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Fractal concepts in studies of soil fauna

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Abstract

Despite the fact that their objects of study live in a highly complex and irregular environment, soil zoologists have not yet made use of the advantage of fractal geometry in their work. Less than 1% of papers published during the last 3 years that dealt with fractal applications in the field of biological and environmental sciences were directed at studies of soil fauna. This paper tries to initiate a more intensive use of fractals in soil zoology and outlines their potential for different aspects of research. It reviews a fractal approach to describe soil nematode movement patterns in an artificial two-dimensional soil matrix and presents original work on the impact of habitat complexity on the abundance:body size distribution of soil microarthropods and on the potential of detecting scaling regions of microarthropod aggregations by identifying scale-dependent changes of a fractal exponent. © 1999 Elsevier Science B.V. All rights reserved.

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1. Introduction

A number of years ago Frontier (1987) and Sugihara and May (1990) outlined the potential of fractal concepts to address some important issues of ecological research. Their list of possible applications included (1) the measurement of available habitat space—e.g., surface availability for invertebrates on plants (Lawton, 1986); (2) the detection of functional hierarchies—e.g., identification of hierarchical size scales by determining different apparent dimensions of forest patches at different scales of observation (Krummel et al., 1987); (3) the analysis of shape and spatial distribution of organisms—e.g., structure of root

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systems (Tatsumi et al., 1989) or the structure of plankton swarms (Frontier, 1987); (4) the analysis of animal movement (Dicke and Burrough, 1988); (5) the analysis of time series—e.g., the estimation of the persistence of rare species (Hastings and Sugihara, 1993); and (6) the use of fractals in an abstract representational space—e.g., strange attractors in the dynamics of ecological systems or characterisation of species diversity as a fractal feature of a community (Frontier, 1987).

Frontier (1987) and Sugihara and May (1990) acknowledged fractal geometry as a particularly attractive approach to address problems of scale and hierarchy and expected it to become of fundamental interest for the analysis and modeling of ecosystems. However, their suggestions seem to have had little impact on the study of soil fauna.

A survey of recent literature published between May 1994 and August 1997 reveals a striking dearth of fractal concepts in soil zoological research. Of the 230 articles that include fractal concepts (listed by Current Contents/Agriculture, Biology and Environmental Sciences®) 27.0% (62 articles) explicitly deal with soil research. The majority of these are soil physical papers and describe or model water and solute transport through soil, soil aggregation and related topics. Eleven articles (4.8%) focus on the analysis of root systems and eight articles (3.5%) focus on the analysis of soil microbial growth patterns. Only 0.9% (two articles) refer to soil animals which corresponds to less than 0.5% of all soil zoological papers listed by Current Contents/Agriculture, Biology and Environmental Sciences® in the same time period. These two articles are an analysis of free-living soil nematode movement in an artificial experimental arena (Anderson et al., 1997) and a description of the body-size distribution of microarthropods and its possible relationship to available habitat space in soil (Kampichler, 1995). Also the review by Senesi (1996) on the use of fractals in soil biology and biochemistry reports a rich literature on the fractal nature of humic substances, proteins, enzymes and patterns in microbial morphology but only two articles refer to soil animals (Crawford et al., 1993; Kampichler and Hauser, 1993).

It is unclear whether the lack of fractal applications in studies of soil fauna is caused by ignorance or rejection of the theoretical approach or whether it is a consequence of the methodological difficulties in studying subterranean organisms. Direct observation is generally not possible and destructive sampling is often required (e.g., extraction of soil cores). In this paper I will try to point out that despite these obvious methodological difficulties it actually is possible to apply fractal concepts to various soil zoological questions. I will highlight selected applications: (1) the analysis of animal movement within a pore network referring to the work by Anderson et al. (1997), (2) the analysis of available habitat space for microarthropods of different size following Kampichler and Hauser (1993) and Kampichler (1995) as well as presenting original results, and (3) the identification of ecological hierarchies in aggregations of

Collembola (original data). In each of these sections, I will outline the underlying principle of the application in a short introduction. Finally I will give a few suggestions for further possibilities of fractal applications in studies of soil fauna. All methodological terminology refers to Hastings and Sugihara (1993).

2. Analysis of soil animal movement

2.1. Outline of principle

Frontier (1987) and Dicke and Burrough (1988) were the first to suggest the description of animal movement trajectories by means of fractal geometry. Dicke and Burrough (1988) argue that the tortuosity of an animal trail may be characterised by its fractal dimension D. The fractal dimension of a trail (or any other curve) usually is determined by the dividers method (cf. Hastings and Sugihara, 1993). This method involves stepping along the trail with a pair of dividers of distance δ (or with a ruler of length δ). The apparent length L of the trail is the number N of straight-line segments that can be fitted to the trail multiplied by the measurement scale δ (the length of a single segment). By decreasing δ the irregularities of the trail can be traced closer and closer, thus the length of the trail will increase with measurement on finer scales. Lenght L depends on measurement scale δ according to the simple power law

$$L(\delta) \propto \delta^{1-D} \tag{1}$$

D can easily be determined by measuring L at different δ and calculating a linear regression of log $L(\delta)$ on log δ. D is derived as 1 − slope-value of the regression line. Smooth trails have a D close to 1 with $D = 1$ for a straight line —i.e., the slope-value is 0, apparent lenght is independent of measurement scale —, tortuous trails have larger D with D approaching 2 in the theoretical case of the trail filling the plane completely.

The suggestions of Frontier (1987) and Dicke and Burrough (1988) have been followed by a number of ecologists analysing trajectories of terrestrial arthropods (e.g., Fourcassié et al., 1992; Johnson et al., 1992; Wiens et al., 1995).

A highly magnified portion of a mathematical fractal line—e.g., of the Koch curve (Mandelbrot, 1982)—resembles the line itself, and successive magnifications always show the same structure. This property is called self-similarity (Mandelbrot, 1982). Natural objects, however, usually exhibit self-similarity only within a certain range of scales. For example, a theoretical tree branches ad infinitum, whereas the finest ramifications of a natural tree do not ramify any more, but they bear leaves, and on the other end of the scale, a natural tree does not belong to a larger one, but to a forest (Frontier, 1987). Also animal trails cannot be expected to be self-similar over all spatial scales—i.e., there is no uniform linear relationship between log $L(\delta)$ and log δ across all values of

δ—and their fractal dimension often may not be constant over some biologically relevant range of spatial scales. Such self-similarity, however, is required if one wants to extrapolate mechanisms from a small to a large spatial scale. This gave rise to criticism on an inappropriate use of the fractal approach: in various articles the fractal dimension of an animal movement trajectory is assumed to be scale-independent without testing this assumption prior to the use of a fractal model (Turchin, 1996). On the other hand, this led to the development of more sophisticated estimators that determine fractal dimension at different spatial scales, give a measure of variance and are able to combine data from separate trail segments measured at various spatial scales (Nams, 1996).

2.2. Application: movement of soil nematodes in an artificial heterogeneous environment

Anderson et al. (1997) were the first to analyse the movement of endogenic animals, namely of free-living soil nematodes, and quantified the interaction between nematode movement along a chemical gradient and a structurally heterogeneous environment. They used 9 cm Petri dishes with a homogeneous layer of nutrient agar as experimental units and applied four different treatments: units with or without a bacterial food-source (*Escherichia coli*, placed left of centre), and units with or without structural heterogeneity established by adding a monolayer of sand grains to the agar surface. Pore space between the grains amounted to approximately 40%. Twenty replicate Petri dishes were used for each treatment. A single specimen of *Caenorhabditis elegans* was placed right of centre of each Petri dish. Their trails were videotaped and the fractal dimension of the movement pathways measured by the dividers method (cf. Hastings and Sugihara, 1993).

The nematode trails from units without structural heterogeneity and without a bacterial food source acting as attractant had the greatest fractal dimension ($D = 1.22 \pm 0.02$ standard error). Movement pathways in these environments were more tortuous, consisting of loops and spirals and were significantly ($p \leq 0.01$) more space filling than the trails in units with bacteria ($D = 1.08 \pm 0.03$ standard error), in units with heterogeneity ($D = 1.08 \pm 0.02$ standard error), and in units with both bacteria and heterogeneity ($D = 1.08 \pm 0.01$ standard error). The presence of a bacterial food source led to a more linear movement, directed towards the bacterial source, most probably due to the influence of a chemical gradient. Also, movement between sand grains led to more linear trajectories even without an attractant being present.

Anderson et al. (1997) also measured the turning-angle distribution of the nematode trails. In the environment without heterogeneity, small changes in direction tended to occur more often than in the environment with heterogeneity. The restrictive pore network minimizes the looping behaviour—pathways with many small changes in angles—and the nematodes follow a trail which is dictated by the physical structure of the environment. If a blocked pore is encountered, nematodes react with a rapid withdrawal followed by a large change in direction. Anderson et al. (1997) assume that this strategy in a physically structured environment aids the nematodes in escaping structural traps, such as 'dead-end' pores, and then reacting to the attractant gradient again.

As Wiens et al. (1995) point out, different combinations of ecological and behavioural features may produce trails with identical fractal dimensions. Thus, they suggest the use of fractal concepts in concert with other scale-dependent measures. The study of Anderson et al. (1997) reiterates this suggestion; although carried out in only a two-dimensional medium, this experiment illustrates the potential of including fractal concepts in the analysis of faunal interactions with the physical framework of soil.

3. Analysis of available habitat space for soil animals

3.1. Outline of principle

Animals live in complexly structured habitats, be it a three-dimensional structure like a tree canopy, a two-dimensional one like a soil surface or a one-dimensional one like a coast-line. Fractal geometry provides a valuable tool for the description of shape and form of natural objects.

The idea of characterising a habitat's complexity by its fractal dimension has mainly been taken up by researchers investigating relationships between plant architecture and its animal community including insects and spiders on vascular plants (Morse et al., 1985; Lawton, 1986; Gunnarsson, 1992), microarthropods on lichens (Shorrocks et al., 1991) and the epifauna on marine macroalgae (Gee and Warwick, 1994a; Davenport et al., 1996). These studies have shown that the greater abundance of small animals can be associated with a greater plant complexity. This is due to the fact that animals of different size perceive their habitat at a different resolution; that is, animals of different size act as 'pair of dividers' or as 'rulers' at different scales δ (cf. Section 2.1) and according to Eq. (1), habitable space in a fractal habitat is larger for smaller animals than for larger ones. The greater D is, the larger the habitat becomes for a small animal and thus the larger should be density of small animals. Some authors also try to relate species diversity to the fractal geometry of the habitat (e.g., Gee and Warwick, 1994b). The majority of ecologists that apply fractal concepts accept this presumed relationship between the fractal scaling of the habitat and species richness. Fenchel (1993) on the other hand argues that if nature actually shows self-similarity at all scales, the environment should in fact 'appear equally complex to a monkey in a forest, to a tardigrade in a moss cushion or to a protozoan in a bacterial mat, and so there should be equally many habitat niches available irrespective of body size'. Whether it is habitat space or habitat diversity that most affect species richness at different spatial scales is still under debate. The relationship between the habitat fractal geometry and species number, however, must not be confounded with the much more straight-forward relationship between the habitat fractal geometry and the number of individuals of different size. This section will only deal with the frequency distribution of individuals of different size.

Few attempts have been undertaken to quantify complexity of soil pore surfaces at a scale relevant for soil microarthropods. Since these animals are incapable of digging and thus confined to the surfaces of soil crevices, fractal geometry should permit the measurement of the surface area that is available for them.

3.2. Application: habitat space for soil microarthropods in a spruce forest soil

By applying the area-perimeter exponent—the area and the perimeter of two-dimensional patches are related by $P \propto A^{D/2}$ with D being the fractal dimension of the patch boundary line (cf. Hastings and Sugihara, 1993)—to thin-sections of three different soils, Kampichler and Hauser (1993) estimated the surface dimension D of pores with a sectional area of at least 0.003 mm^2 to range between 2.26 and 2.39. Kampichler (1995) found a similar surface dimension with values between 2.33 and 2.38 and the average at 2.36 by measuring outlines of hollow spaces in the humus layer of a spruce forest with the dividers method (cf. Hastings and Sugihara, 1993). Inserting $D = 1.36$—intersections with a plane of dimension D_{areal} have the dimension $D_{\mathrm{linear}} = D_{\mathrm{areal}} - 1$ (Mandelbrot, 1982)—into Eq. (1) gives

$$L \propto \delta^{1-1.36} \tag{2}$$

For example, halving the scale of linear measurement δ leads to a $0.5^{-0.36} = 1.28$-fold increase in linear distance. According to Morse et al. (1985), squaring the increase in linear distance gives an estimate for the increase in surface area. Therefore, the respective increase in surface area is $(0.5^{-0.36})^2 = 1.65$. If the way in which soil microarthropods perceive their environment is proportional to their body length we may expect that number of individuals N also scales as

$$N \propto (\delta^{-0.36})^2 \tag{3}$$

Following the reasoning by Morse et al. (1985), let us combine the fractal argument with the assumption that animals with a lower per capita energy demand are able to establish proportionally larger numbers of individuals. This holds independent of habitat complexity. In this case abundance N and biomass W should scale as

$$N \propto W^{-b} \tag{4}$$

where b is the exponent of the allometric relationship $M \propto W^b$ between biomass W and metabolic rate M and equals 0.81 for edaphic arthropods (Ryszkowsky, 1975).

If body mass W and body length L relate as $W \propto L^3$ and $L \propto W^{1/3}$, respectively, Eq. (3) can be written as

$$N \propto \left((W^{1/3})^{-0.36} \right)^2 \tag{5}$$

Consequently the combination of the fractal and the metabolic assumptions leads to $N \propto ((W^{1/3})^{-0.36})^2 \times W^{-0.81}$ and finally

$$N \propto W^{-1.05} \tag{6}$$

Considering that large hollow spaces with large diameter are less abundant than pores with small diameter, large animals have access to fewer crevices than small animals. Thus the expected slope of a plot of log biomass vs. log abundance should be somewhat steeper than -1.05. Kampichler (1995) compared this prediction with a sample of soil microarthropods from the same humus layer. He found the slope to equal -0.80 which is shallower than the expected slope. His report, however, was based only on a subset of the entire sample (6 out of 17 soil cores). This paper contains a more elaborate analysis of that data-base.

The sample consisted of 17 cylindrical soil cores of 5 cm diameter and 10 cm depth. They were extracted by Berlese–Tullgren-funnels and yielded a total of 5749 mites (predominantly oribatid mites) and collembolans, accounting for 98% of all extracted microarthropods. Therefore, subsequent analysis was restricted to these two taxa. All specimens were measured to the nearest 5 μm using a Wild–Censor binocular microscope and were converted into biomass data using the body length:biomass relationships provided by Edwards (1967), where

$$\mu\text{g biomass}_{\text{Oribatida}} = (4.92 \times \mu\text{m body length})^3 \tag{7}$$

$$\mu\text{g biomass}_{\text{Collembola-Arthropleona}} = (2.64 \times \mu\text{m body length})^3 \tag{8}$$

In a double-logarithmic plot of biomass and abundance, a unimodal curve with the mode in one of the lower size-classes can be expected. Eq. (6) should be valid for the distribution to the right of the mode. Blackburn et al. (1992) showed that the choice of number of size classes can significantly alter the slope of the body-size frequency distribution. They recommend dividing the data to the right of the distribution mode into a number of size classes between 6 and 15 for calculating the slope, since lower numbers produce less acurate and more variable estimates and higher numbers systematically overestimate the slope. Based on their guideline the biomass was divided into octaves (i.e., class limits at $\ldots, 2^{-1}, 2^0, 2^1, \ldots$), and semi-octaves (i.e., class limits at $\ldots, 2^{-1}, 2^{-0.5}, 2^0, 2^{0.5}, 2^1, \ldots$). This yielded 8 and 15 classes—the last semi-octave class was empty—to the right of the mode. The abundance within each size-class was also $\log_2$-transformed.

The slope of the regression line is -1.37 (octaves) (Fig. 1a) and -1.39 (semi-octaves) (not shown), respectively. These values fall in line with the prediction of the slope to be somewhat steeper than -1.05. They are not statistically different from -1.05 ($t = 1.20$ and $t = 0.94$; $p > 0.05$) when tested according to $t = (|b_{\text{obs}} - b_{\text{exp}}|)/s_{\text{b}}$, where b_{obs} is the observed slope, b_{exp} is the value of a given slope against which b_{obs} is to be compared, and s_{b} is the standard deviation of b_{obs} (Lozán, 1992).

Obviously, the approximate correspondence between data and prediction does not prove that the fractal nature of soil pore surface adds to an increase of individuals as body size of microarthropods gets smaller. Therefore more studies are needed on the relationship between the shape of the body size distribution

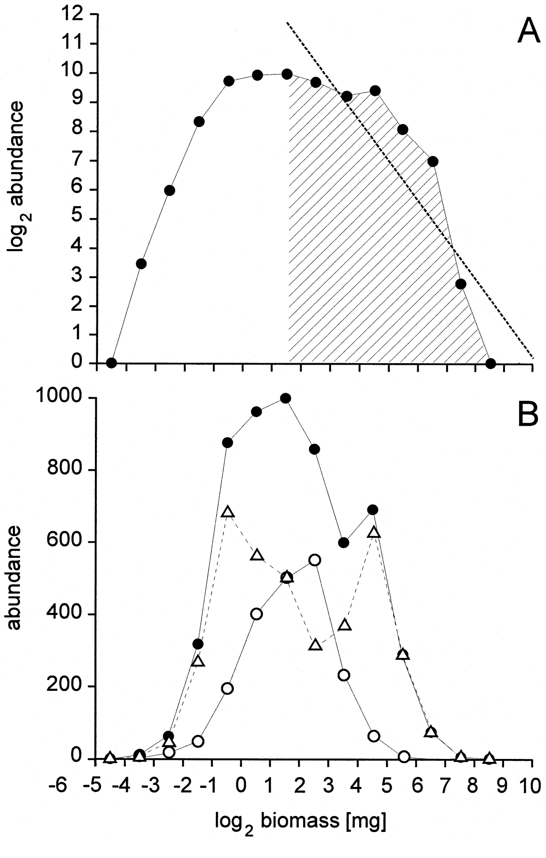

Fig. 1. Body-size distribution of a micoarthropod community (total number of individuals in each size class) in a spruce forest soil (a) in a double-logarithmic plot to show the slope ($b = -1.37$) to the right of the mode (hatched part of the distribution), (b) in a semi-logarithmic plot to show the additive composition of the overall body size distribution (black circles) by the body size distributions of Acarina (white triangles) and Collembola (white circles).

and the fractal geometry of the soil pore surface to find out whether or not different values D actually are reflected in different slopes of a fitted line. Gunnarsson (1992) for example reported that the body size distribution of spiders in tree canopies did not in every case numerically agree with the expected slope for a given D (with D characterising space-filling properties of branches and leaves). A positive relationship between fractal dimension and the slope of the body size distribution, however, was clearly visible. This means, even though the fractal dimension is a weak predictor for a certain value for the slope of the body size distribution, there is obviously a relationship between the fractal dimension and the slope. It must be the aim of future surveys of microarthropod communities to investigate this relationship rather than simply compare prediction and observation in 'one site, one point in time' studies. Patterns of abundance per size-class as well as habitat structure exhibit temporal dynamics: Collembola community patterns for example change distinctively in the course of a year (e.g., Vegter, 1987; Kampichler, 1992), and pore diameter distribution and fractal dimension of pore surface must also be expected to undergo seasonal changes due to biotic (comminution, bioturbation, decomposition, etc.) and abiotic (pressure of a snow cover, etc.) processes.

Despite the appealing simplicity of relating number of individuals in a size-class to the amount of available habitat space, there are some methodological problems in the quantitative analysis of body size:abundance plots (see Loder et al. (1997) for a detailed discussion of these problems in interpreting analogous plots of the body size:species number distribution).

(1) The number of classes into which body size is divided can significantly alter the shape and slope of the body size:abundance distribution. Loder et al. (1997) report on a data-set of North American butterflies, where the fitted slope varies between -2.05 (80 size classes) and -3.36 (five size classes). In keeping to the recommendations by Blackburn et al. (1992) slopes for the body size distribution of soil microarthropods are obtained that are reasonably similar (-1.37 with eight size classes, -1.39 with 15 size classes). However, there is no a priori reason to choose any particular number of size classes. Since any slope value reported on in the literature is likely to be largely subjective, the problem arises of how to compare slopes from different distributions. Loder et al. (1997) regard this to be a probably intractable problem.

(2) Body size:abundance distributions will sometimes include empty classes, particularly at the right-hand side of the distribution. Again, there is no a priori reason to include or exclude these size classes containing no individuals from the regression analysis. If their inclusion is desired, the $\log(x+1)$ transformation to the abundance axis correctly represents empty classes. Loder et al. (1997) regard the potential errors of this procedure to be small. It will, however, depend on how fragmented the distribution is.

(3) In particular when using a high number of size classes, the distribution will sometimes have multiple modes. Again there is no a priori reason to use

either mode. Even when the body size distribution shows a hump rather than an unmistakeable mode (Fig. 1a) the slope value may be affected by the choice of the size classes included in the regression. For example, if the size class left to the mode which contains nearly as many individuals (962) as the modal class (1000) (Fig. 1) is included, the fitted slope changes from -1.37 to -1.15.

(4) The relationship of body size and abundance to the right of the modal class is often curvilinear rather than linear (e.g., Fig. 1a and figures in the works of Gee and Warwick (1994a) and Gunnarsson (1992)). The fractal/metabolic argument predicts a straight line for the right-hand side of the body size distribution in a double logarithmic plot. It cannot yet be determined whether the bulged curve reflects inefficiencies in the extraction process of smaller animals or whether it is a characteristic feature of the body size distribution of soil microarthropods. However, linear regression may be reasonably well fitted to curvilinear data and may explain much of their variance (e.g., $R^2 = 0.82$ when divided into eight size-classes, $R^2 = 0.81$ when divided into 15 size-classes). Thus the slope value may serve as a heuristic tool for finding out whether or not there actually is a relationship between the fractal geometry of the habitat and the body size distribution. However, more detailed knowledge of the exact shape of the distribution which might be obtained in the future could call for a modification of the initial hypothesis.

These are the methodological problems that may arise in the analysis of soil microarthropod communities. However, at the moment we simply do not know whether empty classes, multiple modes or a curvilinear shape are recurrent patterns in the body size distribution of microarthropods. A few guidelines to be followed in a closer analysis can be given.

(1) The quantitative extraction of small individuals in a soil sample is extremely important, since the number of individuals in the lower size classes may strongly influence the location of the mode. The combination of fractal and metabolic arguments applies only to the right-hand side of the distribution. That fact that small individuals are less abundant than the mode suggests, that there are some other factors than metabolic rate, fractal scaling of the habitat or soil porosity which shape the left-hand part of the body size:abundance relationship. Thus the ‘breakpoint’ between left-hand and right-hand side of the distribution must by identified as precisely as possible. The location of the median in a middle size-class indicates that smaller individuals have possibly been missed in the extraction process. For future studies it would therefore be advisable to float the soil samples after dynamic extraction in order to minimize such losses, e.g., by using sugar flotation (Snider and Snider, 1997). Loring et al. (1981), for example, report that only 3% of *Tullbergia granulata*, a tiny collembolan species, could be collected by using Tullgren funnels alone.

(2) The analysis must cover the entire microarthropod community. The tradition most zoologists adhere to, namely to deal with single taxonomical groups (cf. Gunnarsson, 1992), would lead to erroneous conclusions. This is

illustrated by the body size distributions of Collembola and oribatid mites which show extremely different shapes (Fig. 1b). While the collembolans have a unimodal distribution with its peak close to the global mode, the oribatids form two distinct modes with a local minimum in the size-class of the collembolan mode. These peaks are due to a set of large species (e.g., *Nothrus silvestris*, *Atropacarus striculus*) and a set of small species (e.g., *Oppiella nova*, *Microppia minus*). Similar bimodal distributions of oribatid mites have recently been observed in a tropical forest in Puerto Rico (L. Heneghan, personal communication). It is yet too early to draw conclusions from a single data-set. The interesting pattern of interwoven peaks, however, suggests that apart from the hypothetical overall effects of habitat fractal geometry and metabolic demands by the individuals within different size-classes, interactions between taxa shape the internal structure of the body size distribution. Whether these interactions act on an ecological—e.g., medium-sized Collembola outcompeting oribatid mites of the same size—or an evolutionary time-scale—different size-specific rates of speciation in Collembola and oribatid mites—must be addressed by future investigations.

4. Detecting hierarchical scales

4.1. Outline of principle

Ecosystems can be described as hierarchical systems with processes occurring at various spatial and temporal scales (O'Neill et al., 1986). Sugihara and May (1990) explicitly refer to fractals as a means to address problems like the determination of boundaries between hierarchical levels or the determination of scaling rules within a level. The underlying idea is that changes in dynamics across scales should express themselves in changes of spatial or temporal patterns and thus should be recognisable in the fractal exponents quantifying those patterns. The identification of scaling regions is easy: since fractal scaling rules are expressed by power laws—cf. formulae (1) and (2)—, fractal dimension normally is determined by linear regression on log-transformed data. Therefore one has to find out whether the data are sufficiently well characterised by a global regression or whether they are better fitted using piece-wise linear regression, either by applying a 'rolling regression'—moving a window of a fixed number of points over the entire data-set—or by estimating one or more breakpoints and performing regressions separately for each scaling region (Hastings and Sugihara, 1993). A shift in the slope of the regression line may indicate a shift in the underlying ecological process and may thus help in objectively defining boundaries between different scaling regions. This approach has been mainly undertaken by landscape ecologists (e.g., Krummel et al., 1987; Meltzer and Hastings, 1992).

4.2. Application: scaling regions in aggregation patterns of Collembola

In an early work using fractals in ecology, Hastings et al. (1982) applied the determination of the Korcak exponent B to the study of fractal patterns in the distribution of vegetation patches. B was introduced by Korcak (1938) and Mandelbrot (1982) showed it to be a fractal exponent. The Korcak exponent B and fractal dimension D are related by the simple formula $B = D/2$ for fractal islands in the plane and by $B = D/n$ for fractal islands in a n-dimensional Euclidean space. The number N of vegetation patches of a size of at least a follows the relationship

$$N(\text{area} > a) \propto a^{-B} \tag{9}$$

Thus, the larger B is, the patchier (= more small patches) is the distribution. Hastings and Sugihara (1993) (pp. 123–124) proved that the Korcak exponent B can also be used in the form

$$N(a \leq \text{area} < ca) \propto a^{-B} \tag{10}$$

where c is a constant. Now let the patches be soil cores and characterise them not by their area but by the numbers of soil animals they contain, thus translating the Korcak exponent B from Euclidean space to an abstract representational space sensu Frontier (1987). Then Eqs. (9) and (10) rewrite to

$$N\,(\text{number of individuals} > n) \propto n^{-B} \tag{11}$$

and

$$N\,(n \leq \text{number of individuals} < cn) \propto n^{-B} \tag{12}$$

with larger B denoting larger patchiness. A plot of the number of cores N ($n \leq$ number of individuals $< cn$) as a function of n—keeping c constant—will be noisier than the analogous plot of N (number of individuals $> n$), but according to Hastings and Sugihara (1993) it should be easier to recognise break points between scaling regions. Moreover, by applying Eq. (12) rather than Eq. (11) the behaviour at large scales will not interfere with the behaviour at smaller scales (H.M. Hastings, personal communication).

I analysed data on numbers of endogenic and hemiedaphic Collembola in a sample of 400 soil cores from the Scheyern experimental farm of the FAM Munich Research Association for Agricultural Ecosystems (Fromm et al., 1993; Fromm, 1997). The cores (7.8 cm diameter, 5 cm depth) were taken at 400 points distributed over a $50 \times 50\ \text{m}^2$ sampling grid laid over the experimental farm in April 1991. Total numbers of Collembola per core ranged from 0 to 420. I divided that range in semi-octaves ($n = 2^0, 2^{0.5}, 2^1, 2^{1.5}, \ldots$) and chose $c = \sqrt{2}$. Subsequently the number N of soil cores falling in each semi-octave was determined. Fig. 2 shows the graphs for total Collembola and for two

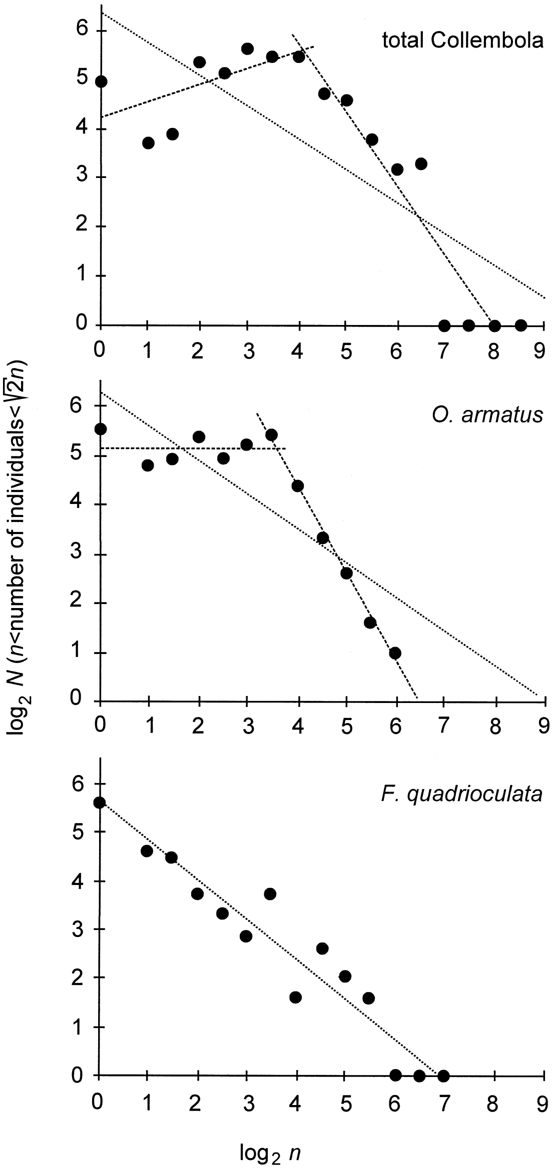

Fig. 2. Relationship between $\log_2 N$ (number of soil cores containing individual numbers $> n$ and $< \sqrt{2} n$) and $\log_2 n$. Hatched lines: regression lines to the left and the right of the breakpoint (breakpoint determined by eye); dotted lines: regression lines of a global regression. See Table 1 for statistics.

dominant species, *Onychiurus armatus* and *Folsomia quadrioculata*. Total Collembola as well as *O. armatus* show distinct breakpoints at an abundance of $2^4 = 16$ and $2^{3.5} \approx 11$ individuals per core, respectively, while the distribution of *F. quadrioculata* is best fit by a global regression (Table 1). Collembola

Table 1
Slope ($-B$) and explained variance (R^2) of linear regressions of $\log_2 N$ (number of soil cores containing individual numbers $>n$ and $<\sqrt{2}\,n$ = dependent variable) on $\log_2 n$ (independent variable) (cf. Fig. 2)

	Range of linear regression	$-B$	R^2
Total Collembola	left of breakpoint	0.35	0.39
	right of breakpoint	−1.41	0.89
	global	−0.64	0.60
O. armatus	left of breakpoint	0.00	0.00
	right of breakpoint	−1.75	1.00
	global	−0.71	0.71
F. quadrioculata	global	−0.81	0.92

exhibit vectorial (e.g., aggregations at food sources or microsites with suitable abiotic conditions), social (e.g., aggregations due to pheromone emission) and reproductive (e.g., patches of juveniles slowly dispersing from an egg cluster) clumping patterns (cf. Usher, 1976; Ekschmitt, 1993). It is plausible to assume that the densities above and below the breakpoints are caused by different combinations of these patterns; below-breakpoint densities possibly also show the lack of any aggregation process.

The fractal analysis clearly has an advantage over the widely used approach of fitting the frequency:abundance distribution to a statistical distribution and of taking a distribution parameter as an index of aggregation (e.g., parameter k of the negative binomial distribution; Southwood, 1978). Such a global index cannot distinguish between different scaling regions within the range of observed abundance.

5. Further suggestions

These three topics certainly do not exhaust the range of possible applications of fractal concepts in soil zoology. Various bacterial and fungal species have been shown to demonstrate fractal patterns in growth and morphology (cf. Senesi (1996) and Boddy et al. (1999)). Jones et al. (1994) regard fractal dimension as a useful parameter for quantifying the space-filling properties and the degree of self-similarity of fungal mycelia and relate these features to the efficiency of explorative and exploitative growth mechanisms. Several authors successfully quantified the morphological response of fungal growth to nutrient status (Ritz and Crawford, 1991; Crawford et al., 1993) and abiotic conditions like temperature or water potential (Donnelly and Boddy, 1997) by determining the change of the fractal dimension of the hyphal network. Also interactions with fungal grazers cause a significant modification of fungal growth patterns as shown by Hedlund et al. (1991). However, these modifications have not yet been quantified by means of fractal geometry. The analysis of the response of fungal mycelia to grazing by microarthropods or of bacterial colonies to grazing by protozoans or nematodes could provide valuable insight into the mechanisms of interaction between microbivorous organisms and their prey and its consequences for nutrient cycling and energy flow in soil. If grazing on fungi and bacteria actually modifies their strategies of resource acquisition, e.g., by switching from explorative to exploitative growth patterns, this will have major consequences for defining the role of soil animals in decomposition processes.

Crawford et al. (1993) pointed out that soil structure should have a tremendous impact also on the population dynamics of bacteria due to the fact that the area accessible to bacteria but not accessible to their predators is a function of complexity of soil pore walls. They pointed out that at a fractal dimension of pore surface of $D_s = 2.36$, almost half of the habitable area for bacteria (size ≈ 5 μm) is to be regarded as a refuge area where they are safe from protozoan predators (size ≈ 30 μm). Although fractal soil features set the limits for predator–prey interactions on the very basis of the bacterial energy channel of below-ground food webs—thus representing an important factor for the dynamics of cycling and transport of nutrients through microbial populations—this concept has not yet been taken up by soil zoologists.

6. Summary and conclusions

The examples presented in this paper highlight the diverse range of possibilities for applying fractals to soil zoological problems. These investigations into fractal applications for soil zoologists should be viewed as preliminary, however, as these problems require further research. The measurement of habitat complexity in the pore-space of soils and organic layers needs further development before its impact on the body size distribution of microarthropods can be assessed. Body size most probably is a major factor determining the possible mechanisms of interaction between microarthropods and microflora. Smaller species have access to smaller soil crevices; they should thus be able to exploit additional microbial food resources not available to larger microarthropods and a larger amount of energy should be channelled through populations of smaller species. The slope to the right of the body size distribution mode of -1.37 in fact indicates that the amount of energy flowing through a size-class rises approx. 1.5-fold at half the body size ($0.5^{0.81-1.37} = 1.474$). Also, the approach of detecting scaling regions in the aggregation patterns of microarthropods needs careful consideration. The relationships between different types of statistical distributions fitted to frequency:abundance distributions of soil animals (e.g., the negative binomial distribution) and the power law scaling presented above are entirely unknown.

Undoubtedly fractal geometry has the potential to contribute to a number of important questions in studies of soil fauna. Soil zoologists are encouraged to make use of this unique instrument for the analysis of complex patterns.

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