat{l}_{iN}(t)$  and  $\hat{l}_{NIN}(t)$  have to be considered as expected mean values, but are not necessarily the metric distance between two sites: they may also reflect the time intervals between two events taking place. When visiting a rock-breeding colony of sea birds (e.g. the Gannet, *Sula bassana*), it appears that the close distance of breeding couples is determined by the limited space available and the protection against predators, that may rob the nests when they are unattended (e.g. the time window for an attack) (Figure 4).

The characterization of the foraging-sheltering dipoles also reveals a cascade of trophic levels, where producer-, competitor-, parasite- or predator species can be identified at each level. However, similarities as well as dissimilarities may

(17) See for instance the BBC documentary-series “The Americas with Simon Reeve” (5x1 hours).

exist at different trophic levels, resulting in a number of similarity terms with increasing index  $m$  (see 3.1), in which the (time-dependent) expected  $\hat{U}(t)$  takes the role of similarity dimension:

$$\sum_m f s_{-i/+i}^{\hat{U}(t)} \approx 1$$

The terms of the expression above add up to unity, so these terms may be regarded as successive probability terms of a biodiversity index, reflecting the successive probabilities of the occurrence of certain indicator species, characteristic for the quality of an ecosystem.

Also, the proportions  $P_{ON}$ ,  $P_{NON}$ , of occupied-, resp. non-occupied niches to the maximal number of different niches to be likely found at a certain location may be derived from:

$$P_{NON} = 1 - P_{ON} \approx 1 - \sum_i \frac{\ln N_i I_{IN}}{\ln N_i f s_{-i/+i}^{-i/+i}} \quad \text{or} \quad P_{NON} \approx 1 - \frac{B_{loc}}{B_{opt}}$$

where  $B_{loc}$ ,  $B_{opt}$  represent the local, resp. optimal biodiversity of a given ecosystem.

According to Mandelbrot [8], in order to translate the critical percolation probability ( $p_{crit}$ ) into a critical threshold for fractal clusters or ‘curds’, defining the upper and lower bounds to a critical fractal dimension ( $D_{crit}$ ) also depends on the dimensional diameter ( $E = \text{volume}^{1/E}$ )<sup>(10)</sup>. For Mandelbrot, estimating the content of the intersection of a fractal cluster (curd) with an Euclidean space, e.g. a plane (perpendicular to some axis), is equivalent to defining the topological dimension of the overlapping space. This in turn, is helpful to determine the critical percolation of a fragmented network (so-called stratified), or to answer whether or not the cluster is connected or falls asunder.

For a stratified random fractal, Mandelbrot [8]<sup>18</sup> uses a lattice divided into  $b^E$  subintervals ( $b$  is called the lattice base). Then, with  $E$  the dimensional diameter of the cluster as defined, Mandelbrot [8] derives the following expressions for the upper, resp. lower bound on the critical fractal dimension ( $D_{crit}$ ):

$D_{crit}$ , upper bound:  $D_{crit}$  satisfies  $b^{D_{crit}} > b^E + \frac{1}{2} b^{E-1}$  (for  $b \geq 3$ , this makes percolation ‘almost certain’)<sup>(18)</sup>, and:

$D_{crit}$ , lower bound:  $D_{crit}$  satisfies  $D_{crit} > E + \log_b p_{crit}$  (for  $b \gg 1$  and  $p_{crit}$  the critical probability in Bernoulli percolation)<sup>(18)</sup>. It remains to be demonstrated which model best suits multi-species ecological networks, either the latter bounds of  $D_{crit}$ , or, the rather manageable formula of  $P_{crit}$  for H. A. Bethe (1906-2005) lattices with coordination number  $z$  (as suggested in immune networks)<sup>(11)</sup>, namely:

$$P_{crit} = \frac{1}{z-1} \quad [24].$$

## 4. Estimating Biodiversity Dynamics in an Ecological Framework

### 4.1. Biodiversity Decline and the Biodiversity Tensor Equation

It has been reported in the island theory of McArthur and Wilson [28, 29], that biodiversity decline causes a gap in the ecological food web. This is for instance exemplified by large whales that consume high amounts of krill, hereby controlling a maximum number of species. However, when whales die, especially in the arctic region, only a few number of predators take benefit (e.g. polar bears). Hence, large predators have a far greater impact on the biodiversity than primary producers.

Under the present conditions of a globally declining biodiversity [30], there is an urgent need to understand the dynamics of biodiversity changes. Compared to the models presented in theoretical studies (see 2), the matrix representation has to be extended to include biomass (e.g. per age class), i.e. it has to be regarded as a volume metric. Theoretically, a biodiversity tensor may be constructed containing all relevant data on (1) species number per trophic level, (2) abundance per species and (3) biomass per age class. Then the following (differential) equation may be constructed for the *Global Biodiversity Loss* as a function of time:

$$\frac{dB_{global}^{1-}}{dt} = -\frac{dB_{local}^{2+}}{dt} + \nabla B_{global}^{1+} - T \cdot \Delta S$$

with  $B^{1-}$ ,  $B^{2+}$  the biodiversity at top level (impaired), at a sub-top level  $B^{2+}$  (increased) or  $\nabla B_{global}^{1+}$  when global dispersal at top level taking place, etc. The last, ‘‘increase of entropy’’ factor ( $T\Delta S$ ) is well established at the level of chemical reactions (between atoms and molecules) and even at the scale of black holes and galaxies [31], but there is quite some reserve among theoretical physicists to apply the notion of entropy at the level of macroscopic, biological objects like in (meta-) populations. So far, there is not another approach for estimating the entropy change, except for the relation of the notion of information state ( $H$ ) defined as negentropy [32]:

$$H = -\sum_{i=1}^n p_i \log p_i$$

According to the second law of thermodynamics, in a closed system the entropy production is zero, implicating that a change in entropy is always reflected by a change in heat or work, so this also holds for the negentropy of the system. The problem with the Earth’s biosphere however, is whether or not it may be regarded truly as a closed system? And, consequently, we cannot conclude that the biosphere as a whole is (or is not) a robust, sustainable hyper-equilibrium system, in analogy with the notion of hyper-object as formulated by Morton and others [33].

(18) BB Mandelbrot (*ibidem*), p. 210 ff.

## 4.2. Integral Operators and Lebesgue Measure Applied to Non-differentiable Functions (Theory)

However, a more important caveat results from the uncertainties resulting from a lack of knowledge about the time-dependency of the abundances of species, when not only growth and reproduction, but also migration parameters are allowed. Strictly, the relationship between biodiversity and the first time-derivative (speed of biodiversity change), as well as with the second time-derivative (declining or increasing speed of biodiversity change) are not known. Also, it has not been elucidated yet whether the biodiversity matrix (represented in 2.3) is a differentiable function<sup>19</sup>. In mathematical theory, the use of an integral operator  $L_K$  is suggested for such non-differentiable functions. For a measurable function  $K$  on  $\mathfrak{R}^2$  ( $K$  is called the kernel of the integral operator), this integral operator is defined as:

$$L_k f(x) = \int_{-\infty}^{\infty} K(x, y) f(y) dy$$

which operator has the properties of being linear and bounded, based on an important property of the Čebyšev norm<sup>20</sup>:

$$\|L_k f(x)\| \leq |b - a| \cdot \max(\{L_k(x, y) | (x, y) \in (a; b)^2\}) \cdot \max(\{f(x) | x \in (a; b)\})$$

$$\|L_k\|_0 \leq |b - a| \cdot \max(\{L_k(x, y) | (x, y) \in (a; b)^2\}) \quad [35]$$

The aim of the above described integral equation is to establish its order (1<sup>st</sup>, 2<sup>nd</sup> or 3<sup>rd</sup>) by investigating the solutions for the equation

$$h(s) = \int_a^b K(s, t) x(t) dt \quad \text{for which the form of the solution is}$$

given by the product of the arbitrary functions  $g$  and  $h$ , satisfying the linear form (with  $\lambda \in \mathfrak{R}$  or  $\lambda \in \mathbb{C}$ )

$$g \cdot h = h + \lambda K(x) \quad [35].$$

According to Heil [34], the integral operator thus defined is a natural generalization of the ordinary matrix-vector product. With  $A$  an  $m \times n$  matrix with entries  $a_{ij}$ , and let  $u$  be a vector in  $\mathbb{C}^n$ , then the product  $Au \in \mathbb{C}^m$  and its components are given by

$$(Au)_i = \sum_{j=1}^n a_{ij} u_j \quad \text{with } i = 1, \dots, m.$$

Intuitively, the importance of the (Lebesgue) integral

operator may be inferred from the nature of the *Exterior Lebesgue Measure (E)*, which can be interpreted as the infimum taken over all finite or countable collections of boxes  $Q_k$  in  $\mathfrak{R}^d$ , satisfying  $E \subseteq \bigcup_k Q_k$ , or

$$|E|_e = \inf \left\{ \sum_k \text{vol}(Q_k) \right\} \quad \text{with the box volume defined as}$$

$$\text{vol}(Q) = \prod_i (b_i - a_i) \quad [36].$$

From the (Lebesgue) measurable set of (nonnegative) functions on a measurable set  $E \subseteq \mathfrak{R}^d$ , Heil [36] defines the  $L^p$ -norm as  $\|f\|_p = \left( \int_E |f(t)|^p dt \right)^{1/p}$  then  $L^p(E)$  is the space of all functions for which  $\|f\|_p$  is finite. Moreover, it can be shown that  $L^p(E)$  is a Banach space, allowing us to define an (essential) supremum norm for the function  $f(t)$  ( $t \in E$ ) [36].

When  $t$  represents time, this would not only allow for calculating biodiversity changes (although it is strictly not known how biodiversity changes with time), but also for studying the seasonality of population changes, using so-called Euler (1707-1783) differential equations. According to Reinhardt and Soeder<sup>21</sup>, cycloid arches may be obtained at solution of these equations, of the form:

$$f(t) = c - r(1 - \cos \alpha)$$

However, these formulas so far lack an adequate translation in known ecological systems, predominantly due to a lack of empirical data from the field. Nevertheless, they may become supportive to several thought experiments, in which the evolution of global biodiversity is represented by paraboloid, hyperboloid or ellipsoid convolution spaces (see 2.3).

Alternatively, a timeless approach for describing biodiversity dynamics in analogy with the notion of stepping stones and Fibonacci sequences could be useful in a fractal theory of ecosystems (see 4.3). In theory, using the mathematical constructs for fractal phenomena, the notion of being measurable and bounded is extended to so-called ‘monstrous’ functions<sup>(13)</sup>, with properties that are not valid everywhere, or non-differentiable or discontinuous in their domains. In this respect, it is interesting to recall Mandelbrot’s interpretation of the Liouville (1809-1882) theorem and ergodicity principle of spaces considered as hyper-volumes, using the Peano-like dispersion construction<sup>22</sup>.

## 4.3. Timeless Fibonacci Series and Local Biodiversity

The number of species interacting with one another are an important parameter for defining the coordination number of the ecological network, and, (in analogy with immune networks) also the critical percolation probability (see 3.2). We may benefit from an analogy with the notion of stepping stones and a (partly) posthumously published theory of Alan

(19) Given the similarity with Mandelbrot’s analogy with Cantor dusts (see 3) and Koch curves (where the drawing of a tangent is impossible!), it is very likely that these are non-differentiable functions.

(20) According to Heil [34], the here presented integral operator refers to the Lebesgue integral and Lebesgue measure, after the work of the mathematician Henri Lebesgue (1875-1941). An important property is that if the kernel  $K$  is a square-integrable function on  $\mathfrak{R}^2$ , then  $L_k$  is a bounded mapping on  $L^2(\mathfrak{R})$ , satisfying the Euclidean norm  $\|L_k\| \leq \|K\|_2$ . Combined with the Banach space property, the limits of these mappings are characterized by the *Banach Fixed Point Property* [35] (see also [25]).

(21) F Reinhardt & H Seder [35], p. 369.

(22) BB Mandelbrot (*ibidem*), p. 62.

M. Turing (1912-1954)<sup>23</sup> on the series of Fibonacci (pseudonym of Leonardo de Pisa, ca. 1170-1250). Namely, in an optimal, space-filling network, such as occurring in plant phyllotaxis [9], the coordination numbers tend to the numbers of a Fibonacci series. Turing remarked that not only the well-known sequence 0,1,1,2,3,5,8,13... but also other sequences satisfy the Fibonacci law<sup>(23)</sup>. Given  $F_{n-1}$ ,  $F_n$ ,  $F_{n+1}$ .. the consecutive terms of the above series, then not only applies  $F_n^2 - F_{n-1}F_{n+1} = (-1)^n$  (which is easily verified, starting from the numbers 1,2,3..), but also the equations of the form  $p_n = p_0F_{n-1} + p_2F_n$  yielding various applications derived from these Fibonacci numbers, such as the following set of equations:

$$p_{n+1} = p_n + p_{n-1} \quad \text{for each } n \text{ (}^{23}\text{)}$$

$$q_{n+1} = q_n + q_{n-1} \quad \text{then for each } n \text{ also follows:}$$

$$p_{n+1}q_n - p_nq_{n+1} = (-1)^n (p_1q_0 - p_0q_1) \quad \text{(which is independent of } n\text{)} \text{ (}^{23}\text{)}.$$

Hence, according to Turing, if the terms  $p_n$ ,  $p_{n+1}$ ,  $q_n$ ,  $q_{n+1}$  satisfy the Fibonacci equation  $F_{n+1} = F_n + F_{n-1}$ , then the linear combination above represents an invariant property, called Wronskian property of the Fibonacci equation<sup>(23)</sup>. So far, applications of this property have been described in plant phyllotaxis [9] (Figure 5). The property refers to a similarity index, that in theory may be useful for predicting (local) biodiversity decline or resilience too, when the coordination numbers of the ecological network are well characterized.

#### 4.4. Biodiversity Resilience Strength (BRS)

It remains to be demonstrated what the relation is between the biodiversity index  $P_{ON}$  of a given ecosystem, the critical (percolation) probability ( $P_{crit}$ ) of that ecosystem (see 3.2), and the *Biodiversity Resilience Strength* (BRS), as being the capability of a strained system to recover after deformation caused by survival stress in a global system of limited resources. The vulnerability of an ecosystem is known to be especially great in the case of the (local) extinction of large predators and within island populations [28], but also in anthropogenic, monotonous plants with high uniformity index. Mathematically, these events indicate far-from-equilibrium situations, for instance in nonlinear systems with forced oscillations where amplitudes becoming infinite. Or, the amplitude (A) of the oscillation with frequency ( $\omega$ ) approaching a critical value ( $\omega_0$ ) tends to infinity:

$$A \propto \left( \frac{N\omega\omega_0}{\omega^2 - \omega_0^2} \right).$$

In ergodic systems [39], describing dynamical systems that are deterministic of nature, it is assumed that no random perturbations or noise may influence the dynamic equations.

In ecological systems, however, the perturbations are essential to the dynamics of the system. Making use of the box volume measuring method (see 4.2), we may rewrite the critical percolation probability ( $P_{crit,i}$ ), representing the risk for an ecosystem to collapse, in terms of the *critical biodiversity*,  $B_{crit}$ . By definition, an ecosystem consists of more than one trophic level (namely: primary producers, primary and secondary predators,...). For an ecosystem at the  $i$ -th trophic level, then:

$$P_{crit,i} = \frac{B_{loc,i}}{\prod_i (|B_{loc,i} - B_{crit,i}|)^{1/m}}$$

This would implicate that if the biodiversity has reached a critical value at one of the trophic levels, the ecosystem would already collapse. Therefore, the *BRS* not only has to be defined in terms of the absolute value of the distance of the local biodiversity ( $B_{loc}$ ) from the critical biodiversity, scaled to the optimized biodiversity average for a given ecozone (see formula below), but also migration terms ( $M_{i,j}$ ) for invading species from neighboring areas at distance  $R_{ij}$  have to be incorporated. For, it has been demonstrated that ‘extinction debt’ and ‘immigration credit’ (and species turnover) are important mechanisms for keeping the local biodiversity in balance [39].

$$BRS \propto \sum_i N_i \frac{B_{loc} - B_{crit,i}}{N_{opt} B_{opt,i}} - \sum_{i,j} (B_{loc} - B_{crit,i}) \frac{M_{i,j}^{1/2}}{R_j^2}$$

This implicates, however, that the biodiversity and *BRS* do not depend solely on the local characteristics or mean field descriptions of an ecosystem, but they also depend on the interactions at short distance and sometimes also at long distance (especially in case of birds or species that can invade islands from overseas). Also it is well known that in pristine, newly formed territories (e.g. after volcanic eruptions) an important role in occupying the new territories is played by pioneer species.

To conclude, not only the application of the formulas presented above needs empirical field data, also the mathematical solvability of the equations needs further research. In the case of representing biodiversity distribution and its disturbances as deviations of for instance a paraboloid convolution space (Figure 6), we suggest the mathematical counterpart of these questions could be similar to the problem of “decomposing a polynomial as a sum of squares” or the problem of “finding the loci of the points in  $\mathfrak{R}^3$  satisfying the general second-degree equation” [15] (see 2.3). To our opinion, this question may remain an interesting challenge for future mathematical modeling applied to a biological problem.

## 5. Discussion

Mathematical modeling has proven to be very successful in describing the quantitative fluctuations and ecological interactions between a limited number of species (e.g. rabbits

(23) The subsequent exposition of the “Wronskian property of solutions of the Fibonacci equation” belongs to unpublished notes from A.M. Turing kept at King’s College Archive Center (KCC/AMT/c/25/34), that were also not included in the *Collected Works of A.M. Turing*, Volume Morphogenesis, edited by P.T. Saunders [9]. They are reproduced with permission from King’s College Archive Center (© PN Furbank, London; see also [37]).

and foxes) in a homogeneous area<sup>24</sup>. Further improvements have been presented to incorporate heterogeneous areas, or to describe patchy spread within an area or interactions between a larger number of species, or within hosts and species with multiple (sexual and asexual) reproductive cycles like in fungi<sup>25</sup>. So far, only limited success has been achieved in describing biodiversity changes in a dynamic, multispecies system such as presented by Vandermeer and Lin [13], but also here only very few trophic levels are included (see 2.2). We previously noted the usefulness of the notion of ‘permanence’ of certain keystone species in a multi-species dynamic system [5, 14].

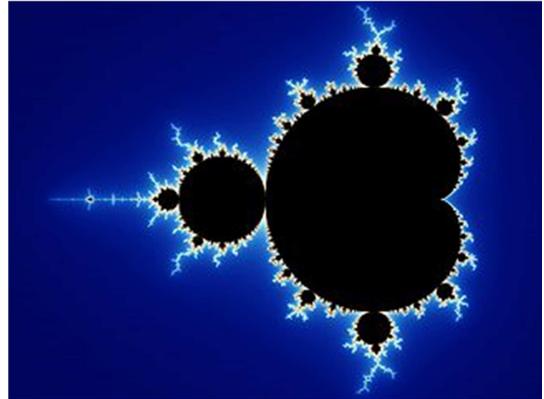
In the present study an approach is followed in order to comprehend biodiversity changes in complex ecological webs. Hereby, the analogy with the methods of describing the fractal geometry of nature according to Mandelbrot [8] appears useful, the more since a lot of species have a profound impact on shaping the landscape, for instance through their effect on vegetation, which in turn depends on / affects physical and, in long term, also geological parameters (take for instance the influence of either rain forest or sand desert on the microclimate, but also the dependence of microclimate on geological structures like mountain ranges).

In order to apply the fractal geometry of nature to ecosystems, a dual approach is followed. First, a translation of the fractal dimension in terms of similarity dimension [8] or mass dimension [21] is applied to patterns of self-similarity in ecological webs, using the notion of an inverse uniformity index. The probability terms of this uniformity index, based on the occurrence of certain indicator species, may constitute a tool for characterizing the quality of an ecosystem (see 3.2). A notion used in percolation theory, namely the critical (percolation) probability, suggested by Mandelbrot [8] to represent the critical dimensionality of a hierarchical cluster below which it falls apart, was found to be useful in formulating a critical biodiversity threshold (see 4.4).

Moreover, an attempt is given to formulate an equation describing the biodiversity changes in a global, dynamic world, called the biodiversity tensor equation. However, in contrast to the well-known dynamic systems describing multiple (non-linear) equilibria or chemical dynamic equilibria, the present global ecosystem is thermodynamically not well characterized. In particular, the second law of thermodynamics requiring a closed ecosystem, is not validated globally due to energetic exchanges and processes affecting the planet as a whole, like accumulation of greenhouse gases and global warming. Nevertheless, relatively novel mathematical techniques may become useful to become applied to the complex, non-differentiable functions found to approximate the fractal patterns of ecosystems and their dynamic behavior. Mathematical modeling may also corroborate intuitive notions, like the notion that biodiversity cannot be adequately described in terms of local or mean field approximations, but requires (long)

distance interactions to account for extinction ‘debts’ and immigration ‘credits’ [39]. The stratified nature of a fractal ecosystem moreover implicates that these extinction/immigration balances may occur at different trophic level, which further enhances the notion of unpredictability of changes in a large ecosystem at the verge of a global collapse, like these induced by climate warming.

However, more research will be needed both in terms of collecting empirical field data as well as in terms of developing new mathematical tools and new heuristics to combine both worlds of science: ecology and applied mathematics.



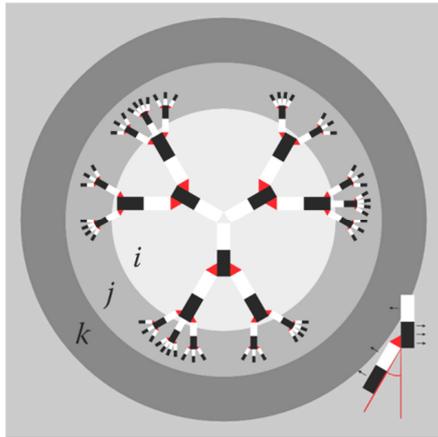
**Figure 1.** a. Initial image of a Mandelbrot Set (© Wikimedia Commons: Mandelbrot Set). The Mandelbrot Set represents a complex generalization of the iteration of the quadratic polynomial  $P_c : z \rightarrow z^2 + c$  with  $c$  a complex parameter. The coloured image is obtained by depicting in black if a point  $c$  belongs to the subset of the plane given by the formula  $M = \{c \in \mathbb{C} : \sup_{n \in \mathbb{N}} |P_c^n(0)| < \infty\}$ . More colors are obtained by defining the color of points not belonging to  $M$  according to how quickly the sequence  $|P_c^n(0)|$  diverges to infinity.



**Figure 2.** Image of plant leaf of *Cyclamen* sp. showing a colour pattern resembling the Mandelbrot Set in Figure 1 (© 2009 Biological Publishing A&O; van der Linden [42]). The (contest) question for readers of the journal *bi-logical* (Vol. 2 [2]) was to give an explanation or a mechanism of a biological reaction-diffusion system, in the sense of Turing, that could generate a pattern resembling the Mandelbrot Set, like observed in these *Cyclamen* plants.

(24) See JD Murray [40].

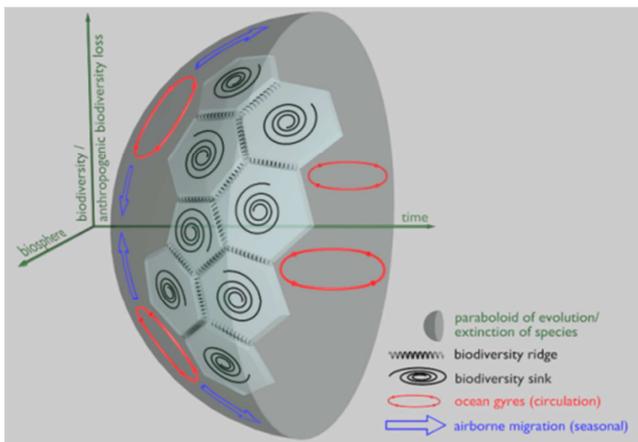
(25) Reviewed in W Allaerts [41].



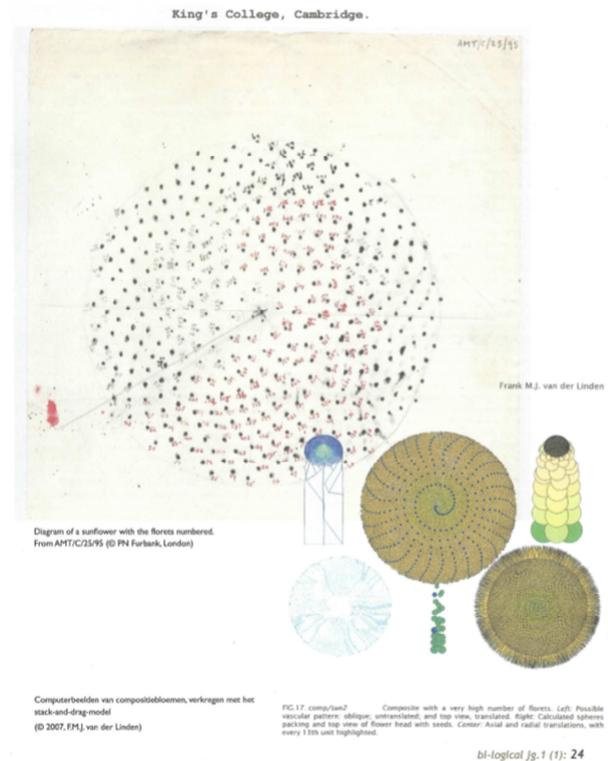
**Figure 3.** Scheme representing a hypothetical ecosystem consisting of foraging-sheltering dipoles ( $f_{s_{-i/+i}}$ ) and interspecies interactions between trophic levels  $i, j, k..$  The overall picture is that of a Bethe lattice with interactions through foraging/predating (white), sheltering (black) and parasitic (red) elements. When going down from top-predator level to the level of primary producers, the number of interspecies interactions increase, defining the coordination number. In addition to the number of interacting species, the coordination number is also influenced by the interaction between individuals of the same species (repulsion arrows, inset).



**Figure 4.** Breeding colony of the Gannet (*Sulla bassana*). The distance between breeding couples is determined by the available space and the time window for protection against an attack of the nest by predators (© Mint images, reproduced from Alamy Stock pictures).



**Figure 5.** Scheme representing the parameters for global biodiversity change (evolution) or anthropogenic biodiversity loss (in time). The global dynamics of speciation (and concomitant extinction, whether or not anthropogenic) during evolution is represented by a paraboloid centered along the time axis. The relationship between global and local biodiversity changes is not only characterized by biodiversity sinks and ridges (high biodiversity regions) on a manifold (hypothetical image of the biosphere), but depends also on migration patterns, both airborne and in ocean migration patterns.



**Figure 6.** Diagram of a sunflower with the florets numbered (from KCC/AMT/C/25/95; © PN Furbank, London) and computer image following the stack-and-drag model developed by F van der Linden (see Allaerts [37]).

Similar to their use in phyllotaxis (in the sense of Turing) [43], the connectivity numbers of interacting species in an ecosystem, when forming a Fibonacci series, offer an alternative approach for estimating biodiversity changes (based on the Wronskian properties of solutions of the Fibonacci series).

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